

STABLE DEMOGRAPHIC LIMIT CYCLES
IN LABORATORY POPULATIONS
OF *TRIBOLIUM CASTANEUM*

BY ROBERT A. DESHARNAIS AND LAIFU LIU*

*Laboratory of Populations, The Rockefeller University, 1230 York Avenue, New York,
New York, 10021-6399, U.S.A.*

SUMMARY

(1) We present a general population matrix model in which the age-specific vital rates depend upon the age structure of the population. The fecundity and survivorship of each age-class are assumed to decrease exponentially at rates which depend on the densities of each age-class. We specialize this model to describe the physiological and behavioural interactions among eggs, larvae, pupae and adults in laboratory populations of *Tribolium* flour beetles.

(2) A non-trivial equilibrium age structure exists provided the population can grow without density dependence. If such an equilibrium exists, it is unique. We linearize the model in the neighbourhood of its equilibrium and state the necessary and sufficient conditions for local asymptotic stability.

(3) Using several simplifying assumptions, we estimate the parameters of the model using data from our own work and from the literature. With these estimates we predict the existence of an unstable equilibrium age structure.

(4) Computer simulations are used to compare the behaviour of the model with census data from experimental populations of *Tribolium castaneum*. After 70 days of culture, the experimental populations were subjected to demographic perturbations. Both the simulations and the experimental populations exhibit stable oscillations. In general, there is good agreement between the model and the data.

(5) We simulated the model using a variety of parameter values. We show how each parameter affects the equilibrium and stability of the model. Increases in the rates of mortality or rates of egg and pupal cannibalism by adults are stabilizing, while high rates of fecundity or egg cannibalism by larvae lead to demographic oscillations. For each parameter, we obtain numerical estimates of the threshold between a stable and unstable point equilibrium.

(6) Considering the variation in the rates of survivorship, reproduction, and cannibalism reported in the literature for different species and genetic strains of *Tribolium* under different environmental conditions, we conclude that laboratory populations of *Tribolium* can exhibit dynamic behaviours ranging from stable equilibria to demographic limit cycles.

* Present address: Department of Mathematics, Beijing Normal University, Beijing, People's Republic of China.

INTRODUCTION

In an age-structured population, negative density dependence involves inhibition of the reproduction and survivorship of one or more age-classes. In an effort to extend the linear matrix formulations of Bernardelli (1941), Lewis (1942), and Leslie (1945), many authors have incorporated density dependence by making the elements of the population projection matrix vary with the age distribution or density of the population (Leslie 1948, 1959; Williamson 1959, 1974; Pennycuick, Compton & Beckingham 1968; Usher 1972; Allen & Basasibwaki 1974; Cook & Léon 1976; Guckenheimer, Oster & Ipaktchi 1977; Levin & Goodyear 1980; Fisher & Goh 1984; Ziebur 1984; Desharnais & Cohen 1986; Liu & Cohen 1987). These types of models can exhibit very complicated dynamics, ranging from stable points to strange attractors. Their application requires detailed biological information on the mechanisms of density dependence which is unavailable for most species. For this reason, density-dependent matrix models are seldom confronted with experimental data (for exceptions, see Pennycuick 1969; Beddington 1974; McKelvey *et al.* 1980; and the continuous-time formulations of Botsford & Wickham 1978; Nisbet & Gurney 1982; Gurney, Nisbet & Lawton 1983).

Flour beetles of the genus *Tribolium* have been used extensively in ecological research for almost 60 years. (For reviews, see Mertz 1972; King & Dawson 1972; Sokoloff 1972, 1974, 1977.) There exist well documented density-dependent interactions among the life stages including, most importantly, cannibalism (Park *et al.* 1965). Regular cycles in the age classes are often observed, even under constant laboratory conditions (Chapman 1933; Mertz 1969). These attributes make *Tribolium* populations attractive subjects for demographic analysis using density-dependent matrix models.

Since Chapman's (1928) pioneering use of *Tribolium* in population research, there have been numerous theoretical studies of the population dynamics of these beetles. Sokoloff (1974; pp. 536–562) provides a chronological summary of many of the mathematical models. Although these models run the gamut from simple difference and differential equations to complex computer programs, to our knowledge, there have been no investigations of the population dynamics of *Tribolium* using the standard matrix approach.

In the current study, we present a general model by Liu & Cohen (1987) which allows age-dependent interactions to suppress the reproduction and survivorship of each age-class. With assumptions based on the biology and behaviour of flour beetles, we apply this model to the complex dynamics of laboratory populations of *Tribolium castaneum* Herbst. We estimate the parameters of the model using data from the literature and evaluate the performance of the model using the data of Desharnais & Costantino (1980). Our results support the view that demographic oscillations in *Tribolium* can be viewed as a stable demographic limit cycle.

MATRIX MODELS

General matrix model

Consider the logistic model of population growth,

$$dN/dt = [r - \gamma N(t)] N(t). \quad (1)$$

In the case of discrete time, assume that $N(t)$ remains constant in the interval $k \leq t < k + 1$, where $k = 0, 1, 2, \dots$. Dividing model (1) by $N(t)$ and integrating from k to $k + 1$ gives

$$N(k+1) = \exp[r - \gamma N(k)] N(k) = \lambda \exp[-\gamma N(k)] N(k). \tag{2}$$

$\lambda = e^r$ is the rate of increase of the population without density dependence and γ measures the sensitivity of population growth to increase in density. This difference equation has been studied extensively by May (1974), May & Oster (1976), and Fisher & Goh (1984).

Liu & Cohen (1987) propose the following density-dependent matrix model as a natural extension of model (2):

$$\mathbf{N}(k+1) = \mathbf{M}[\mathbf{N}(k)] \mathbf{N}(k), \tag{3}$$

where $\mathbf{N}(k) = [n_1(k), n_2(k), \dots, n_\omega(k)]^T$ is a column vector representing the age structure of the population at time k (the superscript T stands for matrix transposition) and

$$\mathbf{M}[\mathbf{N}(k)] = \begin{pmatrix} f_1 \bar{E}_1[\mathbf{N}(k)] & f_2 \bar{E}_2[\mathbf{N}(k)] & \dots & f_{\omega-1} \bar{E}_{\omega-1}[\mathbf{N}(k)] & f_\omega \bar{E}_\omega[\mathbf{N}(k)] \\ s_1 E_1[\mathbf{N}(k)] & 0 & \dots & 0 & 0 \\ 0 & s_2 E_2[\mathbf{N}(k)] & \dots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & \dots & s_{\omega-1} E_{\omega-1}[\mathbf{N}(k)] & 0 \end{pmatrix}. \tag{4}$$

The constants f_i and s_i represent the density-independent fertility and survivorship, respectively, of an individual of age i . Density-dependence is incorporated through the exponential functions

$$\bar{E}_i[\mathbf{N}(k)] = \exp\left[-\sum_{j=1}^{\omega} \bar{\gamma}_{ij} n_j(k)\right], \quad i = 1, 2, \dots, \omega, \tag{5a}$$

$$E_i[\mathbf{N}(k)] = \exp\left[-\sum_{j=1}^{\omega} \gamma_{ij} n_j(k)\right], \quad i = 1, 2, \dots, \omega, \tag{5b}$$

where $\bar{\gamma}_{ij}$ measures the sensitivity of the fertility of an individual of age i to the density of individuals of age j and γ_{ij} is defined similarly for survivorship. Since eqns (3)–(5) are a multidimensional extension of model (2), Liu & Cohen (1987) call this model the *logistic matrix model*.

The vector \mathbf{N}^* is called an *equilibrium population* if $\mathbf{N}^* = \mathbf{M}(\mathbf{N}^*)\mathbf{N}^*$. Conditions for the existence, uniqueness, and stability of \mathbf{N}^* are presented in Liu & Cohen (1987). We now focus our attention on an application of the logistic matrix model to *Tribolium*.

Tribolium matrix model

Populations of flour beetles of the genus *Tribolium* are composed of four life stages (eggs, larvae, pupae, and adults), among which there are behavioural interactions. For several genetic strains of the species *T. castaneum* and *T. confusum*, Park *et al.* (1965) have shown that under crowded conditions adults and larvae cannibalize eggs and adults cannibalize pupae. Larvae were also shown to cannibalize pupae in some strains, but the magnitude of this interaction seems less important. In addition to cannibalism, Rich (1956) has also shown that the fecundity of females decreases with increases in the density of adults. Although other life-stage interactions have been documented, they seem to be less important in the regulation of population densities, and so we shall specialize the logistic matrix model based on the following assumptions: (i) larvae and adults cannibalize eggs at rates independent of the ages of the eggs; (ii) adults cannibalize pupae

at rates independent of the ages of the pupae; (iii) larval and adult mortality is density-independent; and (iv) the density of the immature life stages does not affect the fecundity rates of females.

