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Optimal life-history strategies in seasonal consumer-resource dynamics

A.R. Akhmetzhanov[1], F. Grognard[1] and L. Mailleret[2,1]

[1]: INRIA, BIOCORE Team, Sophia Antipolis, France

[2]: INRA, UR 880, Sophia Antipolis, France

Abstract

The interplay between individual adaptive life histories and populations dynamics is an important issue in ecology. In this context, we considered a seasonal consumer-resource model with non-overlapping generations. We focused on the consumers decision-making process through which they maximize their reproductive output *via* a differential investment into foraging for resources or reproducing. Our model takes a semi-discrete form, and is composed of a continuous time within-season part, similar to a dynamic model of energy allocation, and of a discrete time part, depicting the between seasons reproduction and mortality processes. We showed that the optimal foraging-reproduction strategies of the consumers may be ‘determinate’ or ‘indeterminate’ depending on the season length. More surprisingly, it depended on the consumers population density as well, with large densities promoting indeterminacy. A bifurcation analysis showed that the long-term dynamics produced by this model were quite rich, ranging from both populations’ extinction, co-existence at some season-to-season equilibrium or on (quasi)-periodic motions, to initial condition dependent dynamics. Interestingly, we observed that any long-term sustainable situation corresponds to indeterminate consumers’ strategies. Finally, a comparison with a model involving typical non-optimal consumers highlighted the stabilizing effects of the optimal life histories of the consumers.

Keywords: Individual behavior, population dynamics, semi-discrete model, foraging-reproduction trade off.

1 Introduction

Life history traits of a species, such as its growth pattern, age or size at maturity, and the environment in which the species lives are tightly interdependent and need to be considered concurrently. Life histories of organisms have important effects on their environment, considerably affecting food webs, which may have important consequences within (Polis et al. 1996) and even across ecosystems (Knight et al. 2005; Schreiber and Rudolf 2008). In turn, life histories of organisms can plastically respond to changes in the environmental conditions (Stearns 1992; Day and Rowe 2002). Thus, both life histories and environment interact in a complex feedback loop. For instance, resource (food) level is known to influence life histories in many consumer taxa (see *e.g.* Twombly (1996); Morey and Reznick (2000); Wildy et al. (2001)), modifications which in turn may act on both resource and consumers levels through variations in trophism and reproduction rates. At the populations scale, the consequences of such complex feedbacks are difficult to predict, but they clearly constitute an important issue. In this article, we are interested in the population dynamics consequences of the interaction between a resource species and a consumer species with adaptive life history. Although resource-consumer systems form the fundamental building blocks of most terrestrial and aquatic ecosystems, literature remains scarce on this issue. Actually, most recent life history theory literature seems to focus on the effect of various phenomena (resource abundance, predation pressure, etc...) on the life history strategies of organisms, but largely disregards its interactions with population dynamics (*e.g.* Charnov et al. (2001); Irie and Iwasa (2005);

Yamamura et al. (2007); Ejsmond et al. (2010); Higginson and Ruxton (2010b)). Although some contributions acknowledge the importance of this issue (Higginson and Ruxton 2010a), the only reference we are aware of which specifically focuses on the interplay between adaptive life histories and population dynamics is (Takimoto 2003). This latter contribution considers organisms with complex life cycles (Wilbur 1980) and studies the influence of adaptive timing in ontogenetic niche shifts on consumer resource dynamics.

Yet, since life histories are eventually consequences of individual decisions, it has to be noted that there exists an important number of models studying the interplay between adaptive individual behavior and population dynamics. It can be divided into two main groups: 'top-down' (or 'phenomenological') models and 'bottom-up' (or 'mechanistic') models (Sumpter and Broomhead 2001; Eskola and Geritz 2007).

Top-down models usually encapsulate behavioral terms in demographic parameters that are difficult to interpret at the individual level. The power of such modeling lies in the relative simplicity and the mathematical tractability of the models, but they can not properly describe complex life histories (for examples on consumer-resource systems, see *e.g.* Holt (1983); Krivan and Sirot (1997); Abrams (1992)). Conversely, bottom-up models are based on assumptions at the individual level and their consequences at the population level are emergent properties of the systems. This is the idea underlying individual based (computer) models (IBM) (DeAngelis and Mooij 2005). Dynamic Energy Budget (DEB) theory is an alternative approach that also focuses on the individual level (Kooijman 2010). It proposes a mathematical framework to infer the population dynamics from sound energetic and physiological principles. In both IBM and DEB frameworks, the analysis of the models remains hindered by their mathematical complexity. Another mechanistic approach that has recently received some attention is semi-discrete modeling (Singh and Nisbet (2007); Pachepsky et al. (2008); Mailleret and Lemesle (2009); see also previous examples on consumer-resource dynamics in Godfray et al. (1994); Murdoch et al. (2003)). Semi-discrete models explicitly assume that intra-generational processes like foraging, predation *etc.*, are of a continuous nature, while inter-generational processes (reproduction) are of a discrete nature. As such, this type of modeling allows to explicitly take into account complex (Rohani et al. 1994) and adaptive (Takimoto 2003) behaviors or life histories, while keeping some nice mathematical tractability properties.

In this contribution, we consider a consumer resource system in which consumers must, at any time of their life, choose whether they should reproduce or forage for resources. Such a foraging-reproduction trade-off is closely related to the ‘cost of reproduction’ trade-off between current and future reproduction which is very classical in life-history theory (Lessells 1991; Stearns 1992): delaying reproduction to forage for resources contributes to increase the fecundity but also diminishes the time period available for reproduction; this makes the choice between the two critical and can result in various complex life history patterns.

To investigate the foraging-reproduction trade-off at the intra-generational level as well as its consequences at the inter generational level, we adopt a semi-discrete modeling framework, and consider a consumer-resource model of two annual species. Both species are supposed to reproduce through the generation of dormant immature individuals along the season. These immatures will grow into matures at the beginning of the next season. The resource population is supposed to produce descendants at a constant *per capita* rate, while the consumer individuals have to trade-off between foraging for resources to increase their reproductive capacities or investing in reproduction in order to maximize their number of descendants. The optimal pattern of investment in resource acquisition or reproduction depends both on the environment (here, the resource density) and the physiological state of a consumer (McNamara and Houston 1996). Hence, to determine the optimal life history of a consumer, it is convenient to integrate physiological variables in the model (McNamara and Houston 1996; Lika and Kooijman 2003). Consumers are thus described by two variables, their internal energy (physiological variable) and their population density, while the resource population is described by its density only.

The number of progeny maximization problem translates into a sort of “dynamic model of energy allocation and investment" (Perrin and Sibly 1993), with some original peculiarities. Actually, most energy allocation models appear to be 'individual-centered' in the sense that they focus on the life history of solitary individuals, and do not take into account potential density-dependent environmental feedback; see the review by (Perrin and Sibly 1993) and *e.g.* (Perrin et al. 1993; Iwasa 2000; Ejsmond et al. 2010). The model considered here describes the depletion of the resource as consumers forage for it, and thus accounts for the influence of the consumer population density as well as that of the reproduction-foraging behavior of the consumers. Hence, in our model, density-dependent environmental feedback is explicit.

The standard way to deal with such dynamical optimization problems is to make use of techniques coming from optimal control theory, see examples in *e.g.* (Schaffer 1983; Iwasa and Cohen 1989; Perrin et al. 1993; Gilchrist et al. 2006; Yamamura et al. 2007). In the following, using such techniques, we identify the foraging-reproduction behavior of the consumers that maximizes their number of descendants in the next generation in a closed loop form, *i.e.* for any given environment and consumer density, how the consumers should behave along the season to maximize their reproductive output. In a second step, we investigate the long term inter-generational dynamical patterns of the model as consumers follow such an adaptive optimal strategy and compare these to those produced by typical 'non-optimal' consumers.

2 The Model

Following Takimoto (2003) or Geritz and Kisdi (2004), we studied an annual consumer-resource system in which both species are active during a season of length T within year $n = 0, 1, 2, \ldots$ Let $R_n(t)$ denote the (mature) resource population density at time $t \in [0, T]$ within year n, $C_n(t)$ the (mature) consumer population density and $E_n(t)$ the internal energy of a (mature) consumer. We model the behavior of a consumer through a, possibly time-varying, variable $u_n(t) \in [0, 1]$ that represents the fraction of the consumer's activity devoted to foraging for resources (the ‘foraging ratio’ in the following) to accumulate energy, in a sense to grow; the remaining part, $(1-u_n(t))$, is assumed to be devoted to reproduction and will be denoted ‘reproduction ratio’. Thus, $u_n = 1$ indicates that a consumer feeds on the resource only, $u_n = 0$ that it reproduces only, and $u_n \in (0,1)$ that it adopts a mixed foraging-reproduction behavior.

2.1 Within year: consumer-resource interactions

For the sake of simplicity, we assume that neither the consumers nor the resource suffer natural mortality. The resource population, however, is depleted by the consumers according to the law of mass-action, *i.e.* at a rate proportional to its own density, $R_n(t)$, to the consumer population density, $C_n(t)$, and to the foraging ratio $u_n(t)$. In other terms, the mature consumers explicitly compete for resources through a functional response which is linear. Due to maintenance costs, the internal energy of a consumer is supposed to experience a natural decay at a constant rate, but increases proportionally to the resource population density, $R_n(t)$, and to the foraging ratio, $u_n(t)$. The former assumption implies that a consumer needs to forage for resources otherwise its energy will drop to zero. The latter is consistent with the law of mass-action describing the resource depletion. Indeed, considering the energy of all the consumers, and not of a single individual, lead to recover a classical ‘energy conservation’ principle. These assumptions yield the following within-year n model (dependence in t is omitted)

$$\begin{aligned} \frac{dC_n}{dt} &= 0, \\ \frac{dE_n}{dt} &= -aE_n + bu_nR_n, \\ \frac{dR_n}{dt} &= -cu_nR_nC_n, \end{aligned} \tag{1}$$

where a is the *per* unit rate of decrease of energy, b the conversion parameter of resource into energy and c is the *per capita* consumption rate of the resource, *per* resource unit. A simplifying assumption of model (1) is that the energetic cost of reproducing and of foraging are equal.

2.2 Between years: reproduction and mortality processes

It is assumed that throughout the year both species produce dormant immature individuals (like eggs, seeds). This dormancy hypothesis on the immatures implies that they do not interact with matures and thus do not intervene in the within-year model (1) equations.

