

Statistical Scaling Laws for Competing Biological Species

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Universality classes are defined for an idealized nonlinear system that governs the competition between biological species. The decay to asymptotic steady state is examined for supercritical Hopf bifurcation by considering a phenomenological approach supported by numerical simulations and confirmed by an analytical description. The formalism is general and it is expected to be universal for systems exhibiting Hopf bifurcations.

Keywords: scaling properties; critical exponents; prey-predator; Hopf bifurcation

1. Introduction

In statistical mechanics, scaling laws are generally associated with changes in the spatial structure of dynamical systems due to variations of control parameters [1–4]. A bifurcation is the scientific terminology given to these particular qualitative changes in the dynamics [5]. In the local bifurcation theory, when an equilibrium point changes stability from stable to unstable and a stable limit cycle shows up, we say the system has undergone a Hopf bifurcation [6, 7]. In general, the study of the Hopf bifurcation is of great practical concern as well as of fundamental scientific interest, since it is present in a variety of systems, including electrical circuits [8–10], dynamical population [11, 12], lasers [12, 13] and many others. Some of the basic questions that remain to be explored about Hopf bifurcation are the regimes for which certain scaling laws exist and whether the exponents obtained for systems obeying certain kinds of dynamics are valid for others.

In this paper, we examine the dynamics of interacting biological species modeled by the Lotka–Volterra prey-predator equations. The Lotka–Volterra mathematical model [14–16] describes, considering assumptions not necessarily realizable in nature, the dynamical behavior governing the growth, decay and evolution of two competing biological species, one as predator and the other as prey.

Our main goal in this paper is to apply the scaling formalism to explore the mathematical model of prey-predator near the Hopf bifurcation. Here, two different procedures are adopted. The first is mostly phenomenological, with scaling hypotheses ending up with scaling laws of seven critical exponents. The second considers an analytical description confirming the results obtained by numerical simulation. The scaling analysis presented in this paper suggests that the same critical exponents as well as the scaling properties studied should also be valid for other multidimensional systems that exhibit Hopf bifurcation [17].

This paper is organized as follows. In Section 2, an idealized theoretical model for the prey-predator system is presented and its normal form is derived. Section 3 is devoted to describing the phenomenological approach based on scaling hypotheses leading to critical exponents and hence to scaling laws. In Section 4, an analytical description is made and scaling exponents are derived through the direct solution of the differential equations. Moving on, conclusions are made in Section 5.

2. The Dynamics and Normal-Form Computation

2.1 The Mathematical Model and Dynamics

The evolution of ecological systems has different models, depending on the number of assumptions about the population and environment [15, 16, 18–20]. For the purposes of this work, we consider two interacting populations: a prey (rabbits) species x_1 and its predator (foxes) x_2 . The dimensionless form of the rate equations for a simple predator-prey system [21] is given by

$$\begin{cases} \dot{x}_1 = rx_1(b + x_1)(1 - x_1) - cx_1x_2 \\ \dot{x}_2 = (c - d)x_1x_2 - bdx_2, \end{cases} \quad (1)$$

where x_1, x_2, r, c and $b \in \mathbb{R}$. For further developments, r and c are assumed constant, and b is treated as a control parameter. The model expressed in equation (1) has one fixed point at

$$P_0 = \left(\frac{bd}{c-d}, \frac{bd}{c-d} \left(1 - \frac{bd}{c-d} \right) \right). \quad (2)$$

Near the fixed point P_0 , we have the Jacobian matrix

$$J_{P_0} = \begin{pmatrix} \frac{brd(c+d)}{(c-d)^2} \left(\frac{c-d}{c+d} - b \right) & -\frac{bdc}{c-d} \\ br \frac{c-d(1+b)}{c-d} & 0 \end{pmatrix}. \quad (3)$$