Let the interger $\omega > 0$ represent the maximum age of a beetle in some discrete time unit. Let E be a subset of the intergers $\{1, 2, \dots, \omega\}$ such that a beetle of age i is an egg if and only if $i \in E$. Let the sets $L, P,$ and A be defined similarly for the larval, pupal, and adult stages, respectively. Considering assumptions (i)–(iii) above, we let $\gamma_{ij} = \gamma_{Ej}$ for $i \in E$ and $j \in L, A$; $\gamma_{ij} = \gamma_{Pj}$ for $i \in P$ and $j \in A$; otherwise $\gamma_{ij} = 0$. Assumption (iv) implies $\bar{\gamma}_{ij} = 0$ whenever $j \in E, L,$ or P . For the *Tribolium* model we have

$$n_1(k + 1) = \sum_{j \in A} n_j(k) f_j \exp[- \sum_{h \in A} \bar{\gamma}_{jh} n_h(k)], \tag{6a}$$

$$n_{i+1}(k + 1) = n_i(k) s_i \exp[- \sum_{j \in L} \gamma_{Ej} n_j(k) - \sum_{j \in A} \gamma_{Ej} n_j(k)], \quad i \in E, \tag{6b}$$

$$n_{i+1}(k + 1) = n_i(k) s_i, \quad i \in L, \tag{6c}$$

$$n_{i+1}(k + 1) = n_i(k) s_i \exp[- \sum_{j \in L} \gamma_{Pj} n_j(k)], \quad i \in P, \tag{6d}$$

$$n_{i+1}(k + 1) = n_i(k) s_i, \quad i \in A, i \neq \omega. \tag{6e}$$

Equation (6a) describes the rate at which eggs enter the population and (6b)–(6e) describe the survivorship of eggs, larvae, pupae, and adults, respectively.

Equilibrium and stability

Under what conditions does the *Tribolium* model possess a non-trivial equilibrium? Can the model possess multiple non-trivial equilibria? Answers to these questions are given as follows.

Theorem 1. Let \mathbf{N}^* represent a non-trivial (positive) equilibrium vector of the model (6). \mathbf{N}^* exists if and only if $s[\mathbf{M}(\mathbf{0})] > 1$, where $s(\mathbf{M})$ denotes the spectral radius of the matrix \mathbf{M} . If \mathbf{N}^* exists, it is unique.

This theorem is proved in the appendix. In the proof it is shown that the problem of calculating \mathbf{N}^* can be reduced to the problem of finding the unique real root of a single non-linear equation.

The matrix $\mathbf{M}(\mathbf{0})$ represents the linear projection matrix with no density dependence. Our theorem says that if the population grows without density dependence ($s[\mathbf{M}(\mathbf{0})] > 1$), then with density dependence a single unique equilibrium vector exists.

The local stability of the equilibrium can be investigated in the usual way by linearizing model (6) in the neighbourhood of \mathbf{N}^* . Let $\Delta(k) = \mathbf{N}(k) - \mathbf{N}^*$ represent deviations from the equilibrium. Substituting into model (6) yields

$$\Delta(k + 1) = \mathbf{Z} \Delta(k) + O(|\Delta|^2), \tag{7}$$

where

$$\mathbf{Z} = [z_{ij}] = [\partial n_i(k + 1) / \partial n_j(k)]_{\mathbf{N} = \mathbf{N}^*}, \quad i, j = 1, 2, \dots, \omega. \tag{8}$$

The first row of \mathbf{Z} is given by

$$z_{1j} \begin{cases} = 0 & j \in E, L, P, \\ = F_j^* - \sum_{h \in A} \bar{\gamma}_{hj} n_h^* F_h^* & j \in A, \end{cases} \tag{9a}$$

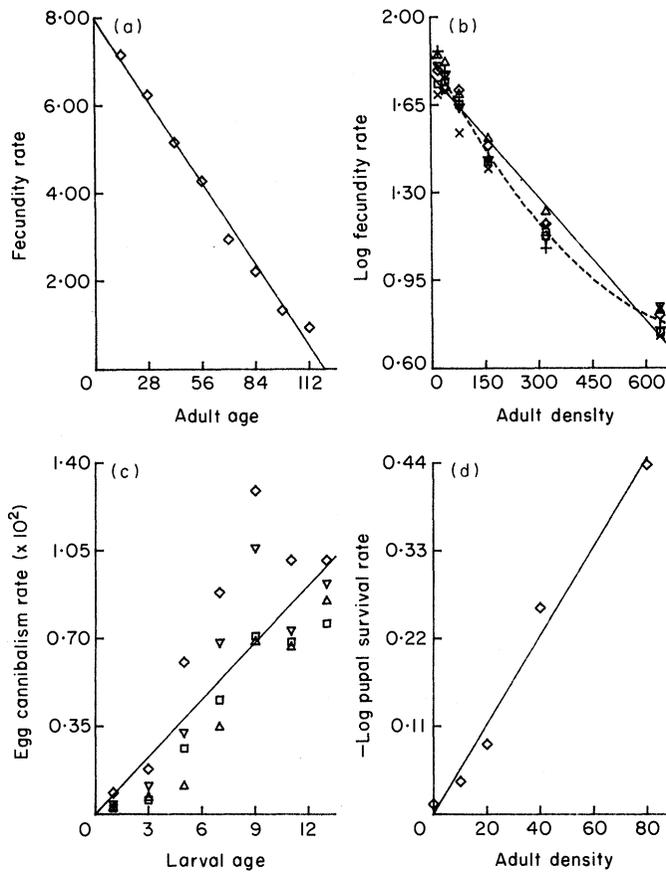


FIG. 1. Data used to estimate several of the parameters of the *Tribolium* matrix model. See text for details.

where

$$F_j^* = f_j \exp\left[-\sum_{h \in A} \bar{\gamma}_{jh} n_h^*\right] \text{ for } j \in A,$$

and the remaining elements are obtained using

$$z_{i+1,j} = \begin{cases} = n_{i+1}^*/n_i^*, & j = i, \quad i \neq \omega. \\ = -\gamma_{Ej} n_{i+1}^*, & j \in L, A, i \in E. \\ = -\gamma_{Pj} n_{i+1}^*, & j \in A, \quad i \in P. \\ = 0, & \text{elsewhere.} \end{cases} \quad (9b)$$

We state without proof the usual condition for stability as:

Theorem 2. The non-trivial equilibrium N^* is asymptotically locally stable if and only if $s(\mathbf{Z}) < 1$.

PARAMETER ESTIMATES

Using various sources of data from our own work and from the literature, we have obtained crude estimates of the parameters of the model (6). To make the model more tractable and to make parameter estimation easier, we have made several simplifications.

TABLE 1. Parameter estimates for the *Tribolium* matrix model

Parameter	Description	Estimated value	Source of data
α	Maximum fecundity	7.96 ± 0.20	Moffa (1976)
β	Decrease in fecundity with age	0.0664 ± 0.0028	Moffa (1976)
K	Decrease in fecundity from crowding	0.00164 ± 0.00006	Rich (1956)
μ_L	Larval mortality	0.251 ± 0.002	Present study
μ_A	Adult mortality	0.0130 ± 0.0009	Desharnais & Costantino (1980)
C_{EL}	Larval cannibalism of eggs (slope)	0.000760 ± 0.000047	Park <i>et al.</i> (1965)
C_{EA}	Adult cannibalism of eggs	0.00252 ± 0.00016	Rich (1956)
C_{PA}	Adult cannibalism of pupae	0.00558 ± 0.00026	Jillson & Costantino (1980)

Our strategy has been to keep the number of parameters as small as possible while trying to retain the significant aspects of *Tribolium* physiology and behaviour.

We begin by fixing the duration of each life stage at values which are consistent with the biology of the corn oil sensitive (*cos*) strain of *Tribolium castaneum* which we maintain in our laboratory. (For a description of the biology of the *cos* mutant, see Scully & Costantino (1975) and Moffa & Costantino (1977).) Using a basic time unit of one day we have $E = \{1, 2, 3\}$, $L = \{4, 5, \dots, 23\}$, $P = \{24, 25, 26\}$, and $A = \{27, 28, \dots, \omega = 300\}$. We emphasize that these values are particular to our own culture conditions and may not be appropriate for other *Tribolium* species and genetic strains.

The fecundity of *Tribolium* females tends to peak early and decrease with age. The simplest assumption is a linear rate of decrease, so we use

$$f_j \begin{cases} = [\alpha - \beta(j - \varepsilon)], & j \in A, \quad j \leq \varepsilon + \text{int}(\alpha/\beta), \\ = 0, & \text{elsewhere,} \end{cases} \quad (10)$$

where $\varepsilon = \min(A)$. In Fig. 1a we have plotted the data of Moffa (1976; p. 51) for the *cos* strain of *T. castaneum*. Since *Tribolium* populations generally maintain a 1:1 sex ratio, we define the fecundity rate as one-half the number of eggs laid per female per day. Parameters α and β were estimated using linear least-squares regression. The regression line of Fig. 1a is highly significant ($P < 0.001$). The estimates of α and β and their standard errors are given in Table 1.

The data of Rich (1956) indicate that fecundity drops as adults become crowded. We have assumed that all adults contribute equally this effect and that all females are equally sensitive to crowding. In eqn (6a) we used

$$\bar{\gamma}_{ij} \begin{cases} = K, & j \in A, \quad i \in A, \\ = 0, & \text{otherwise,} \end{cases} \quad (11)$$

where K is the rate of decrease in fecundity with adult crowding. Using the data of Rich (1956) Table IV, we have plotted the natural logarithm of the daily fecundity rate as a function of adult density in Fig. 1b. So that all parameter estimates are commensurate with the population experiments which we present later, here and throughout we express density in numbers per 20 g of media. In Fig. 1b, the different symbols represent different durations of exposure in the experimental design (Rich 1956). Pooling these data, we fit

linear (solid line) and quadratic (broken line) functions by the method of least squares. Although both functions fit well ($P < 0.001$), a test for lack of fit (Searle 1971; p. 103) suggests that the linear model is inadequate (lack of fit is significant at $P < 0.001$). Nevertheless, to preserve the exponential assumption, we have used the linear regression. Parameter K was estimated as the absolute value of the slope of the solid line in Fig. 1b. The estimate value and its standard error appear in Table 1.