The (mature) resource population is assumed to reproduce at a constant *per capita* rate γ throughout the season, so that the total number of immature resources produced during year n is

$$\int_0^T \gamma R_n(\tau) d\tau. \tag{2}$$

The (mature) consumers reproduce at a *per capita* rate proportional to their own energy and to the reproduction ratio $(1-u_n)$. The total number of immature consumers produced during year n is thus $\int_0^T \theta(1-u_n(\tau))E_n(\tau)C_n(\tau)d\tau$, where θ is the, *per capita*, per unit energy, reproduction rate of a consumer when it reproduces only. Such dependency of the reproduction output in the consumer energy, ultimately a proxy for body mass, is fairly classical in life history modeling (Charnov et al. 2001). Since from model (1) mature consumers population is constant throughout a season, the total number of immature consumers produced during year n reduces to

$$\theta C_n(0) \int_0^T (1-u_n(\tau))E_n(\tau)d\tau. \tag{3}$$

Although no intrinsic mortality of the species is considered in the within-year model, these species die out at the end of a season. Immature populations are assumed to develop between the seasons so that, from (2) and (3), the initial populations at time $t=0$ of year $(n+1)$ are

$$\begin{aligned} C_{n+1}(0) &= \alpha\theta C_n(0) \int_0^T (1-u_n(\tau))E_n(\tau)d\tau, \\ R_{n+1}(0) &= \beta\gamma \int_0^T R_n(\tau)d\tau, \end{aligned} \tag{4}$$

with α and β respectively the proportion of immature consumers and resources that survived the between years (winter) and the maturation process.

At the beginning of year $(n+1)$, mature consumers have just emerged from their immature stage so that we consider they begin their life cycle with an internal energy equal to zero. Hence

$$E_{n+1}(0) = 0. \tag{5}$$

2.3 Optimal life histories of the consumers

It is usual in life history theory to consider that an individual behaves 'optimally' if it maximizes the number of its descendants that survive to reproductive age, *i.e.* its lifetime reproductive success $\mathscr{R}_0$ (Schaffer 1983; Perrin and Sibly 1993; Perrin et al. 1993; Kozlowski 1993; Ejsmond et al. 2010); see also *e.g.* (Iwasa and Cohen 1989; Iwasa 2000; Yamamura et al. 2007) on plant growth modeling as well as (Gilchrist et al. 2006) on pathogen life history modeling.

The number of progeny of an individual is the integral over its lifetime of its instantaneous reproductive rate. Here, only the mature consumers can (and actually do) reproduce, so that the per consumer number of mature descendants in the next generation is, in view of (4), $C_{n+1}(0)/C_n(0)$. At any time $t \in [0,T]$, optimal consumers would then choose $u_n(t)$ solving

$$\max_{u_n(t)\in\mathscr{U}} \left(\alpha\theta \int_0^T (1-u_n(\tau))E_n(\tau)d\tau \right), \tag{6}$$

with $\mathscr{U}$ the set of measurable functions from $[0,T]$ to $[0,1]$. Such an assumption on the admissible $u_n(t)$ allows various complex life histories to be tackled, such as determinate patterns, in which foraging stops at first reproduction (*i.e.* at maturity), or indeterminate ones, in which foraging continues after maturity and the pure foraging phase (Perrin and Sibly 1993). Such a property is particularly important since except for birds, insects or mammals, indeterminate life history strategies are ubiquitous (Charnov et al. 2001). It makes also an important difference with the model by Takimoto (2003), which considered only determinate strategies to be possible.

The optimization problem (6) is closely related to what Perrin and Sibly (1993) called a dynamic model of energy allocation and investment. However, a particular feature of our approach is that the environment is time-varying: the resource R_n is depleted by the foraging consumers, while this is usually neglected in energy allocation models (Schaffer 1983; Iwasa and Cohen 1989; Perrin et al. 1993; Yamamura et al. 2007), but see *e.g.* (Gilchrist et al. 2006) for an exception; as we will see, this does have some consequences.

The statement of the model is now complete: it combines a continuous-time system (1) and an optimal control problem (6) describing the within-season dynamics with a discrete-time system (4-5) that depicts the between years reproduction and mortality processes. Even though every model is a compromise between realism, precision and generality (Levins 1966), these equations can fairly well apply to annual producer-grazer systems, in which the grazer can plastically respond to its environment, like *e.g.* freshwater or land gastropods (Hunter 1961; Iglesias et al. 1996). In fact, the resource equations can also, to some extent, represent perennial, and not annual, primary producers: many of them lose their vegetation during winter seasons, but the number of photosynthetic organs in a given year is directly linked to the amount of energy gathered by photosynthetic organs during the previous year (equation (4)). In view of this, the present model may also represent the population dynamics of mono-cyclic plant pathogens (those with one generation per year), in which growth-reproduction patterns are complex (Agrios 2005). In this latter case however, the terminology used throughout this paper would need to be a little rephrased: resource population would correspond to the host (plant) population, consumer population would be the set of pathogens induced lesions on their hosts, energy would be lesions size, and foraging would correspond to host depletion by a lesion.

3 Within-Year Dynamics

We analyze the optimal control problem presented above and defined by (1) and (6) for all initial conditions $C_n(0), E_n(0)$ and $R_n(0)$ and do not restrict ourselves to initial conditions defined in (4, 5). Doing so allows us to solve any within-year optimal control problem, which results in explicitly computing the optimal life history strategy of the consumers for any initial consumer and resource density as well as initial internal energy.

3.1 Dimensionless model

In the following we solve the optimal control problem for any initial conditions, and thus for any year n, so that we can first drop the n subscripts in equations (1). Moreover the first equation of (1) is useless in the within year context so that we do not consider it either. Let us redefine some of the variable units, respectively time t, consumer population density C and resource density R, as

$$t \triangleq at,\ C \triangleq \frac{c}{a} C,\ R \triangleq \frac{b}{a} R, \tag{7}$$

so that model (1) is equivalent to

$$\begin{aligned} \frac{dE}{dt} &= -E + uR, \\ \frac{dR}{dt} &= -uRC. \end{aligned} \tag{8}$$

In this model, t and C are dimensionless quantities while E and R are expressed in ‘energy’ units. Dividing these two variables by one unit of energy renders model (8) dimensionless. Since it does not vary with time t, C plays here the role of a model parameter.

The maximization problem (6) is equivalent to finding the function $u(t)$ on $[0,T]$ that solves

$$\max_{u(t)\in\mathscr{U}} \int_0^T (1-u(\tau))E(\tau)d\tau. \tag{9}$$

In the following we investigate the optimal control problem defined by the simplified model (8, 9). Before proceeding, it has to be noted that the dynamics of the ratio of a consumer's energy over the resource density $x = E/R$ is entirely determined by itself and by u. Indeed, from (8), we get

$$\frac{dx}{dt} = (uC-1)\,x + u. \tag{10}$$

This feature will prove useful in illustrating the optimal behavior pattern of a consumer.

3.2 Optimal life history pattern

Two types of methods can be used to solve optimal control problems of the form (8, 9): either Bellman's principles of dynamic programming (Bellman 1957) or Pontryagin's maximum principle (Pontryagin et al. 1962). Pontryagin's maximum principle has previously been used in biological modeling for instance by Schaffer (1983), Iwasa and Cohen (1989), Perrin and Sibly (1993), Gilchrist et al. (2006) or Yamamura et al. (2007). Here we prefer Bellman's approach and make use of the method of characteristics to solve the Hamilton Jacobi Bellman (HJB) equation arising from the optimal control problem. Mathematical details of the analysis are reported in Appendix A.

The optimal behavior pattern is numerically illustrated in Figure 1 for a typical consumer population density C. The energy-resource ratio x is plotted against the reverse time $t' = T - t$, which is convenient to compare different season lengths on the same figure. Different optimal trajectories of model $(8, 9)$ are represented with solid lines. The (t', x) plane is separated out in two regions where $u = 0$ and $u = 1$, respectively. Where $u = 0$ it is optimal for the consumers to reproduce, while where $u = 1$ it is optimal to forage resources. The curve separating the two regions is composed of a ‘switching curve’ (dashed-line) whose equation reads

$$x(t') = 1 - e^{-t'} \text{ for } t' < \log(2), \tag{11}$$

and of a ‘singular line’ (dashed-dotted line) whose equation is

$$t' = -\log(x) + \frac{2}{xC} - \frac{4}{C} \text{ for } t' \geq \log(2). \tag{12}$$

On the one hand, as a trajectory crosses the switching curve in natural time, it is optimal for the consumers to switch from foraging for resources ($u = 1$) to reproducing ($u = 0$). On the other hand, as a trajectory hits the singular line it is optimal for the consumers to adopt a mixed behavior, obeying

$$u^{\sigma} = \frac{2x}{xC + 2},$$

which makes the model trajectories follow the singular line.

Generically, depending on the initial consumer energy - resource density ratio $x(t = 0) = x(t' = T) = x_0$ and on the season’s length T, different behaviors emerge. In natural time t, these correspond to: (i) reproduction only (x_0 large, T not too large), (ii) reproduction only / mixed / reproduction only (x_0 large, T large), (iii) foraging only / mixed / reproduction only (x_0 small, T large), (iv) foraging only / reproduction only (x_0 small, T small).

Cases (i) and (ii) can be interpreted as follows (we comment on (iii) and (iv) below): (i), if at the beginning of a season, x_0 is large, *i.e.* the initial consumer energy is large compared to the initial resource density, and the season is short, it is useless for a consumer to forage for resources. The energy gained through foraging is not worth the time wasted not reproducing. (ii), if the season is long, foraging for resources is still useless at the beginning of the season. However, as the consumer energy decreases and drives the x-ratio towards the singular trajectory (25) it turns out to be more efficient to follow a mixed reproduction-foraging behavior to increase the x-ratio until it reaches $\bar{x}$ at $t = T - \log(2)$, and then switch back to reproduction only.

Though they are predicted by the proposed modeling framework, behaviors of type (i) or (ii) are not relevant for model (1, 4-6). Indeed, at the beginning of a season, the consumers are considered to have just grown from the immature stage and to begin their mature life with 0 energy, so that $x_0 = 0$.

