OPTIMAL LIFE-HISTORY STRATEGIES IN SEASONAL CONSUMER-RESOURCE DYNAMICS

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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 nonoverlapping 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, coexistence 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 nonoptimal consumers highlighted the stabilizing effects of the optimal life histories of the consumers.

KEY WORDS: Foraging-reproduction trade-off, individual behavior, population dynamics, semi-discrete model.

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 plasticly 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, because 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 relatively simplicity and the mathematical tractability of the models, but they cannot 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) and Murdoch et al. (2003). Semi-discrete models explicitly assume that intragenerational processes such as foraging, predation etc. are of a continuous nature, whereas intergenerational 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 intragenerational level as well as its consequences at the intergenerational 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, whereas the consumer individuals have to trade-off between foraging for resources to increase their reproductive capacities or investing in reproduction 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, whereas 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 also 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 (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, that is 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 intergenerational dynamical patterns of the model as consumers follow such an adaptive optimal strategy and compare these to those produced by typical “nonoptimal” consumers.

**The Model**

Following Takimoto (2003) and 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 acquire 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.

**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, that is 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, leads to recover a classical “energy conservation” principle. These assumptions yield the following within-year $n$ model (dependence in $t$ is omitted):

$$\frac{dC_n}{dt} = 0,$$

$$\frac{dE_n}{dt} = -aE_n + bR_n u_n,$$

$$\frac{dR_n}{dt} = -cR_n u_n R_n C_n, \quad (1)$$

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 costs of reproducing and of foraging are equal.

**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 $\nu$ throughout the season, so that the total number of immature resources produced during year $n$ is

$$\int_0^T \nu R_n(\tau) d\tau. \quad (2)$$

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 $\int_0^T (1 - u_n(\tau))E_n(\tau)C_n(\tau) d\tau$, where $\nu$ 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). Because from model (1) mature consumers population is constant throughout a season, the total number of immature consumers produced during year $n$ reduces to

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

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

$$C_{n+1}(0) = \alpha \theta C_n(0) \int_0^T (1 - u_n(\tau))E_n(\tau) d\tau,$$

$$R_{n+1}(0) = \beta \gamma \int_0^T R_n(\tau) d\tau, \quad (4)$$

with $\alpha$ and $\beta$, respectively, the proportion of immature consumers and resources that survive 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

$$E_{n+1}(0) = 0. \quad (5)$$
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, that is its lifetime reproductive success $R_0$ (Schaffer 1983; Perrin and Sibly 1993; Perrin et al. 1993; Kozlowski 1993; Ejsmond et al. 2010); see others (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 $u_c(t)$ solving

$$\max_{u_c(t) \in \mathcal{U}} \left( a \int_0^T \left( 1 - u_c(\tau) \right) E_c(\tau) d\tau \right),$$

with $\mathcal{U}$ the set of measurable functions from $[0, T]$ to $[0, 1]$. Such an assumption on the admissible $u_c(t)$ 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 because except for birds, insects, or mammals, indeterminate 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 because 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 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 apply fairly well to annual producer–grazer systems, in which the grazer can plastically respond to its environment, such as 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 (eq. 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 article 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.

Within-Year Dynamics

We analyze the optimal control problem presented above and defined by (1) and (6) for all initial conditions $C_c(0)$, $E_c(0)$ 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.

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 not useful for 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

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

so that model (1) is equivalent to

$$\begin{align*}
\frac{dE}{dt} &= -E + uR, \\
\frac{dR}{dt} &= -uRC.
\end{align*}$$

In this model, $t$ and $C$ are dimensionless quantities whereas $E$ and $R$ are expressed in “energy” units. Dividing these two variables by one unit of energy renders model (8) dimensionless. Because 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 $u_c(t)$ on $[0, T]$ that solves

$$\max_{u_c(t) \in \mathcal{U}} \int_0^T \left( 1 - u_c(\tau) \right) E_c(\tau) d\tau.$$
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

\[
\frac{dx}{dt} = (uC - 1) x + u \quad (10)
\]

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

**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), and 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 S1.

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 for resources. The curve separating the two regions is composed of a “switching curve” (dashed-line) whose equation reads

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

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

\[
t' = -\log(2) \frac{C}{x} \quad \text{for} \ t' \geq \log(2) \quad (12)
\]

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

\[
u^\sigma = \frac{2x}{x C + 2},
\]

which makes the model trajectories follow the singular line.

Generically, depending on the initial consumer energy over 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 (1) and (2) can be interpreted as follows (we comment on (3) and (4) below): (1), if at the beginning of a season, \( x_0 \)...
is large, that is the initial consumer energy is large compared to the initial resource density, and the season is short, it is not useful for a consumer to forage for resources. The energy gained through foraging is not worth the time wasted not reproducing. (2), if the season is long, foraging for resources is still not useful at the beginning of the season. However, as the consumer energy decreases and drives the x-ratio toward the singular trajectory (12) it turns out to be more efficient to follow a mixed reproduction-foraging behavior to increase the x-ratio until it reaches \( x = T - \log(2) \), and then switch back to reproduction only.

