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Frequency–Phase Response of a Periodically Forced Two-Species Lotka–Volterra Competition Model

Tombotamunoa W. J. Lawson[1,*], Eze Chikwem[1]

[1] Department of Mathematics, Ignatius Ajuru University of Education, Rumuolumeni, Port Harcourt, Nigeria

*** Corresponding author:** tombotamunoa.lawson@iaue.edu.ng

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Abstract

Periodic forcing is a standard feature of ecological competition models, but the response of a coexistence state is often summarized by numerical trajectories or by a high-frequency approximation. We derive two complementary diagnostics for a two-species Lotka–Volterra competition system with sinusoidal forcing of intrinsic growth rates and constant competition coefficients. First, every positive solution with the forcing period has cycle means exactly equal to the equilibrium of the unforced system; this follows from averaging the per-capita log-growth equations and is independent of forcing amplitude, frequency, and phase. Second, for small forcing, the complex population response is given by a resolvent, $(i\omega I - J)^{-1}$, acting on the species-specific forcing vector, where J is the coexistence Jacobian. This formula predicts amplitudes and phase shifts, including the cross-species effects of competition. Numerical integrations for a positive-coexistence parameter set validate the response formula over a broad frequency range and show strong sensitivity of oscillation amplitude to the relative phase of the two growth cycles, even though cycle means remain fixed. The computed periodic orbit is locally attracting, with both Floquet multipliers inside the unit circle. The contribution is a compact frequency–phase response analysis and a mean-invariance result for a classical periodically forced competition model; it is not a claim that periodic Lotka–Volterra competition is new. The simulations are illustrative and are not fitted to empirical population data.

Keywords: Lotka–Volterra competition; periodic forcing; frequency response; phase lag; averaging; Floquet multipliers; coexistence

1. Introduction

Competition models have long served as a mathematical framework for describing the interaction of populations that draw on common limiting resources. The logistic and Lotka–Volterra formulations provide tractable reference systems, while resource-explicit models clarify when density dependence can permit coexistence [1, 2, 3, 4, 5, 6, 7, 8, 9, 10]. Environmental variability adds temporal structure to these interactions. Classical studies established that periodic coefficients can alter coexistence, invasion, and stability, and that the outcome depends on the structure and timing of environmental variation [11, 12, 13, 14, 15, 16]. Broader coexistence theory emphasizes that variability promotes coexistence only through mechanisms that create stabilizing differences or temporal niches; forcing alone is not a universal coexistence mechanism [17, 18, 19, 20, 21].

The mathematical behavior of periodically forced ecological systems has been studied using periodic-orbit, invasion, and averaging methods. Averaging theory provides systematic approximations when a system is weakly or rapidly forced [22, 23], while Floquet theory characterizes the local stability of periodic responses, within the general theory of nonlinear population dynamics and dynamical systems [24, 25]. The present paper focuses on a specific question that is complementary to existence and coexistence analyses: given a stable interior equilibrium in the unforced two-species model, how do forcing frequency and relative phase determine the amplitude and timing of the resulting population oscillations?

We study sinusoidal modulation of intrinsic growth rates while holding the competition matrix fixed. Our main analytical findings are: (i) any positive solution that is periodic with the forcing period has exactly the same cycle-mean population vector as the unforced coexistence equilibrium; (ii) for small forcing, the leading periodic response is governed by the matrix transfer function $(i\omega I - J)^{-1}$; and (iii) this formula reduces to the familiar $1/\omega$ amplitude scaling at high frequency, but also quantifies finite-frequency cross-species filtering and phase shifts. We then compare the linear response with nonlinear numerical orbits and compute Floquet multipliers. This is a focused analysis of response properties within an established model class, not a new general theory of seasonal coexistence. Prior studies by Lawson and colleagues address computational oscillator models, oscillator thermodynamics, and steady-state population modelling in related but distinct settings [26, 27, 28]; they motivate the authorship and modelling context but are not evidence for the ecological results derived here.