3.3 Implications for model (1, 4-6)

In model (1, 4-6) the trajectories of interest start with $x_0 = 0$, whatever the initial value of the resource population $R(t = 0) > 0$. For a fixed consumer population size C, a given (x_0, T) determines a unique optimal foraging-reproduction behavior $u^*(t)$. Since $x_0 = 0$ independently of $R(0)$, we can deduce that a population of density C of optimal consumers will adopt the very same behavior independently of the initial resource level: they will forage for resources and reproduce identically, as well as adopt the same singular behavior, if any. As a consequence, both the number of immature consumers and resources produced through some season are proportional to the initial number of resource in that season (see also appendix B for a mathematical derivation of this point). This property is most likely related to the linearity of the functional response of the consumers and will prove useful to compute the long-term dynamics of the full model (1, 4-6).

Only two behavioral patterns are possible with $x_0 = 0$, depending on whether the season length T is larger or smaller than a critical value $\tilde{T}$. If T is smaller than $\tilde{T}$, the optimal behavior of a consumer is of type (iv): first, it forages for resources to increase its energy. Then, as its energy reaches higher values and the resource density becomes low (*i.e.* the x-ratio reaches the switching curve (22)), it switches to reproduction only: the reproductive benefit gained through resource foraging cannot outweigh the disadvantage of having less time available for reproducing. As already mentioned, such a strategy that a consumer ceases accumulating energy as it starts reproducing is referred to as determinate in the literature (Perrin et al. 1993). Otherwise, if a consumer continues accumulating energy after the onset of reproduction, it is called indeterminate. This is what happens in our model when $T > \tilde{T}$: between the pure foraging/energy accumulation phase, and the pure reproduction phase, a consumer follows a mixed reproduction-foraging behavior. Such a mixed strategy prevents consumers energy from reaching high levels, which would induce large maintenance costs because of the $\dot{E}$ equation in (1). As such, indeterminate foraging-reproduction patterns keep the consumers from squandering the resource.

Determinate and indeterminate life-history patterns have been observed for various species and investigated theoretically with individual-centered optimal energy allocation models (Perrin and Sibly 1993). It is interesting to note that our population modeling framework also predicts that such patterns are, in certain situations, optimal. However, contrarily to individually-centered models, the season lengths for which determinate or indeterminate strategies are optimal do not rely on the biological characteristics of the consumers only, but also on the size of their population.. Indeed, from the within-year model it is possible to compute $\tilde{T}$ explicitly; we get

$$\tilde{T}(C) = \frac{\log(C+1) + (C-2)\log(2)}{C-1}, \tag{13}$$

with $\tilde{T}(1) = \log(2) + 1/2$, so that $\tilde{T}$ is a function of the quantity C which, through the change of parameters (7), represents both the consumer density and its influence on the environment. Though seasonality, and especially seasons length, is known to have an influence on growth strategies, there is little evidence from the literature that, as in the present study, density-dependence plays a role in promoting (in)determinate strategies (see the review by Heino and Kaitala (1999)). This dependence is the consequence of the interaction between the two phenomena that are modelled through parameter C: non-constant environment, since the resource is actually depleted by consumers, and explicit consideration of a population of consumers competing for the resource. If either is ignored, density-dependence does not arise in discriminating between determinate and indeterminate strategies: on the one hand, the environment not being depleted by the consumers imposes $c = 0$ in equations (1), which through (7) implies $C = 0$ in the computation of $\tilde{T}$ independently of the actual consumer density; on the other hand considering an individual consumer and not a population, would trivially render $\tilde{T}$ independent on C. In both these cases, the threshold $\tilde{T}$ would not depend on consumers density. Thus, although few contributions actually focused on this point, the present study suggests that density dependence, here competition for resources, may affect the evolution of foraging-reproduction, and presumably growth-reproduction, life history patterns. More specifically, analyzing (13), we have that $\tilde{T}(.)$ is a continuous decreasing function of the consumer population density C. Then, for a given season length T, a large consumer population density C results in a small $\tilde{T}$, and is likely to promote an indeterminate strategy. Alternatively, small consumer population densities tend to favor determinate strategies. These two situations are illustrated for the same season length T, but with different consumer densities C, on Figure 2. Notice however that from (13), $\tilde{T}(C)$ is restricted to the interval $(\log(2), 2\log(2))$ so that the strategy necessarily is determinate for $T < \log(2)$ and indeterminate for $T > 2\log(2)$. This has some consequences on the life history patterns we may observe during long-term dynamics of the model (see section 4.2).

4 Long-Term Dynamics

Here, we will investigate the long-term population dynamics of model (1, 4-6) in which consumers are optimal adaptive foragers. The first step is to compute the number of consumer and resource offspring produced throughout a typical season n to explicitly couple season

$(n+1)$ initial population densities to the consumer-resource interactions that had occurred during season n.

4.1 Computation of the number of offspring

The number of offspring for the consumer and the resource populations are defined by equation (4). Since we will still be working with the dimensionless variables defined in (7), and upon reinserting the season numbering index, the number of offspring of season n that forms the initial consumer and resource populations of season $(n+1)$ is computed as

$$C_{n+1}(0) = \frac{\alpha\theta}{a} C_n(0) \int_0^T (1-u_n^*(\tau))E_n(\tau)d\tau, \text{ and } R_{n+1}(0) = \frac{\beta\gamma}{a}\int_0^T R_n(\tau)d\tau. \tag{14}$$

As noted previously, one can prove that, whatever the season length, the initial number of consumers and resource of season $(n+1)$ are strictly proportional to the initial number of resource of season n (see Appendix B). We can thus write the complete model (1, 4-6) in the compact form

$$C_{n+1}(0) = \rho_C C_n(0) R_n(0)\,\Phi_C(C_n(0),T), \text{ and } R_{n+1}(0) = \rho_R R_n(0)\,\Psi_R(C_n(0),T), \tag{15}$$

where $\rho_C = \alpha\theta/a$ and $\rho_R = \beta\gamma/a$. The functions $\Phi_C(.)$ and $\Psi_R(.)$ have complicated forms but are dependent on $C_n(0)$ and T only (see Appendix B). Due to this complexity, we needed to rely on numerical simulations to confirm our intuition that both $\Phi_C(.)$ and $\Psi_R(.)$ were increasing functions of the season length T. We also showed that the number of resource offspring at the beginning of season $(n+1)$ is a decreasing function of the number of consumers of season n, $C_n(0)$, and that it decreases to 0 as $C_n(0)$ becomes large; so does $\Psi_R(.)$. Similarly, we obtained analytically that $C_{n+1}(0)$ is an increasing function of $C_n(0)$, while the per capita number of consumer offspring $\dfrac{C_{n+1}(0)}{C_n(0)}$ is a decreasing function of $C_n(0)$; this confirms the intuition that the more consumers there are, the more offspring the population can have, but that the *per-capita* number of offspring is diminished. Such form of interferences among consumers is known to generically have stabilizing effects on consumer-resource dynamics (Murdoch et al. 2003), which happens to hold in the present model as well.

4.2 Bifurcation analysis

One can notice from equations (15) that the long term (multi-seasonal) dynamics of model $(1, 4\text{-}6)$ depend upon the parameters ρ_R, ρ_C and T only. Actually, the dependence in ρ_C can even be omitted through a change in the resource units. Indeed, redefining the resource as $R_n \triangleq \rho_C R_n$ does not change the model but eliminates ρ_C from (15), a situation which is exactly similar to the classical model by Nicholson and Bailey (1935). It is thus only necessary to analyze the influence of ρ_R and T on the dynamics of model $(1, 4\text{-}6)$, so that the results can be presented with a bifurcation diagram in the (T, ρ_R) plane. We detail the mathematics employed to compute the bifurcations in Appendix C.

The bifurcation diagram in the (T, ρ_R) plane is presented on Figure 3. The bifurcation curves $\rho_R^*(T)$, $\rho_R^\circ(T)$ and $\rho_R^\infty(T)$ define five regions in which the behaviors of model $(1, 4\text{-}6)$ are qualitatively different. Region I corresponds to the natural extinction of the resource, that drives the consumer population to 0 as well. As the parameters cross the bifurcation curve $\rho_R^*(T)$, an unstable positive equilibrium appears; this is similar to overexploitation of the resource by the consumer population as displayed *e.g.* in the Nicholson and Bailey (1935) model. In the present model however, this phenomenon does not necessarily lead to extinction of the populations through oscillations of increasing amplitude in populations densities: if T is large enough (region II) the unstable positive equilibrium may indeed be surrounded by a stable limit cycle on which both populations undergo long-term oscillations whose period or quasi-period can last several seasons. If T is smaller, however, we recover the extinction phenomenon linked to the overexploitation of the resource (region III). The transition between the two types of behaviors occurs on the curve $\rho_R^\infty(T)$. From region III, increases in the parameters ρ_R and T leading to region IV, generates a dynamical pattern that depends on the initial population densities. In this region there is actually an unstable limit cycle that surrounds the stable equilibrium point: depending on the initial conditions, either the population densities converge to a season-to-season equilibrium, or there is overexploitation of the resource, leading to a crash of both populations. From regions II and IV, increases in both parameters ρ_R and T lead to region V in which the dynamical behavior is much simpler since both populations converge globally to a stable season-to-season equilibrium point.

Figure 4, illustrates typical temporal behaviors of model (1, 4-6) with parameters T and ρ_R in region V (case (a)) and II (case (b)), respectively. Except when parameters are in region I on Figure 3, we always observed oscillating season-to-season dynamic behavior. These oscillations may be damped in which case the system converges towards a stable positive equilibrium (Figure 4, (a)), be sustained (Figure 4, (b)) or grow unbounded depending on ρ_R and T values. Interestingly, sustained situations (positive equilibrium or cycle) displaying a determinate reproduction-foraging strategy never occur: even though determinate strategies can happen during transients, long-term dynamics are always characterized by indeterminate strategies. This result is a direct consequence of the fact that $T \geq 2\log(2)$, which is the largest value $\tilde{T}(C)$ can achieve, in almost all of regions II, IV and V, which generate sustained situations; this prevents determinate strategies in these parts, even in the transients. The only situation where determinate strategies could occur is in the small part of region IV having $T < 2\log(2)$, where the sustainable population dynamics patterns are the stable equilibria $C^*(T, \rho_R)$. We have computed the locus of the (T, ρ_R) parameters such that, at the equilibrium , we have $\tilde{T}(C^*) = T$; this locus yieds a curve such that, on its left, the strategy at equilibrium is determinate, and on its right, it is indeterminate. We found out that this curve lies on the left of $\rho_R^\circ(T)$, so that all sustained patterns of regions IV correspond to indeterminate strategies.

