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AN EXACTLY SOLUBLE KOLMOGOROV MODEL FOR TWO INTERACTING SPECIES

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Abstract

We present an exactly soluble predator-prey model for two species interacting according to a non-linear Kolmogorov-type of equation. We obtain simple analytical expressions for *i*) the parametric equations of the cycles, *ii*) the cycles in the phase space, *iii*) the Hamiltonian and the corresponding integrating factor, showing that the dynamics is globally conservative. In a second part, we propose a general method to construct similar classes of population models. As a particular example we derive the evolution equation describing the time dependent behavior of a two-players, two-strategies asymmetric game.

Keywords: Population dynamics; Exactly solvable predator-prey model; Asymmetric games; Canonical-dissipative system

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1. Introduction and main result

Two-species predator-prey systems with population size dependent per capita growth rates are generically described by a system of ODEs of the Kolmogorov type [2]:

$$\dot{u}(t) := \frac{d}{dt}u(t) = u(t)f\big(u(t), v(t)\big) \tag{1}$$

$$\dot{v}(t) := \frac{d}{dt}v(t) = v(t)g\big(u(t), v(t)\big), \tag{2}$$

verifying

$$f_v(u, v) > 0 \qquad and \qquad g_u(u, v) < 0 \tag{3}$$

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and where $u(t) > 0$ and $v(t) > 0$ stand for the population sizes (or concentrations) of the predators respectively the prey. The Lotka-Volterra (L-V) model which obviously is the most famous illustration of this class is obtained when:

$$f(u, v) = -k_1 + v \qquad \text{and} \qquad g(u, v) = k_2 - u \tag{4}$$

with $k_1 > 0$ and $k_2 > 0$ being two real constants respectively denoting the spontaneous birth and death rates of the predators and the prey. Even for an elementary evolution such as the one given by the L-V model, the explicit time dependent form of trajectories $u(t)$ and $v(t)$ solving the system (1-1) is very hard to write analytically. It is the aim of the present note to expose a simple, though intrinsically non-linear Kolmogorov-type model, for which $u(t)$ and $v(t)$ are expressible in terms of elementary (trigonometric) functions. To the best of our knowledge, this is so far the only nonlinear Kolmogorov-type predator-prey model for which the trajectories are explicitly available. We can summarize our main result in the following

Proposition 1. *For* $(u_0, v_0) \in \Omega := (\frac{1}{2} - \frac{1}{2\sqrt{2}}, \frac{1}{2} + \frac{1}{2\sqrt{2}}) \times (0, 1)$*, the system:*

$$\begin{aligned} \dot{u}(t) &= u(t)\big(1 - u(t)\big)\big(2v(t) - 1\big), & (5)\\ \dot{v}(t) &= v(t)\big(1 - v(t)\big)\big(1 - 2u(t)\big)\Big(2 + \frac{1}{\sqrt{v(t)\,(1 - v(t))}}\Big) & (6)\end{aligned}$$

admits the solution:

$$u(t) = \frac{1}{2} - \frac{A \sin\Big(\frac{t}{\sqrt{1+A^2}} + \phi\Big)}{2\sqrt{1 + A^2}}, \tag{7}$$

$$v(t) = \frac{1}{2} - \frac{A \cos\Big(\frac{t}{\sqrt{1+A^2}} + \phi\Big)}{1 + A^2 \cos\Big(\frac{t}{\sqrt{1+A^2}} + \phi\Big)^2}, \tag{8}$$

where $A \in (0, 1)$ *and* $\phi \in (0, 2\pi)$ *are determined by the initial conditions* $u(0) = u_0$ *and* $v(0) = v_0$*. Moreover the function* H *defined by*

$$H(u, v) = \frac{1 - 2\sqrt{v(1 - v)}}{2u(1 - u)(1 - 2v)^2}, \tag{9}$$

is constant and equals $1 + A^2$ *along the orbits* $\big(u(t), v(t)\big)$ *(i.e.* H *is a constant of motion).*

Note that the per capita growth rates $\dot{u}/u = f(u, v)$ and $\dot{v}/v = g(u, v)$ of the proposed system verify the conditions expressed in eq. (3) which enable to interpret (5-6) as a predator-prey model. The time dependent solutions eqs.(7) and (8) and the resulting cycles in the $u - v$ phase plane are sketched in Fig.1 respectively Fig.2 for several initial conditions.