Although 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 \( x_0 = 0 \).

**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 \( u^{\text{opt}} \). Because \( x_0 = 0 \) 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 S2 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 (11), 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 acquiring 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 \( E \) 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, contrary 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

\[
\tilde{T}(C) = \frac{\log(C + 1) + (C - 2)\log(2)}{C - 1},
\]

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. Although seasonality, and especially season 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 modeled through parameter \( C \): nonconstant environment, because 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 \( \tilde{T}(\cdot) \) 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

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OPTIMAL LIFE-HISTORY STRATEGIES

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.

$T$, but with different consumer densities $C$, in Figure 2. Notice however that from (13), $T(C)$ 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 Long-Term Dynamics, subsection Bifurcation Analysis).

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

COMPUTATION OF THE NUMBER OF OFFSPRING

The number of offspring for the consumer and the resource populations of season $(n + 1)$ is computed as

$$C_{n+1}(0) = \frac{a_0}{a} C_n(0) \int_0^T (1 - u^c_\tau(\tau)) E_n(\tau) d\tau,$$

$$R_{n+1}(0) = \frac{\beta_\tau}{a} \int_0^T R_n(\tau) d\tau.$$

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 S2). We can thus write the complete model (1, 4–6) in the compact form

$$C_{n+1}(0) = \rho_C C_n(0) R_n(0) \Phi_C(C_n(0), T),$$

$$R_{n+1}(0) = \rho_R R_n(0) \Psi_R(C_n(0), T).$$

where $\rho_C = a_0/a$, and $\rho_R = \beta_\tau/a$. The functions $\Phi_C(\cdot)$ and $\Psi_R(\cdot)$ have complicated forms but are dependent on $C_n(0)$ and $T$ only (see Appendix S2). Due to this complexity, we needed to rely on numerical simulations to confirm our intuition that both $\Phi_C(\cdot)$ and $\Psi_R(\cdot)$ 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 consumer density $C_n(0)$, and that it decreases to 0 as $C_n(0)$ becomes large; so does $\Psi_R(\cdot)$. Similarly, we obtained analytically that $C_{n+1}(0)$ is an increasing function of $C_n(0)$, whereas the per-capita number of consumer offspring $\frac{C_{n+1}(0)}{C_n(0)}$ 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.

BIFURCATION ANALYSIS

One can notice from equations (15) that the long-term (multi-seasonal) dynamics of model (1, 4–6) depend upon the parameters $\rho_R, \rho_C$, and $T$ only. Actually, the dependence in $\rho_C$ can even be omitted through a change in the resource units. Indeed, redefining the resource as $R_n \overset{\text{def}}{=} \rho_C R_n$ does not change the model but eliminates $\rho_C$ from (15), a situation that is exactly similar to the classical model by Nicholson and Bailey (1935). It is thus only necessary to analyze the influence of $\rho_R$ and $T$ on the dynamics of model (1, 4–6), so that the results can be presented with a bifurcation diagram in the $(T, \rho_R)$ plane. We detail the mathematics employed to compute the bifurcations in Appendix S3.

The bifurcation diagram in the $(T, \rho_R)$ plane is presented in Figure 3. The bifurcation curves $\rho_R^L(T)$, $\rho_R^T(T)$, and $\rho_R^U(T)$ define five regions in which the behaviors of model (1, 4–6) 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 $\rho_R^L(T)$, an unstable
positive equilibrium appears; this is similar to overexploitation of the resource by the consumer population as displayed for example 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 $\rho_R^*(T)$. From region III, increases in the parameters $\rho_R$ 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 $\rho_R$ and $T$ lead to region V in which the dynamical behavior is much simpler because both populations converge globally to a stable season-to-season equilibrium point.

Fig. 3. Bifurcation diagram of model (1,4–6) in the $(T, \rho_R)$ plane. The $\rho_R$ axis is in log scale while the $T$ axis is in linear scale. The methods used to compute the different bifurcation curves $\rho_R^*(T)$, $\rho_R^0(T)$ and $\rho_R^\infty(T)$ are detailed in Appendix S3. These curves define regions of the plane where the model has different dynamical behaviors: extinction of the populations (I), coexistence through sustained oscillations (II), over-exploitation of the resource resulting in population crashes (III), coexistence 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.

**NONOPTIMAL CONSUMERS**

To evaluate the significance of the previous investigations, we compared the long-term dynamics produced by the model with optimal consumers (1,4–6) to long-term dynamics obtained with consumers adopting a nonoptimal behavior. As a benchmark,
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).