4.3 Non-optimal consumers

To evaluate the significance of the previous investigations, we compared the long-term dynamics produced by the model with optimal consumers $(1, 4\text{-}6)$ to long-term dynamics obtained with consumers adopting a non-optimal behavior. As a benchmark, we considered that the non-optimal consumers behave constantly along any season: they dedicate a fixed fraction $\tilde{u} \in (0,1)$ of their time to foraging the resources, while the other part $(1-\tilde{u})$ is alloted to reproduction. With such a simple consumer behavior, the within and between season parts of the model can be conveniently summed up into the following season-to-season discrete time model:

$$\begin{aligned} C_{n+1}(0) &= \rho_C\, R_n(0) \frac{(1-\tilde{u})\left(C_n(0)\tilde{u}(1-e^{-T}) - (1-e^{-C_n(0)\tilde{u}T})\right)}{C_n(0)\tilde{u}-1}, \\ R_{n+1}(0) &= \rho_R\, R_n(0) \frac{1-e^{-C_n(0)\tilde{u}T}}{C_n(0)\tilde{u}}, \end{aligned} \tag{16}$$

where the energy equation is useless since $E_{n+1}(0) = 0$ by assumption. It can easily be checked that model (16) pretty much resembles Nicholson and Bailey's model, see *e.g.* (Murdoch et al. 2003). It has actually the same dynamical properties: either $\rho_R < 1/T$ and the resources go extinct and drives the consumers population to zero as well, or both population densities undergo sustained oscillations of increasing amplitude that lead to extinction of both populations. It is noteworthy that the corresponding bifurcation curve in the (T, ρ_R) plane is independent of the value of $\tilde{u}$, and is identical to $\rho_R^*(T)$ for the model with optimal consumers as well as the bifurcation condition in the Nicholson and Bailey model. This shows that the optimal adaptive consumers has stabilizing effects on the consumer-resource interactions.

5 Discussion

To investigate the interplay between individual adaptive life histories and populations dynamics, we concentrated on one of the cornerstones of ecological models, a consumer-resource system

(Murdoch et al. 2003). Considering populations with non-overlapping generations, we explicitly modeled consumers behavior assuming that, at each moment of their lifetime, they must adjust their investment into foraging for resources or reproducing. This resulted in a life-history trade-off closely related to the classical trade-off between current and future reproduction (Lessells 1991).

5.1 Modeling framework

We adopted a hybrid mathematical formalism, modeling the within-season consumer-resource interactions with a system of ordinary differential equations and the season-to-season processes with discrete maps. Such semi-discrete models have recently received considerable attention since they are capable of accurately representing and coupling within and between generation population processes (Briggs and Godfray 1996; Geritz and Kisdi 2004; Singh and Nisbet 2007; Pachepsky et al. 2008; Mailleret and Lemesle 2009). Another advantage of such modeling is its ability to take into account traits that can change during the lifetime of individuals in the computation of long-term population dynamics. Such a framework has been used to address the timing of sharp life-history transitions (Takimoto 2003; Hackett-Jones et al. 2009) or to model life history traits which may vary more gradually (Eskola 2009; Ejsmond et al. 2010). As such, the former studies can only consider determinate-like life histories, while the latter can in addition address smooth transitions between life history states, *e.g.* growth and reproduction. We followed an approach similar to Ejsmond et al. (2010) and Eskola (2009), in considering continuously varying investment efforts into resource foraging and reproduction through the introduction of the consumer foraging ratio $u(t)$ and its counterpart the reproduction ratio $(1-u(t))$. However, our model stems from a population interaction point of view, contrarily *e.g.* to the individual one in Ejsmond et al. (2010), and explicitly takes resource dynamics into account, what is seldom done (but see Takimoto (2003) for an example).

5.2 Within-season consumer strategies

Assuming that consumers behave optimally, in the sense that they maximize their expected lifetime reproductive success $\mathscr{R}_0$, we studied the within season optimal foraging reproduction strategy of the consumers through optimal control techniques (Bellman 1957; Vincent and Grantham 1997). We have shown that, depending on the environmental conditions (merely the season length and the consumers density), optimal consumer foraging reproduction strategies were either determinate or indeterminate (Heino and Kaitala 1999). In particular, we recovered the result that short season length tends to favor determinate strategies, while long seasons length promote indeterminate strategies (see Perrin and Sibly (1993), Figure 6). Moreover, we unveiled the influence of another important factor which is consumers density. Low consumer densities tend to select for determinate strategies, while large ones encourage indeterminate ones. As detailed in section 3.3, this influence stems from the coupling between a non-constant environment and the explicit consideration of a population of consumers. To our knowledge, life history modelling literature has mostly concentrated on a single individual in constant (Iwasa and Cohen 1989; Perrin and Sibly 1993; Yamamura et al. 2007) or varying (Gilchrist et al. 2006) environments, but fairly overlooked the potential density dependent feedback of populations. These studies succeeded in showing that various mechanisms can cause life history patterns to be (in)determinate (Heino and Kaitala 1999), but were not able to pinpoint the influence of population sizes.

To keep the developments as clear as possible, we made several simplifying assumptions in the derivation of the within-season equations. Although we do not show the details here, we relaxed some of these which yielded variations of model (1). For instance, we investigated the situation in which energetic costs of foraging and reproduction differ. We have shown that, although the precise formulation of the switching curves and the singular arc were slightly altered, our conclusions on the influence of season length and consumer density were still valid.

Considering that the consumers may suffer from within-season mortality leads also to fairly similar results with consumers displaying a more cautious behavior, *i.e.* starting reproducing at lower ratios of energy over resources than in the absence of mortality. The influence of within-season consumers mortality is actually rather complex and should probably deserve additional research efforts. We also considered the case where the consumers maintenance coefficient a was equal to 0. In such a situation our energy variable E is much more similar to a size variable as in *e.g.* (Takimoto 2003; Ejsmond et al. 2010) and optimal consumer strategies are determinate whatever the environmental factors. Hence, maintenance cost is the main factor promoting indeterminate strategies (see also Charnov et al. (2001)).

5.3 Season-to-season population dynamics

We examined the influence of optimal consumer life histories on the population dynamics of the model. We identified various long-term dynamical patterns, ranging from both population extinction driven by the non-sustainability of the resource dynamics, to a globally stable co-existence season-to-season equilibrium between consumers and resources. We also observed extinctions of the populations through overexploitation cycles, *i.e.* oscillations of population densities of increasing amplitude, or co-existence on periodic or quasi-periodic trajectories. All these dynamical patterns are frequently observed in classical consumer-resource systems (Murdoch et al. 2003). We have also shown that any sustainable situation always corresponds to consumers' indeterminate strategies, and not to determinate ones, which appears to give some cues regarding the ubiquity of indeterminate strategies in nature (Heino and Kaitala 1999). The analysis performed in section 4.3 focused on a generation-to-generation inflexible, *i.e.* non-plastic, behavior. This lead to a highly unstable season-to-season pattern typical of the Nicholson and Bailey model which implies both populations extinction. Such dynamics should in fact be expected since non-plastic behaviors almost always imply successive wasteful over- and conservative under-exploitation of resources, which does not naturally lead to stable situations. Conversely, the optimizing consumers adapt their behavior to the within-season environmental conditions and can exhibit a foraging-reproduction strategy which differs quantitatively if not qualitatively from their parents' strategy. This adaptive optimal consumer behavior tends to promote persistence and stability of the consumer-resource interaction, a property which is actually rather generic in consumer-resource systems, see *e.g.* (Fryxell and Lundberg 1994; Krivan and Sikder 1999; Van Baalen et al. 2001; Takimoto 2003). Nonetheless, in maximizing their *per capita* number of first generation offspring, consumers can well be in the situation to cause considerable damage to the resource. This could prevent it to reproduce sufficiently during the season, what eventually leads to a degraded environment for their children (see *e.g.* Figure 4 during transients (a) or on the periodic motion (b)). This is a form of resource over-exploitation and explains that unsustainable consumer-resource interactions can still occur in our model, despite the adaptive behavior of the consumers.

When season length goes large, long-term dynamics tend to get more stable and over-exploitation or cyclic behaviors are replaced by season-to-season population equilibria. This phenomenon is consistent with observations on many taxa over environmental gradients, which have shown that populations tend to cycle less in places with short winters, *i.e.* longer growing seasons (Ims et al. 2008). As far as our model is concerned, this seems to be caused by season lengths improving reproductive capacities of the resource (section 4.1) which optimal consumers happen to benefit more than non-optimal ones. Better reproductive capacities of the optimal consumers allow them to take advantage of higher reproductive capacities of the resource, facilitating their recovery from low densities. In return, consumer populations becoming larger prevent the resource population from reaching too high levels. These effects act jointly to prevent the system from undergoing over-exploitation cycles and appear thus to be central to the stabilizing properties of the optimal adaptive life histories of the consumers. This point is also supported by the fact that increasing ρ_R, which has positive effects on the resource reproductive capacities as well, exhibits similar, but not equivalent, stabilizing properties.

5.4 Final words

A last remark should be made on the optimality principle we considered in the maximization of $\mathscr{R}_0$. The question of the ‘right’ fitness measurement has actually been the subject of important debates during the last two decades (Metz et al. 1992; Mylius and Diekmann 1995; Metz et al. 2008), the conclusion seemingly being that there is no such unique correct fitness measurement. $\mathscr{R}_0$ maximization has been frequently used in energy allocation models describing the growth patterns of one individual (Perrin and Sibly 1993; Iwasa 2000; Ejsmond et al. 2010).