2. Model and unforced coexistence

Let $x(t)$ and $y(t)$ be positive densities of two competing species. We consider

$$\dot{x} = x\left[\mu_1 + A_1\cos(\omega t) - c_{11}x - c_{12}y\right], \tag{2.1}$$

$$\dot{y} = y\left[\mu_2 + A_2\cos(\omega t + \phi) - c_{21}x - c_{22}y\right], \tag{2.2}$$

where $\mu_i > 0$ are mean intrinsic growth rates, $A_i \geq 0$ are forcing amplitudes, $\omega > 0$ is the angular frequency, and ϕ is the relative phase. The competition coefficients satisfy $c_{ij} > 0$, with c_{ii} describing intraspecific density dependence and c_{ij} $(i \neq j)$ interspecific competition. The forcing period is $T = 2\pi/\omega$. In vector form, with $z = (x, y)^\top$, $\boldsymbol{\mu} = (\mu_1, \mu_2)^\top$, and

$$C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \qquad \boldsymbol{a}(t) = \begin{pmatrix} A_1 \cos(\omega t) \\ A_2 \cos(\omega t + \phi) \end{pmatrix},$$

the system is $\dot{z} = \operatorname{diag}(z)(\boldsymbol{\mu} + \boldsymbol{a}(t) - Cz)$.

The unforced system ($A_1 = A_2 = 0$) has an interior equilibrium

$$z^* = C^{-1}\boldsymbol{\mu} = \frac{1}{\Delta}\begin{pmatrix} c_{22}\mu_1 - c_{12}\mu_2 \\ c_{11}\mu_2 - c_{21}\mu_1 \end{pmatrix}, \qquad \Delta = c_{11}c_{22} - c_{12}c_{21}. \tag{2.3}$$

A positive coexistence equilibrium requires $\Delta \neq 0$ and both components of z^* positive. Its Jacobian is

$$J = -\operatorname{diag}(z^*)C. \tag{2.4}$$

We assume throughout that $z^* > 0$ and that J is Hurwitz (all eigenvalues have negative real parts), so the unforced coexistence equilibrium is locally asymptotically stable. These are local assumptions: they do not assert global stability for every positive competition matrix or for arbitrary forcing amplitudes. Classical competition theory gives the broader ecological context and conditions for coexistence and exclusion [7, 8, 29].

3. Analytical results

3.1. Exact cycle-mean identity

The periodic terms in (2.1)–(2.2) have zero temporal mean. This yields an exact constraint on any positive solution with period T.

Theorem 3.1 (Cycle means)**.** *Suppose $z(t) = (x(t), y(t))^\top$ is a positive T-periodic solution of (2.1)–(2.2). If C is invertible, then*

$$\overline{z} := \frac{1}{T}\int_0^T z(t)\,dt = C^{-1}\boldsymbol{\mu} = z^*. \tag{3.1}$$

Proof. Because $x(t) > 0$ and is periodic, integrating its per-capita log-growth equation over one period gives

$$0 = \frac{1}{T}\int_0^T \frac{\dot{x}}{x}\,dt = \mu_1 + A_1\overline{\cos(\omega t)} - c_{11}\overline{x} - c_{12}\overline{y}.$$

The cosine mean vanishes and similarly the equation for y gives $c_{21}\overline{x} + c_{22}\overline{y} = \mu_2$. Thus $C\overline{z} = \boldsymbol{\mu}$, and invertibility gives (3.1). □

Remark 3.2. The result concerns the arithmetic time mean of density on a positive T-periodic orbit. It does not imply that the instantaneous densities are constant, that their geometric means equal z^*, or that arbitrary initial conditions converge to a periodic orbit. It also depends on constant competition coefficients and zero-mean additive forcing of the per-capita growth rates. If competition coefficients vary in time, or forcing changes density dependence, the identity generally need not hold.

3.2. Small-forcing response and stability

Write $z(t) = z^* + u(t)$ and suppose A_1, A_2 are small. To first order, the perturbation satisfies

$$\dot{u} = Ju + \operatorname{diag}(z^*)\boldsymbol{a}(t) + O(\|u\|^2 + \|\boldsymbol{A}\|\,\|u\|), \qquad \boldsymbol{A} = (A_1, A_2)^\top. \tag{3.2}$$

The real-valued forcing can be represented as the real part of a complex harmonic input.

