Join forces or cheat: evolutionary analysis of a consumer-resource system

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Abstract In this contribution we consider a seasonal consumer-resource system and focus on the evolution of consumer behavior. It is assumed that consumer and resource individuals live and interact during seasons of fixed lengths separated by winter periods. All individuals die at the end of the season and the size of the next generation is determined by the the consumer-resource interaction which took place during the season. Resource individuals are assumed to reproduce at a constant rate, while consumers have to trade-off between foraging for resources, which increases their reproductive abilities, or reproducing. Firstly, we assume that consumers cooperate in such a way that they maximize each consumer individual fitness. Secondly, we consider the case where such a population is challenged by selfish mutants who do not cooperate. Finally we study the system dynamics over many seasons and show that mutants eventually replace the original cooperating population, but are finally as vulnerable as the initial cooperating consumers.

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1 Introduction

Among the many ecosystems found on Earth, one can easily identify many examples of resource-consumer systems like *e.g.* plant-grazer, prey-predator or host-parasitoid systems known in biology [12]. Usually, individuals involved in such systems (bacteria, plants, insects, animals, *etc.*) have conflicting interests and models describing such interactions are based on principles of game theory [14, 8, 2, 7]. Hence, the investigation of such models is of interest to both game theoreticians and behavioral and evolutionary biologists.

One of the main topics of evolutionary theory is addressing whether individuals should behave rationally throughout their lifetime. Darwin's statement of the survival of the fittest indicates that evolution selects the best reproducers, so that the evolutionary process should result in selecting organisms which appear to behave rationally, even though they may know little about rationality. Evolutionary processes may thus result in organisms which actually maximize their number of descendants [17]; this is true in systems in which density dependence can be neglected, or in which the relation between the organisms and their environment is fairly simple [13]. Otherwise, such a rule may not apply and evolution is expected to yield a population which employs an evolutionarily stable strategy; such a strategy will not allow them to get the maximum possible number of descendants, but cannot be beaten by any strategy a deviant organism may choose to follow [10, 19]. In the following, since we will be concerned with populations in which some organisms may deviate from the others, we will use the terminology from Adaptive Dynamics [6] and designate by 'mutants' the organisms adopting a strategy different from the one of the main population, which will be referred to as the resident population.

In this work we study the fate of mutants based on an example of a seasonal consumer-resource system with optimal consumers as introduced by [1] using a semi-discrete approach [9]. In such a system, consumer and resource individuals are active during seasons of fixed length T separated by winter periods. To give an idea of what such a system could represent, the resource population could be annual plants and the consumer population some univoltine phytophagous insect species. All consumers and resources die at the end of the season and the size of the next generation is determined by the number of offspring produced during the previous season (*i.e.* offspring are made of seeds or eggs which mature into active stages at the beginning of the season). We assume that consumers have to share their time between foraging for resources, which increases their reproductive abilities, or reproducing. The reproduction of the resource population is assumed to occur at a constant rate.

In nature several patterns of life-history can be singled out, but they frequently contain two main phases: *growth phase* and *reproduction phase*. The transition between these two phases can be strict when the consumers only feed at the beginning of their life and only reproduce at the end, or there could exist an *intermediate phase* between them where growth and reproduction occur simultaneously. Such types of behaviors are called *determinate* and *indeterminate growth patterns* re-

spectively [15]. Time-sharing between laying eggs and feeding for the consumers will be modeled by the variable u: $u = 1$ means feeding, $u = 0$ on the other hand means reproducing. Intermediate values $u \in (0,1)$ describe a situation where, for some part of the time, the individual is feeding and, for the other part of the time, it is reproducing.

Firstly, we consider a population of consumers maximizing their common fitness, all consumers being individuals having the same goal function and *acting for the common good*; these will be the residents. We then suppose that a small fraction of the consumer population starts to behave differently from the main population, and accordingly will call them mutants. The aim of this paper is to investigate how mutants will behave in the environment shaped by the residents, and what consequences can be expected for multi-season consumer-resource systems.

2 Main model

2.1 Previous work

Let us first consider a system of two populations: resources and consumers without any mutant. The consumer population is modeled with two state variables: the average energy of one individual p and the number of consumers c present in the system, while the resource population is described solely by its density n. We suppose that both populations are structured in *mature* (adult insects/plants) and *immature* stages (eggs/seeds). During the season, mature consumers and resources interact and reproduce themselves. Between seasons (during winter periods) all mature individuals die and individuals become mature in the next season.

We suppose that no consumers have any energy ($p = 0$) at the beginning of the season. The efficiency of reproduction is assumed to be proportional to the value of p; it is thus intuitive that consumers should feed on the resource at the beginning and reproduce at the end once they have gathered enough energy. The consumers thus face a trade-off between investing their time in feeding ($u = 1$) or laying eggs ($u = 0$). According to [1], the within season dynamics are given by

$$\dot{p} = -\kappa p + \eta n u, \quad \dot{n} = -\delta c n u, \tag{1}$$

where we assume that neither population suffers from intrinsic mortality; κ, η and δ are constants. After rescaling the time and state variables, the constants κ and η can be eliminated and the system of equations (1) can be rewritten in the simpler form:

$$\dot{p} = -p + n u, \quad \dot{n} = -c n u, \tag{2}$$

where c is a rescaled parameter which is proportional to the number of consumers present in the system.
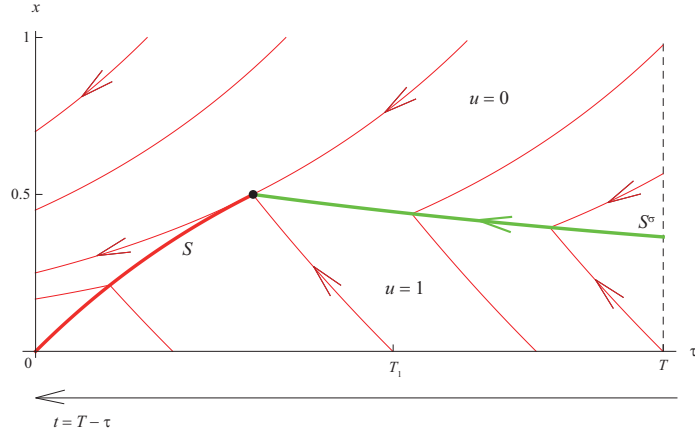
Fig. 1 Optimal collective behavior of the residents illustrated in the (τ, x) plane (see eq. (4)) where τ is reverse time. On the figure, solutions are then initiated at $(T, p(0)/n(0))$ where T is the length of the season.

The amount of immature offspring produced during the season depends on the sizes of the populations

$$J = \int_0^T \theta c (1 - u(t)) p(t) \, dt, \quad J_n = \int_0^T \gamma n(t) \, dt, \tag{3}$$

where θ and γ are constants.

We assume that consumers maximize the value J, their number of descendants, which is a classical measure of fitness. We see that this is an optimal control problem which can be solved using dynamic programming [3] or the Pontryagin maximum principle [16]. To compute the solution of this problem, the constants c, θ and γ can be omitted from (3), without loss of generality.

All the equations describing the problem are homogeneous of degree one in the state variables, which can be only positive. This is a particular case of Noether's theorem in the calculus of variations about problems which are invariant under a group of transformations [4]. Hence, the dimension of the phase space of the optimal control problem (2-3) can be lowered by one unit by the introduction of a new variable $x = p/n$. In this case its dynamics can be written in the form:

$$\dot{x} = -x(1 - cu) + u, \tag{4}$$

and the Bellman function $\tilde{U}(p, n, t) = \int_{T-t}^{T}(1 - u(s))p(s)ds$ with the starting point at $(p(t), n(t)) = (p, n)$ can be expressed as $\tilde{U}(p, n, t) = nU(x, t)$.

The solution of the optimal control problem (2-3) has been obtained in [1] and the optimal behavioral pattern for $c = 1.5$ and $T = 2$ is shown on Fig. 1. These solutions are not restricted to the case where consumers have no energy at the initial time. The region with $u = 1$ is separated from the region with $u = 0$ by a switching

curve S and a singular arc S^σ such that

$$S: \quad x = 1 - e^{-\tau} \tag{5}$$

$$S^\sigma: \quad \tau = -\log x + \frac{2}{xc} - \frac{4}{c}, \tag{6}$$

where $\tau = T - t$. They are shown on Fig. 1 by thick curves. Along the singular arc S^σ the consumer uses intermediate control $u = \hat{u}$:

$$\hat{u} = \frac{2x}{2 + xc}. \tag{7}$$

When $P(0) = 0$, one might identify a bang-bang control pattern for *short seasons* $T \leq T_1$ and a bang-singular-bang pattern for *long seasons* $T > T_1$. The value T_1 is computed as

$$T_1 = \frac{\log(c+1) + (c-2)\log 2}{c-1}, \tag{8}$$

so that it depends on the number of consumers present in the system.

The optimal value of the amount of offspring produced by an individual can be computed using this solution. In the following, we focus on the behavior of mutants appearing in a population of consumers adopting the type of behavior given in Fig. 1.

2.2 Consumer-mutant-resource system

Suppose that there is a subpopulation of consumers that deviate from the residents' behavior. Let us assume that these are selfish and maximize their own fitness, and not the fitness of the whole population, taking into account that the main resident population acts as if the mutants were kin (*i.e.* residents do not understand that mutants are selfish). This means that the residents adjust their strategy by changing the control whenever its level is intermediate. Such adjustment is possible only when some certain conditions are satisfied and mutant subpopulation is small enough (see section 3.2)

Denote the proportion of mutants in the whole population of consumers by ε and the variables describing the state of the mutant and resident populations by symbols with subscripts "m" and "r" respectively. Then the number of mutants and residents will be $c_m = \varepsilon c$ and $c_r = (1 - \varepsilon)c$ and the dynamics of the system can written as

$$\dot{p}_r = -p_r + nu_r, \quad \dot{p}_m = -p_m + nu_m, \quad \dot{n} = -nc\left[(1-\varepsilon)u_r + \varepsilon u_m\right], \tag{9}$$

similarly to (2). The variable $u_m \in [0, 1]$ defines the decision pattern of the mutants. The control $u_r \in [0, 1]$ is the decision pattern of the residents and defined by the solution of the optimal control problem (2-3).

The number of offspring in the next season is defined similarly to (3):

$$J_r = \int_0^T \theta(1 - u_r(t)) c_r p_r(t) \, dt, \ J_m = \int_0^T \theta(1 - u_m(t)) c_m p_m(t) \, dt, \ J_n = \int_0^T \gamma n(t) \, dt,$$

(10)

where the mutant chooses its control u_m striving to maximize its fitness J_m.

We can see that the problem under consideration is described in terms of a two-step optimal control problem (or a hierarchical differential game): in the first step we define the optimal behavior of the residents (see section 2.1), in the second step we identify the optimal response of the mutants to this strategy.

3 Optimal free-riding

Since θ and γ are constants, they can be omitted from the description of the optimization problem $J_m \to \max_{u_m}$. In this case the functional $J_m/(\theta c_m)$ can be taken instead of the functional J_m.