The eigenvalues of the matrix in equation (3) considering the fixed point P_0 are

$$\lambda_{1,2} = \alpha(b) \pm i\beta(b), \quad (4)$$

where

$$\alpha(b) = \frac{brd(c+d)}{2(c-d)^2} \left(\frac{c-d}{c+d} - b \right), \quad (5)$$

$$\beta(b) = \sqrt{rc^2 \frac{d(c-d)}{(c+d)^3}}.$$

According to the linear stability theory, when $\alpha < 0$ the fixed point turns into a stable spiral whose sense of rotation depends on β . For $\alpha = 0$, a stable spiral still dictates the dynamics; however, the speed of convergence is different from $\alpha < 0$. Finally, for $\alpha > 0$, there is an unstable spiral at the origin, and a stable and periodic limit cycle bifurcates from the fixed point.

2.2 The Normal-Form Computation

In the study of local bifurcation, the normal-form theory is an advantageous approach, since it corresponds to the simpler analytical expression at which a dynamical system can be rewritten through a convenient choice of a coordinate system without losing or changing the phase space topology of the original given system being studied.

To compute the normal form of the dynamical system in equation (1), use Theorem 1.

Theorem 1. Consider a two-dimensional dynamical system described by the equations

$$\begin{aligned} \dot{x} &= f(x, \mu), \\ x &\in \mathbb{R}^2, \\ \mu &\in \mathbb{R}, \end{aligned} \quad (6)$$

where f is a smooth function of its variables and time, having for all sufficiently small μ the fixed point $x_0 = 0$ with eigenvalues

$$\lambda_{1,2} = \alpha(\mu) \pm i\beta(\mu). \quad (7)$$

If for $\mu = 0$ the following conditions are satisfied:

1. $\alpha(0) = 0$, $\beta(0) \neq 0$ (non-hyperbolicity)
2. $\left. \frac{d\alpha(\mu)}{d\mu} \right|_{\mu=0} \neq 0$ (transversality)
3. $l_1(0) \neq 0$ (non-degeneracy)

where l_1 is the first Lyapunov coefficient

then, the dynamical system expressed in equation (4) can be rewritten in the following normal form:

$$\begin{cases} \dot{y}_1 = \alpha(\mu)y_1 - \beta(\mu)y_2 + (ay_1 - by_2)((y_1)^2 + (y_2)^2), \\ \dot{y}_2 = \alpha(\mu)y_2 + \beta(\mu)y_1 + (ay_2 + by_1)((y_1)^2 + (y_2)^2). \end{cases} \quad (8)$$

Theorem 1 says for a generic dynamical system in two dimensions, if it is proved that it satisfies the conditions of the Hopf bifurcation theorem, then its normal form is known to be described by equation (8). A proof of this theorem is outlined in other sources [7]. From Theorem 1 follows its corollary:

Corollary 1. Imagine the two-dimensional system

$$\begin{aligned} \dot{x} &= f(x, \mu), \\ x &\in \mathbb{R}^2, \\ \mu &\in \mathbb{R}, \end{aligned} \quad (9)$$

and x_0 its fixed point. At $\mu = 0$, the dynamical system equation (9) is said to exhibit a Hopf bifurcation. Suppose further that for $\mu < \mu_0$ ($\mu > \mu_0$), equation (9) has a pair of complex-conjugate eigenvalues with positive real part and, for $\mu > \mu_0$ ($\mu < \mu_0$), equation (9) has a pair of complex-conjugate eigenvalues with negative real part. Then,

1. For $l_1 < 0$, which happens when $a < 0$, the fixed point x_0 is said to be asymptotically stable at $\mu = \mu_0$. Although, at $\mu > \mu_0$ ($\mu < \mu_0$) a unique stable (unstable) curve of periodic solutions bifurcates from the unstable (stable) fixed point. In this case, the dynamical system exhibits the so-called supercritical Hopf bifurcation.
2. For $l_1 > 0$, which happens when $a > 0$, the fixed point x_0 is said to be unstable at $\mu = \mu_0$. However, at $\mu < \mu_0$ ($\mu > \mu_0$) a unique unstable (stable) curve of periodic solutions bifurcates from the stable (unstable) fixed point. In this case, the dynamical system exhibits the so-called subcritical Hopf bifurcation.
3. For $l_1 = 0$, nothing can be said about the dynamics.

