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Population Biology

Proceedings, Edmonton 1982

Edited by H. I. Freedman and C. Strobeck

PERIODIC LOTKA-VOLTERRA SYSTEMS AND TIME

SHARING OF ECOLOGICAL NICHES

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1. PERIODIC LOTKA-VOLTERRA SYSTEMS

The Lotka-Volterra system

$$P_1' = P_1(b_1 - a_{11}P_1 - a_{12}P_2), \quad P_2' = P_2(b_2 - a_{21}P_1 - a_{22}P_2) \tag{1}$$

with positive, periodic coefficients $b_i = b_i(t) \geq 0$ $(\neq 0)$, $a_{ij} = a_{ij}(t) \geq 0$ $(\neq 0)$ was studied in Cushing (1980) where it was shown that to a large extent the dynamics of (1) with such periodic coefficients mimics that of the familiar classical case of (1) with positive constant coefficients. With constant coefficients (1) has a (unique) positive equilibrium if and only if b_2 lies in a certain interval determined by b_1 and the a_{ij} (namely, the interval with endpoints $b_1 a_{21}/a_{11}$ and $a_{22}b_1/a_{12}$) and this positive equilibrium is stable if and only if $\Delta = a_{11}a_{22} - a_{12}a_{21} > 0$. In Cushing (1980) it is shown more generally that with positive, periodic coefficients (1) has a positive periodic solution if the average of $b_2(t)$ lies in a certain interval (whose endpoints are averaged quantities which reduce to those above for the constant coefficients case) and that this periodic solution is stable if a certain averaged quantity (which reduces to Δ/a_{11} for constant coefficients) is positive.

The purpose of this note is to describe some more specific results for (1) when the periodic coefficients are derived from the MacArthur-Levins theory and to relate them to the idea of time sharing an ecological niche.

In the MacArthur-Levins theory of competition for a one dimensional resource niche the coefficients in (1) are given by

$$b_i = w_i \int_{-\infty}^{+\infty} R(\rho)f_i(\rho)d\rho, \quad a_{ij} = w_i w_j \int_{-\infty}^{+\infty} f_i(\rho)f_j(\rho)d\rho$$

where $w_i f_i(\rho) \geq 0$, $\int_{-\infty}^{+\infty} f(\rho)d\rho = 1$, is a *resource utilization function* for species i and $R(\rho)$ is the availability rate of the resource ρ (Christiansen and Fenchel 1977, May 1974). The simplest case is when the utilization functions are Gaussian:

$$f_i(\rho) = (2\pi W^2)^{-\frac{1}{2}}\exp(\rho - D_i)^2/2W^2$$

and $R(\rho) = R > 0$ is constant. Here W is the "niche width" and $d = |D_1 - D_2|$ the "niche separation". Then

$$b_i = w_i R, \quad a_{ii} = w_i^2/(4\pi W^2)^{\frac{1}{2}}, \quad a_{ij} = \delta w_i w_j/(4\pi W^2)^{\frac{1}{2}},$$

$$\delta = \exp(-(d/2W)^2) \leq 1 \tag{2}$$

and (1) has a positive, stable equilibrium as long as $d/W > 0$. Stability is weakened as $d \to 0$, however, in the sense that the smallest real part of the eigenvalues of the linearized system is a monotonically increasing function of d/W which vanishes at $d/W = 0$ when the niches coincide, (see the final graph in Section 3 ($\lambda = 0$) below).

A biological case can be made for time fluctuations and periodicities in any of the quantities R, W, d and w_i. Such periodicities in (2) lead to a system (1) which falls within the purview of the general theory in Cushing (1980). In this note, attention will be restricted to the case when all parameters are constant except the w_i which will be assumed periodic in time. Thus, as in classical theory, the resource availability, niche positions and niche separation are constant in time. Only resource utilization will vary periodically in time. Specifically, it will be assumed that

$$w_1 = w(1 + \lambda \cos \omega t), \quad w_2 = w(1 + \lambda a \cos(\omega t + \gamma))$$

$$0 \leq \lambda \leq 1, \quad 0 \leq a\lambda \leq 1, \quad 0 \leq \gamma \leq \pi$$