In an explicit population context, natural selection is expected to maximize $\mathscr{R}_0$ when density dependence and environmental feedback are fairly simple (Mylius and Diekmann 1995). This is for instance the case in (Gilchrist et al. 2006) which focused on saprophytic fungi life histories. This study has substantial similarities with ours. However, in the present work, the resource-mediated feedback of the consumers onto their population is actually more involved since it encompasses both consumers adaptive life history and population density effects. In fact, the formulation of equations (1) implicitly assumes that all consumers follow the same life history strategy. Maximizing $\mathscr{R}_0$ is then equivalent to assuming that every individual cooperates with the others in agreeing to adopt a common strategy which in turn has to be beneficial to each of them. A very similar property holds for instance in (Takimoto 2003), and to a lesser extent in *e.g.* Krivan and Sikder (1999); Van Baalen et al. (2001), though the underlying cooperation assumptions are not emphasized. This modelling angle is supported by the fact that cooperation is widespread in nature as it can have various direct or indirect positive influence on the transmission success of cooperators’ genes (Sachs et al. 2004). Yet, cooperation can also be harmful to offspring through local and/or inter-generational competition effects (West et al. 2002). Cooperative communities are also fairly vulnerable to defectors in a variety of settings. In the present framework, defection can be represented by selfish consumer individuals applying a strategy which can differ from the optimal cooperative strategy. Analyzing whether such defecting individuals may take advantage of the cooperation agreement of the rest of the consumer population is particularly important to characterize the resilience of the latter. To do so, a first step would be to consider rare defectors facing a large population of cooperators, bringing the study close to an Adaptive Dynamics (AD) framework (Geritz et al. 1997; Dercole and Rinaldi 2008). This would entail adding a ‘defector consumer’ population in the model, represented by its own energy and reproduction objective, and analyze if it can do better than the cooperators in an environment shaped by these latter. This would undoubtedly complicate the analysis since this would require to solve a non-zero sum differential game involving two populations of players, the cooperators and the defectors, which have unrelated objectives. Analyzing the evolutionary dynamics of complex life histories, which involve traits that may change along the lifetime of an individual, is currently receiving increasing interest in the AD litterature. For instance, Eskola (2009) and Eskola et al. (In Press) very recently studied the evolution of the timing of reproduction in a seasonal stage structured population model. Yet, their modelling framework is simpler than the one presented here; for instance the total *per capita* reproductive output is not constrained by the environment and life history strategies are essentially non-plastic (Eskola et al. In Press). It seems thus that a comprehensive methodological framework has yet to be developed to tackle such complex problems. This constitutes a rather important, though probably difficult, avenue for future works.

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Appendix A Optimal behavior computation

A.1 General equations

Let us denote the number of descendants that are produced playing behavior $u(\cdot)$ between time t and the end of the season if the state is at the value (E,R) at time t

$$J(t,E,R,u(\cdot)) = \int_t^T (1-u(\tau))E(\tau)d\tau$$

We can now define the Bellmann function

$$V^*(t,E,R) = \sup_{u(\cdot)\in\mathscr{U}} J(t,E,R;u(\cdot)), \tag{17}$$

which is actually the optimal value function, *i.e.* the maximal number of descendants that can be produced between time t and the end of the season.

Bellmann's principle of optimality indicates that (17) should be satisfied for any $t \in [0,T]$ as the optimal behavior $u^*(t)$ is played on $[0,T]$. This actually translates into solving the following partial differential equation, which is called the Hamilton Jacobi Bellman (HJB) equation

$$\begin{aligned} -\lambda_t &= -\lambda_E E + E + \max_{u\in[0,1]} \left[u(\lambda_E R - \lambda_R RC - E)\right], \\ &= -\lambda_E E + E + \left[u^*(\lambda_E R - \lambda_R RC - E)\right] \end{aligned} \tag{18}$$

with $\lambda_w = \partial V^*/\partial w$ (for $w = E,R$ and t). We refer to Chapter 7 in (Vincent and Grantham 1997) for a comprehensive derivation of the HJB equation and explanation of Bellman's dynamic programming principle.

Bellman's principle is usually investigated starting from the terminal time $t = T$ working backward in time, so that it is convenient to introduce the reverse time $t' = T - t$. Then, in reverse time t', the characteristic equations which define the solution of the HJB partial differential equation are (see *e.g.* Melikyan (1998))

$$\begin{aligned} \frac{dE}{dt'} &= E - u^*R, \quad & \frac{d\lambda_E}{dt'} &= -\lambda_E + 1 - u^*, \\ \frac{dR}{dt'} &= u^*RC, \quad & \frac{d\lambda_R}{dt'} &= (\lambda_E - \lambda_R C)u^*. \end{aligned} \tag{19}$$

Now, from the definition of the function V^*, one can notice that $V^*(t'=0)=0$ for all values of E and R so that we get, from the definition of λ_E and λ_R, the following 'transversality conditions'

$$\lambda_E(t'=0)=0, \; \lambda_R(t'=0)=0. \tag{20}$$

The remaining part of the analysis essentially consists in integrating the characteristic system (19) under the constraint (18) from the end of the season at initial conditions (20) for all positive $E(t'=0)=E_T$ and $R(t'=0)=R_T$ to calculate the optimal behavior u^*. Indeed, we do not need to consider $E(t')=0$ or $R(t')=0$ since, on the one hand, $E(t'=0)=0$ can only be achieved in the non-optimal solution where $E(t=0)=0$ and $u(t)=0$ for all times, and, on the other hand, $R(t'=0)=0$ only occurs in the non-relevant situation where $R(t=0)=0$. We thus only have to consider positive E_T and R_T.

A.2 Further computations

The quantity $\mathscr{A} = \lambda_E R - \lambda_R RC - E$ is important to the calculation of the optimal behavior pattern $u^*(t)$. Actually from the HJB equation (18), $u^* \in [0,1]$ must maximize the term $u\mathscr{A}$; then, when $\mathscr{A}$ is positive, u^* must be equal to 1, while when $\mathscr{A}$ is negative, u^* must be equal to 0. However, if $\mathscr{A}=0$, u^* cannot be derived from this kind of argument. In this situation we expect an intermediate ('singular') foraging ratio $u^* \in (0,1)$ corresponding to a mixed reproduction-foraging behavior, which can be defined from additional considerations.

We begin by considering the end of the season $t=T$, *i.e.* in reverse time, $t'=0$. From the transversality conditions (20), $\mathscr{A}(t'=0) = -E(t'=0) < 0$ and hence $u^*(t'=0) = 0$. $u^*(t')$ remains equal to 0 as long as $\mathscr{A}(t')$, determined by the characteristic equations (19), remains negative. To determine at which t' the quantity $\mathscr{A}$ vanishes, we then integrate system (19) from (20), E_T and R_T with $u^* = 0$. This gives, as long as $\mathscr{A}(t') < 0$,

$$\begin{aligned} E(t') &= E_T e^{t'}, \quad \lambda_E(t') = 1 - e^{-t'}, \\ R(t') &= R_T, \qquad \lambda_R(t') = 0. \end{aligned} \tag{21}$$

Then, from the definition of $\mathscr{A}$, u^* possibly changes when

$$(1-e^{-t'})R(t') - E(t') = 0 \;\Leftrightarrow\; x(t') = x_T e^{t'} = 1 - e^{-t'}, \tag{22}$$

with x_T the ratio of a consumer's energy over the resource density at the end of the season. Since the function $e^{-t'}(1-e^{-t'})$ (which is central to (22)) has a single maximum at $t' = \log(2)$ equal to $1/4$, it is straightforward that if $x_T > 1/4$ there does not exist any t' such that (22) holds. Hence the optimal foraging ratio in this situation is $u^* = 0$ (consumer reproduce) all over the season.

If $x_T < 1/4$, there exist times t' at which $\mathscr{A}$ vanishes. It can be easily checked that if such t' are lower than $\log(2)$, $d\mathscr{A}/dt'$ is positive what actually indicates that $\mathscr{A}$ becomes positive, and thus that u^* switches from 0 to 1 in reverse time. Then the curve in the (x,t') plane

$$x(t') = 1 - e^{-t'} \text{ for } t' < \log(2), \tag{23}$$

is called the 'switching curve'. After (in reverse time) this switch, the procedure is similar to what has been done previously from the end of the season: we integrate the characteristic equations (19) from the switching curve and the conjugate variables values defined by (21) with $u^* = 1$. The main difference with what was done previously for $u^* = 0$ is that the consumer population density C comes into play in the characteristic equations (19). The calculations show that, whatever the value of C, there is no subsequent change of u^*. Hence, in this situation, the optimal behavior of a consumer is (in natural time t): first, forage the resource only until the ratio of consumer's energy over the resource density reaches the switching curve, and then reproduce only until the end of the season.

A critical case arises when $x_T = 1/4$: the corresponding trajectory of the characteristic equations (19) is tangent to the curve (22) at $t' = \log(2)$, *i.e.* right at the moment it ceases to be a switching curve, at the value $\bar{x} = 1/2$. At this point on the optimal trajectory, not only do we have $\mathscr{A} = 0$ by definition of the switching curve, but one can also show that $d\mathscr{A}/dt = 0$ so that we cannot conclude anything about u^*.

The analysis of the optimal behavior presented above is shown on Figure 1. Computations are done for a typical consumer population density C. What has been calculated so far corresponds to the light-shaded area. However there is still a large part of the (t', x) plane in which we do not know what the optimal behavior is.

The critical case identified at the point $(\log(2), \bar{x})$ indicates the possible emergence of a singular trajectory corresponding to an optimal foraging ratio u^* which is a mixed reproduction-foraging behavior, *i.e.* u^* lies strictly between 0 and 1. From equation (18), for such a singular behavior to be optimal, a consumer should make the quantity $\mathscr{A} = 0$ invariant with respect to the reverse time t'. Denote this singular optimal foraging ratio u^σ, then, for the invariance property to hold, it is at least required that

$$\mathscr{A}(u^\sigma) = 0, \ \ \frac{d\mathscr{A}}{dt'}(u^\sigma) = 0, \text{ and } \ \frac{d^2\mathscr{A}}{dt'^2}(u^\sigma) = 0.$$

From the first two equations we can infer the values of the conjugate variables λ_E and λ_R on the singular trajectory. We get that $\lambda_E = 1 - x$ and $\lambda_R = (1 - 2x)/C$. If we substitute these values into the last equation, we recover the value of the singular foraging ratio

$$u^{\sigma} = \frac{2x}{xC+2}.$$

The corresponding singular trajectory can be computed from the energy-resource ratio x dynamics in reverse time t' and the u^{σ} expression. We get that the singular trajectory is the solution of the ordinary differential equation

$$\frac{dx}{dt'} = -\frac{x^2 C}{xC+2}, \tag{24}$$

with an initial condition at the critical point $(\log(2), \bar{x})$. Then the singular trajectory corresponding to the foraging ratio u^{σ} can be written as, for $t' \geq \log(2)$

$$t' = -\log(x) + \frac{2}{xC} - \frac{4}{C} \;. \tag{25}$$

To guarantee that u^{σ} is optimal on the singular trajectory (25), two other conditions must be checked. First u^{σ} along the trajectory (25) must lie between 0 and 1 (this holds since, from (24), x decreases from $\bar{x} = 1/2$ on this trajectory). Second, the so-called ‘Kelley-condition’ (Melikyan 1998) must also be fulfilled, *i.e.* one must have $\frac{\partial}{\partial u}\left(\frac{d^2\mathscr{A}}{dt^2}\right) \geq 0$, on the singular trajectory (25). Some elementary algebra show that this condition holds true, so that u^{σ} is optimal on (25).

