Genetic analysis of a population of *Tribolium*. VIII. The stationary stochastic dynamics of adult numbers

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A stochastic differential equation model for the rate of change of adult numbers was used to analyze data from two genetically differentiated groups of laboratory populations of the flour beetle, *Tribolium castaneum*. The first group of populations was homozygous for the corn oil sensitive allele and the other group was polymorphic at this genetic locus. Previous work has shown that mean larval viability is increased in the polymorphic populations. This suggests that the average number of potential recruits was higher in the polymorphic populations when compared to the homozygous ones. The stochastic model was used to derive predictions for the stationary distributions and the serial correlations at demographic equilibrium. These predictions were evaluated using 66 weeks of census data from both groups of populations while adult numbers were fluctuating in the region of their steady states. The data supported the following theoretical predictions: (*i*) the fluctuations in adult numbers can be described using a gamma probability density function; (*ii*) increased recruitment in the polymorphic populations results in a larger mean and variance for adult numbers; (*iii*) the autocorrelation of adult numbers decays exponentially with time; and (*iv*) increased recruitment in the polymorphic populations results in a faster rate of decay in the autocorrelations. These results suggest that genetically based fitness differences among populations can be reflected in the stationary stochastic dynamics of population size.

Key words: *Tribolium*, population dynamics, stochastic models, stationary distributions, gamma distribution.

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Un modèle sous forme d'équation différentielle stochastique du taux de changement du nombre d'adultes a été utilisé pour analyser des données sur deux groupes génétiquement différentiés de populations de laboratoire de tribolium rouge de la farine, *Tribolium castaneum*. Le premier groupe de populations était homozygote pour l'allèle sensible à l'huile de maïs et l'autre groupe était polymorphique à ce locus génétique. Des travaux antérieurs ont démontré que la viabilité moyenne des larves est accrue dans les populations polymorphiques. Ceci suggère que le nombre moyen de recrues potentielles a été plus élevé chez les populations polymorphiques en comparaison des populations homozygotes. On a utilisé le modèle stochastique pour émettre des prédictions sur les distributions stationnaires et les corrélations des séries du nombre d'adultes au stade de l'équilibre démographique. Ces prédictions ont été évaluées en utilisant les données de recensement de 66 semaines des deux groupes de populations au moment où le nombre d'adultes fluctuait dans la région de leur état stationnaire. Les données supportent les prédictions théoriques suivantes: (*i*) les fluctuations du nombre d'adultes peuvent être décrites au moyen d'une fonction de densité à probabilité gamma; (*ii*) l'augmentation du nombre de recrues chez les populations polymorphiques se traduit par une moyenne et une variance plus grandes du nombre d'adultes; (*iii*) l'autocorrélation du nombre d'adultes diminue exponentiellement avec le temps; et (*iv*) l'augmentation du nombre de recrues chez les populations polymorphiques se traduit par un taux plus rapide de diminution dans les autocorrélations. Ces résultats suggèrent que les différences de vigueur à base génétique chez les populations peuvent se refléter sur la dynamique stochastique stationnaire du niveau de population.

Mots clés: *Tribolium*, dynamique des populations, modèles stochastiques, distributions stationnaires, distribution gamma.

[Traduit par le journal]

Introduction

One concern of population genetic research is the interaction between the genetic structure of a population and its demographic behaviour. In our earlier report published in this journal, Desharnais and Costantino (1980) showed that homozygosity for the corn oil sensitive allele in the flour beetle (*Tribolium castaneum*) was an unstable genetic equilibrium. Homozygous laboratory cultures which were altered by the introduction of the wild-type allele converged to a polymorphic genetic equilibrium. Furthermore, the average number of adults increased in the polymorphic cultures as compared to the homozygous controls. This demographic response to a genetic shift is in agreement with several models which predict that natural selection will maximize the equilibrium size of a population (MacArthur 1962;

Anderson 1971; Roughgarden 1971, 1976; Charlesworth 1971, 1980; Ginzburg 1977; Asmussen and Feldman 1977; Hastings 1978; Gregorius 1979; Desharnais and Costantino 1983). However, adult numbers in the experimental cultures did not converge to a fixed equilibrium point. Instead, the populations were found to fluctuate around a mean value.

In the present report, we extend the analysis of Desharnais and Costantino (1980) by considering the fluctuations in adult numbers at equilibrium. Our study incorporates an additional 48 weeks of new census data. We begin by applying the theory of stochastic differential equations to an elementary model for population growth in *Tribolium* and then establish several testable theoretical predictions. We relate the differences in the stationary stochastic dynamics of the homozygous and polymorphic populations to differences in recruitment rates based upon the biology of the corn oil sensitive and wild-type genotypes. This report combines a theoretical analysis of stochastic population dynamics with experimental data.

