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Kolmogorov and population dynamics

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Translated from the French by Elizabeth Strouse

9.1 Introduction

During his childhood, Andreï Nikolaievitch Kolmogorov found biology very
interesting. In fact, in the book *Kolmogorov in Perspective*, one can read that
he made the following comment about himself as a schoolboy:

*"I was one of the best in my class in mathematics, but my real scientific
passions were, first of all biology, and then russian history"* ([Kol00], p. 5)

He kept these centers of interest for the rest of his life. Thus, in 1940,
Kolmogorov dared to confront the feared Lysenko by defending Mendel's laws
– a very dangerous move to make in the middle of Stalin's regime. And,
according to V. I. Arnold, the last research done by Kolmogorov [KB67],
published in 1967, was motivated by biological ideas about the structure of
the brain ([Kol00], p. 94).

In fact, Kolmogorov made only a few isolated contributions to biomath-
ematics; but they all demonstrate, as one would expect, a remarkable origi-
nality. In particular, the short note [Kol36] about the predator-prey equation
is a model of perspicacity and has had great influence on the deterministic
theory of population dynamics. It is one of the rare articles that Kolmogorov
published in Italian, doubtlessly in honor of the mathematician Vito Volterra
who inaugurated what would later be called *The Golden Age of biomathemat-
ics* [SZ78]. Kolmogorov's note represents a qualitative jump in the theory of
predator-prey systems.

9.2 From Volterra equations to Gause equations

The beginning point of the study of Kolmogorov discussed here is the famous model that Volterra[1] used, as early as 1925, to explain a surprising discovery of his son in law, the ecologist Umberto D'Ancona [Kin85]. Because of his research in marine biology, based on statistics from fish markets. D'Ancona noticed that during World War 1, the number of predators among Adriatic fauna had increased while the number of prey had diminished. This seemed to be an effect of the reduction of fishing due to the Austro-Italian hostilities: but why did it work in this manner and not in another?

Volterra based his argument on an ordinary differential equation: if $x(t)$ and $y(t)$ are the densities of prey and of predators, respectively, then the rate of increase $\dot{x}/x$ of the prey should be a decreasing function of y, positive for $y = 0$, and the rate of increase $\dot{y}/y$ an increasing function of x, negative for $x = 0$. If we suppose that these functions are linear, we see that

$$\dot{x} = x(a - by) \tag{9.1}$$

$$\dot{y} = y(-c + dx) \tag{9.2}$$

where the constants a, b, c, d are positive. In the positive quadrant, the phase portrait consists of periodic orbits around the equilibrium position $(\bar{x}, \bar{y}) = (c/d, a/b)$. Volterra showed that the temporal averages of $x(t)$ and $y(t)$ along periodic orbits coincide with the values $\bar{x}$ and $\bar{y}$, which gave him a way to explain D'Ancona's observation: in fact, the supplementary contribution due to the fishermen's work diminishes the quantity a (the rate of increase of the prey in the absence of predators) and increases c (the rate of decrease of predators in the absence of prey), without affecting the values of the coefficients b and d, which measure the effects of the interaction between the predators and their prey. The corresponding effect on the temporal averages of the densities of the two populations is just that which D'Ancona observed.

The elegance of Volterra's reasoning stands in clear contrast with the plausibility of his equation. In fact, (9.1)–(9.2) is unstable from many points of view. In particular, the model implies that a prey population, in the absence of predators, would grow exponentially towards infinity. This evident flaw in the (9.1) can be easily corrected, one way is to introduce a self-limiting term for the growth of the prey, reducing the equation, for $y = 0$, to a logistic model $\dot{x} = ax(1 - x/K)$. Georgii Frantsevitch Gause proposed another system of much more general equations ([Gau34], [GSW36]), which, using modern notation, take the following form:

$$\dot{x} = xg(x) - yp(x) \tag{9.3}$$

$$\dot{y} = yq(x) \tag{9.4}$$

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[1] We note that Alfred Lotka introduced the same model, at approximately the same time. independently of Volterra, and in a different context. (Editor's note.)

Here, g describes the rate of increase of prey when the predators are absent: it is a function which is positive on an interval $[0, K]$ and negative for $x > K$ (because, for example, the food resources being limited, the prey are in competition with each other when there are too many of them), and the density of prey thus converges, in the absence of predators, towards the limit K. The functions p and q, which are called the response functions, describe the predator-prey interaction: we suppose that p is a positive function with $p(0) = 0$, while q is strictly increasing for $x > 0$, has a negative limit when x decreases to 0, and a positive limit when x increases to $+\infty$ (an abundance of prey). These equations are much more reasonable and more flexible than (9.1)-(9.2).