Let one introduce the Bellman function $\tilde{U}_m$ for the mutant population. It satisfies the Hamilton-Jacobi-Bellman (HJB) equation

$$\frac{\partial \tilde{U}_m}{\partial t} + \max_{u_m} \left[\frac{\partial \tilde{U}_m}{\partial p_r}(-p_r + n u_r) + \frac{\partial \tilde{U}_m}{\partial p_m}(-p_m + n u_m) - \right.$$
$$\left. \frac{\partial \tilde{U}_m}{\partial n} nc((1 - \varepsilon) u_r + \varepsilon u_m) + p_m(1 - u_m) \right] = 0. \quad (11)$$

Introducing new variables $x_r = p_r/n$ and $x_m = p_m/n$ and using a transformation of the Bellman function of the form $\tilde{U}_m(p_r, p_m, n, t) = n U_m(x_r, x_m, t)$, we can reduce the dimension of the problem by one using Noether's theorem. The modified HJB-equation (11) takes the following form

$$\mathscr{H} \doteq -\nu + \max_{u_m} \left\{ \lambda_r \left[-x_r(1 - c((1 - \varepsilon) u_r + \varepsilon u_m)) + u_r \right] + \right.$$
$$\lambda_m \left[-x_m(1 - c((1 - \varepsilon) u_r + \varepsilon u_m)) + u_m \right] -$$
$$\left. U_m c((1 - \varepsilon) u_r + \varepsilon u_m) + x_m(1 - u_m) \right\} = 0, \quad (12)$$

where the components of the gradient of the Bellman function are denoted by $\partial U_m/\partial x_r = \lambda_r$, $\partial U_m/\partial x_m = \lambda_m$ and $\partial U_m/\partial \tau = \nu$, variable τ denotes backward time, $\tau = T - t$. The optimal control can be defined be $u_m = \text{Heav}(\mathscr{A}_m)$, where $\mathscr{A}_m = \partial \mathscr{H}/\partial u_m = \lambda_r x_r \varepsilon c + \lambda_m(1 + x_m \varepsilon c) - U_m \varepsilon c - x_m$ and $\text{Heav}(\cdot)$ is *a unit step function* whose value is *zero* for negative argument and *one* for positive argument.

One of the efficient ways to solve the HJB-equation is to use the method of characteristics (see *e.g.* [11]). The system of characteristics for equation (12) is

$$x'_r = x_r(1 - c((1-\varepsilon)u_r + \varepsilon u_m)) - u_r, \ x'_m = x_m(1 - c((1-\varepsilon)u_r + \varepsilon u_m)) - u_m,$$
$$\lambda'_r = -\lambda_r, \ \lambda'_m = -\lambda_m + 1 - u_m, \ U'_m = -U_m c((1-\varepsilon)u_r + \varepsilon u_m) + x_m(1 - u_m),$$
$$(13)$$

where the prime denotes differentiation with respect to backward time τ. The terminal condition $U_m(x_r, x_m, T) = 0$ gives $\lambda_r(T) = \lambda_m(T) = 0$. Thus $\mathscr{A}_m(T) < 0$ and $u_m(T) = 0$ (mutants should reproduce at the very end of their life).

3.1 First steps

If we emit the characteristic field from the terminal surface $t = T$ with $u_r = u_m = 0$, then

$$x'_r = x_r, \quad x'_m = x_m, \quad \lambda'_r = -\lambda_r, \quad \lambda'_m = -\lambda_m + 1, \quad U'_m = x_m,$$
$$\lambda_r(T) = \lambda_m(T) = 0, \quad U_m(T) = 0.$$

We get the following equations for state and conjugate variables and for the Bellman function: $x_r = x_r(T)\mathrm{e}^\tau$, $x_m = x_m(T)\mathrm{e}^\tau$, $\lambda_r = 0$, $\lambda_m = 1 - \mathrm{e}^{-\tau}$, $U_m = x_m(1 - \mathrm{e}^{-\tau})$.

From this solution we can see that there could exist a switching surface S_m:

$$S_m: \quad x_m = 1 - \mathrm{e}^{-(T-t)}, \tag{14}$$

such that $\mathscr{A}_m = 0$ on it and where the mutant changes its control. Equation (14) is similar to (5). However, we should take into account the fact that there is also a hypersurface S_r, where the resident changes its control from $u_r = 0$ to $u_r = 1$ independently of the decision of the mutant. Hence it is important to define which surface, S_r or S_m the characteristic intersects first, see Fig. 2. Suppose that this is the surface S_r. Since the control u_r changes its value on S_r, the HJB-equation (12) also changes and, as a consequence, the conjugate variables v, λ_r and λ_m could possibly be discontinuous. Let us denote the incoming characteristic field (in backward time) by "$-$" and the outcoming field by "$+$". Consider a point of intersection of the characteristic and the surface S_r with coordinates $(x_{r_1}, x_{m_1}, \tau_1)$. Thus $x_{r_1} = 1 - \mathrm{e}^{-\tau_1}$ and the normal vector ϑ to the switching surface is written in the form

$$\vartheta = \nabla S_r = (\partial S_r/\partial x_r, \partial S_r/\partial x_m, \partial S_r/\partial \tau)^T = (-1, 0, 1 - x_{r_1})^T.$$