Experimental observations

The detailed *Tribolium* culture techniques together with the demographic and genetic analyses for the first 80 weeks of this experiment are contained in Desharnais and Costantino (1980). For continuity, the general procedure is outlined here. Twenty-two cultures of the flour beetle (*Tribolium castaneum*), homozygous for the corn oil sensitive allele (*cos/cos*), were initiated with 64 adults, 16 pupae, 20 large larvae, and 70 small larvae. Each population was contained in a one-half pint milk bottle with 20 g of corn oil medium and kept in an unlighted incubator at 33 ± 1°C and 56 ± 11% relative humidity. The cultures were censused and placed in fresh medium every 2–3 weeks. At the end of the first 10 weeks, the wild-type allele was introduced into 9 of the 22 cultures. In these populations, the frequency of the wild-type allele converged to a polymorphic equilibrium. The remaining 13 replicates were not genetically altered.

It is the adult census data from weeks 62 to 128 that are examined in this report. Two of the 13 homozygous cultures and three of the nine polymorphic cultures became diseased prior to week 128 and were eliminated from the analysis. Thus our data set consists of 29 consecutive censuses on 11 *cos/cos* homozygous populations (319 observations) and six polymorphic populations (174 observations) obtained while adult numbers were fluctuating in the region of their steady states.

Theoretical background

Deterministic model

A deterministic model for the dynamics of laboratory populations of the *Tribolium* flour beetle can be formulated from a consideration of the behavioural interactions which occur among the various life stages (eggs, larvae, pupae, and adults). In the species *T. castaneum* and *T. confusum*, an important interaction is the cannibalism of pupae by adults. If we let C be the per capita rate at which adults cannibalize pupae and we assume that adults act independently, then the proportion of pupae which survive to adulthood is $\exp(-CN)$, where N is the total number of adults. Coupling this density-dependent function with density-independent rates of reproduction and mortality, we have

$$[1] \quad dN/dt = N(X \exp(-CN) - D)$$

as a simple differential equation for the rate of change in adult numbers. The parameter X represents the rate at which potential recruits (large larvae and pupae) are produced per adult, and D is the per capita adult mortality rate. Although this equation is a gross oversimplification of the true complexity inherent in *Tribolium* populations, it has served as a useful paradigm in many studies on *Tribolium* population dynamics (Crombie 1946; Neyman et al. 1956; Lloyd 1968; Desharnais and Costantino 1980, 1981, 1982*a*, 1982*b*), in fisheries biology (Ricker 1954; Levin and Goodyear 1980; May 1980), and in general population theoretical studies (Moran 1950; May 1974, 1976; Smith 1968, 1974; Hoppensteadt 1975; Oster 1976; May and Oster 1976; Thieme 1979; Hunt 1980; Fisher et al. 1979; Cull 1981; Desharnais and Costantino 1983). Using [1] we sacrifice reality for generality.

The dynamics of the deterministic model [1] are quite simple. If $X > D$, the equilibrium number of adults given by $N^* = \log(X/D)/C$ will be approached asymptotically for any initial condition $N(0) > 0$. If $X < D$, then the population will go extinct. In the neighborhood of N^*, the rate of approach to equilibrium is given by the eigenvalue $\lambda = D \log(D/X)$.

Stochastic model

Costantino and Desharnais (1981) have shown that the deterministic model [1] can be converted to a stochastic model be assuming that either the mortality rate D or the recruitment rate X is subject to random fluctuations. This is accomplished by introducing a "white noise" random variable $\gamma(t)$ which has an expected value of zero and a constant spectral density which equals one. In the case of stochastic mortality we have

$$[2] \quad dN/dt = N(X \exp(-CN) - (D + \sigma\gamma)$$

as our stochastic differential equation. A similar model is obtained assuming recruitment is stochastic. The parameter σ is used here as a measure of the amplitude of the random fluctuations. Of course, a more general model would assume that all three parameters D, X, and C fluctuate. For the sake of brevity and mathe-

matical tractability, we will only consider model [2]. For an analysis of the case when the parameter X fluctuates, see Costantino and Desharnais (1981).

Stationary distribution

With the stochastic Eq. 2 it is possible to obtain an expected steady-state distribution for adult numbers. The density function f for this distribution is obtained through the use of the Kolmogorov equation

$$[3] \quad f(N) = (K/v(N)) \exp\left(2 \int_0^N (m(\epsilon)/v(\epsilon))d\epsilon\right)$$

where, loosely speaking, m and v are the mean and variance of the rate of population change, and K is a scaling factor which makes the integrated probability equal to one. Unfortunately, mathematical ambiguities arise in the analysis of stochastic differential equations, and two types of stochastic calculi are commonly used to calculate m. To simultaneously present our results for both types of calculi, we follow the example of Dennis and Patil (1984) and define the following indicator variable:

$$[4] \quad \xi = \begin{matrix} 0 & \text{Stratonovich calculus} \\ \sigma^2/2 & \text{Ito calculus} \end{matrix}$$

For D stochastic, $m(N) = N(X \exp(-CN) - (D + \xi) + (\sigma^2/2))$ and $v(N) = N^2\sigma^2$. Substituting these into [3] gives

$$[5] \quad f(N) = KN^{2((X-D-\xi)/\sigma^2)-1} \times \exp\left(2(X/\sigma^2) \sum_{n=1}^{\infty} (-CN)^n/(nn!)\right)$$

for the expected probability distribution of adult numbers.