We now consider survivorship. As a first approximation, we will assume a homogeneous mortality rate within each age-class. Let μ_S denote the density-independent mortality rate for age-class S , where $S = E, L, P$, or A . In general, the density-independent survival rates of the immature stages are high. For eggs and pupae, we set $\mu_E = \mu_P = 0$. However, for the *cos* strain of *T. castaneum*, larval viability is decreased when the media contains unsaturated fatty acids (Scully & Costantino 1975). To estimate larval survivorship, we used unpublished data from the experimental study of Desharnais & Costantino (1980). They isolated adults from each of four of their control populations and placed them on standard media for 24 h. A total of 250 eggs were collected from each group of adults and placed on corn oil media. Larvae were recovered 16 days later. For each batch of eggs, we use the natural logarithm of the survivorship divided by the duration of time spent as larvae (13 days = 16 days - 3 days as eggs) as a crude estimate of the larval mortality rate. The average of the four mortality rates is our estimate of μ_L . This average and its standard error appear in Table 1. For adult mortality, we used the census data from the four control populations of Desharnais & Costantino (1980). Since they censused the populations every 2 weeks, we divided the number of dead adults at week $n+2$ by the average number of live adults at weeks n and $n+2$ for $n=0, 2, \dots, 36$. We subtracted these ratios from one, took their natural logarithms, and divided by the census period (14 days) to obtain mortality rates. The average of these seventy-six observations is our estimate of μ_A (Table 1). To check for density dependence, we plotted these mortality rates against the corresponding number of live adults. No functional relationship was noticeable ($r = -0.055$, $P > 0.6$). To summarize, we have in model (6)

$$s_i \begin{cases} = 1, & i \in E \\ = \exp(-\mu_L), & i \in L \\ = 1, & i \in P \\ = \exp(-\mu_A), & i \in A \end{cases} \quad (12)$$

We estimated the rates of egg cannibalism by larvae. From hatching to pupation, larvae increase in size and in the voracity at which they eat eggs. Park *et al.* (1965) examined the age-specific rates at which larvae of several genetic strains eat eggs. In their Table 10, they report the percentage of 100 eggs of *T. castaneum* eaten by groups of fifty larvae of *T. castaneum* after 48 h in 8 g of media. To convert to cannibalism rates per larvae per day for 20 g of media, we subtracted the percentage eaten from one, took the natural logarithm, and divided by 250 ([50 larvae/8 g] \times [2 days] \times [20 g]). These rates are plotted as a function of larval age in Fig. 1c. The different symbols represent the four genetic strains. As an approximation, we assumed that egg cannibalism rates by larvae increase linearly from zero as larvae get older. Let C'_{EL} denote the slope of this relationship. Our estimate of C'_{EL} is the slope of the regression line in Fig. 1c, which is statistically significant ($P < 0.001$). This estimate and its standard error can be found in Table 1. Although a test for lack of fit suggests that a non-linear curve would not reduce the sums of squares significantly ($P > 0.09$), a visual inspection of the data in Fig. 1c suggests that a sigmoidal curve may be

more appropriate as a general description of the relationship between larval age and cannibalism rates.

For adults eating eggs, we have assumed a common cannibalism rate for all adult ages. We denote this rate as C_{EA} . In his study of egg cannibalism by adults of *T. confusum*, Rich (1956) Table IV, computed 24-h per capita rates for 8 g of media. Although his rates vary with adult density and duration of exposure to cannibalism, we scaled his estimates to correspond to 20 g of media, and pooled these values to obtain an overall average. This estimate of C_{EA} and its standard error appear in Table 1.

Finally, we turn to cannibalism of pupae by adults. Again we have assumed no age dependence among adults. We let C_{PA} denote this cannibalism rate. Using the *cos* strain of *T. castaneum*, Jillson & Costantino (1980) exposed groups of twenty-six larvae to varying densities of adults on 26 g of standard media. In Fig. 1d we have plotted the negative logarithm of the survival rate through the pupal stage ($-\log_e[\text{proportion surviving}]/3$ days as pupae) against the adult density per 20 g of media. A least-squares regression confirms a significant linear relationship ($P < 0.001$) which goes through the origin. Our estimate of C_{PA} and its standard error appear in Table 1.

To summarize our results for cannibalism, in model (6) we used

$$\gamma_{Ej} \quad \begin{cases} = C'_{EL} (1 + j - \sigma), & j \in L, \\ = C_{EA}, & j \in A, \end{cases} \quad (13)$$

where $\sigma = \min(L)$, for the rates of egg eating by larvae and adults, and

$$\gamma_{Pj} = C_{PA}, \quad j \in A, \quad (14)$$

for the rate at which adults eat pupae. In our notation, C_{IJ} is the rate at which life stage J eats life stage I .

EXPERIMENTAL DATA AND SIMULATION RESULTS

Experimental design

In the analysis that follows, we compare the behaviour of our model with the experimental data of Desharnais & Costantino (1980). They assessed demographic stability in laboratory populations of the *cos* strain of *T. castaneum* by deliberately perturbing populations which were near equilibrium. We begin with a brief outline of the experimental design.

Thirteen cultures were initiated with sixty-four young adults, sixteen pupae, twenty large larvae, and seventy small larvae. All beetles were homozygous for the *cos/cos* allele. Each population was contained in a half-pint milk bottle with 20 g of corn oil media (90% wheat flour, 5% brewer's yeast, and 5% liquid corn oil) and kept in an unlighted incubator at $33 \pm 1^\circ\text{C}$ and $56 \pm 11\%$ relative humidity. Every 2 weeks all age-classes, except eggs, were censused and all age-classes, including eggs, were placed in fresh media. This procedure was followed for 38 weeks.

After 10 weeks of culture, each population was randomly assigned to one of four treatments. Three of the treatments, each with three replicates, involved demographic perturbations and one treatment, with four replicates, served as a control. For the demographic perturbations they (i) added 100 adults, (ii) removed all adults, and (iii) removed all immatures. The control cultures were not disturbed.

TABLE 2. Census data for the experimental populations

Day	Life stage*	Treatment and replicate												
		Control				Adults added			Adults removed			Immatures removed		
		a	b	c	d	a	b	c	a	b	c	a	b	c
0	A	64	64	64	64	64	64	64	64	64	64	64	64	64
	LL+P	35	35	35	35	35	35	35	35	35	35	35	35	35
	SL	70	70	70	70	70	70	70	70	70	70	70	70	70
14	A	78	88	77	86	76	74	77	74	78	79	76	83	86
	LL+P	4	4	12	12	23	18	5	14	7	14	10	4	9
	SL	263	198	176	249	116	183	257	148	192	189	199	251	195
28	A	78	84	79	80	76	71	77	77	76	76	76	82	84
	LL+P	109	77	71	100	69	103	86	103	58	68	55	108	75
	SL	75	75	87	28	106	76	46	97	73	63	57	31	48
42	A	77	80	76	88	73	79	83	78	69	75	74	90	80
	LL+P	28	18	44	18	41	43	27	68	22	15	12	11	26
	SL	125	111	96	181	74	107	171	55	135	134	197	186	93
56	A	61	69	61	80	67	86	70	73	61	66	63	70	71
	LL+P	77	40	31	61	23	34	71	26	63	49	70	86	63
	SL	203	226	180	173	186	303	229	331	187	169	108	214	165
70	A	85	77	46	75	39	48	67	54	67	58	96	82	87
	LL+P	71	67	72	47	88	167	92	182	81	112	20	70	48
	SL	57	31	13	76	17	18	19	8	30	24	77	45	51
						Perturbation			Perturbation			Perturbation		
70	A	85	77	46	75	139	148	167	0	0	0	96	82	87
	LL+P	71	67	72	47	88	167	92	182	81	112	0	0	0
	SL	57	31	13	76	17	18	19	8	30	24	0	0	0
84	A	102	98	72	76	122	127	142	171	62	86	71	63	57
	LL+P	36	11	7	36	10	7	13	1	36	11	0	0	0
	SL	182	246	222	254	289	246	206	159	136	183	298	361	434
98	A	104	88	69	77	102	111	118	168	72	89	71	56	57
	LL+P	136	127	132	119	106	94	82	20	67	49	202	189	265
	SL	27	48	125	29	35	60	46	379	195	204	10	50	11
112	A	120	100	105	110	107	106	100	169	75	90	139	124	178
	LL+P	35	8	59	27	11	18	23	112	102	87	11	18	19
	SL	265	302	146	286	277	149	254	0	33	21	329	149	205
126	A	122	90	106	106	103	83	97	162	82	93	121	116	154
	LL+P	76	154	125	62	125	82	112	17	40	39	78	128	64
	SL	32	35	101	8	43	117	26	218	323	366	11	46	2
140	A	132	120	99	108	123	105	122	147	92	92	113	113	128
	LL+P	28	20	49	5	9	45	5	71	141	157	15	14	53
	SL	309	213	124	411	325	98	416	24	57	33	370	311	212
154	A	120	107	96	99	113	100	106	137	131	154	98	105	117
	LL+P	252	156	82	232	159	56	227	7	32	15	247	181	136
	SL	8	109	156	28	54	180	50	245	248	314	18	64	20
168	A	113	115	98	120	118	89	125	121	126	140	130	140	115
	LL+P	5	48	87	6	20	94	19	146	108	120	4	34	13
	SL	360	178	69	308	251	46	350	68	14	8	304	338	354
182	A	97	119	95	93	97	92	111	150	124	137	119	137	98
	LL+P	236	141	38	193	151	34	142	12	12	6	214	214	186
	SL	24	171	164	52	112	157	96	284	420	319	11	38	14
196	A	136	121	94	132	117	88	114	134	107	121	140	147	123
	LL+P	20	73	99	12	41	151	40	200	177	170	65	12	86
	SL	357	59	80	213	216	56	151	90	11	24	371	336	365
210	A	122	127	108	115	106	118	96	125	111	118	121	121	108
	LL+P	176	75	47	130	157	34	51	36	28	17	183	192	163
	SL	13	299	187	114	113	261	105	250	385	289	3	69	2
224	A	117	117	98	134	116	111	98	117	109	102	144	134	136
	LL+P	7	114	107	52	49	122	72	241	202	204	12	27	13
	SL	373	9	69	92	181	22	81	148	9	31	568	163	412
238	A	105	121	106	117	115	131	108	141	125	132	130	111	108
	LL+P	189	54	38	81	167	49	77	57	28	22	201	237	174
	SL	14	419	293	217	206	316	346	247	372	295	4	83	4
252	A	120	113	88	134	149	130	126	134	107	113	145	137	123
	LL+P	12	157	121	73	58	146	131	180	143	135	59	19	33
	SL	404	3	42	75	144	7	47	86	13	19	526	199	382
266	A	99	125	106	139	150	119	157	131	104	105	130	110	111
	LL+P	226	9	22	63	155	30	139	27	18	8	192	129	158
	SL	2	351	215	164	204	365	240	238	307	271	0	159	6