9.3 The Kolmogorov equations

Kolmogorov did not mention these equations in his note [Kol36], even though he must have known about the work of Gause -- who also lived in Moscow in the thirties and, at the age of twenty-two, revolutionized mathematical biology with his book *The Struggle for Existence* [Gau34]. After noticing that, in Volterra's work, there was an arbitrary postulate of linear rates of increase that could not be justified as anything but a first approximation of real rates of increase, Kolmogorov considered the most general case possible

$$\dot{x} = xS(x, y) \tag{9.5}$$

$$\dot{y} = yW(x, y) \tag{9.6}$$

and was led to postulate (assuming that the rates of increase S and W were continuously differentiable) some minimal conditions which are satisfied in any realistic predator-prey interaction.

The first group of conditions requires that, if the number of predators increases, then the rates of increase of the two populations decrease:

$$\frac{\partial S}{\partial y} < 0, \qquad \frac{\partial W}{\partial y} < 0. \tag{9.7}$$

These conditions (the second of which was not satisfied in Volterra's and Gause's models) are, in general, accepted without objection by ecologists (even though, for example, one can imagine predators who only manage to attack their prey when there are enough of them to surround it, which would imply that the second condition is not valid for small values of y). The immediate consequence of the postulate (9.7) is that the two isoclines in the interior of the positive quadrant, $\{(x, y) : \dot{x} = 0\}$ and $\{(x, y) : \dot{y} = 0\}$, can be viewed as the graphs of two functions of x. Their intersections are, evidently, the fixed points of (9.5)--(9.6), which correspond to equilibria of the system with coexistence of the two populations.

The other conditions of [Kol36] describe the behavior of (9.5)–(9.6) on the boundary of the positive quadrant, that is, in the absence of one population or of the other. They imply, more precisely, that the unique equilibrium $(K, 0)$ which is composed of prey but not of predators, can be invaded by predators, so that

$$W(K, 0) > 0. \tag{9.8}$$

This implies that there is at least one equilibrium with coexistence of the two species.

What is still missing is a condition to guarantee that there is only one such equilibrium, that is, a unique point in the intersection of the two isoclines in the interior of the first quadrant. This would be a simple consequence of a condition analogous to (9.7):

$$\frac{\partial S}{\partial x} < 0, \qquad \frac{\partial W}{\partial x} > 0. \tag{9.9}$$

Kolmogorov noticed that the validity of this condition is not clear if x, the number of prey, is small. Today, all ecologists are familiar with the Allee effect, which is the fact that the rate of increase (of a prey population for example) can decrease and even become negative if the density of the population is sufficiently small. Kolmogorov, who could not yet know of this effect, seems to have suspected that there was such a mechanism, even though the argument he gave, invoking the presence of a large number of predators, does not seem very clear. According to a note on the bottom of a page, as long as the density x of the prey is small, the probability of survival of the prey would be an increasing function of x (maybe because the predators have eaten their fill, while the competition effect within the prey species can not yet be felt). Having understood that (9.9) is not necessarily valid, Kolmogorov introduced another condition, that S decrease and W increase along rays starting at the origin. This is therefore a condition concerning directional derivatives. Today this condition is often written in the form

$$x\frac{\partial S}{\partial x} + y\frac{\partial S}{\partial y} < 0, \qquad x\frac{\partial W}{\partial x} + y\frac{\partial W}{\partial y} > 0. \tag{9.10}$$

Imagine, indeed, that a large habitat become smaller because of some external force. In this case the densities x and y increase while the ratio between them stays constant. The individuals would be obliged to get closer to each other, the predators would have less distance to travel to find their meal, and each prey would be tracked by more predators. Thus, the predators would have the benefit of the new circumstances, while the prey would suffer from them.

The condition (9.10) implies that there is only one equilibrium $\mathbf{Z}$ in the interior of the positive quadrant, and that it is divided by the isoclines (which intersect in $\mathbf{Z}$) into four regions depending on the signs of $\dot{x}$ and of $\dot{y}$.

