The Theory of Population Dynamics:
I. Back To First Principles

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Models in population dynamics theory have been based on the following principle: the relative growth rate of a population is a function of the environment in which it lives. Parameters of the environment have included the size of the population under consideration and the sizes of other populations interacting with it. This has led to the description of communities as systems of first order rate-based differential equations, beginning with the Lotka–Volterra equations and including most of their known generalizations. A new proposal is to replace this principle by the following: the rate of change of the population relative growth rate is a function of environmental changes and an environment. The new principle interprets the Malthusian exponential growth as an undisturbed motion. This implies the description of interactions based on relative acceleration rather than the growth rate. The new approach leads to second order differential equations which can be integrated to traditional equations only in special cases. The "forces" that establish equilibria in ecological systems and the criteria of their stability change drastically within the new scheme. Experiments needed to validate or reject the proposal are discussed.

1. Malthusian Law

The founders of theoretical physics conceived an interesting trick: to relate complex and unknown phenomena to "initial conditions" and those that are accessible to study to the laws of nature (Wigner, 1970). Newtonian mechanics describes, for example, the Earth's motion around the Sun in such a way that it is possible to calculate the future motion of the Earth given its initial relative position and speed. "Why the Earth has (or ever had) its current position and speed" is outside of the scope of theoretical mechanics though it is not, *a priori*, a nonsensical question. Everything is explained by Newton's laws, which establish the invariance of physical laws with respect to uniform straight-line motion. We are so accustomed to this statement, that we sometimes forget that it is no more than a generalization (and in some way, an extrapolation) of our experience but is not a self-evident truth (Mach, 1983; Wigner, 1970; Cartwright, 1983). The history of pre-Newtonian physics includes unsuccessful attempts to develop theoretical mechanics considering speed as the quantity which is influenced by "external forces". The 2000-year experience of this unfruitful but quite natural approach shows that the transition to the invariance postulate of mechanical laws with respect to the Galilean transformation was difficult and counterintuitive. The modern viewpoint has been rather successful, but at the same time, it has substantially narrowed the subject of what is called

physics. In modern terminology, the Newtonian revolution was basically the change in the form of the description of the dynamic state of the system from only "position" to "position and speed".

From the point of view of this historical analogy, the models of population dynamics can be classified as Aristotelian. All known models of population dynamics, disregarding internal structure, are based on the population size as the complete descriptor of the dynamic state. We can write this central assumption of traditional theory as follows

$$\frac{1}{N}\frac{dN}{dt} = f(E)$$

where N is the population size, $(1/N)/(dN/dt)$ is the relative growth rate (average number of surviving offspring per parent per unit of time), and $f(E)$ is a function of the environment, with the understanding that population size itself might be one of the environmental parameters.

To construct a community model, we write such an equation for each of the populations in the ecosystem. The environment, E, for a given population includes sizes of other populations, and that is how we obtain the system of equations designed to describe the dynamics. The differences between models are due to different assumptions concerning the functions f.

Let me call "constant unlimited" all environments in which a given population increases (or decreases) exponentially. There is no external way to determine such a constancy. One can, in principle, do it by enumerating: food is sufficient, oxygen is present in necessary quantities, temperature is constant, etc. But there is no need to enumerate the separate causes. Environmental invariability *for a given population* from the population-dynamics point of view can be established by examining the population itself, since only if the population size is constant or changes exponentially is the environment constant.

I will write down the Malthusian law $N(t) = N_0 e^{rt}$ in a slightly unusual form

$$\frac{d^2}{dt^2}(\ln N) = 0.$$

Paraphrasing Hutchinson (1975); Populations preserve exponential growth unless they do not. Although sounding tautological, this bears, in my opinion, a meaning analogous to Newton's first law, describing what happens when "nothing happens in the environment". In the suggested form, the equation has no parameters and requires two initial conditions: population size and the growth rate.

I would like to conclude this section by noting that the Malthusian law is the only formula in population dynamics to which the word "law" has been applied; all the rest were "models". I completely agree with this usage of words, stressing exponential growth as a background for all events happening in population dynamics. In this paper I will try to reconstruct the principles of population dynamics based on an extended notion of the dynamic state.