* Notation: A = adults; LL + P = large larvae plus pupae; SL = small larvae.

The census data appears in Table 2 and Figs 2–6. We have combined the data into three age groups: adults (A), large larvae plus pupae (LL + P), and small larvae (SL). Since the populations exhibited oscillations which are sometimes out of phase, we have presented the data for individual replicates. Figs 2–6 allow a direct comparison of the experimental populations to predictions of the model. The observations are represented by symbols and were connected with continuous curves using cubic spline interpolation. When viewing these data, it should be kept in mind that the census period is coarse in relation to the period of the oscillations predicted by the model. We discuss this problem in more detail below.

Equilibrium and stability

We begin by using Theorem 1 to make a specific prediction for the equilibrium of the *Tribolium* populations. Using the parameter estimates of the previous section (Table 1) in eqn (A6) of the appendix, we computed the real dominant eigenvalue λ of the density-independent matrix $\mathbf{M}(\mathbf{0})$ by the method of bisection. We found $\lambda = 1.1396$. This gives an intrinsic rate of increase $r = \log_e(\lambda) = 0.1307$ per day, which compares favourably with other estimates for *T. castaneum* under similar conditions of temperature and humidity (Sokoloff 1974; Table 11.22). Since the spectral radius $s[\mathbf{M}(\mathbf{0})] = \lambda > 1$, Theorem 1 guarantees the existence of a unique non-trivial equilibrium vector \mathbf{N}^* . We computed \mathbf{N}^* using eqns (A2)–(A5) of the appendix. To compare the simulation results with the experimental data, we divided the larval age groups (days 4–23) into two sets of equal size: small larvae (days 4–13) and large larvae (days 14–23). For the equilibrium we predict 87.87 adults, 68.53 large larvae plus pupae and 75.15 small larvae.

To evaluate stability, we used \mathbf{N}^* in eqn (9) to compute the elements of the matrix \mathbf{Z} . The eigenvalues of this 300×300 matrix were kindly computed by Jane Cullum at the IBM Research Center in Yorktown Heights, New York, using a new algorithm for large sparse non-symmetric matrices (Cullum & Willoughby 1986). Using $i = (-1)^{1/2}$, we report the following observations: (i) all the eigenvalues are distinct; (ii) all the eigenvalues are complex conjugates; (iii) the dominant pair of eigenvalues are $\lambda_1, \lambda_2 = 1.0001 \pm 0.2277i$; (iv) the largest subdominant pair of eigenvalues are $\lambda_3, \lambda_4 = 0.9872 \pm 0.1973i$; (v) $|\lambda_1| > 1 > |\lambda_3|$; that is, only the dominant eigenvalues have a modulus that exceeds unity. Since $s(\mathbf{Z}) = |\lambda_1| = 1.0257 > 1$, from Theorem 2 we predict that \mathbf{N}^* for the *Tribolium* populations is an *unstable* equilibrium. Finally, since λ_1 and λ_2 dominate the long-term behaviour of the linearized model (7), we can use these eigenvalues to obtain an estimate of the period of the cycles near \mathbf{N}^* (Gurney & Nisbet 1985). Letting $\log_e(\lambda_1) = a + bi$, the period is approximately $p = 2\pi/b$. In our case, $\log_e(\lambda_1) = 0.0254 + 0.2234i$ and $p = 28.06$ days. This is close to the generation time of 27 days and compares favourably with the period of 26.76 days obtained from a spectral analysis of the simulation results. Details of the spectral analysis are presented in a later section.

Control populations

The adult densities for the four control populations are plotted in Figs 2a–d. The horizontal dashed line in each figure is the expected equilibrium number of adults. We iterated the model (6) using the same initial conditions as the experimental populations, with a uniform distribution of individuals within the small larval, large larval, and pupal age groups, and with all adults at 27 days of age. The adult densities from the simulation are presented in Fig. 2e. Although the experimental data shows some fluctuations in adult density, there are no regular small amplitude oscillations as in the simulation results.

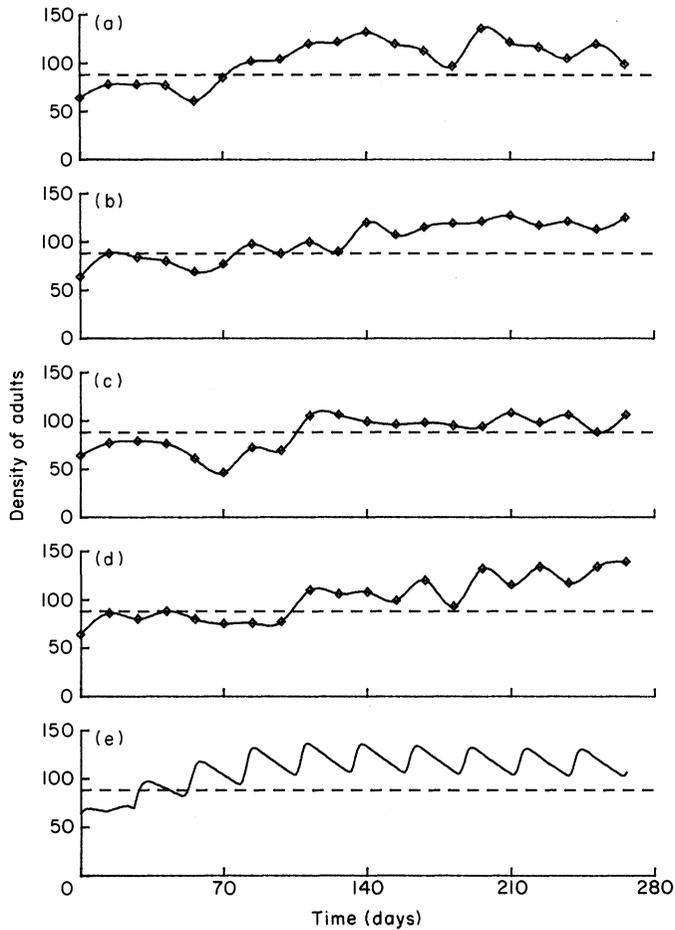


FIG. 2. Density of adults versus time for the four control populations (a–d) and the *Tribolium* matrix model (e). The census points (diamonds) were interpolated using cubic splines. The horizontal dashed lines represent the predicted equilibrium density of adults.

From the observed differences between replicates, it seems possible that stochastic sources of variation overwhelm these oscillations. It is also possible that the census period is too coarse to detect small amplitude oscillations. In any case, the overall densities of the experimental populations agree quite well with the stimulation results. In particular, it is interesting that the adult densities fluctuate at levels which *exceed* the predicted equilibrium value (dashed line). This suggests that a time average of adult density would be poor predictor of the equilibrium in an unstable system.