The rest of the reasoning is surprisingly simple. The equilibrium with only the prey population present, which is given by $\mathbf{B} = (K, 0)$, is necessarily made

up of a saddle point, and the two orbits which converge there are situated on the x-axis. Thus the positive quadrant contains a unique orbit having $\mathbf{B}$ as α-limit, that is, such that $\lim x(t) = K$ and $\lim y(t) = 0$ for $t \to -\infty$. This orbit stays in a compact domain, and thus must have a non-empty ω-limit[2]. If this ω-limit contains a fixed point, it must be $\mathbf{Z}$. In this case, it is easy to see that all the orbits, in the interior of the positive quadrant, converge to $\mathbf{Z}$. If this is not the case, the theorem of Poincaré-Bendixson implies that the ω-limit is a limit cycle around $\mathbf{Z}$. In this case, all the orbits in the positive quadrant which are in the exterior of this cycle converge to it.

9.4 Technical aspects

Kolmogorov, who didn't like to dwell upon technical details, gave only a rough sketch of his idea. Actually, what he wrote was not totally correct. In fact, there is an obvious contradiction between the two parts of conditions (9.7) and (9.10), as can be easily seen by setting $x = 0$ and considering $y > 0$. This error is not, however, very serious and is easy to correct. For example, in [AGW73] and [AGHW74], it is shown that it suffices to assume that (9.7) and (9.10) are valid in the interior of the positive quadrant and to specify the behavior of S and W along the axes. The same type of proof, with all possible details, can be found in [Fre75] and [Fre80]. Kolmogorov didn't feel the need to give the details of his argument as his milieu was extremely well informed about the methods for studying ordinary non-linear differential equations in two dimensions, and in particular conversant with results that had just been obtained by mathematicians and engineers in the Soviet Union such as Pontryagin, Andronov, Krylov, Bogoliubov, Moiseev and Bautin (see for example [ALGM73]). We remark that in 1939 Moiseev showed that, if the functions S and W are affine then an equation of type (9.5)-(9.6) never admits a limit cycle.

The equations of Volterra (9.1)-(9.2) and of Gause (9.3)-(9.4) are not particular cases of Kolmogorov's equation because neither (9.2) nor (9.4) satisfy the second condition of (9.7): the isocline in both cases is vertical. But the conclusion stays the same. This is also the case for the so-called equation of Holling-Tanner

$$\dot{x} = xr(1 - \frac{x}{K}) - yp(x) \tag{9.11}$$

$$\dot{y} = ys(1 - \frac{hy}{x}) \tag{9.12}$$

(with the constants r, s, h and K positive and the response function p as in (9.3)). Here the growth of prey (without predators) is logistic with a constant

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[2] The ω-limit of the orbit $(x(t), y(t))$ is the set of all points $(\hat{x}, \hat{y})$ such that $\hat{x} = \lim x(t_k)$ and $\hat{y} = \lim y(t_k)$ for a subsequence $t_k \to +\infty$

capacity, and the growth of predators is logistic with a capacity proportional with x. This model seems to be designed to describe real cases of the predator-prey systems, when one has made a suitable choice of the response function p.

Kolmogorov makes clear that his reasoning implies nothing about what happens in the interior of the cycle, but notes that, in the simplest cases, the limit cycle is unique and attracts all the orbits coming from the interior (excepting, of course, equilibrium). Afterwards, a great deal of research was done to find conditions for the global stability of $\mathbf{Z}$, and for the unicity of the limit cycle [Che81], [KF88], [Kua90], [HH95], [GKT97], [Has00]. One often hears the assertion that asymptotic stability of $\mathbf{Z}$ implies its global stability: but this is false, in general (see e.g. [Bul76]).

9.5 The impact

At first the reaction to Kolmogorov's note was rather lukewarm. It was only during the sixties that these results began to be appreciated, mostly because of the appearance at this time of the articles of Rosenzweig and MacArthur [RM63], and of Rescigno and Richardson [RR67]. The detailed study of the explicit form of the response function, in particular that done by Holling [Hol65], also played an important role. It was no longer necessary to convince the ecologists of the reality of non-transitory oscillations in certain systems of predator-prey, or of the robustness of their period and their amplitude. It became evident that models with limit cycles were necessary. Furthermore, by using an elegant criterion proposed by Rosenzweig and MacArthur, one could determine whether the equilibrium $\mathbf{Z}$ of the system (9.3)–(9.4) was locally stable or not. Thus, the emergence of Hopf bifurcation became easy to verify. Sometime around 1972 there was a real stampede toward limit cycles due to three articles in *Science* written by Rosenzweig, Gilpin and May, respectively ([May72], [Gil72], [Ros72]). In particular, the book of May [May73] spread Kolmogorov's message among ecologists, and showed that the linear analysis of an equilibrium does not always allow one to make conclusions about the global behavior of the system.