Corollary 1 establishes whether the dynamical system being studied exhibits the supercritical or the subcritical case of the Hopf bifurcation.

Returning to the mathematical model expressed in equation (1), the eigenvalues of the Jacobian matrix are

$$\lambda_{1,2} = \frac{brd(c+d)}{2(c-d)^2} \left(\frac{c-d}{c+d} - b \right) \pm i \sqrt{rc^2 \frac{d(c-d)}{(c+d)^3}}.$$

Note that for $b_c = \left(\frac{c-d}{c+d} \right)$, $\alpha(b_c) = 0$ and $\beta(b_c) \neq 0$.

Also,

$$\left. \frac{d\alpha(b)}{db} \right|_{b=b_c} = - \frac{b_c(c+d)rd}{2(c-d)^2} \neq 0. \tag{10}$$

Finally,

$$l_1(b_c) = - \frac{c^2 d^2 r}{\beta(b_c)} \neq 0. \tag{11}$$

Therefore, all the conditions of Theorem 1 are satisfied. Hence, the normal polar form of the dynamical system of equation (1) is given by

$$\begin{cases} \dot{\rho} = \alpha(b)\rho - \rho^3, \\ \dot{\phi} = \beta(b) + \rho^2, \end{cases} \tag{12}$$

where ρ and ϕ describe the radial and angular coordinates, respectively.

In this section, the normal form of the prey-predator model is obtained. The theorem proposed acts as a shortcut to obtain the normal form for dynamical systems characterized by occurrence of the Hopf bifurcation.

3. The Phenomenological Properties of the Steady State

We now outline the derivation of the scaling law for Hopf bifurcation. The scaling analysis presented was carried out in a very similar direction to that discussed in [22], so we present only the main points here, rather than providing the detailed arguments. In our analysis, the first step is to apply the normal-form theory to simplify the form of the dynamics on the center manifold, which yields to the reduced set of equations (12).

To see the scaling properties, we must look at the convergence to the steady state, and the natural variable that describes it is the

distance from P_0 . Besides, the convergence must also depend on the initial condition and hence, the control parameter $\alpha(b)$. The parameter $\alpha(b_c) = 0$ defines the bifurcation point, and the convergence to the equilibrium point for variables ρ and ϕ is shown in Figures 1 and 2, respectively, considering different initial conditions.

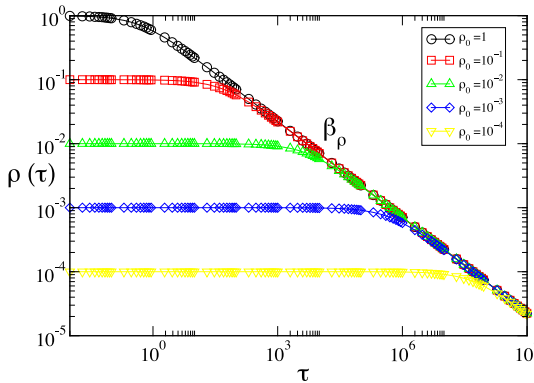


Figure 1. Convergence to the steady state at the fixed point P_0 for different initial conditions as shown in the figure. The parameter used was $\alpha(b_c) = 0$.