The densities of the immature age-classes for the control populations are plotted in Fig. 3a–d. The solid curves represent the small larvae and the broken curves are for the large larvae plus pupae. There is a definite regularity to the fluctuations of the immature age-classes in the experimental populations. These oscillations are very large in magnitude, sometimes going from near zero in one census to over 400 individuals in the next. As with the adult data, irregularities in the observed oscillations could be due in part to stochastic effects. For example, the replicates in Fig. 3a and b seem to be in phase in the first half of

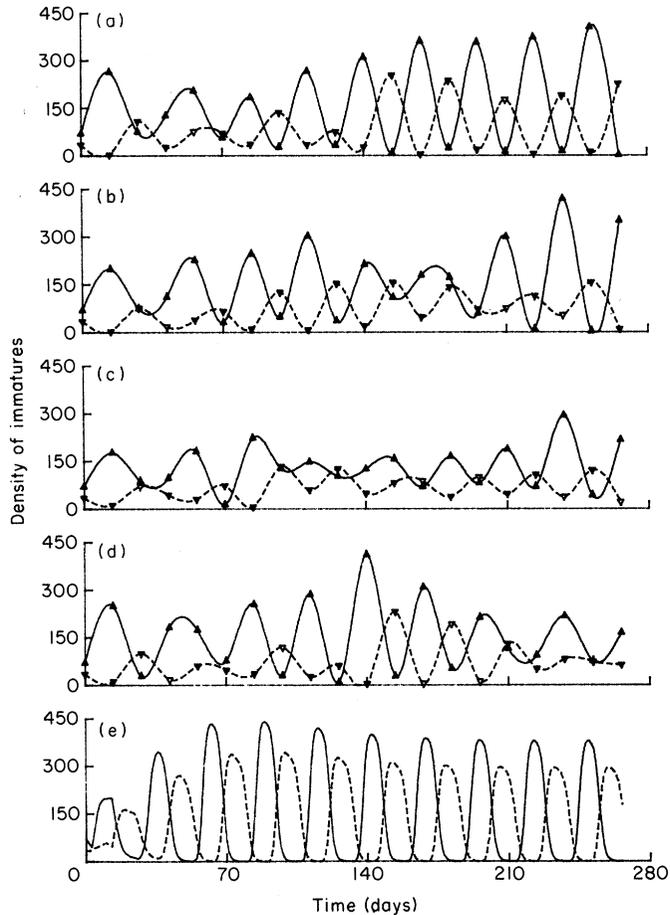


FIG. 3. Density of small larvae (solid curves) and large larvae plus pupae (broken curves) versus time for the four control populations (a–d) and the *Tribolium* matrix model (e). The census points (triangles) were interpolated using cubic splines.

the experiment, but out of phase at the end of the experiment, suggesting that the periodicity may drift. However, with oscillations of this magnitude and period, another potential source of irregularities is the discrete nature of the censusing procedure. The observations are spaced at roughly half the period. Under these conditions, is possible for two or more adjacent observations to capture densities between the peaks and troughs, giving the illusion of little or no fluctuation.

The simulation results appear in Fig. 3e. Qualitatively, there is good agreement between the model's behaviour and the dynamics of the *Tribolium* populations. The amplitudes of the oscillations and their period are roughly equal. The oscillations of the small larvae are also out of phase with the oscillations of large larvae plus pupae. It is not possible to directly compare the shapes of the oscillations, since the curves for the experimental data are determined by cubic splines. However, when the simulation data is periodically sampled every 14 days and these data are interpolated with splines, there is a drift in amplitude of the peaks and troughs, indicating that the periodicity of the simulation data

is not an integral multiple of the census period. A precise estimate of the periodicity of the simulation results is presented in a later section.

Demographic perturbations

In three replicates comprising one treatment, 100 adults were added at day 70. The adult densities for these populations are presented in Fig. 4a–c. The vertical dashed line represents the perturbation. After the perturbation, adult numbers decreased to a density level which is comparable to the controls. In Fig. 4d we show the results for the model (6), which was subjected to the same perturbation. The rate of return of the adult densities to the unperturbed levels is approximately the same for the theoretical model and the experimental populations. In the census periods following the perturbation the densities of the immature stages continue to oscillate in a manner similar to the control population (Table 2).

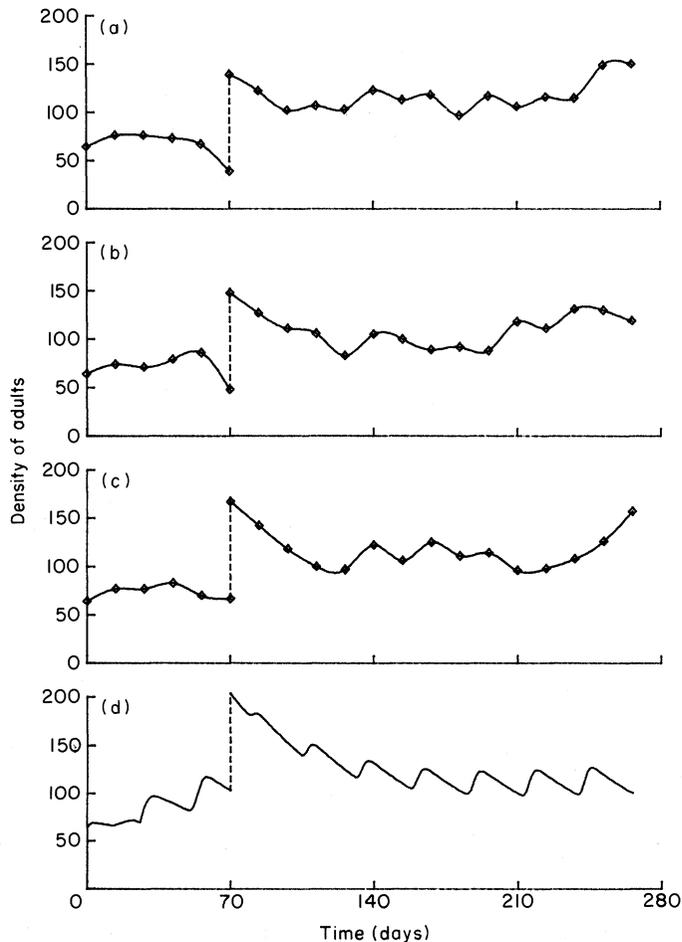


FIG. 4. Density of adults versus time for the three experimental populations (a–c) and the *Tribolium* matrix model (d) where 100 adults were added at day 70. The census points (diamonds) were interpolated using cubic splines. The vertical dashed lines represent the perturbation.

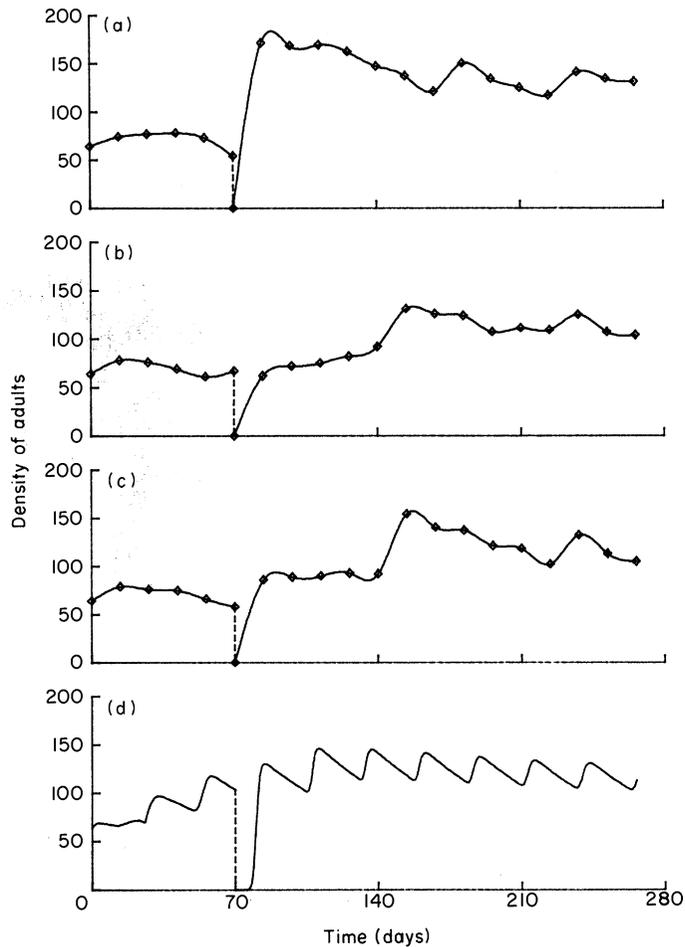
Limit cycles in Tribolium

FIG. 5. Density of adults versus time for the three experimental populations (a–c) and the *Tribolium* matrix model (d) where all adults were removed at day seventy. The census points (diamonds) were interpolated using cubic splines. The vertical dashed lines represent the perturbation.

In Fig. 5a–c, we present the results for the three populations in which all adults were removed at day 70. In two of the populations (Fig. 5b, c), there was a rapid return of adult density to the unperturbed level. This same pattern is predicted by the model (Fig. 5d). The remaining experimental culture overshoots the unperturbed density level and then gradually decreases to the same level as the controls (Fig. 5a). An examination of Table 2 reveals that there was a large cohort of potential recruits (182 large larvae plus pupae) in this population at the time that the adults were removed. In all three experimental populations, the oscillations of the immature life stages persist after the perturbations (Table 2).