The density function given by [5] is rather unwieldy in that it involves an infinite series. Costantino and Desharnais (1981) derived a linear approximation for this series which simplifies the analysis. Using this approximation, [5] becomes a member of the well-known family of gamma distributions whose density function is given by

$$[6] \quad f(N) = (\beta^\alpha \Gamma(\alpha))^{-1} N^{\alpha-1} \exp(-N/\beta)$$

Here $\Gamma(x)$ is the gamma function. This density is only defined for $N > 0$. α is the shape parameter of the distribution and β is a scaling parameter. As α gets large, $f(N)$ approaches a Gaussian normal distribution (Johnson and Kotz 1970). For fluctuations in D, $\alpha = 2(X - D - \xi)/\sigma^2$ and $\beta = (\sigma^2 \log(X/D))/(2C(X - D))$. As σ^2 gets small relative to X and D, α gets large, the importance of ξ diminishes, and the predicted distribution becomes approximately normal.

We examined a numerical example to see how closely the gamma density [6] approximates the exact density [5]. First we chose plausible parameter values such that $N^* = 160$, $X/D = 3.5$, and $\sigma^2/D = 0.10$. Substituting these values into the exact density function, we computed the integration constant K and the first two moments of the distribution. We then fit both a gamma and a normal density function with the same mean and variance as the exact distribution. We measured the closeness of the fit by computing the maximum difference between the cumulative frequencies of the exact distribution and both the gamma and normal approximations (Kolmogorov's statistic). The gamma density provided a close fit with a maximum difference of 0.013. For the normal density the maximum difference was 0.045; the normal density could not match the skewness of the exact distribution. Costantino and Desharnais (1981) evaluated the gamma approximation using a Monte Carlo simulation of [2].

The major advantage of working with a known distribution is that closed form expressions are available for its moments. For the gamma, the mean and variance of adult numbers are given by $E(N) = \alpha\beta$ and $\mathrm{Var}(N) = \alpha\beta^2$, respectively. In terms of the biological parameters of our original model, we have

$$[7] \quad E(N) = N^*(1 - \xi/(X - D))$$

$$[8] \quad \mathrm{Var}(N) = ((\sigma N^*)^2 (1 - \xi/(X - D))) \div (2(X - D))$$

where N^* is the equilibrium point of the deterministic model [1]. With these expressions it is possible to predict the effects of a change in one of the biological parameters on the steady-state distribution of adult numbers.

Stationary time series

If the amplitudes of the random fluctuations are small, then we can obtain a first approximation to the autocorrelation function of adult numbers through time (Nisbet and Gurney 1982). We begin by linearizing our stochastic differential [2] around the point $N(t) = N^*$ and $\gamma(t) = 0$. This gives us

$$[9] \quad dN/dt \simeq (N(t) - N^*)\lambda - \sigma N^* \gamma(t)$$

where λ is the eigenvalue from the deterministic model [1]. (Our data analysis, presented below, will justify the use of this linear approximation.) Using standard Fourier transform techniques, we derive in Appendix 1 the following theoretical function for the autocorrelation of $N(t)$ with $N(t + \tau)$:

$$[10] \quad \rho_N(\tau) = \exp(\lambda|\tau|)$$

With this expression, one can obtain information on the demographic stability of the population by estimating λ from data at the steady state.

Until now, we have assumed that the random vari-

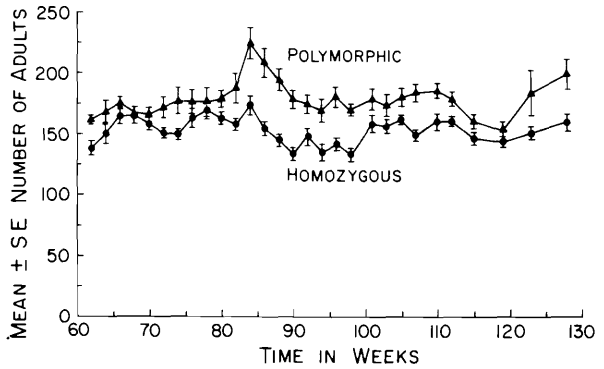

FIG. 1. Mean ± standard error of number of adults plotted against census week for the homozygous populations (●) and the polymorphic populations (▲).