so that the resource utilization functions have the same averages $w > 0$, but vary cosinusoidally in time with period $2\pi/\omega$ and with relative amplitudes a and phase difference γ. A rescaling of time (from t to wRt) and of P_i to $wP_i/R(4\pi W^2)^{\frac{1}{2}}$ leads to (1) with the coefficients

$$b_1 = 1 + \lambda \cos \omega t, \quad a_{11} = (1 + \lambda \cos \omega t)^2, \quad a_{22} = (1 + \lambda a \cos(\omega t + \gamma))^2$$

$$b_2 = 1 + \lambda a \cos(\omega t + \gamma), \quad a_{12} = a_{21} = \delta(1 + \lambda \cos \omega t)(1 + \lambda a \cos(\omega t + \gamma)). \tag{3}$$

The goal is to describe various properties of the positive periodic solution of (1) and (3) and its stability as they depend on the parameters $\lambda, \omega, a, \gamma$ and δ. It is hoped that this will lead to some insights into the phenomenon of time sharing a resource niche as well as the effects that these periodicities have on the fundamental concepts of competitive coexistence and exclusion and of limiting similarity.

2. SOME ANALYTICAL RESULTS

When the amplitude λ is small, regular perturbation techniques can be used to derive lower order approximations to the positive periodic solution of (1) and (3). Tedious, but straightforward calculations show that $P_i(t) = (1+\delta)^{-1} + \lambda y_i(t) + O(\lambda^2)$ where

$$2y_i(t) = (A_1 + (-1)^{i+1} A_2) \cos \omega t + (B_1 + (-1)^{i+1} B_2) \sin \omega t$$

$$A_1 = -[1 + a \cos \gamma + \omega a \sin \gamma]/(1+\delta)(1+\omega^2)$$

$$B_1 = [-\omega(1 + a \cos \gamma) + a \sin \gamma]/(1+\delta)(1+\omega^2)$$

$$A_2 = -(\delta-1)[(\tfrac{\delta-1}{\delta+1})(1 - a \cos \gamma) + \omega a \sin \gamma]/[(\delta-1)^2 + (\delta+1)^2 \omega^2]$$

$$B_2 = (\delta-1)[-(\tfrac{\delta-1}{\delta+1}) a \sin \gamma + \omega(1 - a \cos \gamma)]/[(\delta-1)^2 + (\delta+1)^2 \omega^2].$$

The Floquet exponents of the system linearized at this periodic solution are

$$e_1 = -1 + 0(\lambda), \qquad e_2 = (\delta-1)/(\delta+1) + \theta\lambda^2 + 0(\lambda^3)$$

$$\theta = \theta(\delta) = \omega^2(a^2 - 2a \cos \gamma + 1)/8(1+\omega^2) + 0(|\delta-1|).$$

Of particular interest is the case of very similar niches $\delta \sim 1$ (i.e. $d/W \sim 0$). For $\delta \sim 1$

$$P_i(t) \sim \tfrac{1}{2} + \lambda(A_1 \cos \omega t + B_1 \sin \omega t) + 0(\lambda^2)$$

$$e_2 \sim -\theta(1)\lambda^2 + 0(\lambda^3) \sim -\tfrac{\omega^2}{8}(1+\omega^2)^{-1}(a^2 - 2a \cos \gamma + 1)\lambda^2 + 0(\lambda^3).$$

Note that e_2 is the smallest Floquet exponent and hence determines the strength of the stability of the positive periodic solution.

For small amplitude oscillations $\lambda \sim 0$ and similar niches $\delta \sim 1$ some conclusions which can be deduced from these lower order terms are the following.

1. Since $\theta(1) \geq 0$ and since $\theta(1) = 0$ if and only if $\gamma = 0$, $a = 1$, it is seen that the presence of periodicities in the resource utilization functions $(\lambda \neq 0)$ decreases e_2 and hence promotes the stability of the competitive interaction, except possibly in or near the case of in-phase oscillations $(\gamma = 0)$ of equal amplitudes $(a = 1)$.

2. Since the maximum of $\theta(1)$ occurs for $a = 1$, $\gamma = \pi$, stability is maximized when the oscillations of the utilization functions are out-of-phase $(\gamma = \pi)$ and of equal amplitudes $(a = 1)$.

3. $\theta(1)$ and hence stability is increased by an increase of amplitude λ or frequence ω or relative amplitude $a > \cos \gamma$. Stability decreases with increasing $a \in [0, \cos \gamma]$.

