lousov (1959); Zhabotinsky (1991)], that constitute two milestones of nonlinear dynamics theory.

Mathematical biology is a branch of applied mathematics which studies the changes in the composition of populations. Historically its origins can be traced back to the demographic analysis by Malthus and Verlhust (Sec. 3.1), but, during the years, the development of mathematical biology has greatly expanded till embodying ecology, genetics and immunology. In population biology, we are generally interested in the time variation of the number of individuals of certain species. Species compete, evolve and disperse to seek resources for sustaining their struggle for the existence. Depending on the specific environment and settings, often the interplay among individuals involves a sort of loss-win mechanisms that can be exemplified to the form of predator-prey interactions. In this context, the role of chaos is still a controversial issue, and the common wisdom suggests that a chaotic behavior is the exceptional event rather than a rule. The typical "incorrect" argument raised is the stability of systems that would make chaos improbable. Accordingly, populations are expected to undergo cyclical fluctuations mostly triggered by living cycles, seasonal or climate changes. On the other hand, the alternative line of reasoning recognizes in the extreme variability and in the poor long-term predictability of several complex biological phenomena a fingerprint of nonlinear laws characterized by sensitive dependence on initial conditions.

In Chemistry, where the rate equations have the same structure of those of population dynamics, we have a similar phenomenology with the concentration of reagents involved in chemical reactions in place of the individuals. Rate equations, written on the basis of the elementary chemical rules, can generate very complex behaviors in spite of their simplicity as shown in the sequel with the example of the Belousov-Zhabotinsky reaction [Zhabotinsky (1991)]. We stress that in all of the examples discussed in this section we assume spatial homogeneity, this entails that the phenomena we consider can be represented by ODE of the state variables, the role of inhomogeneity will be postponed to the next Chapter.

11.3.1 *Population biology: Lotka-Volterra systems*

Species sharing the same ecosystem are typically in strong interaction. At a raw level of details, the effects exerted by a species on another can be re-conducted to three main possibilities: *predation*, *competition* or *cooperation* also termed mutualism. In the former two cases, a species subtracts individuals or resources to another one, whose population tends to decrease. In the latter, two or more species take mutual benefit from the respective existence and the interaction promotes their simultaneous growth. These simple principles define systems whose evolution in general is supposed to reach stationary or periodic states. Lotka-Volterra equations, also known as *predator-prey system*, are historically one of the first attempt to construct a mathematical theory of a simple biological phenomena. They consist

in a pair of nonlinear ODE describing the interactions of two species, one acting as predator and the other as prey. Possible realistic examples of predator-prey systems are: resource-consumer, plant-herbivore, parasite-host, tumor cells (virus)-immune system, susceptible-infectious interactions, etc. These equations were proposed independently by Lotka (1910) and Volterra (1926b,a)[43]

$$\frac{\mathrm{d}x}{\mathrm{d}t} = r_1 x - \gamma_1 xy \tag{11.22}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -r_2 y + \gamma_2 xy \tag{11.23}$$

where x is the number of some prey (say, rabbits); y is the number of predators (wolves); r_1, γ_1, r_2 and γ_2 are positive parameters embodying the interaction between the two species. The assumptions of LV-model are the following. In the absence of predators, prey-population grows indefinitely at rate r_1. Thus, in principle, preys have infinite food resources at disposal and the only limitation to their increment stems from predation represented by the term $-\gamma_1 xy$. The fate of predators in absence of preys is "extinction" at rate r_2, condition prevented by the positive term $\gamma_2 xy$, describing hunting.

The dynamics of the model is rather simple and can be discussed conveniently by looking at the phase portrait. There are two fixed points $P_0 = (0,0)$ and $P_1 = (r_2/\gamma_2, r_1/\gamma_1)$, the first corresponds to extinction of both species while the second refers to an equilibrium characterized by constant populations. Linear stability matrices (Sec. 2.4) computed at the two points are

$$\mathbb{L}_0 = \begin{pmatrix} r_1 & 0 \\ 0 & -r_2 \end{pmatrix} \qquad \text{and} \qquad \mathbb{L}_1 = \begin{pmatrix} 0 & -r_2 \frac{\gamma_1}{\gamma_2} \\ r_1 \frac{\gamma_2}{\gamma_1} & 0 \end{pmatrix}.$$

Therefore P_0 admits eigenvalues $\lambda_1 = r_1$ and $\lambda_2 = -r_2$, hence is a saddle, while P_1 has pure imaginary eigenvalues $\lambda_{1,2} = \pm\sqrt{r_1 r_2}$. In the small oscillation approximation around the fixed point P_1, one can easily check that the solutions of linearized LV-equations (11.22)-(11.23) evolve with a period $T = 2\pi/\sqrt{r_1 r_2}$. An important property of LV-model is the existence of the integral of motion,

$$H(x, y) = r_2 \ln x + r_1 \ln y - \gamma_2 x - \gamma_1 y, \tag{11.24}$$

as a consequence, the system exhibits periodic orbits coinciding with isolines of the functions $H(x, y) = H_0$ (Fig. 11.13a), where the value of H_0 is fixed by the initial