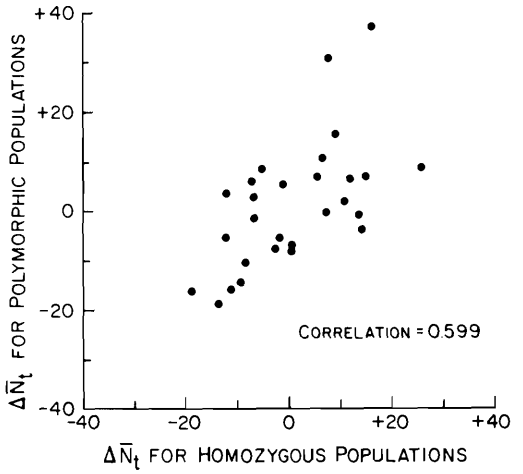

FIG. 2. Scatter diagram of the change in mean adult numbers ($\Delta\bar{N}_t$) for the homozygous versus the polymorphic populations. Each point represents the change over two successive censuses.

able $\gamma(t)$ represents uncorrelated white noise. As an alternative model, we will assume that environmentally induced fluctuations in the parameter D are themselves autocorrelated. Specifically, we now assume that $\gamma(t)$ represents "pink noise," that is, the correlation of $\gamma(t)$ with $\gamma(t + \tau)$ is

$$[11] \quad \rho_\gamma(\tau) = \exp(\mu|\tau|)$$

where $\mu < 0$ is a measure of the rate of decay of the autocorrelations. With this modified definition of $\gamma(t)$ in [9], we show in Appendix 1 that the expected autocorrelation function of adult numbers is

$$[12] \quad \rho_N(\tau) = \begin{cases} (\lambda\exp(\mu|\tau|) - \mu\exp(\lambda|\tau|))/(\lambda - \mu) & \text{for } \lambda \neq \mu \\ (1 - \lambda|\tau|)\exp(\lambda|\tau|) & \text{for } \lambda = \mu \end{cases}$$

By comparing [10] and [12] with actual data, one can evaluate the assumption that the time scale for random environmental fluctuations is much shorter than the time scale for changes in population size.

Results

The mean and standard error of adult numbers over time are plotted in Fig. 1. The polymorphic populations maintain a larger number of adults than the homozygous populations. Desharnais and Costantino (1980) made a similar observation for the census data prior to week 62. In this earlier study, assays of the survivorship of eggs sampled from the experimental cultures indicated an increase in the mean larval viability for the polymorphic populations. This finding, which is consistent with the bioligy of the *cos* mutant, suggests that the average number of potential recruits, parameter X, is higher in the polymorphic cultures than in the homozygous ones. An increase in the parameter X results in an increase in the deterministic equilibrium number of adults N^*, an interpretation which is supported by the experimental data (Fig. 1).

An examination of the fluctuations of mean adult numbers in Fig. 1 suggests that the homozygous and polymorphic populations are correlated in their behaviour. That is, the increases and decreases in population size occur at roughly the same points in time. We investigated this impression by computing the change in the mean number of adults at time t as $\Delta\bar{N}_t = \bar{N}_t - \bar{N}_{t-1}$, pairing the values for the homozygous and polymorphic groups at each census, and plotting these data as a scatter diagram in Fig. 2. This analysis does indicate a significant positive correlation ($r = 0.599$, $P < 0.01$), suggesting that all the populations are responding to the same random input. Because all the cultures were kept on the same shelf in the same incubator, in this experiment the random input may be due to small changes in the incubator's temperature and humidity.

The census data can also be used to obtain estimates of the expected gamma stationary distributions. We pooled the census data for the homozygous and polymorphic populations separately, and generated two observed frequency histograms (Fig. 3). We then fitted the gamma density function [6] by estimating the parameters α and β using the method of maximum likelihood (Johnson and Kotz 1970, p. 189). The fitted distributions are represented by the solid curves in Fig.

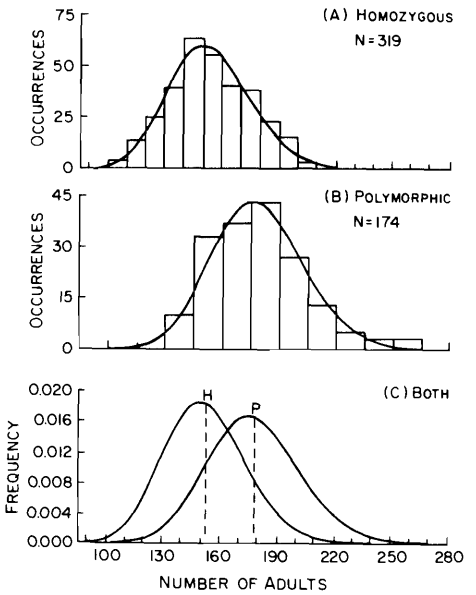

FIG. 3. Stationary distributions of adult numbers for the (A) homozygous and (B) polymorphic populations. The histograms represent the observed distributions and the smooth curves are the fitted gamma density functions. N is the number of observations. Both density functions are plotted on the same scale in (C). The vertical dashed lines in (C) locate the means for each distribution.