In the last treatment, all immatures were removed at day 70. The adult densities for these populations are presented in Fig. 6. As expected, there was a decline in adult density following the perturbation. In two of the cultures (Fig. 6a, b), this decline was followed by

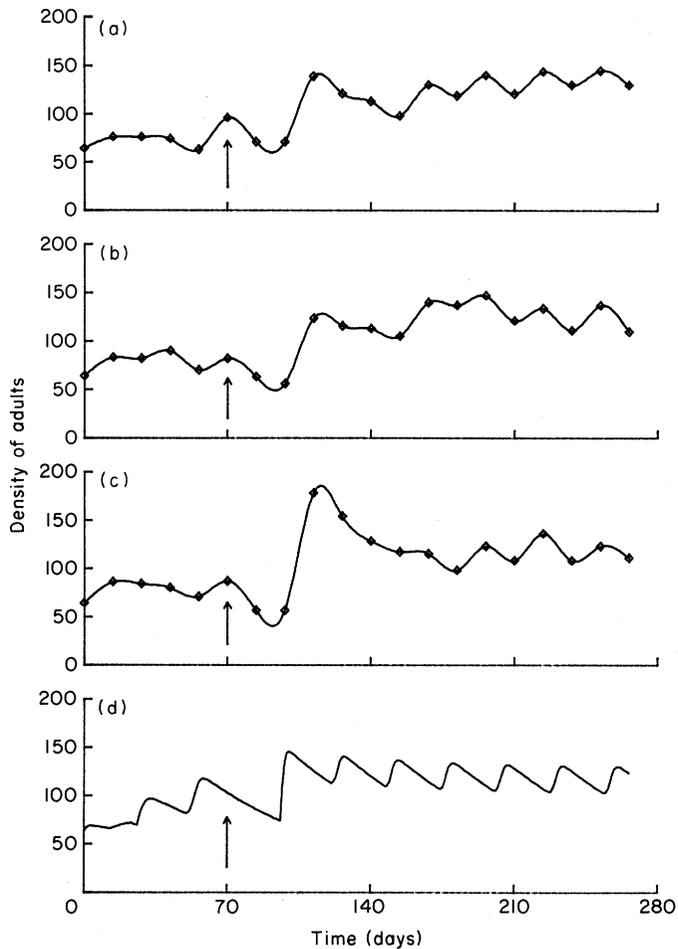


FIG. 6. Density of adults versus time for the three experimental populations (a–c) and the *Tribolium* matrix model (d) where all immatures were removed at day 70. The census points (diamonds) were interpolated using cubic splines. The vertical arrows lines represent the perturbation.

a return to the adult densities of the controls. The model displayed similar behaviour (Fig. 6d). In the population of Fig. 6c, a small overshoot followed the decline in adult density before a return to the unperturbed level. In this treatment, the removal of immatures may have tended to temporarily synchronize the immature cycles with the census periods (Table 2). This could explain the increased regularity of the fluctuations in adult density observed in Fig. 6.

Demographic limit cycle

The local stability analysis and perturbation results suggest that these *Tribolium* populations possess a stable oscillatory attractor. To visualize this idea, we iterated the model (6) using an initial condition which was very close to equilibrium and plotted the proportions of adults, large larvae plus pupae and small larvae in Fig. 7. The arrows

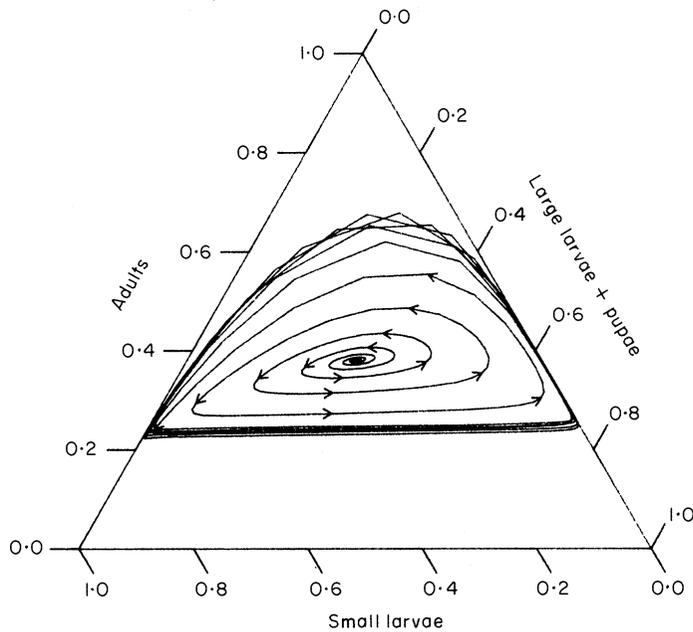


FIG. 7. Triangular coordinate plot of the population of adults, large larvae plus pupae, and small larvae predicted by the *Tribolium* matrix model when the initial condition is near the unstable equilibrium. The arrows indicate the direction of change over time.

indicate the population trajectory as it spirals away from the equilibrium. We tried several other initial conditions, and the trajectories always approach the same loop as the simulation in Fig. 7. We feel the asymptotic behaviour of the model can be characterized as a stable demographic limit cycle.

We conducted a spectral analysis to ascertain the period of the limit cycle. The model was iterated 50 000 times to guarantee asymptotic behaviour. The results from the subsequent $T=1001$ iterations were used to examine the periodicity. Let $N_A(1), N_A(2), \dots, N_A(T)$ represent the sequence of adult densities. Define $y(t) = N_A(t) - [\sum N_A(t)]/T$ and $v = \sum [y(t)]^2$. The quantities $a(\tau)$ and $b(\tau)$ can be thought of as 'correlations' of $x(t)$ with $\cos(\tau t)$ and $\sin(\tau t)$, respectively, where

$$a(\tau) = (v T)^{-1/2} \sum_{t=1}^T y(t) \cos(\tau t), \quad (15a)$$

$$b(\tau) = (v T)^{-1/2} \sum_{t=1}^T y(t) \sin(\tau t), \quad (15b)$$

The spectral density at angular frequency τ is given by

$$\Omega(\tau) = [a(\tau)]^2 + [b(\tau)]^2 \quad (16)$$

(Kendall & Stuart 1968, pp. 410–412). The angular frequency τ is related to the period p by $p = (\pi)/\tau$. For the adult densities, we obtained a large sharp peak in $\Omega(\tau)$ at $\tau = 0.234810$

TABLE 3. Bifurcation values for each parameter

Parameter*	Bifurcation value	Ratio to estimated value	Equilibrium densities at bifurcation	Effect of increasing the parameter
α	0.718	0.0902	(24.1, 6.8, 7.1)†	destabilize
K	0.0211	12.9	(73.0, 44.8, 48.7)	stabilize
μ_L	0.0788	3.14	(66.0, 47.6, 92.1)	stabilize
C_{EL}	0.000146	0.192	(132.2, 212.1, 238.1)	destabilize
C_{EA}	0.00896	3.56	(73.1, 44.9, 48.8)	stabilize
C_{PA}	0.187	33.5	(6.3, 36.5, 41.9)	stabilize

* Oscillations persist for all possible values of β and μ_A when the remaining parameters have their default values.

† Number of adults, large larvae plus pupae, and small larvae, respectively.

which corresponds to a period of $p = 26.7586$ days. An identical result was obtained using the number of small larvae. To corroborate this estimate, we computed the number of days between adjacent maxima of adult numbers. Adult peaks occurred every 26–27 days with an average of 26.75 days. As might be expected, the periodicity of the limit cycle is close to the duration of the life cycle (27 days).

Bifurcation points

How far away are these *Tribolium* populations from the stable region of parameter space? How do the life history and behavioural traits affect stability? We addressed these questions by observing the behaviour of our model for various parameter values. Since the simplified version of the model still possesses eight parameters (Table 1), we made no attempt to map out the entire region of parameter space. Instead, we defined the estimates of Table 1 as the default values, and varied each parameter individually. The method of bisection was used to estimate the thresholds at which the model bifurcates from a stable point equilibrium into a stable limit cycle.

The bifurcation points for each parameter appear in Table 3. Oscillations persist for all possible values of β and μ_A when the remaining parameters maintain their default values. For the other parameters, we have reported the equilibrium densities at the bifurcation point and indicated whether or not the model is stabilized or destabilized when the parameter is increased above its bifurcation value.

The parameters α and C_{EL} are destabilizing and the remaining parameters are stabilizing. This suggests that increases in the reproductive rate of flour beetles has a destabilizing effect while increases in mortality rates are stabilizing. The same phenomenon is true in predator–prey systems (Rosenzweig 1971) and in discrete generation single species models (May 1974). As Chapman & Whang (1934) conjectured from some of the earliest experiments with *Tribolium*, an increase in the cannibalism rate of larvae on eggs can lead to sustained oscillations. It is interesting that the other forms of cannibalism actually have a stabilizing effect. This suggests that the relationship between cannibalism and stability depends upon the relative rates at which the active life stages (larvae and adults) consume the inactive ones (eggs and pupae). However, we cannot rule out the possibility that cannibalism of eggs or pupae by adults are destabilizing for other combinations of parameter values.

In some cases, the bifurcation points are not too far from the estimated values. A 3.14 factor increase in the larval mortality rate, μ_L , would be sufficient for stability. A 3.56 factor increase in the rate at which adults eat eggs, C_{EA} , would have a similar effect.

Decreasing the cannibalism rate of eggs by larvae, C'_{EL} , to 19.2% of its estimated value would also result in a stable equilibrium. Finally, we can reduce the total fecundity and maintain the last age of reproduction by scaling both α and β by the same factor. Using the method of bisection, we found that stability is obtained when the total fecundity is 18.4% of its default value.

