A Resource-consumer Model With Age Structure

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Abstract: Dynamical systems in which agents compete for resources may exhibit chaotic fluctuations. This works improves on Gamarra and Solé's paper. Implicit solutions of the model are obtained. Our main results shows that resource availability at any time depends on the number of potential consumers.

Keywords: Age-structure, Population Dynamics, Resource-consumer, Model.

1. INTRODUCTION

Basic framework for understanding the dynamics of biological populations recognizes that changes in population numbers are the result of two types of processes - on the one hand, there is the deterministic component of population dynamics that results from interactions between individuals and other predictable ecological processes - on the other, there is stochastic component of population dynamics that results from random variations in birth and death rates, for instance owing to the direct effects of weather or disturbance [5]. It is fundamental to understand the dynamics of any population in order to determine the relative roles of these two processes in a year-to-year variation in population numbers. We shall consider the former in the present study.

Partially inspired by the fact that even in the absence of stochastic variations, entirely deterministic systems are capable of producing patterns of population change that are apparently indistinguishable from random noise [11], we propose a resource-consumer mechanism structured by age, and in which a time lag is introduced to account for the time it takes individuals to adapt to changes (in their feeding pattern, environmental changes etc...). Recently, Rao and Rao [13] studied the stability of resource-consumer dynamic models involving distributed delays. They do not take into account the age parameter.

Therefore, in this paper, within-generation dynamics of and age-structured resource-consumer interactions developing in time units *t* is studied. And here we ask: *Does age-dependent vital rates play any important role in the dynamics of resource-consumer model*? The proposed model is interesting in its own right, at least from the mathematical point of view.

The rest of the paper is organized as follows: In the next section, we develop the model and attempt to obtain an implicit solution. The last section concludes the study.

2. THE CONSUMER-RESOURCE MODEL

The model presented in this section generalizes Gamarra and Solé's [6]. By assuming a homogeneous interaction at any continuous time *t*, and by using the notation in [6], where *R* stands for resources and *C* for consumers, we have

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$$\frac{dR(t)}{dt} = \gamma - C(t)\frac{R(t)}{\Gamma}; \qquad R(0) = R_0,$$

$$\frac{dC(t)}{dt} = \lambda - m(1 - \frac{R(t)}{\Gamma})C(t); \quad C(0) = C_0, \tag{1}$$

where $\gamma > 0$ stands for the renewal of resources, and $\lambda > 0$ is a constant growth/renewal rate depicting some immigration of consumers from external pool. m represents the intrinsic death modulus in the absence of resources. $\Gamma = \lim_{t\to\infty} R(t)$ is the carrying capacity of the environment in terms of resources or the maximum available resource ($R \le \Gamma$), a limit which holds only in the absence of consumers.

Equation (1) is solvable, since the functions involved are continuous in $\mathbb{R}^+$ and integrable. Indeed, $R(t), C(t) \in L^1(\mathbb{R}^+; \mathbb{R}^+)$. System (1) is a system of couple differential equations. Considering equation $(1)_1$ independently (this is a crude assumption), using a freshman integration, its first integral is given by

$$R(t) = R_0 + \gamma e^{\left\{-\frac{1}{\Gamma}\int_0^t C(u)du\right\}} \int_0^t e^{\left(-\frac{1}{\Gamma}\int_0^s C(u)du\right)} ds, \tag{2}$$

where u follows the limit described only in the absence of consumers. Equation (2) may be used in estimating the quantity of resources if the number of consumers is known *a priori*. The growth of any population in a restricted environment must eventually be limited by a shortage of resources [12]. If production depends on previous resources, then system (1) now reads

$$\frac{dR}{dt} = \left(\gamma - \frac{C}{\Gamma}\right)R,$$

$$\frac{dC}{dt} = \left[(\lambda - m)\left(1 - \frac{R}{\Gamma}\right)\right]C, \tag{3}$$

where $m > \lambda \ll 1$ Otherwise, for $m < \lambda$, consumers will growth in the absence of resources. This may be due to an implicit assumption that consumers may grow from consumption of alternative resources when the common resources are scarce, a biologically reasonable condition as it relates directly to the adaptation of species. A more detail study on this can be found in [10]. λ and m are the growth rate and the intrinsic mortality rate in the absence of resources, respectively.

The integral representation of equation $(3)_1$ is

$$R(t) = R_0 e^{\gamma t} \exp\left\{-\frac{1}{\Gamma}\int_0^t C(u)du\right\}, \tag{4}$$

which can be interpreted as follows: in the absence of consumers, resources will keep on growing, but will not exceed the carrying capacity Γ, and as a result of overcrowding, will start declining. For instance, plants compete for light, and those that cannot emerge fast die out.