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[43] Volterra formulated the problem stimulated by the observation of his son in law, the Italian biologist D'Ancona, who discovered a puzzling fact. During the first World War, the Adriatic sea was a dangerous place, so that large-scale fishing effectively stopped. Upon studying the statistics of the fish markets, D'Ancona noticed that the proportion of predators was higher during the war than in the years before and after. The same equations were also derived independently by Lotka (1910) some years before as a possible model for oscillating chemical reactions.

conditions $x(0) = x_0$ and $y(0) = y_0$.[44] Therefore, as shown in Fig. 11.13b, the time evolution consists of cyclic fluctuations of the two populations, for which predator population follows the variation of the preys with a certain dephasing, known as the *law of periodic fluctuations*. The biological origin of oscillations is clear: abundance of hunters implies large killing of preys, that, on the long term, means shortage of food for predators thus their decline. This decrease, in turn, causes the increase of preys and so on, in cyclical alternates.

Another interesting property of LV-model concerns the average over a cycle of number of prey/predator populations that, independently of initial conditions, reads

$$\langle x \rangle = r_2/\gamma_2, \qquad \langle y \rangle = r_1/\gamma_1 . \tag{11.25}$$

This result, known as *law of averages*, can be derived writing, e.g., Eq. (11.22) in logarithmic form and averaging it on a period T

$$\frac{\mathrm{d}\ln x}{\mathrm{d}t} = r_1 - \gamma_1 y \qquad \frac{1}{T}\int_0^T \mathrm{d}t\, \frac{\mathrm{d}\ln x}{\mathrm{d}t} = r_1 - \gamma_1 \langle y \rangle .$$

The periodicity of $x(t)$ makes the left hand side vanishing and thus $\langle y \rangle = r_1/\gamma_1$. The law of averages has the paradoxical consequence that, if the birth rate of preys decreases $r_1 \to r_1 - \epsilon_1$ and, simultaneously, the predator extinction rate increases $r_2 \to r_2 + \epsilon_2$, the average populations vary as $\langle x \rangle \to \langle x \rangle + \epsilon_2/\gamma_2$ and $\langle y \rangle \to \langle y \rangle - \epsilon_1/\gamma_1$, respectively (*law of perturbations of the averages*). This property, also referred to as *Volterra's paradox*, implies that a simultaneous changes of the rates, which causes a partial extinction of both species, favors on average the preys. In other words, if the individuals of the two species are removed from the system by an external action, the average of preys tends to increase. Even though this model is usually considered inadequate for representing realistic ecosystems because too qualitative, it remains one of the simplest example of a pair of nonlinear ODE sustaining cyclical fluctuations. For this reason, it is often taken as an elementary building block when modeling more complex food-webs.

The main criticism that can be raised to LV-model is its structural instability due to the presence of a conservation law $H(x, y) = H_0$ conferring the system an Hamiltonian character. A generic perturbation, destroying the integral of motion where orbits lie, changes dramatically LV-behavior. Several variants have been proposed to generalize LV-model to realistic biological situations, and can be expressed as

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= F(x, y)x \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= G(x, y)y \,, \end{aligned} \tag{11.26}$$

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[44]The existence of integral of motion H can be shown by writing the Eqs. (11.22,11.23) in a Hamiltonian form through the change of variables $\xi = \ln x, \eta = \ln y$

$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = r_1 - \gamma_1 \mathrm{e}^\eta = \frac{\partial \mathcal{H}}{\partial \eta} \qquad \frac{\mathrm{d}\eta}{\mathrm{d}t} = -r_2 + \gamma_2 \mathrm{e}^\xi = -\frac{\partial \mathcal{H}}{\partial \xi} ,$$

where the conserved Hamiltonian reads $\mathcal{H}(\xi, \eta) = r_2\xi - \gamma_2 \mathrm{e}^\xi + r_1\eta - \gamma_1 \mathrm{e}^\eta$, that in terms of original variables x, y gives the constant $H(x, y)$.
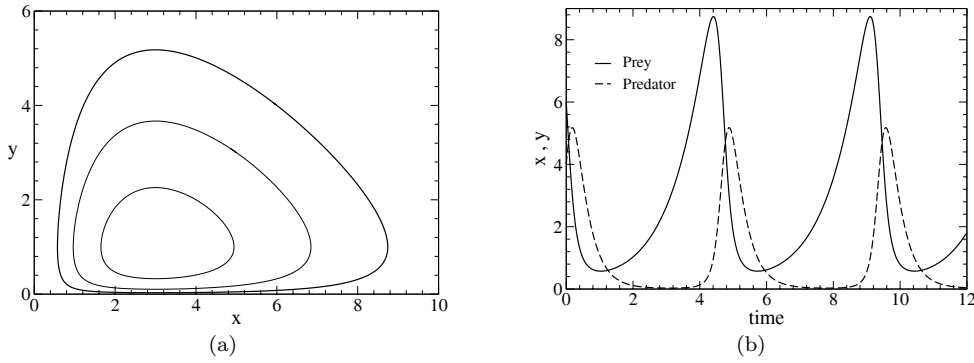
Fig. 11.13 (a) Phase-space portrait of LV-system described by the isolines of $H(x, y)$ (11.24). (b) Oscillating behavior in prey-predator populations of LV-equation for $r_1 = 1.0$, $r_2 = 3.0$, $\gamma_{1,2} = 1.0$.