From the incoming field we have the following information about the co-state $\lambda_r^- = 0$, $\lambda_m^- = x_{r_1}$, $v^- = x_{m_1}(1 - x_{r_1})$. Since the Bellman function is continuous on the surface S_r, we have: $U_m^+ = U_m^- = U_m = x_{m_1} x_{r_1}$. The gradient ∇U_m has a jump in the direction of the normal vector ϑ: $\nabla U_m^+ = \nabla U_m^- + k\vartheta$. Here k is an unknown scalar. Thus

$$\lambda_r^+ = -k, \quad \lambda_m^+ = x_{r_1}, \quad v^+ = x_{m_1}(1 - x_{r_1}) + k(1 - x_{r_1}) \tag{15}$$

If we suppose that the control of the mutant is the same, $u_m^+ = 0$ (in this case $\mathscr{A}_m^+$ should be negative), the HJB-equation (12) has the form
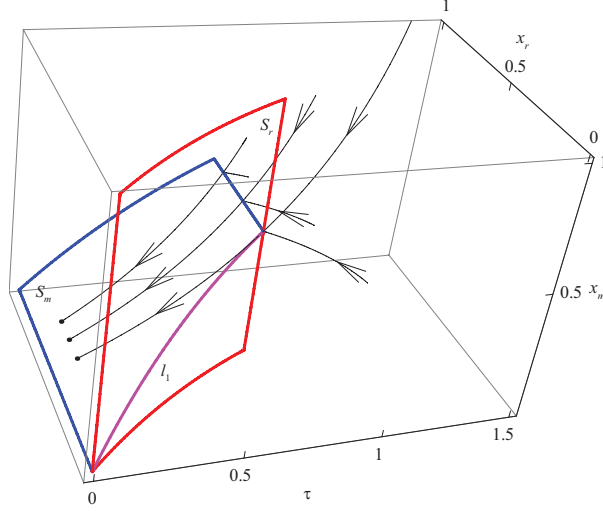
Fig. 2 Some family of optimal trajectories emanating from the terminal surface

$$-v^+ + \lambda^+ [-x_{r_1}(1-(1-\varepsilon)c)+1] - \lambda_m^+ x_{m_1}(1-(1-\varepsilon)c) - (1-\varepsilon)cU_m + x_{m_1} = 0. \tag{16}$$

Substituting the values from (15) into (16) we get: $k[-2(1-x_{r_1})-x_{r_1}(1-\varepsilon)c] = 0$, which leads to $k = 0$ and, actually, there is no jump in the conjugate variables. They keep the same values as in (15) and $\mathscr{A}_m^+ = \mathscr{A}_m^-$.

Conversely, the mutant may react to the decision of the resident and also change its control on S_r from $u_m^- = 0$ to $u_m^+ = 1$. This is fulfilled if $\mathscr{A}_m^+ > 0$. Substitution of the values v^+, λ_r^+ and λ_m^+ from (15) to the HJB-equation (12) gives $k = (x_{r_1} - x_{m_1})/(x_{r_1}c + (1-x_{r_1}))$ and

$$\mathscr{A}_m^+ = \lambda_r^+ x_{r_1}\varepsilon c + \lambda_m^+(x_{m_1}\varepsilon c + 1) - \varepsilon cU_m - x_{m_1} = (x_{r_1} - x_{m_1})\frac{(1-\varepsilon)x_{r_1}c + (1-x_{r_1})}{x_{r_1}c + (1-x_{r_1})},$$

which is positive when $x_{r_1} > x_{m_1}$. In Fig. 2 this corresponds to the points of the surface S_r which are below the line $l_1\colon x_r = x_m = 1 - e^{-\tau}$. For the optimal trajectories which go through such points: $u_r(\tau_1 + 0) = u_m(\tau_1 + 0) = 1$. One can show that there will be no more switches of the control. However, if we consider a trajectory going from a point above l_1, then $u_r(\tau_1 + \delta) = 1$ and $u_m(\tau_1 + \delta) = 0$ with arbitrarily small $\delta > 0$; a switch of the control u_m from zero to one then takes place later (in backward time). After that, there will be no more switches.

Now consider a trajectory emitted from the terminal surface which first intersects the surface S_m rather than the surface S_r. In this case the situation depicted in Fig. 3 takes place: one might expect the appearance of a singular arc S_1^σ there. The following are necessary conditions for its existence

$$\mathscr{H} = 0 = \mathscr{H}_0 + \mathscr{A}_m u_m, \quad \mathscr{H}_0 = -\nu - \lambda x_r - \lambda_m x_m + x_m \tag{17}$$

$$\mathscr{A}_m = 0 = \lambda_r x_r \varepsilon c + \lambda_m (x_m \varepsilon c + 1) - \varepsilon c U_m - x_m \tag{18}$$

$$\mathscr{A}'_m = \{\mathscr{A}_m \, \mathscr{H}_0\} = 0 \doteq \mathscr{A}_{m1}, \tag{19}$$

where the curly brackets denote the Poisson (Jacobi) brackets. If ξ is a vector of state variables and ψ is a vector of conjugate ones (in our case $\xi = (x_r, x_m, \tau)$ and $\psi = (\lambda_r, \lambda_m, \nu)$), then the Poisson brackets of two functions $F = F(\xi, \psi, U_m)$ and $G = G(\xi, \psi, U_m)$ are given by the formula: $\{F \, G\} = \langle F_\xi + \psi F_{U_m}, G_\psi \rangle - \langle F_\psi, G_\xi + \psi G_{U_m} \rangle$. Here $\langle \cdot, \cdot \rangle$ denotes the scalar product and *e.g.* $F_\psi = \partial F / \partial \psi$.