2. The Essence of the Argument

Let us start by considering the statics. On a very gross scale, we can say that population sizes that are observed in ecosystems are dictated by the environment, so that if the environment is changed, the sizes change accordingly. This statement ignores dynamics completely but can be accepted on a very crude level as a reasonable approximation to reality. Of course, even in a static case, interrelations between species can be taken into account, and changing the environment for one of the populations will change the sizes of other populations involved in the network of mutual interactions.

The next step is to consider disturbances and to assume that birth and death rates of the species rather than their abundances, are defined by the environment, and that changes of the environment cause the growth rates to deviate from zero. This will lead us to the traditional rate-based equations.

Accepting exponential growth as a nondisturbed motion and assuming that deviations of the environment cause changes in the growth rates is another step in the same direction. I find it totally impossible, on purely logical grounds, to distinguish between the last two ways of describing dynamics. When a growing population depletes the food supply, is it the growth rate that is itself changing as a function of the declining supply or is it a change in the growth rate that is brought about by the food supply being depleted? Either view seems acceptable. The difference between the two views is, however, quite substantial in certain cases.

With the new view, the growth rate becomes another independent variable which should be supplied in addition to the dynamic equations as an extra initial condition. The question of why a given population in a given environment has a certain growth rate is never addressed. The explanations concentrate only on how growth rate will change given that it is set at a certain initial value. An attempt to construct such a second order equation benefits from its generality (it will describe the essence of the interaction and be valid in a variety of environments) at the expense of not addressing a universe of questions which are reasonable but too hard to answer. Most of us are so used to the rate-based equations that it takes an effort to see the actual impossibility of rejecting the proposed step outright. Consider, for instance, a traditional description of logistic-like growth

$$\frac{1}{N}\frac{dN}{dt} = r - \phi(N).$$

Differentiating the equation, we obtain

$$\frac{d^2}{dt^2}(\ln N) = -\frac{d\phi}{dN}\frac{dN}{dt}$$

with the relative acceleration of the population size being affected by a negative, growth-rate-dependent, "friction-like force". The two equations are, of course, fully equivalent. What if, however, an equation has a more general form

$$\frac{d^2}{dt^2}(\ln N) = -\psi\left(N, \frac{dN}{dt}\right)$$

and is not integrable back to the old model? Why not postulate that in a limited environment the rate of change of the Malthusian parameter is a function of population size and its rate of growth? The self-interaction is then described by this function, and the initial Malthusian parameter must be supplied as an extra initial condition together with the initial size. This extra condition would reflect all the properties of the environment besides the ones that cause density dependence to act.

I do not, in fact, insist on the above equation as a necessary competitor for the much simpler logistic-like model. I believe, however, that this example clearly shows the impossibility of distinguishing between the two views on purely logical grounds without references to observations, or, at least, to intuition based on observations.

Which of the two approaches is "correct" is not a legitimate question to ask at this point. Which one fits better as a description of reality can only be judged by the consequences, not by the internal logic. The philosophical distinction between the "explanatory-mechanistic" versus "metaphoric" models does not exist on the very basic level of primary principles.

The most striking differences between the two views appear in the description of predator–prey interactions. In the next section, I will advocate the new approach for modelling such interactions based on detailed comparison of the behavior of the two models and references to some experimental data.

3. Predation

(A) UNLIMITED ENVIRONMENT

In order to consider predation dynamics in its pure form, let us mentally place a pair of interacting predator and prey populations in an ideal constant and unlimited environment. By unlimited, I imply the absence of density dependence of any sort so that both populations grow (or die) exponentially in the absence of interaction. Adding limitations will, of course, stop exponential expansion of our populations and provide a degree of necessary realism. This will be done in Section 4.

Let me clarify further the concept of an unlimited environment. Sometimes, even when a population grows exponentially, it is said that the growth is limited by a particular substrate that is consumed by the growing population. We mean that increasing the concentration of the substrate in the medium will increase the population growth rate. In this sense, growth is called "limited" by this concentration. This is not the sense in which I use this term. I will call all environments where a particular population grows exponentially *unlimited*. Thus, for a given population, one can have an infinite variety of unlimited environments characterized by a different growth rates. For our purpose *limitations* will appear only when a resource is being used up in the process of population growth and, thus, the growth itself deviates from exponential. A chemostat with bacteria as prey, and protozoa as predators is the closest effective analogy to the abstract environment I have described. Experiments on predator-prey interactions in chemostats are, therefore, relevant to our consideration and we will discuss them at the end of this section.