3. For the homozygous cultures, we estimated $\tilde{\alpha} = 49.92 \pm 3.94$ and $\tilde{\beta} = 3.07 \pm 0.244$, and for the polymorphic populations $\tilde{\alpha} = 54.39 \pm 5.81$ and $\tilde{\beta} = 3.294 \pm 0.354$. The standard errors of these estimates were computed using the asymptotic (large sample) formulas given by Johnson and Kotz (1970, p. 188). In both cases, the estimated values of α and β are highly correlated ($r = -0.995$).

We evaluated the gamma expectation using a χ^2 test for goodness of fit. The expected values for each frequency interval were obtained by numerical integration of the fitted gamma density functions. The computed χ^2 statistics were compared with the table values at the 5% probability level with $n - 3$ degrees of freedom, where n is the number of frequency intervals. For both the homozygous and polymorphic distributions, we accepted the gamma hypothesis.

We also used the χ^2 procedure to test our data for normality. For the homozygous populations, we accepted the normal distribution at the 5% probability level. The observations in the right tail of the observed polymorphic frequency distribution (Fig. 3) forced us to reject the assumption of normality. Nevertheless, the large estimated values of the gamma shape parameters for both groups suggest that the normal distribution is a fair approximation for these data.

Our theoretical results provide us with some predictions concerning the mean and variance of adult numbers. As we have already noted, the polymorphic and homozygous populations differ most significantly with respect to their density-independent rates of recruitment. Assuming that the parameter X is larger in the polymorphic group, we can use [7] and [8] to make qualitative predictions about the relative magnitudes of the means and variances of the two distributions. First, an examination of [7] tells us that an increase in X will result in an increase in $E[N]$, that is, $\partial E[N]/\partial X > 0$. Similarly, [8] implies that, unless X is very large relative to D (unless $X/D > 4.92$), an increase in X causes an increase in the variance ($\partial \text{ Var}(N)/\partial X > 0$). These two hypotheses can be tested with the experimental data.

We compared the means and variances of the homozygous and polymorphic distributions using statistical tests based upon the assumption of normality. Using an approximate student's t-test for unequal variances (Snedecor and Cochran 1967, pp. 114–115), we found that the mean for the polymoprhic distribution ($\bar{N} = 179.2$) is significantly larger than the mean for the homozygous distribution ($\bar{N} = 153.6$) at the 0.001 level of probability. A test for the equality of the variances (Snedecor and Cochran 1967, p. 116) also revealed a significantly larger variance for the polymorphic group ($\text{Var}(N) = 620.3$) when compared to the homozygous group ($\text{Var}(N) = 468.6$) at the 0.05 level of probability. These results support our theoretical predictions provided the ratio of X to D is not too large.

We also used our time series to compute the autocorrelations of adult numbers. We estimated the autocorrelation of order τ by paring the adult census number at week t with the adult number at week $t + \tau$ for each replicate. These paired observations were pooled within the homozygous and polymorphic groups, and an overall correlation coefficient was calculated in the usual way for both groups. This procedure was repeated for values of τ ranging from 2 to 20 weeks at intervals of 2 weeks, which is the average period between censuses. For both groups, this yielded 10 serial correlations of adult numbers. We then corrected the estimated correlation coefficients of order τ by dividing the values by $(1 - (\tau/n))$, where n is the total number of paired data points used in the computation. This procedure removes the bias in an autocorrelation estimate (Bloomfield 1976, p. 184). These corrected estimates are plotted in Fig. 4.

The estimated autocorrelations were used to evaluate the theoretical predictions based upon [9]. First, we note that although these predictions are based upon a linear model, this linear approximation is valid if the fluctuations in population size are not very large. For both our distributions, the coefficient of variation is

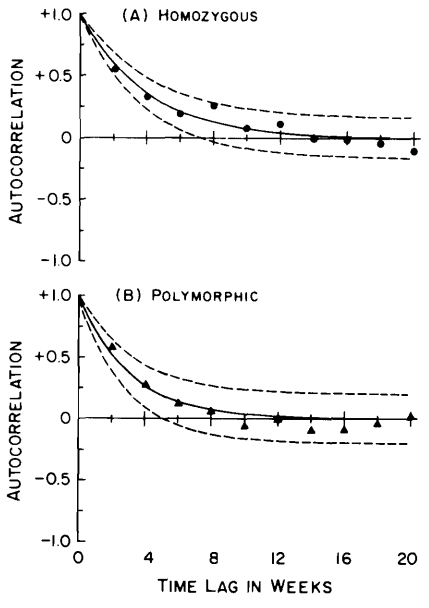

FIG. 4. Stationary autocorrelations of adult numbers versus time lag for the (A) homozygous and (B) polymorphic populations. The circles and triangles are the observed autocorrelations. The solid curves are the fitted theoretical autocorrelation functions obtained from [10]. The dashed curves form confidence bands of ±2 standard errors, and were computed using [14] for the expected variance of the autocorrelations.