After some algebra, (19) takes the form

$$\mathscr{A}_{m1} = \nu \varepsilon c + x_m + \lambda_r x_r \varepsilon c - (x_m + 1)(1 - \lambda_r) = 0 \tag{20}$$

We can derive the variable ν from (17) and substitute it into (20). We get $\mathscr{A}_{m1} = x_m - 1 + \lambda_m = 0$. This leads to $\lambda_m = 1 - x_m$ and

$$\lambda_r = \frac{x_m + \varepsilon U_m + (1 - x_m)(x_m \varepsilon c + 1)}{x_r \varepsilon c},$$

which is obtained from (18).

To derive the singular control $u_m = \tilde{u}_m \in (0,1)$ along the singular arc, one should write the second derivative: $\mathscr{A}''_m = 0 = \{\{\mathscr{A}_m \mathscr{H}\} \mathscr{H}\} = \{\{\mathscr{A}_m \mathscr{H}_0\} \mathscr{H}_0\} + \{\{\mathscr{A}_m \mathscr{H}_0\} \mathscr{A}_m\} \tilde{u}_m$. Thus

$$\tilde{u}_m = \frac{\{\{\mathscr{A}_m \mathscr{H}_0\} \mathscr{H}_0\}}{\{\mathscr{A}_m \{\mathscr{A}_m \mathscr{H}_0\}\}} = \frac{2x_m}{2 + x_m \varepsilon c}, \tag{21}$$

which has the same form as (7).

The equation for the singular arc S_1^σ can be obtained from the system of dynamic equations (13) by substituting $u_r = 0$ and $u_m = \tilde{u}_m$ from (21):
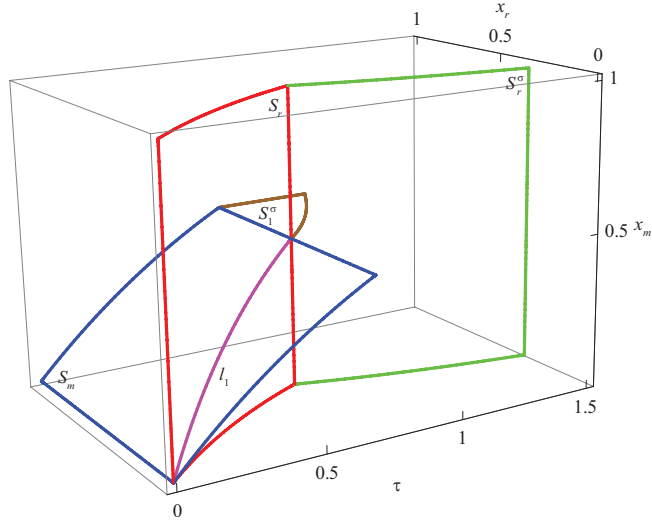
$$x'_m = -\frac{x_m^2 \varepsilon c}{2 + x_m \varepsilon c}, \quad x_m(\tau = \log 2) = 1/2.$$

Finally, we have the analogous expression to (6):

$$S_1^\sigma: \quad T - t = -\log x_m + \frac{2}{x_m \varepsilon c} - \frac{4}{\varepsilon c} \tag{22}$$

for $\varepsilon \neq 0$. If $\varepsilon = 0$, the surface S_m is a hyperplane $x_m = 1/2$.

After these steps we have the structure of the solution shown in Fig. 3.

Fig. 3 Construction of the singular arc S_1^σ

3.2 Optimal motion along the surface S_r^σ

According to the computations done in section 2.1, resident consumers must adopt a behavior u_r which keeps the surface S_r^σ invariant (see Fig. 3). In a mutant-free population, this is done by playing the singular control (7), but if mutants are present in the population, the dynamics of the system are modified and the mutant-free singular control (7) does not make S_r^σ invariant any more. However, residents may still make S_r^σ invariant by adopting a different behavior, denoted $\hat{u}_r$, as long as the mutants' influence, *i.e.* ε, is not too large. To compute $\hat{u}_r$, we notice that it should make x_r follow the dynamics depicted in Fig. 1, *i.e.* $\dot{x}_r = -x_r(1-cu_r) + u_r$ with $u_r = \hat{u}$ defined in equation (7). We get that $\hat{u}_r$ should be computed from:

$$x_r' = -\frac{x_r^2 c}{2 + x_r c} = x_r(1 - c((1-\varepsilon)\hat{u}_r + \varepsilon u_m)) - \hat{u}_r,$$

so that

$$\hat{u}_r = \frac{2x_r(1+x_r c)}{(1+(1-\varepsilon)x_r c)(2+x_r c)} - \frac{x_r \varepsilon c u_m}{1+(1-\varepsilon)x_r c}. \tag{23}$$

Thus, the residents will be able to keep S_r^σ invariant provided $\hat{u}_r \in [0,1]$ for all points belonging to S_r^σ and for all possible values of $u_m \in [0,1]$.

To identify for which parameters of the model this is possible, we may notice that $\hat{u}_r$ is a linear function of u_m and decreasing. Moreover,

$$u_r(u_m = 0) = \frac{2x_r(1+x_r c)}{(1+(1-\varepsilon)x_r c)(2+x_r c)} \leq 2x_r \frac{1+x_r c}{2+x_r c} \leq 1,$$

since $x_r \leq 1/2$. Conversely, when $u_m = 1$, $u_r = \frac{2x_r}{2+x_rc} \frac{1+x_rc-\varepsilon c-\varepsilon cx_rc/2}{1+(1-\varepsilon)x_rc}$. If this value is larger than 0 for any x_r belonging to S_r^σ, invariance of S_r^σ is ensured. A condition for this to occur is

$$\varepsilon < 1/c. \tag{24}$$

It is interesting to notice that $u_r(u_m = 0)$ is larger than the original $\hat{u}$ in (7), since the residents must compensate for the non-eating mutants. Conversely, when $u_m = 1$, $u_r < \hat{u}$. The tipping point takes place when $u_m = \hat{u}$, which ensures $u_r = u_m$; mutants behaving like the original residents allow the residents to behave as such.