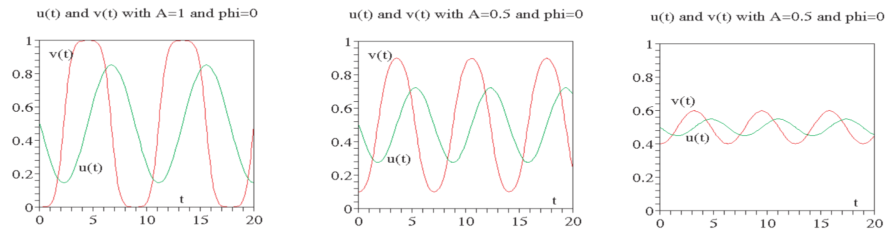

FIGURE 1: Sketch of the solutions $u(t)$ and $v(t)$ of the predator-prey system eqs. (5-6) with $\phi = 0$ and $A = 0.99$, 0.5 and 0.1.

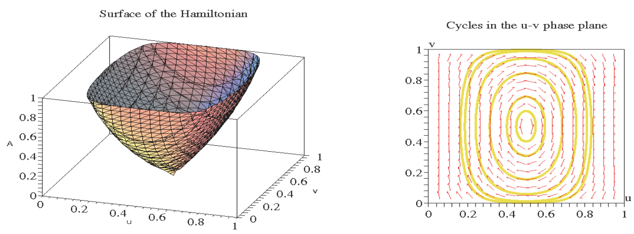

FIGURE 2: Left: Sketch of the Hamiltonian surface $H(u, v) = A$ for $0 < A < 1$. Right: Phase portrait of the eqs. (5-6) with different orbits defined by $A = 0.1; 0.2; 0.4; 0.6; 0.8$ and 0.9. They periodically wind around the rest point $(\frac{1}{2}, \frac{1}{2})$ in a clockwise rotation.

Construction of the model and remarks

Construction. The proposition is proved by straightforward computation. More instructive is the construction of the model. We start with the equation for the explicitly solvable, non-linear harmonic oscillator introduced in [5]:

$$\dot{x} = y, \tag{10}$$

$$\dot{y} = -(1 - y^2)\frac{x}{1 + x^2}. \tag{11}$$

The above system admits the harmonic solution

$$x(t) = A\sin(\omega(A)t + \phi) \tag{12}$$

with $\omega(A) = \frac{1}{\sqrt{1+A^2}}$ the initial condition dependent frequency and with ϕ the initial phase. Introducing the transformation $\dot{x} = y = \tanh(z)$ which confines $\dot{x}$ into the interval $[-1, 1]$ and writing

$$V'(x) = \frac{d}{dx}V(x) \quad := \quad \frac{x}{1+x^2}, \quad \textit{with } V(x) = \frac{1}{2}\ln(1+x^2), \tag{13}$$

$$\mathcal{H}(x,z) \quad := \quad \ln\big(\cosh(z)\big) + V(x), \tag{14}$$

eqs. (10-11) transform into the Hamiltonian system

$$\dot{x} = \tanh(z) \quad = \quad \frac{\partial\mathcal{H}(x,z)}{\partial_z}, \tag{15}$$

$$\dot{z} = -V'(x) \quad = \quad -\frac{\partial\mathcal{H}(x,z)}{\partial_x}. \tag{16}$$

The crucial observation is now that besides $\dot{x}$, the variable $\dot{z}$ is also confined into a bounded interval. We indeed have $\dot{z} \in [\inf_x V'(x), \sup_x V'(x)] = [-\frac{1}{2}, \frac{1}{2}]$. This allows to interpret the evolution equations for these bounded quantities in population dynamical terms. Deriving the above system we find the evolution equations for $\dot{x}$ and $\dot{z}$:

$$\ddot{x} \quad = \quad (1-\dot{x}^2)\dot{z} \tag{17}$$

$$\ddot{z} \quad = \quad -\dot{x}V''\big(V'^{-1}(-\dot{z})\big) = -\frac{1}{2}\dot{x}(1-4\dot{z}^2)\big(1+\frac{1}{\sqrt{1-4\dot{z}^2}}\big). \tag{18}$$

Shifting the orbits $t \mapsto (\dot{x}(t), \dot{z}(t))$ into Ω by introducing the new variables

$$u = \frac{\dot{x}+1}{2}, \quad \textit{and } v = \dot{z} + \frac{1}{2}, \tag{19}$$

we find that in these variables, the eqs. (17) and (18) reduce to the predator-prey system (5-6).