Space is one of the resources and it is assumed to be unlimited. This means that a density of organisms stays constant; population "instantaneously" fills larger space

as it grows. The variable of our interest is the total population size, not the density per unit space. This distinction will be important in future comparisons of proposed equations with classical Lotka–Volterra models which dealt with densities rather than population sizes. In other words, these models included the idea of space limitation even in its "density-independent" version.

A variety of outcomes is conceivable when we place predator and prey together in an unlimited environment. The outcome may depend on their sizes as well as on their respective growth rates.

—The predator may exterminate all prey and then die or continue to grow depending on other sources of food available to the predator.

—The prey may constitute an insufficient source of food to maintain the predator and predator may die out while the prey population will resume its growth.

—The predator may grow but with such a limited growth rate (even with abundant prey) that the prey population will outgrow the predator and will grow asymptotically with the same exponent as if predator were absent. Prey in this case effectively "escape" predation although they are being consumed by slowly increasing number of predators.

—The populations may attain balanced growth, when they co-exist in a certain proportion and grow exponentially. The exponent of such growth can be positive or negative, but is always below the rate at which the prey grows alone. Such stationarity is, or course, a special, and nongeneric, case of exponential growth.

—Populations may oscillate in a sequence of "overexploitation–underexploitation" time periods preserving exponential growth or stationarity on the average.

The Lotka–Volterra equations or their usual generalizations do not allow this variety of outcomes. As will be discussed below, the classical models of predator–prey interaction were, in fact, an attempt to describe these interactions combined with some form of limitations to the population growth. In my opinion, the traditional approach therefore obscured the essence of predation dynamics. Accepting idealized unlimited environments as a starting point for the analysis will allow us to construct much simpler and more universal models. They will include all outcomes listed above, as a set of solutions for a system of second order differential equations. Of course, the specific outcomes will be dependent on initial population sizes and on the initial Malthusian parameters of both populations. The latter are additional initial conditions whose presence allow the equation describing the interactions to remain unchanged across environments.

(B) RATE-BASED HOMOGENEOUS MODEL

Let us start our analysis by constructing the rate-based model in order to compare it to the acceleration based model that will follow. The first and very crucial assumption that we will make here is that joint exponential growth of both populations with the same rate and same ratio of sizes is a required trajectory for any model describing the growth of the predator-prey system in an unlimited environment. The overall rate with which a pair grows in such an environment will certainly depend on the Malthusian growth rates of both populations taken in isolation (r_1

and r_2) as well as on their interaction. As will be seen below, this assumption of the existence of the "balanced growth" trajectory will significantly effect the construction of an appropriate model. It is mathematically equivalent to assuming that in unlimited environments equations of dynamics should be invariant with respect to multiplication of both population sizes by the same constant. If we construct a rate-based model, we should then write

$$\frac{d}{dt} (\ln N_1) = r_1 - g(N_1/N_2)$$

$$\frac{d}{dt} (\ln N_2) = -r_2 + f(N_1/N_2)$$

(1)

where N_1 and N_2 are the sizes of the populations of prey and predator respectively, r_1 and r_2 are their Malthusian parameters in the absence of interactions, and the functions g and f describe the reactions of the Malthusian parameters of both populations to the given relative abundance of prey to predator.

Note that under the Lotka–Volterra scheme

$$\frac{d}{dt} (\ln N_1) = r_1 - \alpha_1 N_2$$

$$\frac{d}{dt} (\ln N_2) = -r_2 + \alpha_2 N_1$$

proportional change in sizes of both populations change the rate of predation. This would be the case if space, for instance, is limited. As will be seen further, space could be one of the constraints affecting the growth, but the action of this constraint will be reflected in the new model quite differently (see Section 4 of this paper).