In this paper we consider only the values of ε satisfying (24), *i.e.* such that the residents are able to adopt their optimal behavior, in spite of the presence of mutants. Otherwise, the influence of the mutants on the system may be too large, and the residents would not have the possibility to stick to their fitness maximization program.

The control $\hat{u}_r = \hat{u}_r(x_r, x_m, \tau, u_m)$ is defined in feedback form, *i.e.* it depends on the time and on the state of the system. The corresponding Hamiltonian (12) needs to be modified to

$$\hat{\mathscr{H}} = \mathscr{H}(x_r, x_m, U_m, \lambda_r, \lambda_m, \nu, \hat{u}_r(x_r, x_m, \tau, u_m), u_m), \tag{25}$$

so that the coefficient multiplying the control u_m becomes

$$\hat{\mathscr{A}}_m = \frac{\partial \hat{\mathscr{H}}}{\partial u_m} = \frac{\lambda_m(1+x_r(1-\varepsilon)c+x_m\varepsilon c)-\varepsilon cU_m}{1+(1-\varepsilon)x_rc} - x_m. \tag{26}$$

This expression allows us to compute the optimal behavior of the mutants on the surface S_r^σ, but the calculations are quite complicated. To make things simpler, let us first consider the particular case of vanishingly small values of ε and study the optimal behavioral pattern.

3.3 Particular case of a vanishingly small population of mutants

3.3.1 On the singular surface S_r^σ

If $\varepsilon \cong 0$, the mutants' influence on the system is negligible and, to make S_r^σ invariant, the resident should apply the mutant-free singular behavior computed in (7): $\hat{u}_r = 2x_r/(2+x_rc)$. In addition, equations (25) and (26) take the following form

$$\hat{\mathscr{H}} = -\nu + \frac{\lambda_r x_r^2 c}{2+x_rc} + \lambda_m \left(-x_m\frac{2-x_rc}{2+x_rc} + u_m\right) - U_m\frac{2x_rc}{2+x_rc} + x_m(1-u_m) \tag{27}$$

$$\hat{\mathscr{A}}_m = \lambda_m - x_m. \tag{28}$$
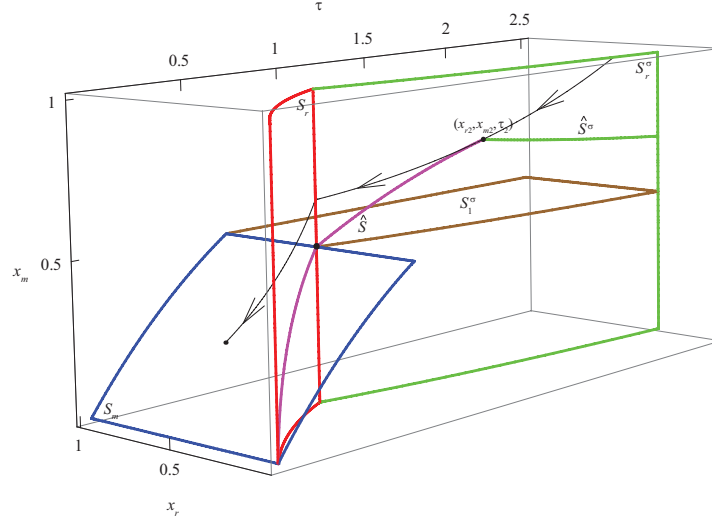
Fig. 4 Optimal behavior on the surface S_r^σ

If the trajectory originates (in backward time) from some point belonging to S_r^σ such that $x_m^\sigma \doteq x_m(\tau = \log 2) > 1/2$, then $u_m(\tau = \log 2) = 0$ and the system of characteristics for the Hamiltonian (27) is

$$x_r' = -\frac{x_r^2 c}{2+x_r c}, \ x_m' = x_m \frac{2-x_r c}{2+x_r c}, \ \lambda_m' = -\lambda_m + 1, \ U_m' = -U_m \frac{2x_r c}{2+x_r c} + x_m \quad (29)$$

with boundary conditions: $\tau = \log 2$, $x_r = 1/2$, $x_m = x_m^\sigma$, $\lambda_m = 1/2$, $U_m = x_m^2/2$. Thus $\lambda_m = 1 - e^{-\tau}$ and there exists a switching curve $\hat{S}$, which is defined as: $x_m = 1 - e^{-\tau}$ in addition to $\tau = -\log x_r + 2/(x_r c) - 4/c$. Thus $\hat{S} = S_m \cap S_r^\sigma$.