4. The population mean values are, to lowest order, equal to $(1+\delta)^{-1}$ and are independent of a, λ, ω and γ.

5. The amplitude $(A_1^2 + B_1^2)^{1/2} = [(a^2 + 2a \cos \gamma + 1)/16(1+\omega^2)]^{1/2}$ of the oscillations in the population sizes $P_i(t)$ is minimized when $\gamma = \pi$. Thus, in this sense too, out-of-phase utilization of resources leads to maximal stability. This

amplitude is also decreased with increased frequence ω, but increased with increased relative amplitude a.

6. When $\gamma \sim 0$, the amplitude of P_1 increases with the phase difference γ while that of P_2 decreases with increases in γ.

7. The population sizes $P_i(t)$ oscillate nearly in-phase, except near $\gamma = \pi$.

Any one of these conclusions can be drastically altered if either $\delta \gg 1$ or $\lambda \gg 0$ or $a \sim 1$ and $\gamma \sim 0$.

3. NUMERICALLY FOUND RESULTS

I have carried out a great many numerical integrations of (1) and (3) for various parameter values. While corroborating the conclusions above these have also revealed some other interesting phenomena. The following graphs show a typical plot of the computed magnitude of the smallest Floquet exponent and the population maxima and minima as they change with the phase difference γ in resource utilization.
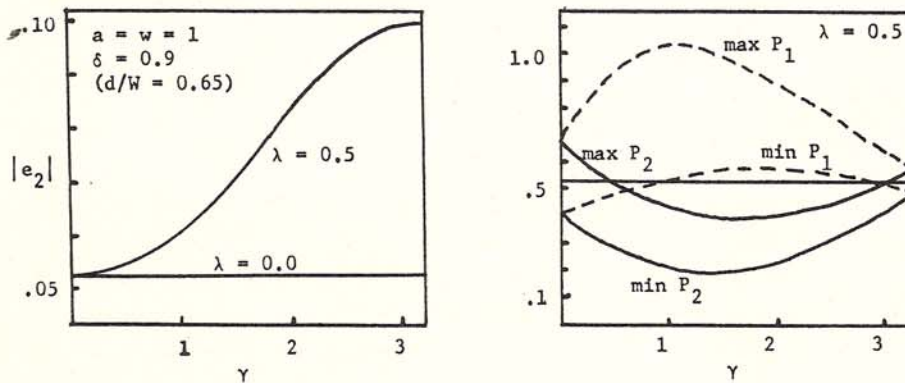

Figure 1

The monotonic increase in stability with increasing γ is however lost as the niches are brought closer together (δ is increased) as is shown in the next pair of graphs. Note not only the drop in system stability, but also the threatened extinction of P_2 (because of low population levels) for interactions only slightly out-of-phase ($\gamma \sim 1$), see Figure 2.