Specific signs of r_1 and r_2 in the equations (1) are assumed here only for simplicity of initial consideration. Both Malthusian parameters can in principle be positive or negative, depending on the properties of the unlimited environment in which this pair is placed. It is very east to see what outcomes are described by this model (1). If the isoclines for the two populations do not intersect, we have relative extinction of prey or predator. By relative extinction, I mean that the ratio of population sizes will tend to zero of infinity while both of them may grow or decline. Whether the actual extinction of one or both populations takes place depends on the absolute values of r_1 and r_2. Stable coexistence (that is, balanced exponential growth) is possible if the isoclines intersect in one of the two imaginable ways.

If we fix the shapes of the functions f and g forcing stable coexistence, the relative outcome of the interaction is fully defined by the difference, $r_1 - r_2$. By changing r_1 or r_2 we move isoclines up or down causing a change in the equilibrium ratio of population sizes

$$x^* = \frac{N_1}{N_2}$$

as well as a change in the balanced growth rate. The value of x^* goes up with r_1 when, for instance, our unlimited environment has better quality food for the prey. The value of x^* goes down if r_2 goes up, when, for instance, the predator obtains another unlimited source of food. In general, within certain limits x^* is a growing function of the imbalance of the predator's and prey's Malthusian parameters. Beyond these limits, relative extinction of one or the other populations takes place. Although one can generalize the model by allowing more than one intersection of isoclines, let us ignore this possibility which will sidetrack us from the major theme of our consideration. Note that the outcome of interaction in this model does not depend on the initial values of N_1 and N_2 (it does in the case of unstable coexistence). Species either coexist and grow in balance or one of them goes extinct. Oscillations are impossible in this model, which is actually equivalent to a first-order differential equation

$$\frac{d}{dt} (\ln x) = r_1 - r_2 - g(x) - f(x)$$

where $x = N_1 / N_2$.

Let me, in summary, list only the properties of this model that I will question in the future, in comparison with the new model:

(1) The outcome of the interaction does not depend on the initial sizes of populations.

(2) Oscillations are impossible.

(3) In the case of coexistance, the balanced ratio of abundances, x^*, is a growing function of $(r_1 - r_2)$.

Other conclusions that can be made based on this model qualitatively coincide with the conclusions from the proposed model.

(C) PROPOSED MODEL

Following the general philosophy described in section 2, I propose to replace the traditional model by the following one

$$\frac{d^2}{dt^2} (\ln N_1) = - G\left(\frac{N_1}{N_2}\right)$$

$$\frac{d^2}{dt^2} (\ln N_2) = F\left(\frac{N_1}{N_2}\right)$$

Here rates of change of the Malthusian growth rates, G and F, are affected by the ratio of population sizes. The model is, again, invariant with respect to proportional changes of both population sizes. Moreover, it is invariant with respect to an arbitrary "Malthusian transformation": that is, multiplication of both population sizes by the same exponential function. Initial growth rates, r_{10} and r_{20} should be supplied in addition to initial population sizes, and they reflect the properties of the particular unlimited environment. The right-hand sides of equations (2) are qualitatively shown on Fig. 1. Formally speaking, this model does not contradict
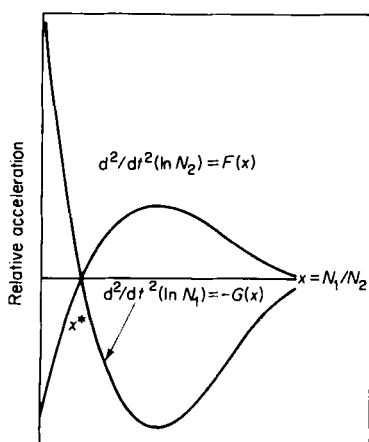
FIG. 1. Accelerations of ln N (rates of change of the Malthusian parameter) as a function of relative abundance of prey and predator according to the proposed model; x^* is the equilibrium ratio of two populations.

the homogeneous rate-based one. Differentiating equations (1), we can obtain equations in the form (2), with

$$G \text{ derived } (x) = \frac{\mathrm{d}g}{\mathrm{d}x} x(r_1 - r_2 - g(x) - f(x))$$

$$F \text{ derived } (x) = \frac{\mathrm{d}f}{\mathrm{d}x} x(r_1 - r_2 - g(x) - f(x)).$$

The fundamental difference between the two models is that I assume that functions F and G in System (2) are *independent* of the initial Malthusian parameters of the populations. These values in the model are defined only by the properties of the environment in which the pair of species is placed. The functions F and G are assumed to be fundamental characteristics of the predation process, and not influenced by merely numerical rates of multiplication of the species'grown in isolation. Of course, the initial rates of growth r_{10} and r_{20} need to be supplied for System (2). I assume that by varying the environment, I can assign these values freely, while preserving equations in the form (2) with functions G and F unchanged.