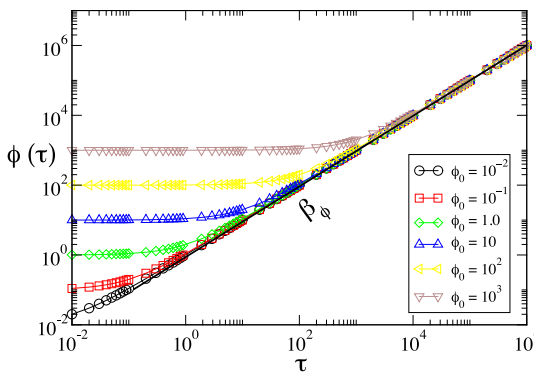


Figure 2. Plot of the angular variable ϕ as a function of time τ for different initial conditions, as labeled in the figure. The parameter used was $\alpha(b_c) = 0$.

Analysis of Figures 1 and 2 indicates that depending on the initial condition, the orbit stays in a constant plateau, and after reaching a crossover time, τ_ρ for ρ and τ_ϕ for ϕ , the orbit suffers a changeover from a constant regime to a power-law decay in the radial coordinate

and a power-law growth in the angular coordinate. Based on the behavior observed from Figures 1 and 2, we can propose the following scale hypotheses:

1. For a short interval of time τ , say $\tau \ll \tau_x$, the convergence to the steady state is given by

$$\begin{cases} \rho(\tau) \propto \rho_0^{\alpha_\rho}, \\ \phi(\tau) \propto \phi_0^{\alpha_\phi}. \end{cases} \tag{13}$$

A quick analysis of Figures 1 and 2 allows us to conclude that critical exponents $\alpha_\rho = \alpha_\phi = 1$.

2. For a sufficiently large τ , say $\tau \gg \tau_x$, the convergence to the steady state is given by

$$\begin{cases} \rho(\tau) \propto \tau^{\beta_\rho}, \\ \phi(\tau) \propto \tau^{\beta_\phi}, \end{cases} \tag{14}$$

where β_ρ gives the decay exponent and β_ϕ gives the growth exponent.

3. The characteristic crossover time τ_x that describes the changeover from a constant regime to a power-law decay in the radial coordinate and to a power-law growth in the angular coordinate is given respectively by

$$\begin{cases} \tau_x \propto \rho_0^{z_\rho}, \\ \tau_x \propto \phi_0^{z_\phi}, \end{cases} \tag{15}$$

where z_ρ and z_ϕ are known as the changeover exponents.

Based on the behavior shown in Figures 1 and 2 and considering the scaling hypotheses, it is possible to describe the ρ and ϕ as homogeneous and generalized functions when $\alpha(b_c) = 0$, as

$$\begin{aligned} \rho(\rho, \tau) &= \ell \rho(\ell^c \rho_0, \ell^d \tau), \\ \phi(\phi, \tau) &= \ell \phi(\ell^{c_1} \phi_0, \ell^{d_1} \tau), \end{aligned} \tag{16}$$

where ℓ is a scaling factor and the c_i and d_i are characteristic exponents. By convenient choices of ℓ , the c_i and d_i exponents are proved to be related to the characteristic exponents α , β and z for both polar variables. We start our analysis considering only the radial coordinate.

As ℓ is a scaling factor, we chose $\ell^c \rho_0 = 1$, therefore leading to $\ell = \rho_0^{-1/c}$. By substituting this expression in equation $\rho(\rho, \tau)$ we end up with

$$\rho(\rho_0, \tau) = \rho_0^{-1/c} \rho(1, \rho_0^{-d/c} \tau). \tag{17}$$

We assume $\rho(1, \rho_0^{-d/c} \tau)$ as a constant for $\tau \ll \tau_x$. Comparing equation $\rho(\rho, \tau)$ with the first scaling hypothesis, we conclude that $\alpha_\rho = -1/c$.