Proposition 3.3 (Linear frequency response)**.** *Assume J is Hurwitz. For each fixed $\omega > 0$, the first-order periodic response is*

$$u_1(t) = \Re\left\{H(\omega,\phi)e^{i\omega t}\right\}, \qquad H(\omega,\phi) = (i\omega I - J)^{-1}\begin{pmatrix} A_1 x^* \\ A_2 y^* e^{i\phi}\end{pmatrix}. \tag{3.3}$$

The leading oscillation amplitude of species i is $|H_i|$, and its phase relative to the common reference $\cos(\omega t)$ is $\arg H_i$. Define positive phase lag to mean that the response peaks after its own forcing; then the lag is $\psi_i - \arg H_i$ modulo 2π.

Proof. For the first-order equation $\dot{u}_1 = Ju_1 + \Re\{qe^{i\omega t}\}$, where $q = (A_1 x^*, A_2 y^* e^{i\phi})^\top$, seek a periodic solution $u_1 = \Re\{He^{i\omega t}\}$. Substitution gives $(i\omega I - J)H = q$. Since J is Hurwitz, $i\omega I - J$ is nonsingular for real ω, yielding (3.3). The implicit function theorem applied to the period-T Poincaré map gives a nearby periodic orbit for sufficiently small forcing: at zero forcing, the derivative of the return map is e^{JT}, which has no unit eigenvalue because J is Hurwitz. Its local attraction persists for small forcing amplitudes. □

Corollary 3.4 (High-frequency limit)**.** *For fixed amplitudes and phase, as $\omega \to \infty$,*

$$H(\omega,\phi) = \frac{q}{i\omega} + O(\omega^{-2}), \qquad u_{1,i}(t) = \frac{A_i z_i^*}{\omega}\sin(\omega t + \psi_i) + O(\omega^{-2}), \tag{3.4}$$

where $\psi_1 = 0$ and $\psi_2 = \phi$ are the species-specific forcing phases. Thus the leading waveform of species i is shifted by its own forcing phase, with cross-species corrections entering at order ω^{-2}. Thus the leading response amplitude decays as $1/\omega$; at finite frequencies the off-diagonal entries of J transmit forcing between species.

4. Numerical design

We selected an illustrative parameter set with no claim of calibration to a specific ecosystem:

$$\boldsymbol{\mu} = (0.8, 0.7)^\top, \quad C = \begin{pmatrix} 1 & 0.4 \\ 0.5 & 1.1\end{pmatrix}, \quad (A_1, A_2) = (0.20, 0.15). \tag{4.1}$$

The determinant is $\Delta = 0.90$, and the unforced coexistence state is $z^* = (2/3, 1/3)^\top$. The Jacobian eigenvalues are approximately -0.7754 and -0.2579, confirming local asymptotic stability. The forcing amplitudes are 25% and about 21% of the respective mean growth rates. We solved the original nonlinear equations with an adaptive Runge–Kutta method (SciPy *solve_ivp*, relative tolerance 10^{-9} and absolute tolerance 10^{-11}). For each frequency and phase offset, trajectories were integrated one period at a time until the successive period-end states differed by less than 2×10^{-10} in the infinity norm, up to 250 cycles. Each converged period was sampled at 1,601 equally spaced times. The linear predictions were evaluated from (3.3). Floquet multipliers were computed by integrating the variational equation $\dot{M} = D_z f(t, z(t))M$, $M(0) = I$, over the converged period. The scripts and figure data are supplied in the source package.

5. Results

5.1. Waveforms and phase dependence

Figure 1 shows the converged periodic waveforms at $\omega = 1.5$ for three relative phases. The response remains positive and periodic. Changing ϕ alters amplitudes and relative timing because the two species are coupled through the off-diagonal competition terms. At $\phi = 0$, half peak-to-trough amplitudes are approximately $(0.07895, 0.02948)$; at $\phi = \pi/2$, they are $(0.07502, 0.03994)$; and at $\phi = \pi$, they are $(0.08140, 0.03626)$. These differences are visible despite the same mean growth rates and forcing magnitudes.