0.14, suggesting that our use of the linear model is reasonable. Using a nonlinear least squares procedure, we fit the predicted [10] to our serial correlations. The fitted functions appear in Fig. 4. For both groups, the regression estimates for the eigenvalues are $\tilde{\lambda} = -0.258 \pm 0.025$ for the homozygous populations and $\tilde{\lambda} = -0.330 \pm 0.035$ for the polymorphic group. Because $\lambda = D(\log(D/X))$, the smaller estimated value for the polymorphic populations is consistent with the assumption that the parameter X is larger for this group. We also used the least-squares procedure to evaluate the alternative prediction [12] which is based on the assumption of random pink noise. For the homozygous autocorrelations, the least-squares fit continued to improve as $\mu \uparrow \infty$, yielding our original estimate of λ from the white noise model. For the polymorphic autocorrelations, [12] did provide a slightly better fit, with a coefficient of variation of 0.94. However, the estimated values of $\tilde{\lambda} = -0.456 \pm 0.173$ and $\tilde{\mu} = -1.144 \pm 0.939$ also suggest that the time scale for the environmental fluctuations is significantly shorter than the time scale for the fluctuations in adult number.

Finally, it is possible to obtain a confidence interval on the expected autocorrelation function. If n is the number of paired observations used to compute the autocorrelation and the parent series is normally distributed, then Bartlett (1946) has shown that the variance of the estimated autocorrelation is given by

$$[13]\quad \mathrm{Var}[\tilde{\rho}_N(\tau)] = (1/n)\sum_{j=-\infty}^{+\infty} (\rho_N(j)^2 + \rho_N(j-\tau) \times \rho_N(j+\tau) - 4\rho_N(\tau)\rho_N(j)\,\rho_N(\tau+j) + 2\rho_N(j)^2\rho_N(\tau)^2)$$

where $\tilde{\rho}_N$ is the estimated autocorrelation and ρ_N is its expected value. In Appendix 2, we show that substitution of [10] into [13] gives

$$[14]\quad \mathrm{Var}(\tilde{\rho}_N(\tau)) = (1/n)\,((1 - \exp(2\lambda\tau)) \times (1 + \exp(2\lambda))\,(1 - \exp(2\lambda))^{-1} - 2\tau\exp(2\lambda\tau))$$

We used our estimated values for λ in [14] to obtain confidence regions of ±2 standard errors on the expected autocorrelations of adult numbers assuming random white noise. These confidence regions are drawn in Fig. 4. All of our estimated autocorrelations fall within these confidence regions.

Discussion

The use of stochastic differential equations has been a recent subject of dispute among population biologists. Nisbet and Gurney (1982) point out that some of the value of the predictions based on stochastic differential equations are lost because of the assumptions used in their derivation. For example, our knowledge of the flour beetle system provides no guide to the choice of integration rule, Ito or Stratonovich. Nevertheless, we were able to evaluate the predictions of our stochastic formulation using experimental data. The data supported our predictions of a gamma distribution for adult numbers and a negative exponential autocorrelation function. More importantly, we were able to relate the genetic differences between the homozygous and polymorphic groups to observable differences in their stationary stochastic dynamics. It is at this level that we feel the theory is most useful.

Perhaps a more difficult question is the nature of the stochasticity itself. In the present study, we chose a model of environmental stochasticity by introducing an exogenous random variable $\gamma(t)$ into the adult mortality rate. An alternative formulation is based on the assumption of demographic stochasticity, where the probabilistic nature of the recruitment and mortality of individuals serves as the only source of variation in population size. We have also found the latter formulation to be applicable to *Tribolium* (Desharnais and Costantino 1982*a*), and at the present time we see no clear-cut reason always to choose one model over the other. However, in the present study we did find a correlation in the dynamical behaviour of separate populations (Fig. 2) which

does suggest environmentally induced fluctuations.

Finally, it is worth mentioning the many statistical difficulties one encounters when analyzing time series observations on replicate populations. On one hand, the stationary distribution of population size is an abstraction which is technically applicable only to a very large (infinite) ensemble of independent populations. On the other hand, the stationary autocorrelation function for adult numbers is an abstraction applicable only to a very long (infinite) time series for a single population. Of course, any realistic experiment will be intermediate to these extremes. Our naive approach has been to pool observations among replicates of the same treatment to perform our analyses. A more powerful approach would take into account observations within and between replicates to compare treatments. We eagerly await the development of such statistical techniques.

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Appendix 1

Here we derive the theoretical autocorrelation functions [10] and [12]. Our methods closely follow those of Nisbet and Gurney (1982).

Assume $N(t)$ is a stationary stochastic process which exists over a very long time interval $(-T/2, T/2)$. The Fourier transform of $N(t)$ is defined as

$$[A1] \quad \tilde{N}(\omega) = \int_{-T/2}^{T/2} N(t) \exp(-i\omega t)\mathrm{d}t$$

and the inverse Fourier transformation is given by

$$[A2] \quad N(t) = (1/2\pi) \int_{-\infty}^{\infty} \tilde{N}(\omega) \exp(i\omega t)\mathrm{d}\omega$$

Here, $i = (-1)^{1/2}$.