All imaginable outcomes of interactions listed in section 3(A) are possible within this model. A particular outcome is defined by a combination of initial conditions including population sizes and their growth rates. A simple analogy is a satellite which can fall to earth, rotate around it or escape gravity depending on its initial position and speed. The law of interaction stays unchanged in all the three cases.

To realize all these outcomes, consider the "forces" acting on two populations as shown on Fig. 1. If the initial position, $x = N_1/N_2$ is close to the balanced growth ratio, x^*, and $r_{20} - r_{10}$ is relatively small, we can linearize our equations around the equilibrium ratio and obtain $x(t)$ oscillating around the mean value, x^*. Then both populations grow (on the average) exponentially with the exponent depending on the initial growth rates. If the initial position is imbalanced favoring predators,

$N_1/N_2 \ll x^*$ and $r_{10} < r_{20}$ we may obtain extinction of prey or predator or both. The precise sequence of events in this case will depend on the absolute values of N_{10} and N_{20}. If, on the contrary, $N_1/N_2 \gg x^*$ then the prey may effectively "escape" predation and $N_1/N_2 \to \infty$, so that the prey will asymptotically attain its independent growth rate while the predator will grow (or decline) with a lower exponent.

Let us summarize all the properties of the proposed model that are different from those of the homogeneous rate-based model developed in the previous section:

(1) The outcome of the interaction depends on both the initial sizes of the populations and their growth rates.

(2) In the case of coexistence, oscillations are superimposed on balanced exponential growth. The frequency of these oscillations in the neighborhood of the equilibrium ratio, x^*, does not depend on the initial growth rates. Since oscillations generally are nonlinear, slight dependence of the period on the initial conditions is expected. The amplitude of the oscillations is always determined by both initial sizes and initial growth rates.

(3) The balanced ratio of abundances in the case of coesistence, x^*, is independent of the initial growth rates.

(D) REQUIRED EXPERIMENTS

Let us contrast the differences between the two models presented above. First, let us compare the three properties listed at the end of sections 3(B) and 3(C).

First, with the traditionally constructed homogeneous model, if $r_1 < r_2$, coexistence is impossible. With the second model, if the initial ratio is significantly imbalanced in favor of the prey, $N_1/N_2 \gg x^*$ and $r_{10} < r_{20}$ balanced growth with superimposed oscillations can emerge.

The second difference is the presence of oscillations in the case of coesixtence. This effect is easiest to see when populations are, on the average, constant. The standard overexploitation–underexploitation cycle typical of predator–prey system is given by the new model. The amplitude depends on initial conditions (including rates), the frequency is basic for the interaction of a given pair of populations.

The third difference relates to the balanced ratio itself. If, for instance, we feed prey with a better (unlimited) food, increasing its rate of multiplication, the balanced ratio of prey to predator stays unchanged under the new model. It goes up according to the traditional model.

In the absence of the precise experimental data, the choice between the two model is a matter of intuition. Both give reasonable descriptions of what might happen. Let us then discuss the experiments which might help in making a choice.

Note, first of all, that beginning with the classical work of Gause (1934), much unsuccessful experience has accumulated in attempts to verify the Lotka–Volterra predator–prey equations and their analogues. This is very much in contradiction with the expectations derived from these equations predicting cyclic behaviour and even stable coexistence in the presence of limiting factors. Note that the frequency of oscillations predicted by the Lotka–Volterra model is strongly dependent on the population's growth rates–in complete contradiction to the model proposed here.

Experiments with competition have been much more successful at realizing model-predicted behaviors. Competitive exclusion as well as coexistence of competitors have been observed experimentally in the laboratory in reasonably good agreement with traditional models (see comments on competition below, in section 4).