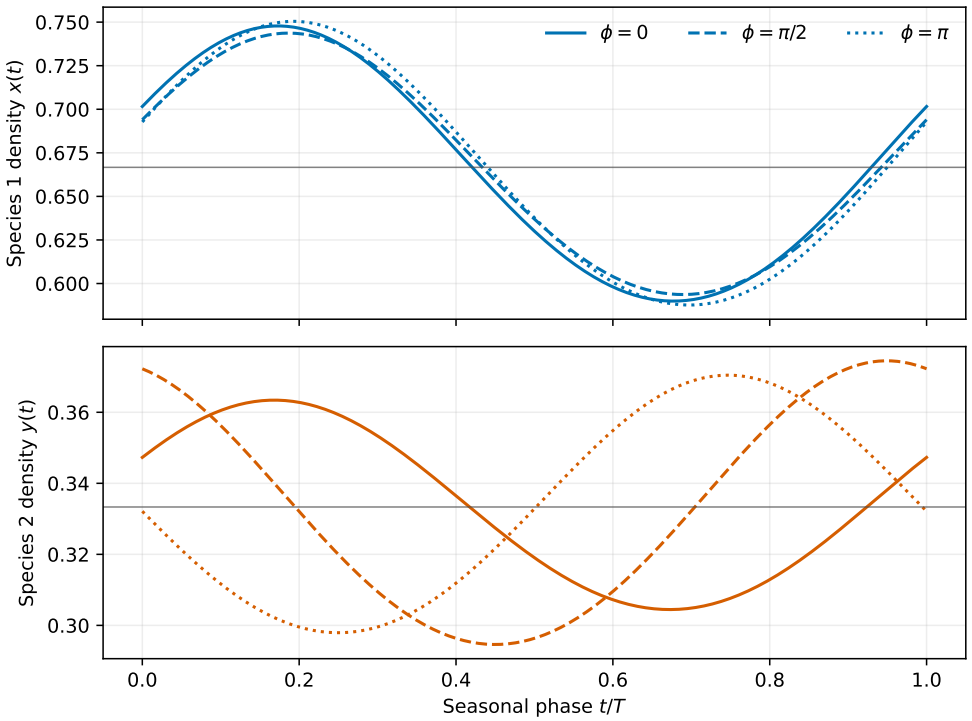


Figure 1: Nonlinear periodic densities for the parameter set in (4.1), forcing frequency $\omega = 1.5$, and relative phases $\phi = 0, \pi/2, \pi$. Horizontal gray lines indicate the unforced equilibrium densities. Curves are model simulations, not observed population data.

5.2. Frequency response

Figure 2 compares nonlinear half peak-to-trough amplitudes across frequencies with the first-order prediction for $\phi = \pi/2$. The amplitude decreases with increasing frequency, consistent with (3.4). At low and intermediate frequencies, species-specific relaxation and cross-species coupling shape the response; the phase offset also changes the amplitude. The first-order response closely tracks the nonlinear simulation for the selected moderate forcing over the plotted range, with the largest expected deviations at the lowest frequencies where forcing acts over longer portions of each cycle. This agreement is a numerical validation for this parameter set, not a general error bound.