Now consider the linear stochastic differential equation

$$[A3] \quad \mathrm{d}N/\mathrm{d}t = f(t) = (N(t) - N^*)\lambda - \sigma N^*\gamma(t)$$

where $\gamma(t)$ represents random noise. As $T \uparrow \infty$, a well-known relationship exists between the Fourier transform of $N(t)$ and the transform of its derivative, $f(t) = \mathrm{d}N/\mathrm{d}t$. The relationship is

$$[A4] \quad \tilde{f}(\omega) = i\omega\tilde{N}(\omega)$$

However, we can use [A3] to calculate $\tilde{f}(\omega)$ directly. This gives

$$[A5] \quad \tilde{f}(\omega) = \int_{-T/2}^{T/2} f(t) \exp(-i\omega t)\mathrm{d}t$$

$$= \lambda\tilde{N}(\omega) - 2N^*\lambda\omega^{-1} \sin(\omega T/2) - \sigma N^*\tilde{\gamma}(\omega)$$

where $\tilde{\gamma}(\omega)$ is the Fourier transform of $\gamma(t)$. If the time interval T is sufficiently large, we may equate [A4] and [A5], obtaining

$$[A6] \quad \tilde{N}(\omega) = N^*(\lambda - i\omega)^{-1} (\sigma\tilde{\gamma}(\omega) + (2\lambda/\omega) \sin(\omega T/2))$$

This can be used to obtain the spectral density of $N(t)$, which is defined as

$$[A7] \quad S_N(\omega) = \lim_{T\to\infty} T^{-1}E(\tilde{N}(\omega)\overline{\tilde{N}(\omega)}$$

where $\overline{\tilde{N}(\omega)}$ is the complex conjugate of $\tilde{N}(\omega)$. Assuming $E(\gamma(t)) = 0$, we also have $E(\tilde{\gamma}(\omega)) = E(\overline{\tilde{\gamma}(\omega)}) = 0$. Because $\sin(\omega T/2)$ is a bounded function,

$$[A8] \quad S_N(\omega) = (\sigma N^*)^2 (\lambda^2 + \omega^2)^{-1} S_\gamma(\omega)$$

First we consider the case where $\gamma(t)$ is random "white noise." By definition, $E(\gamma(t)) = 0$ and $S_\gamma(\omega) = 1$. Substituting into [A8] we obtain,

$$[A9] \quad S_N(\omega) = (\sigma N^*)^2 (\lambda^2 + \omega^2)^{-1}$$

for the spectral density of $N(t)$. The autocovariance function $\mathrm{Cov}_N(\tau) = E((N(t) - N^*)(N(t + \tau) - N^*))$ can be calculated from the inverse transformation of the spectral density using

[A10] $$\mathrm{Cov}_N(\tau) = (1/2\pi)\int_{-\infty}^{\infty} S_N(\omega)\exp(i\omega|\tau|)d\omega$$

$$= (\sigma N^*)^2 (1/2\pi)\int_{-\infty}^{\infty} (\lambda^2 + \omega^2)^{-1}\exp(i\omega|\tau|)d\omega$$

This definite integral is computed easily using the calculus of residues (e.g., Dennery and Krzywicki 1967, pp. 53–60):

[A11] $$\int_{-\infty}^{\infty} (\lambda^2 + \omega^2)^{-1}\exp(i\omega|\tau|)d\omega = 2\pi i \lim_{\omega \to -i\lambda} (\omega + i\lambda)(\lambda^2 + \omega^2)^{-1}\exp(i\omega|\tau|)$$

$$= 2\pi i \lim_{\omega \to i\lambda} (\omega - i\lambda)^{-1}\exp(i\omega|\tau|)$$

$$= (-\pi/\lambda)\exp(\lambda|\tau|)$$

The autocorrelation function [10] is obtained by substituting [A11] into [A10] and computing $\rho_N(\tau) = \mathrm{Cov}_N(\tau)/\mathrm{Cov}_N(0)$.

Now assume that $\gamma(t)$ is random "pink noise" with $E(\gamma(t)) = 0$ and $E(\gamma(t)\gamma(t+\tau))$ given by [11]. The spectral density of $\gamma(t)$ is obtained from the Fourier transform

[A12] $$S_\gamma(\omega) = \int_{-\infty}^{\infty} \rho_\gamma(\tau)\exp(-i\omega\tau)d\tau$$

$$= \int_{-\infty}^{\infty} \exp(\mu|\tau|)\cos(-\omega\tau)d\tau = -2\mu(\mu^2 + \omega^2)^{-1}$$

Substituting [A12] into [A8] gives

[A13] $$S_N(\omega) = -2\mu(\sigma N^*)^2 (\lambda^2 + \omega^2)^{-1}(\mu^2 + \omega^2)^{-1}$$

for the spectral density of $N(t)$. Using [A13] in [A10], we have

[A14] $$\mathrm{Cov}_N(\tau) = (\sigma N^*)^2 (-\mu/\pi)\int_{-\infty}^{\infty} (\lambda^2 + \omega^2)^{-1}(\mu^2 + \omega^2)^{-1}\exp(i\omega|\tau|)d\omega$$