I submit that the failure of experimental verification for the Lotka-Volterra predator-prey model is plausibly a consequence of using a wrong model. In fact, if a model of the sort proposed here is accepted, it is easy to see why it was so difficult to maintain a predator-prey system in the laboratory without adopting special tricks like environmental heterogeneity or or immigration. A very delicate balance of initial sizes *and initial growth rates* is needed to insure coexistence. According to the new model, the best approach is to start with the balanced ratio and create a minimal difference in the initial growth rate, so that the system is minimally deviant from its equilibrium state. This can be achieved by adjusting the properties of the environment in which the pair of populations is placed. These conditions were definitely not satisfied in the attempted experiments. The expectation of stable coexistence independent of initial sizes and (most importantly) growth rates, which was based on the Lotka-Volterra equations, might be responsible for the failure of these experiments. Repeating such experiments with the new model in mind would be a valuable exercise.

A series of experiments where prey and predator were successfully maintained (oscillating usually stopped after 6-7 cycles) came from work with continuous cultures by Fredrickson and his colleagues at the University of Minnesota (Tsuchiya *et al.*, 1972). The oscillations were the result of a three-way interaction, for instance glucose feeding of bacteria which are prey for protozoa. Although glucose is introduced to a chemostat at a constant rate, it fluctuates widely in counterphase to the consumer (prey) abundance. However, the glucose concentration is always so much above the Michaelis constant that it is reasonable to assume that the Mathusian parameter of prey is saturated. I can, therefore, use the results as an example of purely predator-prey oscillatory interaction. In principle, one should monitor the glucose content within the chemostat, adjusting the input concentration in order to keep it constant within the chemostat. Then, the experiment will become even more useful for studying the predator-prey interaction in isolation. Changing the flow rate in chemostat experiments, as well as changing the quality of food supplied for the prey, is a very good way to see the effect of initial growth rates on the fate of the interaction. If the proposed model provides a better description of the system, amplitudes of oscillations should be very sensitive to the changes in flow rate while both frequency of oscillations and mean relative abundance should not be sensitive to such changes. In the set of results reported in Tsuchiya *et al.* (1972), the flow rate was reduced twice and four times between the three experiments. Neither the frequency of oscillations nor the average ratio changed significantly in these experiments, although the amplitude of the oscillations was higher for higher flow rates. This is precisely what would have been predicted based on the now model and is in complete contradiction with traditional models.

4. Constraints

Ideal environments in which we mentally placed our pair of interacting prey and predator populations do not exist. Populations do not indefinitely grow exponentially. Limiting factors, or constraints, reduce and finally stop the growth at some point. This is not to say that considering an unlimited environment was not a useful exercise. It helped to clarify our thinking about the dynamics of predation, and now we will attempt to add realism by placing the system in a limited environment.

Let us start with one population and consider the analogy of the logistic equation

$$\frac{d}{dt}(\ln N) = r - \phi(N).$$

The essence of this equation is the reflection of a limiting resource, such as space, which is being consumed as the population grows.

From the general philosophy of our new approach, we should expect environmental *change* rather than environnment to play the role of the "force" in the population dynamics equations. Differentiating once, we have

$$\frac{d^2}{dt^2}\ln N = -\frac{d\phi}{dN}\frac{dN}{dt}$$

which will become our force to be substituted into the new model. This equation is nothing but a derivative of the logistic-like equation. It is a result of the presence of a constraint in the form of a limited resource. The force generated by the constraint can be called *a reaction of the constraint*. It is a growth-rate dependent, "friction-like" force which decelerates the growth and limits it to the carrying capacity of the environment, defined by the standard equation.

$$r - \phi(N) = 0.$$

Note that here r reflects all other properties of the environment besides the limiting factor and $\phi(N)$ describes the shape of the density-dependence induced by the presence of the constraint. Clearly, if this limitation is the only factor influencing growth, there is no sense in differentiating the logistic-like equation once again in order to obtain the force acting on the acceleration of population size. The old model is fully satisfactory by itself. The new form, however, is absolutely necessary if we want to consider the joint action of predation in combination with the limiting factors.