To complete the computation of the optimal behavior problem, we only have to emit trajectories of the characteristic system (19) from the singular trajectory (25) with $u^* = 0$ and $u^* = 1$, to fill the (t', x) plane with optimal trajectories as is done on Figure 1.

Appendix B Computation of $C_{n+1}(0)$ and $R_{n+1}(0)$

B.1 Short seasons

If $T < \tilde{T}(C_n(0))$, we have seen that solutions with initial conditions satisfying (5) are of the bang-bang type with only one switch. In order to compute the switching time t_{10}, where $u(t)$ switches from the value 1 to the value 0, it then suffices to evaluate when $x_n(t)$ reaches the switching curve (23), defined as $x_n(t) = 1 - e^{-(T-t)}$. Solving (10) with $u = 1$ and initial condition $x_n(0) = 0$ then imposes that the switching instant must satisfy

$$\frac{e^{(C_n(0)-1)t_{10}} - 1}{C_n(0) - 1} = 1 - e^{-(T-t_{10})}. \tag{26}$$

From this, we cannot extract a simple analytical expression of t_{10}, but it uniquely defines it. With that implicit definition of t_{10}, the integrals can easily be computed since, before the switching instant, $E_n(t)$ and $R_n(t)$ are the solutions of (8) with $u = 1$:

$$\begin{aligned} E_n(t) &= \frac{R_n(0)}{C_n(0)-1}(e^{-t} - e^{-C_n(0)t}), \\ R_n(t) &= R_n(0)e^{-C_n(0)t}, \end{aligned}$$

while, after t_{10}, $u = 0$ imposes

$$\begin{aligned} E_n(t) &= \frac{R_n(0)}{C_n(0)-1}(e^{-t_{10}} - e^{-C_n(0)t_{10}})e^{-(t-t_{10})}, \\ R_n(t) &= R_n(0)e^{-C_n(0)t_{10}}, \end{aligned}$$

Taking into account these expressions, the integrals can easily be computed and the number of offspring that can reproduce during the next season is

$$C_{n+1}(0) = \frac{\alpha\theta}{a}\frac{C_n(0)R_n(0)}{C_n(0)-1}(e^{-t_{10}} - e^{-C_n(0)t_{10}})(1-e^{-(T-t_{10})}),$$

and

$$R_{n+1}(0) \quad = \quad \frac{\beta\gamma}{a}R_n(0)\left(\frac{1-e^{-C_n(0)t_{10}}}{C_n(0)} + e^{-C_n(0)t_{10}}(T-t_{10})\right).$$

These expressions explicitly depend on t_{10} which, as is seen from (26), only depends on $C_n(0)$ and T. The way $C_{n+1}(0)$ and $R_{n+1}(0)$ depend on $C_n(0)$ and T is therefore quite complex. Their main feature is thus their linear dependency in $R_n(0)$.

B.2 Long seasons

In the case where $T > \tilde{T}(C_n(0))$, the computations are essentially the same except that we have to deal with the singular arc (24), which leads to an increased complexity. The first switching instant $t_{1\sigma}$ is here defined as the moment $u_n(t)$ switches from the value 1 to the singular control. It occurs at the moment at which a solution $x_n(t) = \frac{e^{(C_n(0)-1)t}-1}{C_n(0)-1}$ of (10) with $u = 1$ reaches the singular arc so that it satisfies the equation

$$-\log\left(\frac{e^{(C_n(0)-1)t_{1\sigma}}-1}{C_n(0)-1}\right) + \frac{2(C_n(0)-1)}{C_n(0)(e^{(C_n(0)-1)t_{1\sigma}}-1)} - \frac{4}{C_n(0)} \quad = \quad T - t_{1\sigma} \tag{27}$$

The switching instant from the singular solution to the zone of exclusive reproduction then takes place at the end of the singular arc, so that it always occurs at time $(T-\log(2))$.

We will then explicitly compute the number of offspring through an evaluation of the contribution of each part of the optimal solution. For the consumer, we need to compute

$$\frac{\alpha\theta}{a}C_n(0)\left[\int_{t_{1\sigma}}^{T-\log(2)}(1-u^{\sigma}(t))E_n(t)\,dt+\int_{T-\log(2)}^{T}E_n(t)\,dt\right].$$

The computation requires that we notice that, along the singular arc the dynamics are described by

$$\begin{aligned}\frac{dE_n}{dt} &= -E_n+R_nu^{\sigma} &&= -\frac{E_n^2C_n(0)}{E_nC_n(0)+2R_n},\\ \frac{dx_n}{dt} &= \frac{x_n^2C_n(0)}{x_nC_n(0)+2} &&= \frac{E_n^2C_n(0)}{R_n(E_nC_n(0)+2R_n)},\end{aligned}$$

so that we have

$$\frac{dE_n}{dt}=-R_n\frac{dx_n}{dt}=-\frac{E_n}{x_n}\frac{dx_n}{dt},$$

which imposes that $E_n(t)x_n(t)=R_n(t)x_n^2(t))$ is constant along the singular arc (e.g. at the value $E_n(t_{1\sigma})x_{1\sigma}$). Using this constancy and the x_n dynamics along the singular arc, we can compute the first integral as

$$\begin{aligned}\int_{t_{1\sigma}}^{T-\log(2)}(1-u^{\sigma})E_n\,dt &= \int_{x_{1\sigma}}^{1/2}\left(1-\frac{2x_n}{x_nC_n(0)+2}\right)\frac{E_n(t_{1\sigma})x_{1\sigma}}{x_n}\frac{x_nC_n(0)+2}{x_n^2C_n(0)}\,dx_n,\\ &= -E_n(t_{1\sigma})x_{1\sigma}\frac{x_nC_n(0)+1-2x_n}{x_n^2C_n(0)}\bigg|_{x_{1\sigma}}^{1/2},\\ &= E_n(t_{1\sigma})x_{1\sigma}\left(\frac{x_{1\sigma}C_n(0)+1-2x_{1\sigma}}{x_{1\sigma}^2C_n(0)}-2\right),\\ &= \frac{R_n(t_{1\sigma})}{C_n(0)}(1-2x_{1\sigma})(x_{1\sigma}C_n(0)+1).\end{aligned}$$

Noting that $E_nx_n|_{t=t_{1\sigma}}=E_nx_n|_{t=T-\log(2)}=E_n(T-\log(2))/2$, we can now compute the second integral as

$$\int_{T-\log(2)}^{T}E_n(T-\log(2))e^{T-\log(2)-t}\,dt=\frac{E_n(T-\log(2))}{2}=R_n(t_{1\sigma})x_{1\sigma}^2$$

Finally, the number of consumers offspring is then

$$C_{n+1}(0) = \frac{\alpha\theta}{a} C_n(0) R_n(t_{1\sigma}) \left(x_{1\sigma}^2 + \frac{(1-2x_{1\sigma})(x_{1\sigma}C_n(0)+1)}{C_n(0)} \right).$$

In order to compute $R_{n+1}(0)$ we now have to evaluate three integrals. During the first phase $\dot{R}_n = -C_n(0)R_n$ so that

$$\int_0^{t_{1\sigma}} R_n \, dt = R_n(0)(1 - e^{-C_n(0)t_{1\sigma}}).$$

The final phase where $u = 0$ yields a constant value of $R_n(t) = R_n(T - \log(2)) = 4R_n(t_{1\sigma})x_{1\sigma}^2$ (where we have used the constancy of $R_n(t)x_n^2(t)$ along the singular arc and $x_n(T - \log(2)) = \frac{1}{2}$). The resulting integral is then

$$\int_{T-\log(2)}^{T} R_n \, dt = 4R_n(t_{1\sigma})x_{1\sigma}^2 \log(2).$$

Finally, we can compute

$$\begin{aligned}
\int_{t_{1\sigma}}^{T-\log(2)} R_n \, dt &= \int_{x_{1\sigma}}^{1/2} \frac{E_n(t_{1\sigma})x_{1\sigma}}{x_n^2} \frac{x_n C_n(0) + 2}{x_n^2 C_n(0)} \, dx_n, \\
&= E_n(t_{1\sigma})x_{1\sigma} \left(\frac{2}{3x_n^3 C_n(0)} + \frac{1}{2x_n^2} \right) \Bigg|_{1/2}^{x_{1\sigma}}, \\
&= R_n(t_{1\sigma})x_{1\sigma}^2 \left(\frac{2(1-8x_{1\sigma}^3)}{3x_{1\sigma}^3 C_n(0)} + \frac{1-4x_{1\sigma}^2}{2x_{1\sigma}^2} \right).
\end{aligned}$$

Finally, we can sum these three integral terms and obtain the number of reproducing resource offspring at the beginning of the next season:

$$\begin{aligned}
R_{n+1}(0) = \frac{\beta\gamma}{a} \Big[& R_n(0)(1 - e^{-C_n(0)t_{1\sigma}}) + 4R_n(t_{1\sigma})x_{1\sigma}^2 \log(2) \\
& + \frac{R_n(t_{1\sigma})(1-2x_{1\sigma})(4 + 8x_{1\sigma} + 16x_{1\sigma}^2 + 3x_{1\sigma}C_n(0)(1+2x_{1\sigma}))}{6x_{1\sigma}C_n(0)} \Big].
\end{aligned}$$

Computations in the line of what was done for the short season then lead to

$$C_{n+1}(0) = \frac{\alpha\theta}{a} R_n(0) C_n(0) e^{-C_n(0)t_{1\sigma}} \left(x_{1\sigma}^2 + \frac{(1-2x_{1\sigma})(x_{1\sigma}C_n(0)+1)}{C_n(0)} \right),$$

and

$$\begin{aligned} R_{n+1}(0) = \frac{\beta\gamma}{a} R_n(0) \Bigg(& \frac{1-e^{-C_n(0)t_{1\sigma}}}{C_n(0)} + 4e^{-C_n(0)t_{1\sigma}} x_{1\sigma}^2 \log(2) \\ & + \frac{e^{-C_n(0)t_{1\sigma}}(1-2x_{1\sigma})(4+8x_{1\sigma}+16x_{1\sigma}^2+3x_{1\sigma}C_n(0)(1+2x_{1\sigma}))}{6x_{1\sigma}C_n(0)} \Bigg), \end{aligned}$$

where $x_{1\sigma} = \frac{e^{(C_n(0)-1)t_{1\sigma}}-1}{C_n(0)-1}$ is the value of $x_n(t)$ at the first switching instant. Again, the only straightforward dependency is the linearity of both expressions in $R_n(0)$.