DISCUSSION

In any attempt to model a biological system, one must confront a trade-off between analytical tractability and realism. In the present study, we tried to retain what we feel are the most important aspects of the biology of *Tribolium* in relation to their population dynamics while keeping the model as simple as possible. Considering that our formulation of the model is based on several crude assumptions and that several of our parameter estimates come from published data for different genetic strains and different species, the agreement between the model simulations and the experimental data is quite good. The relatively small number of parameters in this model allowed us to retain some generality and to probe parameter space for insight into the dynamical properties of *Tribolium* populations. Nevertheless, our work falls far short of a complete analytical treatment.

Two recent papers by Hastings (1986) and Hastings & Costantino (1986) provide a more analytical treatment of egg cannibalism by larvae in *Tribolium*. Because adult longevity is several times the duration of the life cycle, they assume that the interactions between adults and immatures occurs on a slow time-scale relative to the dynamics within the immature age-classes. Using the continuous time McKendrick–von Foerster model, they focus on a window of the life cycle made up of just eggs and larvae. Adult density is a constant in their analysis. With the additional assumption that larvae of all ages eat eggs at the same rate, they were able to derive necessary and sufficient conditions for stability in terms of the original parameters of the model. They go further to demonstrate that their model possesses *simultaneously* a stable equilibrium and a stable limit cycle over a significant range of parameters. The existence of multiple attractors in this egg–larval submodel is proven in a theorem by Hastings (1986). Whether this remarkable result is true for the more realistic case where cannibalism rates depend upon the age of the larvae remains an open question.

Many of the results of the present study are consistent with the findings of Hastings (1986) and Hastings & Costantino (1986). Increases in the rates of fecundity and cannibalism by larvae tend to be destabilizing. Increases in the rates of mortality and cannibalism by adults are stabilizing. In both models, the period of the oscillations is roughly equal to the developmental period. Adult numbers show small oscillations while the immature age-classes oscillate wildly. Since these last two observations hold true for our experimental data, this lends support to the concept of a fast time-scale for egg–larval dynamics and a slow time-scale for immature–adult dynamics.

There exists a large amount of variability in rates of reproduction, mortality, and cannibalism among the various genetic strains and species of *Tribolium* (Park, Mertz & Petruszewicz 1961; Sokoloff 1974). Environmental conditions also affect these biological attributes. This raises the interesting possibility of doing 'comparative population dynamics,' where one experimentally probes for transitions from stable equilibria to stable limit cycles. The numerical work summarized in Table 3 suggests that these transition points occur at parameter values which are of the same order of magnitude as

those currently existing in laboratory populations. Studies of this sort would help place the ideas of Hopf bifurcations and stable limit cycles in population biology on a firmer experimental footing.

Finally, we should point out that our model of cannibalistic interactions, although specific to *Tribolium* in its details, may have relevance to the demography of many natural populations. In reviews of interspecific predation, Fox (1975) and Polis (1981) cite over forty examples where cannibalism is suggested as a regulator of population size. In fish populations, cannibalism by older or larger individuals can cause skewed age or size distributions and can sometimes result in violent fluctuations in recruitment (Ricker 1954; Radovich 1962; Forney 1976; Holcik 1977; Popova & Sytina 1977; DeAngelis, Cox & Coutant 1979). Naturally occurring population cycles have been attributed to age-specific cannibalistic interactions in perch (Menshutkin 1964) and in the Dungeness crab *Cancer magister* (Botsford & Wickham 1978; McKelvey *et al.* 1980). Our results with *Tribolium* may exemplify a more general class of demographic phenomena.

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REFERENCES

- Allen, R. L. & Basasibwaki, P. (1974). Properties of age structure models for fish populations. *Journal of the Fisheries Research Board of Canada*, **31**, 1119–1125.
- Beddington, J. (1974). Age distribution and the stability of simple discrete-time population models. *Journal of Theoretical Biology*, **47**, 65–74.
- Bernardelli, H. (1941). Population waves. *Journal of the Burma Research Society*, **31**, 1–18.
- Botsford, L. W. & Wickham, D. E. (1978). Behaviour of age-specific, density-dependent models and the Northern California Dungeness crab (*Cancer magister*) fishery. *Journal of the Fisheries Research Board of Canada*, **35**, 833–843.
- Chapman, R. N. (1928). Quantitative analysis of environmental factors. *Ecology*, **9**, 111–122.
- Chapman, R. N. (1933). The causes of fluctuations of populations of insects. *Proceedings of the Hawaiian Entomological Society*, **8**, 279–297.
- Chapman, R. N. & Whang, W. Y. (1934). An experimental analysis of the cause of population fluctuations. *Science*, **80**, 297–298.
- Cook, D. & Léon, J. A. (1976). Stability of population growth determined by 2×2 Leslie matrix model with density-dependent elements. *Biometrics*, **32**, 435–442.
- Cullum, J. & Willoughby, R. A. (1986). A practical procedure for computing eigenvalues of large sparse nonsymmetric matrices. *Large Scale Eigenvalue Problems* (Ed. by J. Cullum & R. A. Willoughby), pp. 193–240. Elsevier Science Publishers B.V., North-Holland.
- DeAngelis, D. L., Cox, D. & Coutant, C. (1979). Cannibalism and size dispersal in young-of-the-year largemouth bass: Experiment and model. *Ecological Modelling*, **8**, 138–148.
- Desharnais, R. A. & Cohen, J. E. (1986). Life not lived due to disequilibrium in heterogeneous age-structured populations. *Theoretical Population Biology*, **29**, 385–406.
- 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.

- Fisher, M. E. & Goh, B. S. (1984). Stability results for delayed-recruitment models in population dynamics. *Journal of Mathematical Biology*, **19**, 147–156.
- Forney, J. (1976). Year class formation in the walleye (*Stizostedion vitreum*) population of Oneida Lake, New York, U.S.A. 1966–1973. *Journal of the Fisheries Research Board of Canada*, **33**, 783–792.
- Fox, L. R. (1975). Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, **6**, 87–106.
- Guckenheimer, J., Oster G. & Ipaktchi, A. (1977). The dynamics of density-dependent population models. *Journal of Mathematical Biology*, **4**, 101–147.
- Gurney, W. S. C. & Nisbet, R. M. (1985). Fluctuation periodicity, generation separation, and the expression of larval competition. *Theoretical Population Biology*, **28**, 150–180.
- Gurney, W. S. C., Nisbet, R. M. & Lawton, J. H. (1983). The systematic formulation of tractable single-species population models incorporating age structure. *Journal of Animal Ecology*, **52**, 479–496.
- Hastings, A. (1987). Cycles in cannibalistic egg–larval interactions. *Journal of Mathematical Biology*, **24**, 651–666.
- Hastings, A. & Costantino, R. F. (1987). Cannibalistic egg–larval interactions in *Tribolium*: An explanation for the oscillations in population numbers. *The American Naturalist* (in press).
- Holcik, J. (1977). Changes in fish community of Kikava Reservoir with particular reference to Eurasian perch. *Journal of the Fisheries Research Board of Canada*, **34**, 1734–1747.
- Jillson, D. & Costantino, R. F. (1980). Growth, distribution, and competition of *Tribolium castaneum* and *Tribolium brevicornis* in fine-grained habitats. *The American Naturalist*, **116**, 206–219.
- Kendall, M. G. & Stuart, A. (1968). *The Advanced Theory of Statistics*, Vol. 3. Hafner Publishing Co., New York.
- King, C. E. & Dawson, P. S. (1972). Population biology and the *Tribolium* model. *Evolutionary Biology*, **5**, 133–227.
- Leslie, P. H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183–212.
- Leslie, P. H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213–245.
- Leslie, P. H. (1959). The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. *Physiological Zoology*, **32**, 151–159.
- Levin, S. A. & Goodyear, C. P. (1980). Analysis of an age-structured fishery model. *Journal of Mathematical Biology*, **9**, 245–274.
- Lewis, E. G. (1942). On the generation and growth of a population. *Sankhya*, **6**, 93–96.
- Liu, L. & Cohen, J. E. (1987). Equilibrium and local stability in a logistic matrix model for age-structured populations. *Journal of Mathematical Biology*, **25**, 73–88.
- May, R. M. (1974). Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science*, **186**, 645–647.
- May, R. M. & Oster, G. F. (1976). Bifurcations and dynamic complexity in simple ecological models. *The American Naturalist*, **110**, 573–599.
- McKelvey, R., Hankin, D., Yanosko, K. & Snygg, C. (1980). Stable cycles in multi-stage recruitment models: An application to the Northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 2323–2345.
- Menshutkin, V. V. (1964). Population dynamics studied by representing the population as a cybernetic system. *Voprosy Ikhtologii*, **1**, 23–33.
- Mertz, D. B. (1969). Age distribution and abundance in populations of flour beetles. I. Experimental studies. *Ecological Monographs*, **39**, 1–31.
- Mertz, D. B. (1972). The *Tribolium* model and the mathematics of population growth. *Annual Review of Ecology and Systematics*, **3**, 51–78.
- Moffa, A. M. (1976). *Genetic polymorphism and demographic equilibrium in Tribolium castaneum*. Unpublished doctoral thesis, University of Rhode Island.
- Moffa, A. M. & Costantino, R. F. (1977). Genetic analysis of a population of *Tribolium*. VI. Polymorphism and demographic equilibrium. *Genetics*, **87**, 785–805.
- Nisbet, R. M. & Gurney, W. S. C. (1982). *Modelling Fluctuating Populations*. John Wiley & Sons, New York.
- Park, T., Mertz, D. B. & Petruszewicz, K. (1961). Genetic strains of *Tribolium*: Their primary characteristics. *Physiological Zoology*, **37**, 97–162.
- Park, T., Mertz, D. B., Grodzinski, W. & Prus, T. (1965). Cannibalistic predation in populations of flour beetles. *Physiological Zoology*, **38**, 289–321.
- Pennycuik, C. J., Compton, R. M. & Beekingham, L. (1968). A computer model for simulating the growth of a population, or of two interacting populations. *Journal of Theoretical Biology*, **18**, 316–329.
- Pennycuik, L. (1969). A computer model of the Oxford great tit population. *Journal of Theoretical Biology*, **22**, 381–400.
- Polis, G. A. (1981). The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**, 225–251.
- Popova, O. A. & Sytina, L. A. (1977). Food and feeding relations in Eurasian perch (*Perca fluviatilis*) and pike perch (*Stizostedion lucioperca*). *Journal of the Fisheries Research Board of Canada*, **34**, 1559–1570.
- Radovich, J. (1962). Effects of sardine spawning size and environment on year-class production. *California Fish and Game*, **48**, 123–140.