We considered that the nonoptimal consumers behave constantly along any season: they dedicate a fixed fraction \( \tilde{u} \in (0, 1) \) of their time to foraging for resources, whereas the other part \((1-\tilde{u})\) is allotted 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:

\[
\begin{align*}
C_{n+1}(0) &= \rho_C R_n(0) \frac{(1-\tilde{u})(C_n(0)\tilde{u}(1-e^{-T})-(1-e^{-C_n(0)\tilde{u}T}))}{C_n(0)\tilde{u} - 1}, \\
R_{n+1}(0) &= \rho_R R_n(0) \frac{1-e^{-C_n(0)\tilde{u}T}}{C_n(0)\tilde{u}}.
\end{align*}
\]

where the energy equation is useless because \( E_{n+1}(0) = 0 \) by assumption. It can easily be checked that model (16) pretty much resembles Nicholson and Bailey’s model, see (Murdoch et al. 2003) for example. It has actually the same dynamical properties: either \( \rho_R < 1/T \) and the resources go extinct and drive 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 \((T, \rho_R)\) 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.

**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 nonoverlapping 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).

**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 because these 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). We have shown that, although the former studies can only consider determinate-like life histories, whereas the latter can in addition address smooth transitions between life-history states, for example 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 for example 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).

**WITHIN-SEASON CONSUMER STRATEGIES**

Assuming that consumers behave optimally, in the sense that they maximize their expected lifetime reproductive success \( R_0 \), 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, whereas long season length promotes indeterminate strategies (see Perrin and Sibly 1993; Fig. 6). Moreover, we unveiled the influence of another important factor that is consumers density. Low consumer densities tend to select for determinate strategies, whereas large ones encourage indeterminate ones. As detailed in section Within-Year Dynamics, subsection Implications for Model (1,4–6), this influence stems from the coupling between a nonconstant environment and the explicit consideration of a population of consumers. To our knowledge, life-history modeling 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, 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, that is 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, for example, Takimoto (2003) and 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).

**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 nonsustainability of the resource dynamics, to a
globally stable coexistence season-to-season equilibrium between
customers and resources. We also observed extinctions of the
populations through overexploitation cycles, that is oscillations
of population densities of increasing amplitude, or coexistence
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’ indeter-
minate 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 Long Term Dynamics,
subsection Nonoptimal Consumers focused on a generation-to-
generation inflexible, that is nonplastic, behavior. This lead to a
highly unstable season-to-season pattern typical of the Nicholson
and Bailey model that implies both populations extinction. Such
dynamics should in fact be expected because nonplastic 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 that differs quantita-
tively if not qualitatively from their parents’ strategy. This adap-
tive optimal consumer behavior tends to promote persistence and
stability of the consumer-resource interaction, a property that is
actually rather generic in consumer-resource systems, see for ex-
ample (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 from reproducing sufficiently dur-
ing the season, eventually leading to a degraded environment for
their children [see e.g., Fig. 4 during transients (A) or on the pe-
riodic 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 becomes large, long-term dynamics
tend to get more stable and over-exploitation or cyclic behav-
ors 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, that is longer growing
seasons (Ims et al. 2008). In the present model, longer season
length increases the reproductive capacities of the resource (sec-
tion Long Term Dynamics, subsection Computation of the Num-
ber of Offspring) which in turn increases the optimal consumers
reproduction capacities as well. 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 becoming too large.
These effects act jointly to prevent the system from undergoing
over-exploitation cycles and appear thus to be central to the sta-
bilizing properties of the optimal adaptive life histories of the
consumers. This point is also supported by the fact that increasing
\( \rho_k \), which has positive effects on the resource reproductive
capacities as well, exhibits similar, but not equivalent, stabilizing
properties.

**FINAL WORDS**

A last remark should be made on the optimality principle we
considered in the maximization of \( R_0 \). 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.
\( R_0 \) 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 ex-
pected to maximize \( R_0 \) when density dependence and environ-
mental feedback are fairly simple (Mylius and Diekmann 1995).
This is for instance the case in (Gilchrist et al. 2006) which fo-
cused on saprophytic fungi life histories. This study has sub-
stantial similarities with ours. However, in the present work, the
resource-mediated feedback of the consumers onto their popu-
lation is actually more involved because 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
\( R_0 \) is then equivalent to assuming that every individual coop-
erates with the others in agreeing to adopt a common strategy
that 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, for example, Krivan and Sikder (1999); Van Baalen
et al. (2001), although the underlying cooperation assumptions
are not emphasized. This modeling 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 intergenerational
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 that can differ
from the optimal cooperative strategy. Analyzing whether
such defecting individuals may take advantage of the coopera-
tion agreement of the rest of the consumer population is par-
ticularly 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 the cooperators. This would undoubtedly complicate the analysis because this would require to solve a nonzero 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 literature. For instance, Eskola (2009) and Eskola et al. (2011) very recently studied the evolution of the timing of reproduction in a seasonal stage structured population model. Yet, their modeling 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. 2011). It seems thus that a comprehensive methodological framework has yet to be developed to tackle such complex problems. This constitutes a rather important, although probably difficult, avenue for future works.

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LITERATURE CITED