Appendix C Computation of the bifurcation curves

One can directly derive from (15) that $(0,0)$ is a trivial equilibrium for any ρ_R and T. There may also exist a positive equilibrium (C^*, R^*) which is the solution of

$$\rho_C R^* \Phi_C(C^*, T) = 1, \text{ and } \rho_R \Psi_R(C^*, T) = 1. \tag{28}$$

Before going any further into the analysis of these equilibria, we need to analyze the properties of the functions $\Phi_C(C,T)$ and $\Psi_R(C,T)$. The latter has been shown numerically to be a decreasing function of $C_n(0)$. For $\Phi_C(C,T)$, it can be shown analytically that $C_{n+1}(0)$ is an increasing function of $C_n(0)$ while the per capita number of offspring is a decreasing function of $C_n(0)$. Since $C_{n+1}(0)$ is proportional to $C_n(0)\Phi_C(C_n(0),T)$, it ensues that

$$-\Phi_C < C\frac{\partial \Phi_C}{\partial C} < 0 \tag{29}$$

Onto the bifurcation analysis, since $\Psi_R(.)$ is a decreasing function of C, and tends to 0 as C tends to infinity, a positive equilibrium exists, and is unique, if and only if $\rho_R \Psi_R(0,T) > 1$. The LHS of this equation is actually the *per capita* number of resource offspring in the absence of consumers. In such a situation, the resource population stays constant throughout the season (equation (8)) so that, from the second equation in (14), $R_{n+1}(0) = \rho_R T R_n(0)$. This directly yields that $\Psi_R(0,T) = T$ for all T. This allows us to define a first bifurcation curve $\rho_R^*(T)$ such that $\rho_R = 1/T$. If $\rho_R < 1/T$, the only equilibrium of the model is $(0,0)$. It is moreover globally asymptotically stable since with $\rho_R < 1/T$ the resource goes to extinction by itself, and drives any consumer population to 0 as well. If $\rho_R > 1/T$, the positive equilibrium (C^*,R^*) exists; whether it is stable or not requires further considerations that are presented in what follows. Anyway, we can show through Taylor expansion techniques, that if ρ_R is larger than $(1/T)$, but still close to it, the positive equilibrium is unstable.

We identified two additional bifurcation curves. The first one, denoted $\rho_R^\circ(T)$ corresponds to a Neimark-Sacker bifurcation (Wiggins 2003) in which the stability of the positive equilibrium changes, with the eigenvalues of its associated Jacobian matrix being complex conjugate and crossing the unit circle: a periodic (or quasi-periodic) orbit emanates from the equilibrium point as the parameters ρ_R and T cross the bifurcation curve $\rho_R^\circ(T)$. Such a periodic or quasi-periodic orbit can be stable or unstable. A necessary condition for a Neimark-Sacker bifurcation to occur is that the determinant of the Jacobian matrix associated to the equilibrium point (C^*,R^*) is equal to 1 with complex conjugate eigenvalues. Writing the Jacobian matrix of (15) gives:

$$\begin{pmatrix} \rho_C R_n(0)\,\Phi_C(C_n(0),T) + \rho_C C_n(0) R_n(0)\,\frac{\partial \Phi_C(C_n(0),T)}{\partial C} & \rho_C C_n(0)\,\Phi_C(C_n(0),T) \\ \rho_R R_n(0)\,\frac{\partial \Psi_R(C_n(0),T)}{\partial C} & \rho_R \Psi_R(C_n(0),T) \end{pmatrix}$$

Computing the determinant at equilibrium and writing the constraint for a Neimark-Sacker bifurcation yields

$$\rho_C R^* \Phi_C(C^*,T)\rho_R \Psi_R(C^*,T) + \rho_C C^* R^* \frac{\partial \Phi_C(C^*,T)}{\partial C}\rho_R \Psi_R(C^*,T) \\ - \rho_R R^* \frac{\partial \Psi_R(C^*,T)}{\partial C}\rho_C C^* \Phi_C(C^*,T) = 1$$

Noting that the first term is equal to 1 thanks to (28), we see that this condition can be conveniently rewritten as

$$\left[\frac{1}{\Phi_C}\frac{\partial \Phi_C}{\partial C}\right]_{(C^*,T)} = \left[\frac{1}{\Psi_R}\frac{\partial \Psi_R}{\partial C}\right]_{(C^*,T)},$$

which combined with the second equation of (28) defines the bifurcation curve $\rho_R^{\circ}(T)$.

Elementary computations indicate that the eigenvalues of the Jacobian matrix at equilibrium are complex conjugate if $4 + \rho_C C^* R^* \frac{\partial \Phi_C(C^*,T)}{\partial C} > 0$. In fact, thanks to (29), we have

$$4 + \rho_C C^* R^* \frac{\partial \Phi_C(C^*,T)}{\partial C} > 4 - \rho_C R^* \Phi_C(C^*,T) = 3$$

so that the eigenvalues are complex conjugates and a Neimark Sacker bifurcation generically occurs when crossing the $\rho_R^{\circ}(T)$ curve. We actually found that if T is large, the Neimark-Sacker bifurcation is super-critical, *i.e.* the periodic orbit is stable, while it is sub-critical if T is small, *i.e.* the periodic orbit is unstable.

This last property set us on the trail of another bifurcation curve. This bifurcation actually corresponds to the fact that the periodic or quasi-periodic orbits arising from the Neimark-Sacker bifurcation grow larger and larger and finally escape to infinity and the boundaries of the positive orthant. This curve, which we will denote $\rho_R^{\infty}(T)$, can only be numerically estimated and is thus less accurately defined than the other two.

Figure 1:

Optimal behavior pattern of a consumer presented in the (t', x) plane for a typical consumer population density C. Solid lines represent optimal trajectories of model $(8,9)$. The dash-dotted line is the singular trajectory corresponding to the mixed foraging ratio $u^* = u^\sigma$. Arrows indicate how trajectories are followed in natural time t. The dashed line is the switching curve (11) and the dashed-dotted line is the singular trajectory (12). The shaded area corresponds to the first part of the computation in Appendix A. Black dots (i) to (iv) correspond to x_0 and T yielding the different kinds of behaviors described in the text. The bold trajectory starting at $t' = \tilde{T}(C)$ and $x = 0$ separates behavior patterns of consumers starting the season with $E = 0$ between "determinate" (when $\tilde{T}(C) < T$) and "indeterminate" (when $\tilde{T}(C) > T$) strategies. See the text for computations and comments.

Figure 2:

Illustration of determinate (left column) and indeterminate (right column) consumer's behavioral strategies during a season with consumer energy E (upper row) and resource density (lower row) with respect to within-season natural time t. Pure strategies (foraging only and reproduction only) are represented with plain lines, mixed strategies with dashed dotted lines. In both of these cases, the season length T is equal to 1.2 (dimensionless units), and the simulations only differ by the number of consumers in the system: $C = 0.8$ (case (a), dimensionless units) and $C = 15$ (case (b)). This shows that density dependence influences the type of strategy adopted by the consumers.

Figure 3:

Bifurcation diagram of model $(1, 4\text{-}6)$ in the (T, ρ_R) plane. The ρ_R axis is in log scale while the T axis is in linear scale. The methods used to compute the different bifurcation curves $\rho_R^*(T)$, $\rho_R^\circ(T)$ and $\rho_R^\infty(T)$ are detailed in the text. These curves define regions of the plane where the model has different dynamical behavior: extinction of the populations (I), co-existence through sustained oscillations (II), over-exploitation of the resource resulting in population crashes (III), co-existence at a season-to-season equilibrium for some initial conditions (IV), or for any (V). These behaviors are illustrated on the bifurcation diagram by schematic representations of the corresponding $(C_n(0), R_n(0))$ multi-season phase planes trajectories. On the right of the vertical line $T = 2\log(2)$, only indeterminate strategies can occur.

Figure 4:

Temporal dynamics of model (1,4-6) displaying both within season and between season dynamical behaviors of the consumer population C (top row), their internal energy E (middle row) and the resource population R (bottom row). Pure strategies (foraging only or reproduction only) are represented with plain lines, mixed strategies with dashed dotted lines. Vertical dashed lines in the consumer and resource population dynamics represent the death of the individuals at the end of a season. Case (a): season-to-season damped oscillations and convergence to an equilibrium in population densities corresponding to parameters in region V in the bifurcation diagram (Figure 3) with $\rho_R = 4.5$ and $T = 2.4$ (dimensionless units). A temporal gap is inserted to facilitate the reading and illustrate the transients and the convergence toward the equilibrium. Case (b): sustained oscillations in population densities corresponding to parameters in region II in the bifurcation diagram (Figure 3) with $\rho_R = 1.6$ and $T = 2$ (dimensionless units).