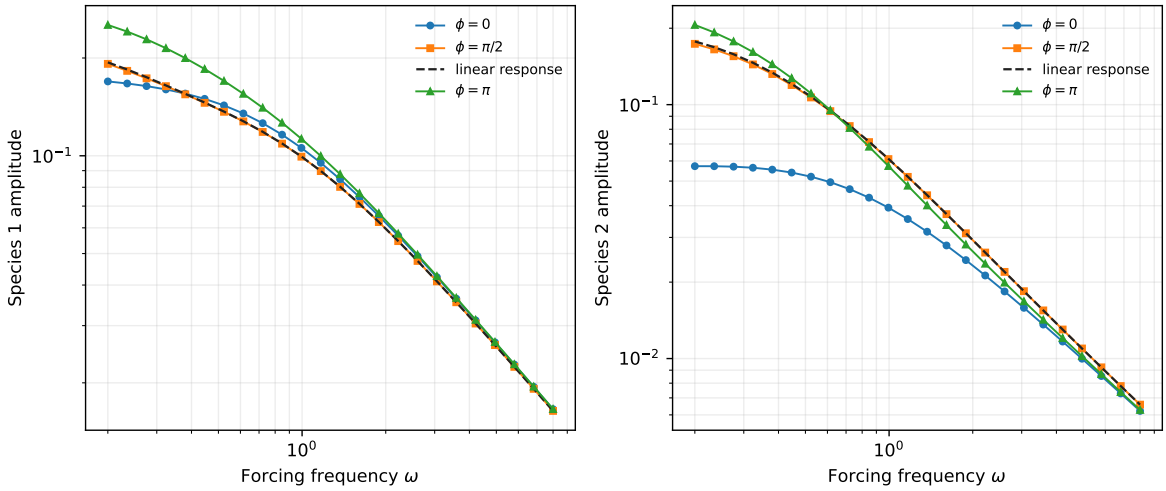


Figure 2: Half peak-to-trough response amplitude versus forcing frequency. Colored symbols/curves show nonlinear simulations for three phase offsets. The black dashed curve is the first-order prediction for $\phi = \pi/2$. Species 1 and 2 are shown in separate panels.

5.3. Exact invariance of the cycle means

The cycle-mean theorem predicts $\overline{x} = 2/3$ and $\overline{y} = 1/3$ for every positive solution with period T under this model, regardless of ϕ. The numerical phase sweep at $\omega = 1.5$ confirms these means to solver precision while the oscillation amplitudes vary with phase (Figure 3). This distinction matters for interpretation: phase can strongly alter peak and trough abundance without altering the long-run arithmetic mean in this particular model. The result follows from the structural form of the equations, rather than from the chosen numerical values.

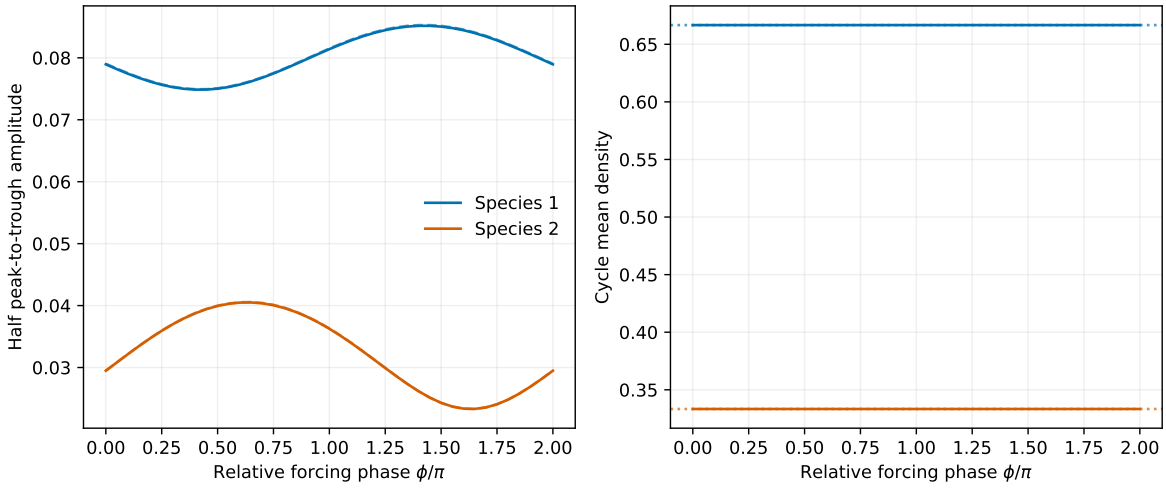


Figure 3: Phase-offset sweep at $\omega = 1.5$. Left: nonlinear oscillation amplitudes (solid) and first-order amplitudes (dashed) over $0 \leq \phi \leq 2\pi$. Right: cycle means, which remain equal to z^* as required by Theorem 3.1; dotted horizontal lines mark the unforced equilibrium values.