The switching curve $\hat{S}$ ends at the point with coordinates $(x_{r_2}, x_{m_2}, \tau_2)$ where the characteristics become tangent to it and the singular arc $\hat{S}^\sigma$ appears (see Fig. 4). Before determining the coordinates of this point, let us define the singular arc, denoted $\hat{S}^\sigma$. From (27-28) we get
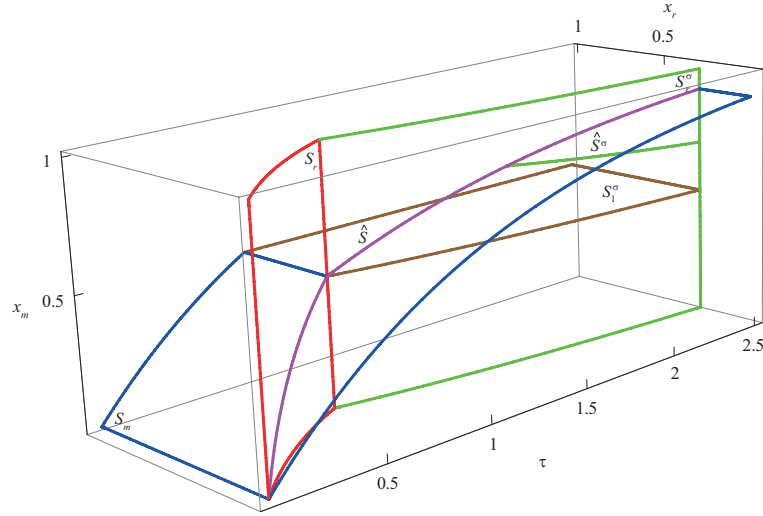
$$v = \frac{\lambda_r x_r^2 c}{2+x_r c} - \lambda_m x_m \frac{2-x_r c}{2+x_r c} - U_m \frac{2x_r c}{2+x_r c} + x_m, \quad \lambda_m = x_m \quad (30)$$

along the singular arc. Substitution of (30) into equation $\hat{\mathscr{A}}_m' = 0$ gives $x_m = (2 + x_r c)/4$.

In addition, the intermediate control $\hat{u}_m$ can be derived from $\hat{\mathscr{A}}_m'' = 0$ and is equal to

$$\hat{u}_m = \frac{1}{2+x_r c},$$

which is positive and belongs to the interval between zero and one.

Fig. 5 Optimal behavioral pattern for $c = 3$

We see that the coordinates x_{r_2}, x_{m_2} and τ_2 can be defined by the following equations

$$x_{m_2} = \frac{2 + x_{r_2} c}{4} = 1 - \mathrm{e}^{-\tau_2}, \quad \tau_2 = -\log x_{r_2} + \frac{2}{x_{r_2} c} - \frac{4}{c},$$

which comes from the fact that the point $(x_{r_2}, x_{m_2}, \tau_2)$ belongs to $\hat{S}^\sigma$ and is located on the intersection of the curves $\hat{S}^\sigma$ and $\hat{S}$. This result is illustrated in Fig. 4.

3.3.2 Outside the singular surface S_r^σ

If the state is outside the surface S_r^σ, things are a little easier since at least the behavior of the residents, u_r, is constant and equal to 0 or 1, depending on the respective value of τ and x_r.

We can actually show that the surface S_1^σ (where $u_r = 0$) can be extended further by considering the situation in Fig. 3. Indeed, the following conditions are fulfilled for this region:

$$\mathscr{H}\Big|_{u_r=0} = -v - \lambda_r x_r - \lambda_m x_m + x_m = 0, \quad \mathscr{A}_m = \lambda_m - x_m = 0, \quad \mathscr{A}'_m = 0.$$

Therefore, $v = -\lambda_r x_r - \lambda_m x_m + x_m$, $\lambda_m = x_m$ and the condition $\mathscr{A}'_m = 0$: $-1 + 2x_m = 0$ gives $x_m = 1/2$, which is precisely the definition of S_1^σ when $\varepsilon = 0$ (see equation (22)).

Consider now the region where x_r is smaller than on the surface S_r^σ (see Fig. 4), where $u_r = 1$. There is a switching surface which extends the surface S_m and is

defined by the same equation (14). However, there could also exist a singular arc S_2^σ starting from some points of S_m. Such an arc must satisfy the following conditions

$$\mathcal{H}\Big|_{u_r=1} = -\nu - \lambda_r(x_r(1-c) - 1) - \lambda_m x_m(1-c) - z U_m + x_m = 0 \qquad (31)$$

$$\mathcal{A}_m = \lambda_m - x_m = 0, \quad \mathcal{A}_m' = 0, \qquad (32)$$

which give a possible candidate for a singular arc S_2^σ: $x_m = 1/(2-c)$. We see that its appearance is possible only for $c < 1$, since x_m must belong to S_m. For $c > 1$ the structure of the solution in the domain below the surface S_r^σ is actually simpler and consists only of the switching surface S_m, see Fig. 5. Notice that in the case $x_r(0) = x_m(0) = 0$ investigated below, the existence of the singular arc S_2^σ is not relevant, since it cannot be reached from such initial conditions.

### 3.4 Computation of the value functions in the case $\varepsilon = 0$

Following [1], we assume that at the beginning of the season the energy of consumers is zero: $x_r(0) = x_m(0) = 0$. Therefore, we should take into account only the trajectories coming from these zero initial conditions. The phase space is reduced in this case to the one shown in Fig. 6. One can see that there are three different regions depending on the length of the season T. If it is short enough, *i.e.* $T \le T_1$ (see equation (8)), then the behavior of the mutant coincides with the behavior of the resident and the main population cannot be invaded: actually, the behavior of the mutant coincides with the behavior of the residents. If the length of the season is between T_1 and T_2, there is a period in the life-time of a resident when it applies an intermediate strategy and spares some amount of the resource for its future use. Mutants are able to use this fact and there exists a strategy that guarantees them better results.

Let us introduce the analogue of the value function $\tilde{U}_m$ for the resident and denote it by $\tilde{U}_r$:

$$\tilde{U}_r(p_r, p_m, n, t) = \int_{T-t}^{T} p_r(s)(1 - u_r(s)) \, ds.$$

The value $\tilde{U}_r(0, 0, n(0), T)$ represents the amount of eggs laid by the resident during a season of length T. Its value depends on the state of the system and the following transformation can be done $\tilde{U}_r(p_r, p_m, n, t) = n U_r(x_r, x_m, t)$. In the following, we omit some parameters and write the value function in the simplified form $U_r(T) \doteq U_r(0, 0, T)$ where the initial conditions $x_r(0) = x_m(0) = 0$ have been taken into account.