We now choose $\ell^c \rho_0 = 1$, yielding $\ell = \tau^{-1/c}$. Substituting in equation $\rho(\rho, \tau)$, we obtain for $\tau \gg \tau_x$ that

$$\rho(\rho_0, \tau) \propto \tau^{-1/d}. \quad (18)$$

A direct comparison of this result with the second scaling hypothesis gives $\beta_\rho = -1/d$. Finally, by comparing the two expressions obtained for the scaling factor ℓ , we arrive at $\tau_x = \rho_0^{\alpha_\rho/\beta_\rho}$. A comparison with the third scaling hypothesis allows us to obtain the following scaling law:

$$z_\rho = \frac{\alpha_\rho}{\beta_\rho}. \quad (19)$$

The knowledge of any two exponents allows determining the third one by substituting equation (19). The scaling hypotheses for the angular coordinate lead to the same scaling, as described in [22]; therefore, we obtain $z_\phi = \alpha_\phi/\beta_\phi$.

Following the procedures already described [22], the analysis obtained from the numerical simulations of ρ has shown the characteristic exponents $\alpha_\rho = 1.00(0)$, $\beta_\rho = -0.499(3)$. Evaluating equation (19) for exponents α_ρ and β_ρ , we obtain $z_\rho = -2.002(8)$. The analysis for ϕ has shown $\alpha_\phi = 1.00(0)$, $\beta_\phi = -0.499(3)$ and $z_\phi = -2.003(6)$.

Once we have discussed the convergence to the steady state at the bifurcation point, we now discuss the dynamics for $\alpha(b) \neq 0$, which characterizes the neighborhood of a Hopf bifurcation. The convergence to the steady state is $\alpha(b)$ marked by an exponential law of the type

$$\rho(\tau) - \rho^* \simeq (\rho_0 - \rho^*)e^{-\tau/\epsilon}, \quad (20)$$

where ϵ is the relaxation time described by

$$\epsilon \propto \alpha(b)^\delta, \quad (21)$$

where δ is a relaxation exponent. Figure 3 shows the behavior of ϵ versus $\alpha(b)$. A power-law fitting gives $\delta = -0.969(9) \simeq -1$.

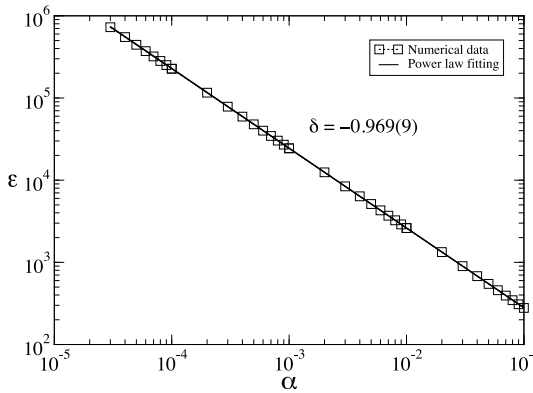


Figure 3. Plot of the behavior of relaxation time ϵ against $\alpha(\sigma)$. A power-law fitting furnishes $\delta = -0.969(9) \approx -1$.

4. Analytical Approach to the Steady State

Our main goal in this section is to investigate the scaling properties observed in the convergence to steady state at the Hopf bifurcation that characterizes the prey-predator dynamical system. Before the bifurcation, the dynamics converge to a fixed point that is asymptotic stable. However, at the bifurcation point, the fixed point loses stability, and after the bifurcation it reveals the dynamics, which converge to a closed orbit in a plane, that is, a limit cycle of period 1. Because the attractor is a closed cycle in a plane, the use of polar coordinates is the better approach to describe the dynamics and hence investigate the scaling properties as well as the critical exponents for the Hopf bifurcation.