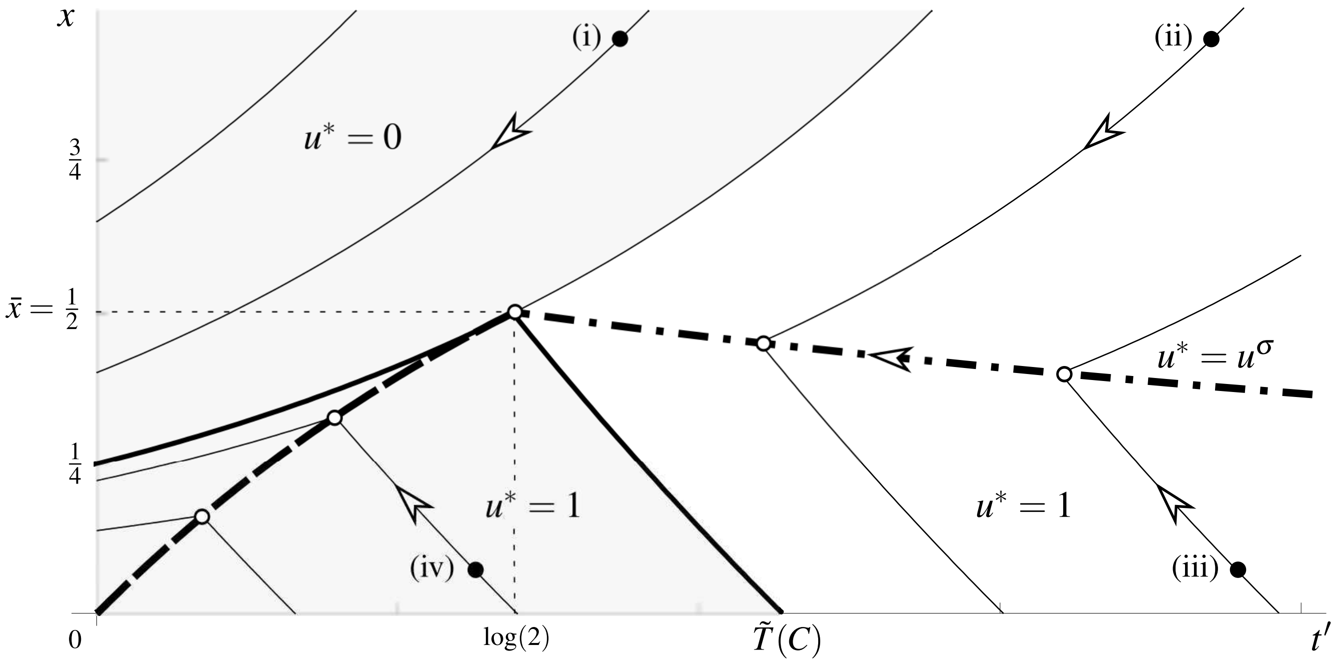
x
$\frac{3}{4}$
$\bar{x} = \frac{1}{2}$
$\frac{1}{4}$
0
log(2)
$\tilde{T}(C)$
t'
(i)
(ii)
(iii)
(iv)
$u^* = 0$
$u^* = 1$
$u^* = 1$
$u^* = u^\sigma$

Figure 1

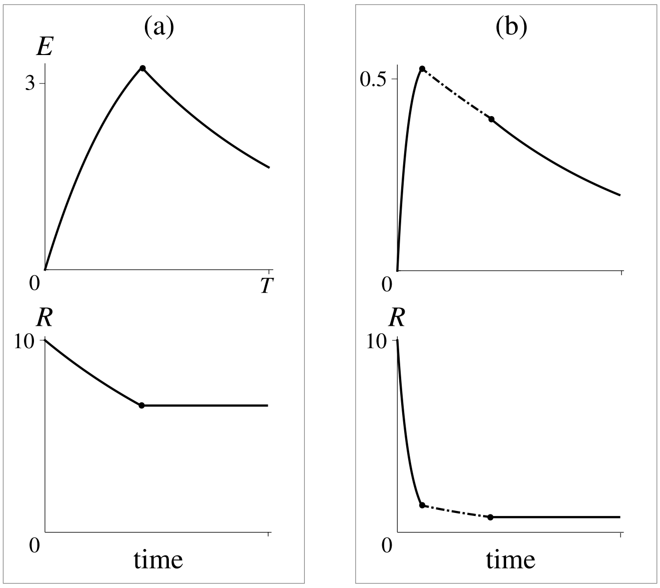

Figure 2

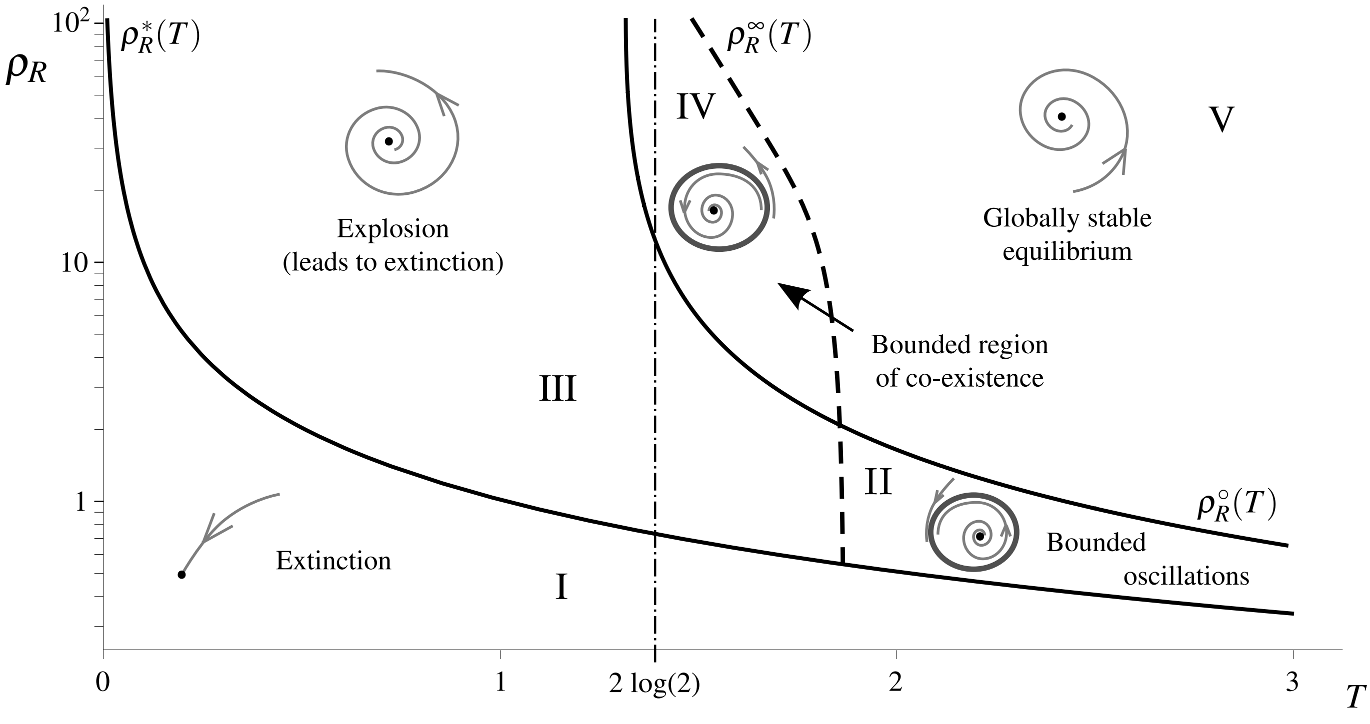
ρ_R
10^2
10
1
$\rho_R^*(T)$
$\rho_R^\infty(T)$
$\rho_R^\circ(T)$
IV
V
III
II
I
Explosion
(leads to extinction)
Globally stable
equilibrium
Bounded region
of co-existence
Bounded
oscillations
Extinction
0
1
2 log(2)
2
3
T

Figure 3

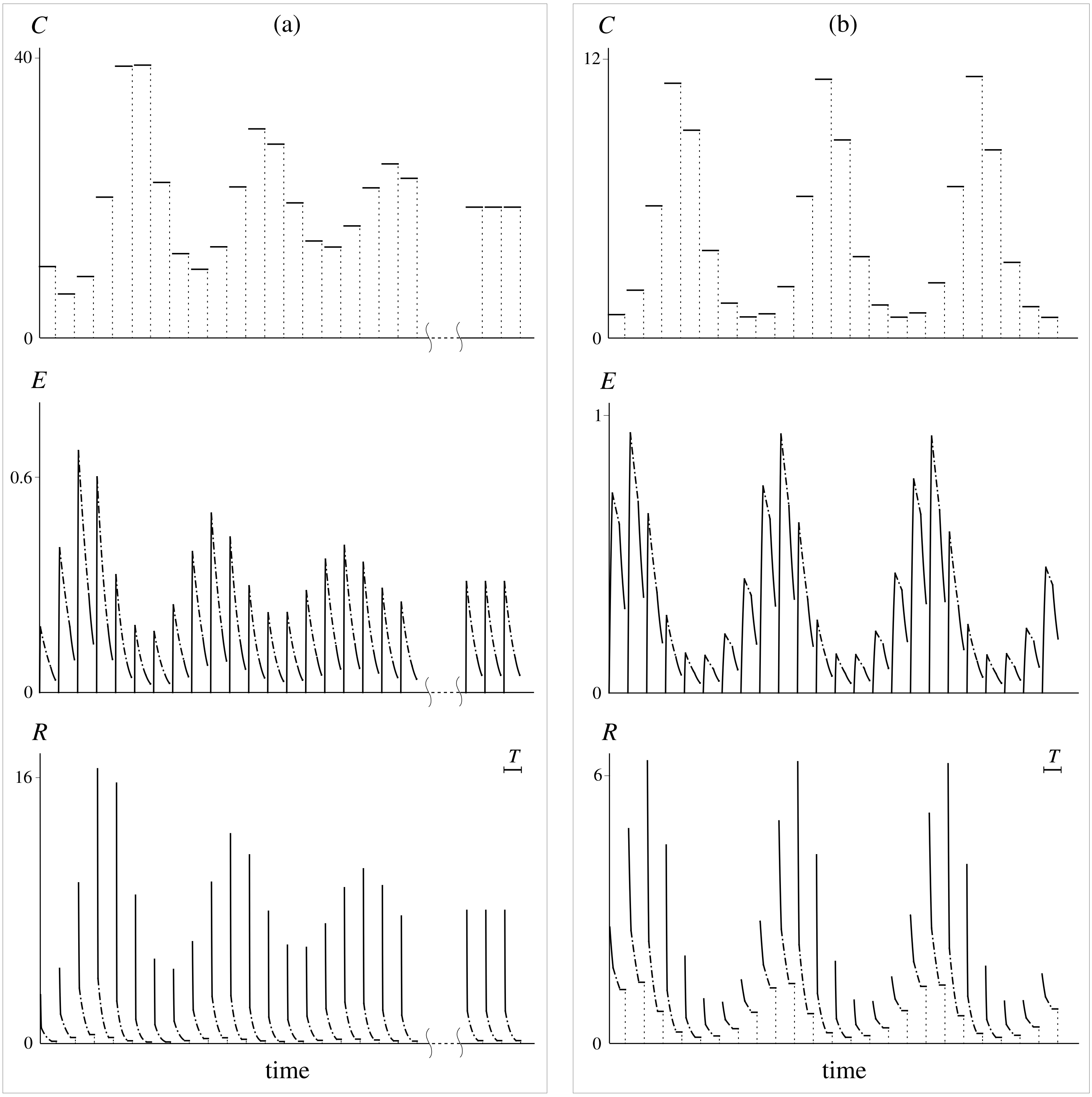

Figure 4