where G and F are the rates at which prey/predator populations change. Following Verhulst, the first improvement can be introduced by considering a logistic growth (Sec. 3.1) of preys in absence of hunting:

$$F(x, y) = r_1 \left(1 - \frac{x}{K}\right) - \gamma_1 y$$

where K represents the *carrying capacity*: the maximal number of individuals an environment can support. More in general, the hunting rate, γ_1, is supposed to contain a saturation effect in predation term, with respect to the standard LV-model. As typical choices of $\gamma_1(x)$, we can mention [Holling (1965)],

$$\frac{a}{b + x}, \qquad \frac{ax}{b^2 + x^2}, \qquad \frac{a[1 - \exp(-bx)]}{x} \ ,$$

that when plugged into Eq. (11.26)) make the rate bounded. Also the rate $G(x, y)$ is certainly amenable to more realistic generalizations by preferring, e.g., a logistic growth to the simple form of Eq. (11.23). In this context, it is worth mentioning *Kolmogorov's predator-prey model*. Kolmogorov (1936) argued that the term $\gamma_2 xy$ is too simplistic, as it implies that the growth rate of predators can increase indefinitely with prey abundance, while it should saturate to the maximum reproductive rate of predators. Accordingly, he suggested the modified model

$$\frac{dx}{dt} = r(x)x - \gamma(x)y$$
$$\frac{dy}{dt} = q(x)y$$

where $r(x)$, $\gamma(x)$ and $q(x)$ are suitable functions of the prey abundance and predators are naturally "slaved" to preys. He made no specific hypothesis on the functional form of $r(x)$, $\gamma(x)$ and $q(x)$ requiring only that:

(a) In the absence of predators, the birth rate of preys $r(x)$ decreases when the population increases, becoming at a certain point negative. This means that a sort of inter-specific competition among preys is taken into account.

(b) The birth rate of predators $q(x)$ increases with prey population, going from negative (food shortage) to positive (food abundance).

(c) The function $\gamma(x)$ is such that: $\gamma(0) = 0$ and $\gamma(x) > 0$ for $x > 0$.

With these three conditions, Kolmogorov obtained a complete phase diagram, showing that a two-species predator-prey competition may lead to, extinction of predators, stable coexistence of preys and predators or, finally, oscillating cycles. He also generalized the differential equation to more than two species,[45] introducing most of the classification nowadays used in population dynamics. Moreover, Kolmogorov pointed to the strong character of the assumptions behind an approach based on differential equations. In particular, he argued that populations are composed of individuals and statistical fluctuations may not be negligible, especially for small populations. In practice, there exists a fourth scenario: at the minimum of a large oscillation, fluctuations can extinguish the prey population, thereby causing the extinction of predators too. In this remark Kolmogorov underscored the importance of discreteness in population dynamics becoming the precursor of what nowadays is termed "agent based formulation" of population biology, where individuals are "particles" of the system interacting with other individuals via effective couplings. An interesting discussion on this subject can be found in Durrett and Levin (1994).

11.3.2 *Chaos in generalized Lotka-Volterra systems*

According to Poincaré-Bendixon theorem (Sec. 2.3), the original Lotka-Volterra model and its two-dimensional autonomous variants as well cannot sustain chaotic behaviors. To observe chaos, it is necessary to increase the number of interacting species to $N \geq 3$. Searching for multispecies models generating complex behaviors is a necessary step to take into account the wealth of phenomenology commonly observed in Nature, which cannot be reduced to a simple 2-species context. However, the increase of N in LV-models does not necessarily imply chaos, therefore it is natural to wonder "under which conditions do LV-models entail structurally stable chaotic attractors?". Answering such a question is a piece of rigorous mathematics applied to population biology that we cannot fully detail in this book. We limit to mention the contribution by Smale (1976), who formulated the following theorem on a system with N competing populations x_i

$$\frac{dx_i}{dt} = x_i M_i(x_1, \ldots, x_N) \qquad i = 1, \ldots, N .$$

He proved that the above ODE, with $N \geq 5$, can exhibit any asymptotic behavior, including chaos, under the following conditions on the functions $M_i(\boldsymbol{x})$: 1) $M_i(\boldsymbol{x})$ is infinitely differentiable; 2) for all pairs i and j, $\partial M_i(\boldsymbol{x})/\partial x_j < 0$, meaning that only species with positive intrinsic rate $M_i(0)$ can survive; 3) there exist a constant C such that, for $|\boldsymbol{x}| > C$ then $M_i(\boldsymbol{x}) < 0$ for all i. The latter constraint corresponds

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[45]See for instance Murray (2002); the generalized version is sometimes referred to as *Kolmogorov model*.