The above comment relates to the description of competition as well. Competition for a resource can be viewed as a form of limitation to growth, where the limiting factor depends on the sizes of the competing populations. Within the proposed scheme, a pure competition equation can be written as a traditional rate-based equation in the same fashion as the logistic-like model. However, in order to combine competition with predation, the "reactions of constraints" of a more general (than logistic) form can be obtained by additional differentiation. Resulting, rate-dependent "friction-like" forces will then need to be superimposed on the predation equations in fundamentally the same way as it is done for the single species density

dependence below. The full analysis of the consequences of this superimposition falls outside the framework of this paper.

To start from a simple case, let us assume that in a predator-prey system, only the prey population is affected by the growth limiting resource. We will then have

$$\frac{d^2}{dt^2}(\ln N_1) = -G\left(\frac{N_1}{N_2}\right) - \frac{d\phi}{dN_1}\frac{dN_1}{dt}$$

$$\frac{d^2}{dt^2}(\ln N_2) = F\left(\frac{N_1}{N_2}\right).$$

Note that an important assumption of additivity is made here. The rate of change of the Malthuisian parameter is a *sum* of the rate induced by predation and the rate induced by the declining resource. This superposition assumption will be discussed separately in the next section.

Without explicit expressions for the functions G, F and ϕ (N), it makes no sense to attempt solving the equations directly. Let us consider the behavior of the system in the neighborhood of the equilibrium, N^*, the root of the equation, $r = \phi$ (N), with $N_1^* = x^* N_2^*$. Omitting the computations, the analysis of the linearized system gives the following result. We have a stable equilibrium around the ratio x^* with damped oscillations if the intensity of density dependence is low (for low values of γ) and a nonoscillatory stability when the intensity of density dependence is high. Note that even with a non-oscillatory stability an overshoot of the equilibrium level is a possibility.

These conclusions seem very similar to the ones obtained from the Lotka-Volterra equations when density dependence is included. There are, however, important differences. Changing both r_{10} and r_{20}, i.e., non-interactive factors of the environment, will affect the equilibrium values of both prey and predator in our model but will preserve the ratio at x^*. In the Lotka-Volterra model the equilibrium level of prey is defined only by r_2 and not r_1 whereas the equilibrium level of the predator depends on r_2, r_1 and γ. The ratio of prey to predator is not preserved in the Lotka-Volterra model, whereas in our model it is invariant to the strength of limiting factors and other noninteractive properties of the environment. Only the total absolute abundance level reached by the system depends on the initial growth rates.

The behavior of the unrestricted predator-prey system in the linear approximation is analogous to the simple mechanical oscillator moving uniformly with friction and oscillating with amplitude defined by relative initial position and speed. The behavior of the predator-prey system with density-dependent factors is analogous to the mechanical oscillator with some level of friction. Oscillations are damped or not present at all (if friction is strong enough) but the relative equilibrium position is not influenced by friction. The absolute final position, on the other hand, depends on the initial speeds and the intensity of friction.

Away from local approximation, there is more complexity to our model. The "friction" intensity is actually position-dependent and the "spring" is strongly nonlinear. The essential features of the analogy, however, are valid. The nonlinearity of "the spring" allows for the predator's extinction in fundamentally the same way

as for the non-restricted case. The existence of an extinction threshold allows for extinction of the prey before the predator, but this was also the case with the classical models.

Adding limiting factors to the predator in addition to the prey will complicate the model. There are more possibilities, depending on whether or not the ratio of separate carrying capacities is above or below x^*, which is purely a predation-defined balanced ratio. If we assume that the density-dependent factors for the predators are either absent or weak compared to those of the prey, our general conclusion of a stable ratio at x^* will hold.

Questions for experimental or even field verification that are raised by this model are whether the equilibrium ratio of prey to predators is the same in different environments, and whether the frequencies of their oscillations are the same when the strength of density dependence is the same.

It is unfortunate that we are attempting to build a theory of population dynamics without a reasonably complete understanding of statics. As can be seen from the analysis above, understanding static relationships holds the key to making a choice between competing models of dynamics. In this regard, the work of Sugihara (1984) on the topology of trophic networks may prove to be extremely important. It might happen that the fact that trophic networks are "mechanically stringent," made up of triangles and tetrahedrons, has a much more literal meaning than it seemed even to the author of this analogy. If trophic relationships act like springs connecting the equilibrium ratios of preys and predators, the stability of the systems itself might impose the property of "mechanical stringency" on the network of trophic relationships.