Remarks. **a)** Using the constant of motion H expressed in eq. (9), the system (5-6) can be rewritten as

$$\dot{u}(t) \quad = \quad \phi(u,v)\frac{\partial H(u,v)}{\partial_v} =: F(u,v) \tag{20}$$

$$\dot{v}(t) \quad = \quad -\phi(u,v)\frac{\partial H(u,v)}{\partial_u} =: G(u,v) \tag{21}$$

where the strictly positive function

$$\phi(u,v) = \frac{2\big[(1-2v)^2 u(1-u)\big]^2 \sqrt{v(1-v)}}{(1-2\sqrt{v(1-v)})^2}, \tag{22}$$

acts as a velocity change for the trajectories. The function ϕ plays the role of an integrating factor and verifies

$$\frac{\partial}{\partial_u}\Big(\frac{F(u,v)}{\phi(u,v)}\Big) + \frac{\partial}{\partial_v}\Big(\frac{G(u,v)}{\phi(u,v)}\Big) = 0, \tag{23}$$

where $F(u,v)$ and $G(u,v)$ are defined in eqs. (20) and (21). The orbits of the system (20-21) therefore coincide with the integration curves of the Hamiltonian system

$$\dot{x}(t) = \frac{\partial H(x,y)}{\partial_y}, \tag{24}$$

$$\dot{y}(t) = -\frac{\partial H(x,y)}{\partial_x}. \tag{25}$$

b) Applying the canonical-dissipative extension of Hamiltonian systems to the eqs. (24) and (25) we can generate limit cycles to our initially conservative system (see e.g., [1, 4, 6]). Here the term "dissipative" is to be understood in the large sense (i.e. with alternating positive and negative nonconservative contributions cancelling over a complete cycle) and "canonical" means that the dissipative and the conservative part of the dynamics are determined by the invariant of motion H. The simplest form for the H-dependent dissipation around a fixed level E is a linear choice $H - E$. Coupling the sign of the dissipation with the dynamics by multiplying with $\dot{v}$ and adding the dissipation to $\dot{u}$, we end up with the most simple canonical-dissipative extension of the system (5-6):

$$\begin{aligned} \dot{x}(t) &= \frac{\partial H(x,y)}{\partial_y} + (H(u,v) - E)\frac{\partial H(x,y)}{\partial_x}, \\ \dot{y}(t) &= -\frac{\partial H(x,y)}{\partial_x}. \end{aligned} \tag{26}$$

The resulting limit cycle for $E = 1.16$ is sketched in figure 3.

c) A generalization to other population dynamics systems with bounded state variables is feasible for a large class of potentials V. The conditions on V are readable in eq. (18) and include – besides the uniform boundedness of V' – the existence of both, the inverse of V' and the second derivative of V. Taking for example

$$V(x) = \ln\big(\cosh(x)\big), \tag{27}$$

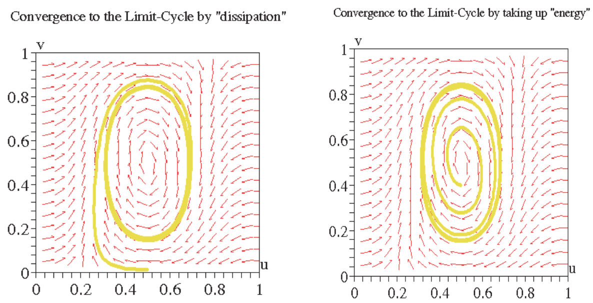

FIGURE 3: Sketch of two orbits in the $x-y$ phase-plane defined by eqs. (24) and (25). The orbits convergence to the limit-cycle constructed by a simple canonical-dissipative extension of the Hamiltonian dynamics eqs. (24) and (25).

these two conditions are satisfied with $V'^{-1}(x) = arc\tanh(x)$ and $V''\big(V'^{-1}(-\dot{z})\big) = 1-\dot{z}^2$. The eqs. (17) and (18) transform into

$$\ddot{x} = (1-\dot{x}^2)\dot{z} \tag{28}$$

$$\ddot{z} = -(1-\dot{z}^2)\dot{x} \tag{29}$$

which, when shifted into $[0,1]^2$ by the transformation

$$u = \frac{\dot{x}+1}{2} \quad and \quad v = \frac{\dot{z}+1}{2}, \tag{30}$$

reduce to the evolution equations

$$\dot{u}(t) = u(t)\,(1-u(t))\,(2v(t)-1)\,, \tag{31}$$

$$\dot{v}(t) = v(t)\,(1-v(t))\,(1-2u(t))\,. \tag{32}$$

It is worthwhile noting that this type of evolution equations is well known in asymmetric games where two players confront their strategies over and over again in order to maximize their payoffs and where $t \mapsto \big(u(t), v(t)\big)$ describes the evolution of the frequencies of the two possible strategies used by the two players (see e.g., [3] Chapt. 10.4).

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