For his own reasons, Kolmogorov himself came back to his model in a short note written in 1972 ([Kol72]). In particular, he applied his method to the Gause equations (again without citing Gause) and gave a classification of possible phase portraits. These arguments were extended in [Baz74] and [SL78].

We conclude this section with several remarks. From an ecologist's perspective it is less important to know whether a certain equilibrium is stable than to know if the system is permanent, that is, if the species under consideration can survive indefinitely; it is of secondary interest to know if their densities converge or oscillate. The role of this notion of permanence in theoretical analyses of the ecology of populations is increasing [HS98]. The associated notion of stability is more like that of Lagrange than that of Lyapunov: it is

formulated as a condition that the border of the phase space (including points at infinity) be repulsive.

It is interesting to notice, in this context, that Kolmogorov explains in his note [Kol36] that the modelization of the ecological system by a deterministic model is not valid if the populations are very small (that is, if one is close to the border of the phase space). No one was better than Kolmogorov at deducing a differential equation from a stochastic model. The fact that he did not try to do this in the case of a predator-prey interaction suggests that he was conscious of the difficulty of doing so: and it is perhaps because he considered it too difficult to deduce the analytic expression corresponding to the vector field given by (9.5)–(9.6) from a stochastic process modelling the encounters between predators and prey, that he decided to do without, and to instead use the general properties (9.7),(9.8),(9.9) and (9.10).

But, what is of primary importance is the general approach used by Kolmogorov: in particular, today, to give a model of biological communities made up of three or more species one frequently uses equations of the type

$$\dot{x}_i = x_i F_i(x_1, ..., x_n) \tag{9.13}$$

(which are called ecological equations, or, more and more often, Kolmogorov equations) and to specify the system, not by giving precise analytic expressions for the rates of growth F_i, but by setting conditions for the signs of their partial derivatives: for example, competitive communities are described by conditions like

$$\frac{\partial F_i}{\partial x_j} \leq 0 \tag{9.14}$$

for $i \neq j$, etc. Thanks to work by Morris Hirsch, Hal Smith and their collaborators (see [Hir88], [Smi95]), this approach now gives some of the results which are most useful for ecological applications and most interesting from a mathematical point of view. More generally, an ordinary differential equation $\dot{x}_i = f_i(x_1, ..., x_n)$ defines a cooperative system if

$$\frac{\partial f_i}{\partial x_j} \geq 0 \tag{9.15}$$

for $i \neq j$, and a competitive system if the inequalities are reversed. One of the principal results concerning such systems is that the flow, restricted to a compact limit set, is topologically equivalent to a flow defined by a system of lipschitzian differential equations on an invariant compact set of $(n-1)$-dimensional space. In particular, we can use this result to obtain a theorem of Poincaré-Bendixson in three dimensions: a compact limit set for a cooperative or competitive system in $\mathbb{R}^3$ which contains no fixed point is actually a periodic orbit. Zeeman [Zee93] used these results in his attack on the problem of classifying the competitive systems of Lotka-Volterra in three dimensions, thus identifying 33 stable equivalence classes, and Hofbauer, Mallet-Paret and

Smith [HMS91] established the existence of stable periodic orbits for "hyper-cyclic" systems.

A particular case of Kolmogorov equations is the set of ecological equations describing the three-species food chains. Hastings and Powell [HP91] showed that these equations often present a chaotic behavior (see also [KH94] and [MY94]). Muratori and Rinaldi [MR89] as well as Kuznetsov and Rinaldi [KR96] studied Hopf bifurcations in the prey-predator-superpredator systems.

Our last remark is that recent work by Hofbauer and Schreiber [HS04] (see also Schreiber and Mielcynski [MS02]) show that there are open sets of Kolmogorov equations containing a dense subset of permanent equations and a dense subset of equations having an attractor on the boundary of $\mathbb{R}_+^n$. For these equations, it is impossible to predict whether or not all species will survive.

Such results are well within the tradition inaugurated by Kolmogorov: in general the study of ecological systems cannot be reduced to a local study of stable equilibria. Only a dynamic global study can account for the complexity of ecological feedback.

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