5. Superposition

The manner in which a number of causes are combined in a mathematical model describing dynamics is crucial in making distinctions between different models. With the traditional rate-based models, we had the relative growth rate itself partitioned into terms: so many offspring per parent per unit time due to consumption of the first kind of food *plus* so many due to consumption of the second kind of food *minus* so many dying due to a limiting factor, etc. In the proposed model we assume the rate of change of the mean number of offspring per parent per unit time to be partitioned into an algebraic sum of terms due to separate causes. We have no direct evidence in support of either of these superposition principles. One can make a judgment only by the consequences of one or another assumption.

In physics, for example, accelerations react additively to two forces applied jointly but speeds do not. Even there this principle is only an approximation although a very good one. For bodies in a very viscous liquid we can safely accept the superposition principle for the speeds. Newtonian law in this case is unnecessary; a mass on the spring will never oscillate but monotonically relax towards an equilibrium and "Aristotelian" mechanics is fully sufficient.

Let us consider the first equation of system (3) of the previous section in this context. Assuming the Malthusian parameter to be of low absolute value in order

to linearize the second term on the right hand side we have

$$\frac{d^2}{dt^2} \ln N_1 = -G\left(\frac{N_1}{N_2}\right) - \gamma \frac{d}{dt} \ln N_1.$$

This is equivalent to a first order integro-differential equation with a distributed delay

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 - \int_0^t K(t, \tau) G\left(\frac{N_1(\tau)}{N_2(\tau)}\right) dt.$$

In this equation $K(t, \tau) = 1$ when $\gamma = 0$ (in the absence of limitations) and $K(t, \tau) \rightarrow \delta(t - \tau)$ when $\gamma \rightarrow \infty$.

In other words, a first order equation in a traditional form can be obtained when the limiting factor is very strong.

Traditional rate-based models incorporating delays have been introduced by many authors and go back to the original work of Vito Volterra. The proposed approach can be looked at as a special case of a general distributed delay reaction model. The specialization, however, is a very particular one. The strength of the limiting factors acts as a parameter which places the model on the spectrum from the simple traditional model in cases of strong limitations to the second order differential equation with only "position-dependent" terms in the case of unlimited environment. Intermediate cases are conveniently expressed in terms of the second order equations with the right hand side subdivided into terms dependent on growth rates as well as populations sizes. This seems to be a very reasonable way to superimpose two causally different influences and express a model as a momentary but a second order differential equation.

6. Previous Attempts

Attempts to introduce second order differential equations in population dynamics modelling have been made in the past. The first independent publications by Clark (1971) and Ginzburg (1972, in Russian) were quite formal and immature approaches to the problem. Two other publications include a response to Clark's work (Innis, 1972) and an analysis and classification of types of behavior in a single population second order model (Yee, 1980). Another approach attempting to interpret adaptation due to natural selection as a cause of "inertia" in population's response to environmental changes was made by Ginzburg (1980) and reiterated in Ginzburg (1982). The position concerning acceleration-based models advocated in the current paper is radically different from all of the above mentioned approaches. The difference is in focusing on prey-predator or, more generally, consumer-resource interactions as a basis for arriving at the second order model.

7. Conclusions

The proposed approach in summary is to consider predation as producing effects on the acceleration of the population growth (changes in Malthusian parameters) rather than on rates. The analysis of "forces" thus defined leads to a description of the coexisting predator-prey system as a stable oscillation around a particular

equilibrium ratio. This ratio stays unaffected by changes in the Malthusian parameters of both populations (initial conditions for growth rates). Density-dependent factors in the proposed model are interpreted as "reactions of constraints". They are responsible for stopping the exponential growth of an otherwise unlimited system, and they influence the frequency and the rate of decay of oscillations.

Experimental work that is needed to reject or support the proposed view should be centered on checking the invariance of the ratio and the oscillation frequencies in prey–predator systems with respect to initial growth rates. These characteristics vary according to the traditional model as a function of r_1 and r_2 (in different directions for different models) and stay unchanged under the proposed model.

I would like to end by encouraging such experimentation. This will not only help to judge the validity of the proposed view but help to make an intelligent choice between different kinds of population dynamics models which have remained in the literature for 60 years without adequate verification.

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