Now we consider two cases. Assume $\mu \neq \lambda$. Let $\omega_1 = i\lambda$ and $\omega_2 = i\mu$. Using the calculus of residues we have

[A15] $$\int_{-\infty}^{\infty} (\lambda^2 + \omega^2)^{-1}(\mu^2 + \omega^2)^{-1}\exp(i\omega|\tau|)d\omega = 2\pi i \sum_{j=1}^{2} \lim_{\omega \to \omega_j} (\omega - \omega_j)(\lambda^2 + \omega^2)^{-1}(\mu^2 + \omega^2)^{-1}\exp(i\omega|\tau|)$$

$$= \pi(\mu^2 - \lambda^2)^{-1}(\mu^{-1}\exp(\mu|\tau|) - \lambda^{-1}\exp(\lambda|\tau|))$$

If $\mu = \lambda$, then ω_1 is a pole of order two. From the theorem of residues

[A16] $$\int_{-\infty}^{\infty} (\lambda^2 + \omega^2)^{-2}\exp(i\omega|\tau|)d\omega = 2\pi i \lim_{\omega \to \omega_1} \mathrm{d}((\omega + i\lambda)^2 (\lambda^2 + \omega^2)^{-2}\exp(i\omega|\tau|))/d\omega$$

$$= (\pi/2\lambda^2)(\tau - \lambda^{-1})\exp(\lambda|\tau|)$$

Substituting [A15] and [A16] into [A14] and dividing by $\mathrm{Cov}_N(0)$ gives $\rho_N(\tau)$ in [12].

Appendix 2

Here we detail the steps used to arrive at [14].

We begin by substituting our expected autocorrelation function [10] into Bartlett's general result [13]. This yields

[B1] $$\mathrm{Var}(\tilde{\rho}_N(\tau)) = (1/n)\sum_{j=-\infty}^{+\infty} (\exp(2\lambda|j|) + \exp(\lambda(|j-\tau| + |j+\tau|)) - 4\exp(\lambda(|j| + |\tau| + |j+\tau|))$$

$$+ 2\exp(2\lambda(|j| + |\tau|)))$$

Now we must consider the values of $|j-\tau| + |j+\tau|$ and $|j| + |\tau| + |j+\tau|$ for $-\infty < j < +\infty$ and $-\infty < \tau < +\infty$. It is easy to see that

[B2] $$|j-\tau| + |j+\tau| = \begin{cases} 2|j| & \text{for } |j/\tau| > 1 \\ 2|\tau| & \text{for } |j/\tau| \leq 1 \end{cases}$$

and

[B3] $$|j| + |\tau| + |j+\tau| = \begin{cases} 2|j| & \text{for } j/\tau < -1 \\ 2|\tau| & \text{for } -1 \leq j/\tau \leq 0 \\ 2|j| + 2|\tau| & \text{for } j/\tau > 0 \end{cases}$$

Assume $\tau \geq 0$. Using [B2] and [B3], we break the doubly infinite series [B1] into five parts and simplify:

$$[B4] \quad n \operatorname{Var}[\tilde{\rho}_N(\tau)] = 2 \sum_{j=-\infty}^{-\tau-1} (\exp(2\lambda(|j| + \tau)) - \exp(2\lambda|j|)) + \sum_{j=-\tau}^{-1} (\exp(2\lambda|j|) - 3\exp(2\lambda\tau) + 2\exp(2\lambda(|j| + \tau)))$$
$$+ 1 - \exp(2\lambda\tau) + \sum_{j=1}^{\tau} (\exp(2\lambda j) + \exp(2\lambda\tau) - 2\exp(2\lambda(j + \tau)))$$
$$+ 2 \sum_{j=\tau+1}^{\infty} (\exp(2\lambda j) - \exp(2\lambda(j + \tau)))$$

The first and last series cancel. The last terms of the two remaining finite series also cancel. This leaves

$$[B5] \quad n \operatorname{Var}(\tilde{\rho}_N(\tau)) = 1 - (2\tau + 1)\exp(2\lambda\tau) + 2 \sum_{j=1}^{\tau} \exp(2\lambda j)$$

Since the terms of the series in [B5] represent a geometric progression, we can write

$$[B6] \quad \sum_{j=1}^{\tau} \exp(2\lambda j) = \exp(2\lambda)(1 - \exp(2\lambda\tau))(1 - \exp(2\lambda))^{-1}$$

Substitution of [B6] into [B5] yields [14].

As a final note, one can repeat this procedure, *mutatis mutandis*, for $\tau \leq 0$ and show that $\operatorname{Var}(\tilde{\rho}_N(-\tau)) = \operatorname{Var}(\tilde{\rho}_N(\tau))$.

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