For widely separated niches ($\delta \sim 0$) the stability dependence on γ is reversed as is shown in the next graph (Figure 3). Thus, being *in*-phase is most advantageous for species with widely separated niches. The next pair of graphs below show the effects on stability of the amplitude λ and how they also qualitatively change for close versus widely separated niches (Figure 4). All of these computations were done with frequency $\omega = 1$.
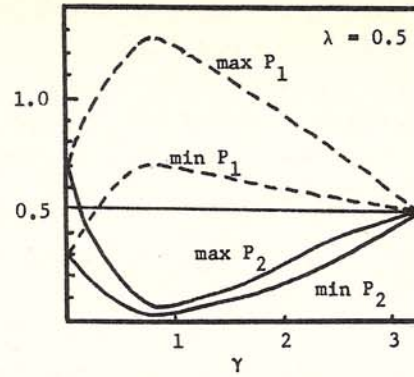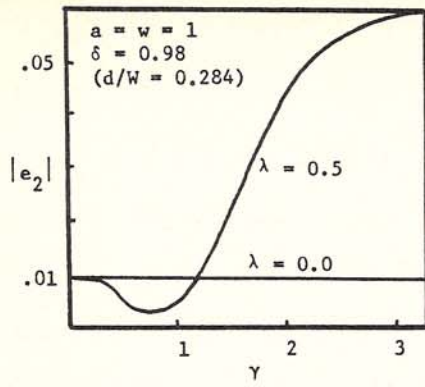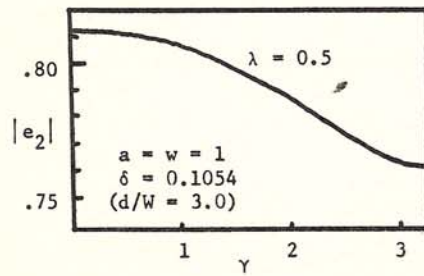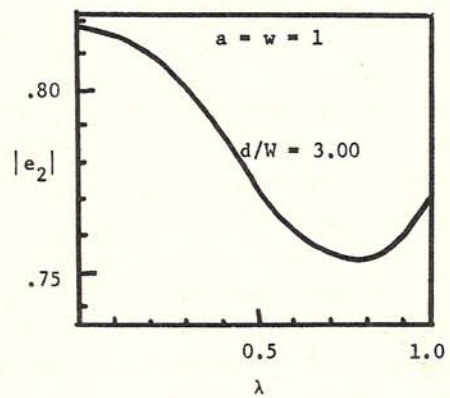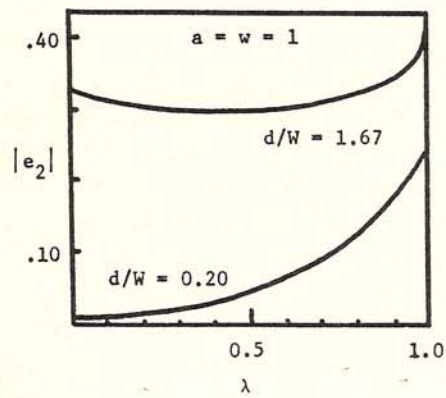
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Figure 2

Figure 3

Figure 4

The final graph (Figure 5) shows the effect on stability of changes in the niches separation to width ratio d/W (for out-of-phase oscillations of maximum amplitude $\lambda = 1$) and allows a comparison with similar graphs of the classical case of constant coefficients $\lambda = 0$ (see Christiansen and Fenchel 1977, May 1974).
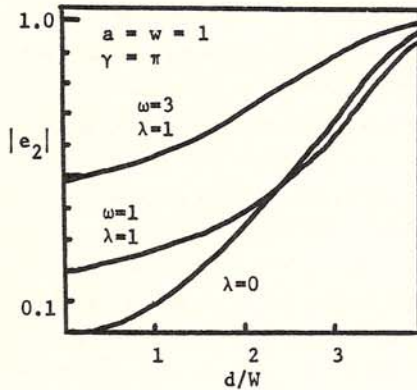

Figure 5

Thus, for frequency $\omega = 1$ it is advantageous to periodically, out-of-phase utilize the resource niches ($\lambda = 1$, $\gamma = \pi$) only for niches sufficiently close together (d/W $\lesssim$ 2). For frequency $\omega = 3$ the graphs for $\lambda = 1$ and $\lambda = 0$ were not found numerically to cross and hence it appears always advantageous to be out-of-phase. The "cross-over" of the graphs for $\lambda = 1$ and $\lambda = 0$ seems to be a complicated function of the frequence ω.

4. CONCLUSIONS

Holding other parameters constant, we considered periodicities in the resource utilization functions of two competing species modeled by the classical Lotka-Volterra-MacArthur-Levins theory. It was found for small niche separations ($\delta \sim 1$) that stable coexistence is enhanced when the periodic oscillations in the utilization functions are out-of-phase ($\gamma = \pi$) and are of maximum amplitude ($\lambda = 1$), i.e. the similar niches are "time shared". Short periods and large relative amplitudes also increased stability. These conclusions, however, may drastically alter and indeed be reversed for widely separated niches ($\delta \sim 0$).

It was also found that for close niches, small phase differences ($\gamma \sim 0$) are disastrous for coexistence (actually worse than in-phase oscillations $\gamma = 0$), the species P_2 whose resource utilization function peaks earliest being threatened with extinction because of very low population levels. This rather unexpected

result could have importance with regard to the possible evolution of time sharing in similar niches by two competing species who begin in a state of in-phase resource utilization. The above result would not allow a continuous evolution of the phase difference γ to an out-of-phase state without threatened extinction of one of the species.

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