Rich, E. L. (1956). Egg cannibalism and fecundity in *Tribolium*. *Ecology*, **37**, 109–120.
 Ricker, W. F. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–623.
 Rosenzweig, M. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, **171**, 385–387.
 Scully, A. M. M. & Costantino, R. F. ((1975). Genetic analysis of a population of *Tribolium*. V. Viability of the unsaturated fatty acid sensitive mutant. *Canadian Journal of Genetics and Cytology*, **17**, 585–590.
 Searle, S. R. (1971). *Linear Models*. Wiley, New York.
 Sokoloff, A. (1972). *The Biology of Tribolium*, Vol. 1. Oxford University Press, Oxford.
 Sokoloff, A. (1974). *The Biology of Tribolium*, Vol. 2. Oxford University Press, Oxford.
 Sokoloff, A. (1977). *The Biology of Tribolium*, Vol. 3. Oxford University Press, Oxford.
 Usher, M. B. (1972). Developments in the Leslie matrix model. *British Ecological Society*, **12**, 29–60.
 Williamson, M. H. (1959). Some extensions of the use of matrices in population theory. *Bulletin of Mathematical Biophysics*, **21**, 13–17.
 Williamson, M. H. (1974). The analysis of discrete time cycles. *Ecological Stability* (Ed. by M. B. Usher & M. H. Williamson), pp. 17–33. Chapman & Hall.
 Ziebur, A. D. (1984). Age-dependent models of population growth. *Theoretical Population Biology*, **26**, 315–319.

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APPENDIX

Proof of Theorem 1. Assume the positive equilibrium vector \mathbf{N}^* exists. From model (6)

$$n_1^* = \sum_{j \in A} n_j^* f_j \exp[-\sum_{h \in A} \bar{\gamma}_{jh} n_h^*], \tag{A1a}$$

$$n_{i+1}^* = n_i^* s_i \exp[-\sum_{j \in L} \gamma_{Ej} n_j^* - \sum_{j \in A} \gamma_{Ej} n_j^*], \quad i \in E, \tag{A1b}$$

$$n_{i+1}^* = n_i^* s_i, \quad i \in L, \tag{A1c}$$

$$n_{i+1}^* = n_i^* s_i \exp[-\sum_{j \in A} \gamma_{Pj} n_j^*], \quad i \in P, \tag{A1d}$$

$$n_{i+1}^* = n_i^* s_i, \quad i \in A, \quad i \neq \omega. \tag{A1e}$$

Let $\rho_1 = 1$ and

$$\rho_j = \prod_{h=1}^{j-1} s_h \quad \text{for } j = 2, 3, \dots, \omega.$$

We denote the earliest ages in L, P , and A using $\sigma = \min(L), \zeta = \min(P)$, and $\varepsilon = \min(A)$. From (A1c) and (A1e) we have

$$n_i^* = n_\sigma^* (\rho_i / \rho_\sigma), \quad i \in L, \quad i = \zeta, \tag{A2a}$$

$$n_i^* = n_\varepsilon^* (\rho_i / \rho_\varepsilon), \quad i \in A. \tag{A2b}$$

Substituting (A2) into (A1a), (A1b), and (A1d) gives

$$n_1^* = n_\varepsilon^* \sum_{j \in A} \delta_j \exp[-\theta_j n_\varepsilon^*], \tag{A3a}$$

$$n_{i+1}^* = n_1^* \rho_{i+1} \exp[-i(n_\sigma^* \eta_1 + n_\varepsilon^* \eta_2)], \quad i \in E, \tag{A3b}$$

$$n_{i+1}^* = n_\sigma^* (\rho_{i+1} / \rho_\sigma) \exp[(\zeta - i - 1) n_\varepsilon^* \eta_3] \quad i \in P, \tag{A3c}$$

where $\delta_j = (\rho_j / \rho_\varepsilon) f_j, \quad \theta_j = \sum_{h \in A} \bar{\gamma}_{jh} (\rho_h / \rho_\varepsilon), \quad \text{for } j \in A,$

and $\eta_1 = \sum_{j \in L} \gamma_{Ej} (\rho_j / \rho_\sigma), \quad \eta_2 = \sum_{j \in A} \gamma_{Ej} (\rho_j / \rho_\varepsilon), \quad \eta_3 = \sum_{j \in A} \gamma_{Pj} (\rho_j / \rho_\varepsilon).$

From (A3c) with $i = \varepsilon - 1$, we have

$$n_\sigma^* = n_\varepsilon^* (\rho_\sigma / \rho_\varepsilon) \exp[(\varepsilon - \zeta) n_\varepsilon^* \eta_3]. \tag{A4}$$

Substituting (A3a) and (A4) into (A3b) with $i = \sigma - 1$ gives

$$\sum_{j \in A} f_j \rho_j \exp[-n_\varepsilon^* (\theta_j + c_1 + c_2 \exp[c_3 n_\varepsilon^*])] = 1 \tag{A5}$$

where $c_1 = (\varepsilon - \zeta)\eta_3 + (\sigma - 1)\eta_2$, $c_2 = (\sigma - 1)(\rho_\sigma / \rho_\varepsilon)\eta_1$, and $c_3 = (\varepsilon - \zeta)\eta_3$. Since $1 < \sigma < \zeta < \varepsilon$, $c_i \geq 0$ for $i = 1, 2, 3$.

Replace n_ε^* with x and consider the LHS of (A5) as a function $G(x)$. If any of the non-negative parameters $\bar{\gamma}_{ij}$, γ_{Ej} , or γ_{Pj} are positive, then $G(x)$ is a monotonic decreasing function for $x > 0$. By assumption, $n_\varepsilon^* > 0$ exists and $G(n_\varepsilon^*) = 1$. The monotonicity of $G(x)$ implies that $G(0) > 1$ and n_ε^* is unique. By substituting backwards from (A4) through (A2), it is obvious that n_ε^* uniquely determines the entire vector \mathbf{N}^* .

Now consider the density-independent Leslie matrix $\mathbf{M}(\mathbf{0})$. It is well known from demographic theory that $\mathbf{M}(\mathbf{0})$, has a real positive eigenvalue λ which is not less in modulus than any other eigenvalue of $\mathbf{M}(\mathbf{0})$. Hence, $s(\mathbf{M}(\mathbf{0})) = \lambda$. The characteristic polynomial of $\mathbf{M}(\mathbf{0})$ is given by

$$W(x) = |\mathbf{M}(\mathbf{0}) - x \mathbf{I}| = x^\omega - \sum_{j \in A} x^{\omega-j} f_j \rho_j, \tag{A6}$$

where \mathbf{I} is the identity matrix. By definition, λ is the largest real root of $W(x) = 0$. From (A5), it is easy to see that $G(0) = 1 - W(1)$. However, the existence of \mathbf{N}^* implies $G(0) > 1$. This implies $W(1) < 0$. Since $\lim_{x \rightarrow \infty} W(x) = \infty$, $W(x) > 0$ for $x > \lambda$ which implies $\lambda = s(\mathbf{M}(\mathbf{0})) > 1$.

Conversely, assume $\lambda = s(\mathbf{M}(\mathbf{0})) > 1$. From Descartes' theorem, we know that the number of real roots of a polynomial is less than or equal to the number of sign changes in its sequence on non-zero coefficients. From (A6), it is obvious that there is one sign change in the coefficients of $W(x)$, which means that λ is the only real positive root of $W(x)$. Since $\lim_{x \rightarrow \infty} W(x) = \infty$ and $\lambda > 1$, $W(1) < 0$. This implies $G(0) > 1$. Since $G(x)$ is monotonic decreasing for $x > 0$, there exists a unique number x^* which satisfies $G(x^*) = 1$. If we set $n_\varepsilon^* = x^*$, then n_ε^* satisfies (A5), and we obtain the unique positive vector \mathbf{N}^* .