We start by considering the evolution toward the fixed point at the bifurcation point, that is, at $\alpha = 0$. The differential equation is written as

$$\frac{d\rho}{d\tau} = -\rho^3. \tag{22}$$

A straightforward integration gives

$$\rho(\tau) = \frac{\rho_0}{\sqrt{1 + 2\tau\rho_0^2}}. \tag{23}$$

Let us now discuss the implications of equation (23) for specific ranges of τ . For sufficiently short time, we realize that $\rho(\tau) \propto \rho_0$. Since this is a constant for short time, the exponent α_ρ obtained from the

hypothesis $\rho(\tau) \propto \rho_0^{\alpha\rho}$, we end up with the conclusion of $\alpha_\rho = 1$. However, for sufficiently long times we have

$$\rho(\tau) \propto \tau^{-1/2}. \quad (24)$$

The hypothesis for long time is that $\rho(\tau) \propto \tau^{\beta\rho}$; therefore, we conclude that $\beta_\rho = -1/2$. From the scaling law $z_\rho = \alpha_\rho/\beta_\rho$, we obtain that $z_\rho = -2$.

We then discuss the case $\alpha \neq 0$, considering the convergence to the steady state at the neighborhood of a Hopf bifurcation. Near a bifurcation, the convergence to the steady state is described by an empirical function of the type $\rho(\tau) - \rho^* = (\rho_0 - \rho^*)e^{-\tau/\epsilon}$, where ρ^* is the value of ρ at the equilibrium, ρ_0 is the initial condition for ρ at $\tau = 0$, $\epsilon \propto \alpha^\delta$, where τ is the relaxation time with α denoting the distance from the bifurcation measured in the control parameter, and δ is the critical exponents driving the speed of convergence to the steady state. We then have to solve the following differential equation:

$$\frac{d\rho}{d\tau} = \alpha\rho - \rho^3.$$

A direct integration gives

$$\rho(\tau) - \sqrt{\alpha} \simeq \frac{\sqrt{\alpha}}{2} e^{-2\alpha\tau}. \quad (25)$$

This result furnishes the relaxation exponent $\delta = -1$.

A next step is to investigate the angular bifurcation function. We consider first the case of $\alpha = 0$. The differential equation, when incorporated with the solution of $\rho(\tau)$, is written as

$$\frac{d\phi}{d\tau} = \beta + \frac{\rho_0^2}{1 + 2\tau\rho_0^2}.$$

After integration we obtain the following:

$$\phi(\tau) = \phi_0 + \beta\tau + \frac{1}{2}\ln(1 + 2\tau\rho_0^2). \quad (26)$$

Let us now discuss the implications of equation (26) for specific ranges of τ . Considering the case where

$$\beta\tau + \frac{1}{2}\ln(1 + 2\tau\rho_0^2) \ll \phi_0,$$

we realize that $\phi(\tau) \propto \phi_0$, leading to $\alpha_\phi = 1$. However, in the case

$$\beta\tau \gg \phi_0 + \frac{1}{2}\ln(1 + 2\tau\rho_0^2),$$

we obtain $\phi(\tau) \propto \tau$, giving $\beta_\phi = 1$. The last case is obtained when

$$\beta\tau = \phi_0 + \frac{1}{2}\ln(1 + 2\tau\rho_0^2) \cong \phi_0,$$

which gives $z_\phi = 1$.

Therefore, the results obtained by the phenomenological approach are confirmed by the direct solution of the differential equations that govern the dynamics.

5. Conclusions

Scaling laws and critical exponents are derived from the investigation of an idealized model for the prey-predator dynamical system. The relative simplicity of the model and the ability to generate a large variety of nonlinear behaviors motivate the choice of the system. In this work, a critical step in the scaling investigation is the representation of the dynamics in the normal form.

The convergence to the steady state was conducted by two different approaches: (i) phenomenological, where scaling hypotheses lead to homogenous functions with critical exponents related by scaling laws; and (ii) analytical, through the direct solution of the differential equations, which is only possible in the normal form.

The scaling properties, as well as the scaling exponents, define a class of universality within which these results should also be valid for other multidimensional systems that exhibit Hopf bifurcation.

Given the importance of the results obtained, it is important to mention that the scaling properties for Hopf bifurcation as well as the scaling properties for other bifurcations, in general, give an alternative form to investigate and classify the type of bifurcation in dynamical systems, for example, electrical circuits, when the set of equations describing the dynamics is not all known.

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