Similarly, equation $(3)_2$ yields

$$C(t) = C_0 \cdot e^{(\lambda - m)t} \exp\left\{\frac{m}{\Gamma}\int_0^t R(\tau)d\tau\right\}. \tag{5}$$

By allowing γ in equation $(3)_1$ to depend on time, an equation similar to that of concentration of drug in the blood stream [7] is obtained, the drug being introduced in dosages $\gamma(t)$ and removed at a rate proportional to R. The main difference is that the constant of proportionality $k := -\dfrac{C(t)}{\Gamma}$, is not a constant. This is extremely important, especially for seasonal or periodic resources. In such cases, it could be assumed that $\gamma(t)$ is periodic, i.e., $\gamma(t-T) = \gamma(t) = \gamma(t+T)$, where T is the period; and the initial resource (stock) depends on T such that $R_0 = R_0(T)$ gives the initial resource at the beginning of each period T.

Also, any periodic change of climate will tend to impose its period upon oscillations of internal origin [8], and incorporating the periodicity of environment (seasonal effects, food supplies, mating habits...) into equation (8) yields

$$R(t+T) = R_0(T)\exp\left\{\int_0^t\left[\gamma(s-T)-\frac{1}{\Gamma}C(s)\right]ds\right\}. \tag{6}$$

As mention earlier, age structure is capital in the Resource-Consumer model because in the case of a food web, it takes some time for the plants to get mature for a proper interaction to take place. It is therefore vital to account for this time retardation. More so, it takes a certain unit of time for consumers to respond to changes in the population size or environment [8,16,17]. Aiyelo and Tchuenche [1] referred to this process as adaptation parameter.

It is of interest to note however that true age of a biological entity is a matter of which sites are active. Hence, true age is a multidimensional variable, and this multidimensional characterization is called physiological age by biologists [3]. By the law of continuum, the evolution equations in (3) with some little modifications take the form of a system of non-linear first order partial differential equations of the McKendrick type, given by

$$\frac{\partial R}{\partial t} + \frac{\partial R}{\partial a} = -k(t,a)R(t,a),$$
$$R(0,a) = R_0(a), \quad R(t,0) = B_R(t), \tag{7}$$

and

$$\frac{\partial C}{\partial t} + \frac{\partial C}{\partial \alpha} = -m\left(1-\frac{R}{\Gamma}\right)C(t,\alpha),$$
$$C(0,\alpha) = C_0(\alpha), \quad C(t,0) = B_C(t) \tag{8}$$

where $k(t,a) = \dfrac{C(t,a)}{\Gamma}$, a is the age of resources while α is the consumer's age. Here we note that how consumers distribute their consumption effort among different ages of the resource population is not discussed (more details will be provided in a follow up paper). It is assumed that available resource is reduced by consumption alone, m is defined as above; $B_c(t)$ and $B_R(t)$ represent the recruitment or renewal of consumers and resources, respectively; $R_0(a)$ and $C_0(\alpha)$ are the appropriate initial densities.

Equations (7) and (8) can readily be solved via the Laplace transform method if the right-hand sides are modified to be of convolution type. The method of characteristics can best be applied if it is heuristically assumed that $\dfrac{C(t,a)}{\Gamma} := k(t)$, a function of time only. In this case the solution is given by

$$R(t,a) = \begin{cases} R_0(a-t)\exp\left\{-\int_0^t k(\tau+a-t)d\tau\right\}; & a > t, \\ B_R(t-a)\exp\left\{-\int_0^a k(\alpha-a+t)d\alpha\right\}; & t \geq a. \end{cases} \tag{9}$$

Similarly, by letting $\dfrac{C(t,a)}{\Gamma} = k(t,a)$, the same method of solution yields

$$R(t,a)\begin{cases} R_0(a-t)\exp\left\{-\int_0^t k(\tau,\tau+a-t)d\tau\right\}; & a > t, \\ B_R(t-a)\exp\left\{-\int_0^a k(\alpha-a+t,\alpha)d\alpha\right\}; & t \geq a. \end{cases} \tag{10}$$

Equation (8) has a similar solution of the form (10) if

$$k(t,a) := m\left(1 - \frac{R(t,a)}{\Gamma}\right).$$

In order to apply the Laplace transform technique (see [18]), introduce a time lag as follows:

$$\frac{\partial R}{\partial t} + \frac{\partial R}{\partial a} = -C(t,a)\frac{R(t-\tau,a)}{\Gamma}, \tag{11}$$

$$\frac{\partial C}{\partial t} + \frac{\partial C}{\partial a} = -m\left(1 - \frac{R(t,a)}{\Gamma}\right)C(t-\tau,\alpha). \tag{12}$$

The introduction of the same time lag swiftly renders the equations analytically tractable if the right hand side is of convolution type.