5.4. Floquet stability

For $\omega = 1.5$ and $\phi = \pi/2$, the computed monodromy matrix has eigenvalues (Floquet multipliers) approximately 0.03881 and 0.33985. Both have modulus less than one, so the numerically computed periodic orbit is locally asymptotically attracting. This is consistent with the perturbative persistence argument for sufficiently small forcing. It does not establish global attraction or persistence for all initial conditions and parameter values.

Table 1: Baseline equilibrium and periodic-orbit diagnostics for the illustrative parameter set.

Quantity	Value
Unforced coexistence equilibrium z^*	$(0.66667,\ 0.33333)$
Forcing frequency ω	1.5
Forcing phase ϕ	$\pi/2$
Period $T = 2\pi/\omega$	4.18879
Nonlinear half peak-to-trough amplitudes	$(0.07502,\ 0.03994)$
Linear-response amplitudes	$(0.07508,\ 0.03999)$
Cycle means	$(0.66667,\ 0.33333)$
Floquet multipliers	$(0.03881,\ 0.33985)$

6. Discussion

The exact mean identity and the frequency-response formula answer different questions. The identity states that, whenever a positive solution periodic with the forcing period exists, its cycle means are pinned to the constant-coefficient coexistence equilibrium. The transfer function describes how the trajectory departs from those means over the cycle. It therefore distinguishes average abundance from seasonal exposure, peak density, and timing. In applications where nonlinear impacts depend on peaks, synchrony, or threshold crossings, phase-dependent oscillations may still matter even when the model's arithmetic mean is invariant.

The response matrix $(i\omega I - J)^{-1}$ also clarifies why separate scalar logistic approximations can miss the coupled response. The off-diagonal competition terms mix the species' forcing signals, while the eigenvalues of J set characteristic relaxation times. At forcing frequencies much larger than the relaxation rates, populations cannot track the environment and the response approaches the $1/\omega$ scaling. At slower frequencies, the relative phase and coupling shape the amplitude and phase lag. This is consistent with the established theory that environmental variation can favor or hinder coexistence depending on how it interacts with species-specific demographic and competitive responses [12, 13, 17, 18, 21, 30].

The present model deliberately isolates direct modulation of intrinsic growth. It does not represent a resource explicitly, include seasonal variation in competition coefficients, incorporate stochastic weather, or model delayed responses, age structure, or spatial movement. Consequently, the cycle-mean invariance should not be interpreted as a general

ecological prediction. In systems with seasonal carrying capacities or resource dynamics, a changed environment can alter mean abundance and the coexistence mechanism itself [7, 29, 20, 21]. More elaborate periodic Lotka–Volterra models may also have multiple positive periodic states and invasion outcomes that depend on initial conditions or parameter phase relationships [15, 16].

Our novelty claim is correspondingly narrow: we combine an exact mean constraint with a two-species complex response formula and demonstrate how it organizes phase and frequency effects in a reproducible nonlinear example. Periodic competition models and seasonal coexistence are not new subjects. The analytical formula is useful as a compact diagnostic, while empirical application would require estimating growth, competition, and forcing parameters from time series and testing whether the model's constant-competition assumptions are adequate. The authors' previous work includes analytical steady-state modelling in biological systems and computational oscillator studies [28, 26, 27]; the present manuscript extends the mathematical modelling agenda to time-periodic competitive population dynamics without conflating the physical oscillator results with ecological evidence.

7. Conclusion

For two competing species with sinusoidally forced intrinsic growth and fixed competition coefficients, every positive solution periodic with the forcing period has cycle means equal to the unforced coexistence equilibrium. Around a stable equilibrium, the first-order periodic response is obtained by applying the resolvent $(i\omega I - J)^{-1}$ to the complex forcing vector. Simulations confirm that this response predicts amplitudes well for the illustrative parameter set, while phase sweeps show that oscillation amplitudes can vary even when cycle means do not. The numerically calculated orbit is locally attracting by its Floquet multipliers. These results provide a testable analysis for a specific periodic competition model; broader ecological claims require models and data that represent additional mechanisms.

Reproducibility and data availability

All numerical results and plots are generated by the accompanying Python script using the parameters reported in (4.1). No empirical data were used. The LaTeX source, figure files, and script are provided together in the source package.

Author declarations

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