Let $\mathcal{L}$ represents the operator of Laplace transform, while $\hat{R}$ is the transform of R with respect to t and $p(\in \mathbb{C})$ the transform variable. Then, equation (11) yields (see [14])

$$\mathcal{L}\left[R_t + R_a + \frac{1}{\Gamma}C(\tau,a)R(t-\tau,a)\right] = 0. \tag{13}$$

That is,

$$\frac{d\hat{R}(p,a)}{da} + \left(p + \frac{1}{\Gamma}\hat{C}(p,a)\right)\hat{R}(p,a) + R_0(a) = 0, \tag{14}$$

which implies,

$$\hat{R}(p,a) = e^{-pa} \exp\left\{-\frac{1}{\Gamma}\int_0^a \hat{C}(p,\alpha)d\alpha\right\} \int_0^a R_0(\xi)e^{p\xi} \exp\left(\frac{1}{\Gamma}\int_0^\xi \hat{C}(p,\alpha)d\alpha\right)d\xi$$

$$+ K(p)\exp\left\{-\int_0^a \left(p + \frac{1}{\Gamma}\hat{C}(p,\alpha)\right)d\alpha\right\}, \tag{15}$$

where $K(p)$ is the constant of integration given by the boundary condition $\hat{B}_R(p)$. By letting

$$\sigma(a) := \exp\left\{-\frac{1}{\Gamma}\int_0^a \hat{C}(p,\alpha)d\alpha\right\}, \tag{16}$$

equation (15) now reads

$$\hat{R}(p,a) = \sigma(a)\left\{\int_0^a e^{-p(a-\xi)}\frac{R_0(\xi)}{\sigma(\xi)}d\xi + \hat{B}_R(p)e^{-pa}\right\}. \tag{17}$$

By inspection (see 15]),
$$R(t, a) = B_R(t-a)(\sigma)H(t-a) + R_0(t-a)(t)H(a-t), \tag{18}$$

where $\sigma(t) := \dfrac{\sigma(a)}{\sigma(a-t)}$, $H(\cdot)$ is the Heaviside function which forces solutions to be right continuous. Hence, they

are positive and biologically relevant.

Integrating equation (17) with respect to a gives

$$\hat{R}(p,a) = e^{-pa}\int_0^a e^{-p\alpha}(R_0(\alpha) - \frac{1}{\Gamma}\hat{C}\hat{R})d\alpha + \hat{B}_R(p)e^{-pa}. \tag{19}$$

Evaluation of the inverse of the first and last expressions on the right-hand side of equation (19) is done by inspection. The middle term is a convolution integral whose inversion is immediate, and a little rearrangement of the solution yields

$$R(t,a) = \left(1 - \frac{C(t,\alpha)}{\Gamma + C(t,\alpha)}\right)\{B(t-a)H(t-a) + R_0(a-t)H(a-t)\}. \tag{20}$$

It is important here to note the absence of the survival function $\sigma(\cdot)$ in equation (20). Nevertheless, this may be taken care of by the expression

$$\left(1 - \frac{C}{\Gamma + C}\right) < 1.$$

The interpretation of equation (20) is not so obvious, but an intuitive look tells us that the quantity of resources available at time t depends on the number of consumers $C(t, \alpha)$, who actually go for the available resources.

In order to further support the need for this study, we note that the passenger pigeon was present in the United States in vast numbers until late in the nineteenth century. It was heavily hunted for sport and for food and

consequently its numbers were drastically reduced by the1880s [2]. Unfortunately, the passenger pigeon could apparently breed successfully only when in a large concentration. The precipitous decline in the passenger pigeon population from huge numbers to extinction calls for great concern and this seems to be one of the basic factors which contributed to the quest for species conservation. Therefore, a study related to resource consumption is ecologically meaningful. The autonomous (time-independent) system is similar to the model studied in [6], but with age derivatives instead of time. Consequently, this paper is an extension of their work, and the stability analysis will be carried out in a forthcoming paper.

3. CONCLUSION

The consumer-resource interaction is a fundamental issue in ecology [9] due to the fact that living organisms do not survive or reproduce without resources [4]. The derivation of the age-structured model describing the dynamical interactions between populations of consumers and resources began with a generalization of the non-linear Gamarra and Solé's model [6], where the fertility coefficients are resource and consumer independent. That is, the effect of overcrowding which often causes fluctuations is not considered. It is generally followed in parallel with depletion of resources, leading to drastic changes of population numbers [4]. But luckily, this problem has been analyzed from the point of view of consumer choices [9, Chapter 3], which depends on the evolutionary history and adaptability of populations. This adaptability justifies the introduction of a time lag in equations (11) and (12), which is necessary to describe the units of time it takes the resource/consumer to respond to changes in the population size or environment.

The interdependence between resource availability and survival of the population (consumers) can be incorporated into equation $(3)_2$. In such a case, the intrinsic growth rate r $(= \lambda - m)$, say, takes the form $r = r(R(t))$ such that in the complete absence of resources $(R(t) = 0)$, $r(0) = r_0 < 0$, and consumers die out. Otherwise, they relocate to new sites (favorable localities) by migration or adapt [1] to new resources (a process that takes time!). The model derived herein is not only an extension, but a study of a resource-consumer model structured by age in its own right. The following biological conclusions can be derived from our analysis:

–   At the non trivial equilibrium, resources reach a constant value R^*, say where $0 < R^* < \Gamma$. Therefore, the existence of resource-free steady state is not conceivable [4].

–   Equation (20) tells us that the quantity of resources available at any time t depends on the number of potential consumers present at that same time.

This model view differently can be considered as predation, where the prey is the resource of the predators, with or without other external resource forms.

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