In the region **A** (see Fig. 6) the value functions for both populations (of mutants and residents) are equal to each other $U_m(T) = U_r(T) = x_1 e^{-c(T-\tau_1)}$. Here the value τ_1 can be defined from the intersection of the trajectory and the switching curve $S_r \cap S_m$:
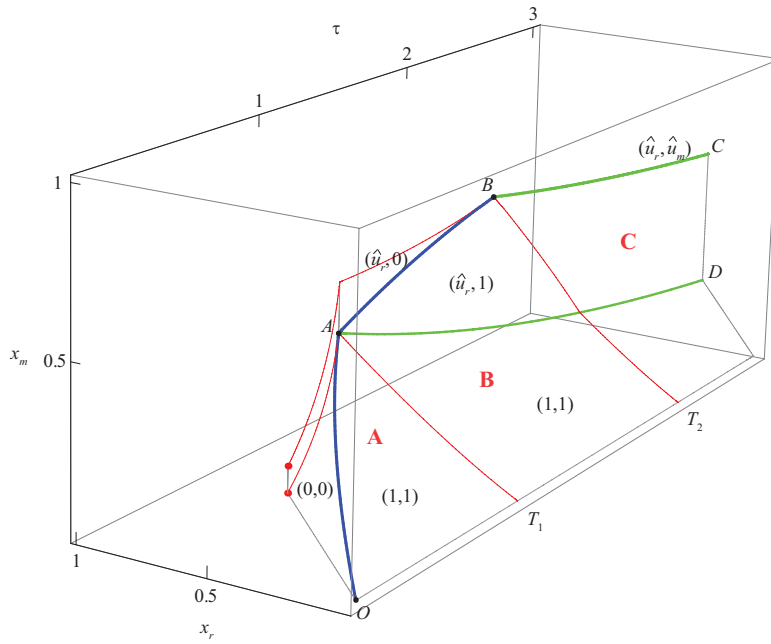
Fig. 6 The reduced optimal pattern for trajectories satisfying the initial conditions $x_r(0) = x_m(0) = 0$ with $c = 3$
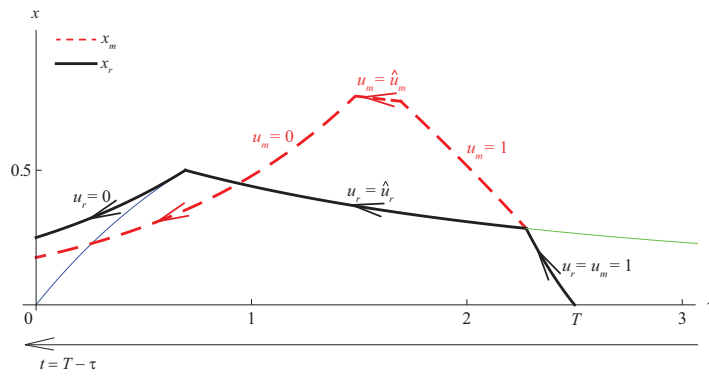
Fig. 7 Optimal free-riding the mutant

$$1 - \mathrm{e}^{-\tau_1} = \frac{\mathrm{e}^{(c-1)(T-\tau_1)} - 1}{c - 1}.$$

To obtain the value functions in the regions **B** and **C**, one must solve the system of characteristics (29) in the case when the characteristics move along the surface S_r^σ and $u_m = 1$. This leads to the following characteristic equations for the Hamiltonian (27):

$$x_r' = -\frac{x_r^2 c}{2 + x_r c}, \quad x_m' = x_m \frac{2 - x_r c}{2 + x_r c} - 1, \quad U_m' = -U_m \frac{x_r^2 c}{2 + x_r c},$$

and consequently

$$x_m = C_1 x_r^2 \mathrm{e}^\tau + x_r z + 1, \quad U_m = C_2 x_r^2, \quad C_1, C_2 = \mathrm{const}, \tag{33}$$

where C_1 and C_2 are defined from the boundary conditions, while equation (6) is also fulfilled.

Along the singular arc $\hat{S}^\sigma$ the mutant uses the intermediate strategy (21). In this case,

$$U_m' = -U_m c\hat{u}_r + x_m(1 - \tilde{u}_m) = -U_m \frac{2x_r c}{2 + x_r c} + \frac{1 + x_r c}{4}.$$

Since $x_r' = -\frac{x_r^2 c}{2 + x_r c}$, we have $\frac{dU_m}{dx_r} = \frac{2U_m}{x_r} - \frac{(1 + x_r c)(2 + x_r c)}{4 x_r^2 c}$. Thus

$$U_m = C_3 x_r^2 + \frac{4 + 3x_r c(3 + 2x_r c)}{24 x_r c}, \quad C_3 = \mathrm{const}. \tag{34}$$

We now undertake to compute the limiting season length T_2 that separates the region **B** from the region **C**. The coordinates of the point B were obtained in the previous section. To define the coordinates of the point $(x_{r_2}^\sigma, x_{m_2}^\sigma, \tau_2^\sigma)$ of intersection of the optimal trajectory with the curve AD, we use the dynamics of motion along the surface S_r^σ with $u_r = \hat{u}_r$ and $u_m = 1$ (33): $x_m = C_1 x_r^2 \mathrm{e}^\tau + x_r z + 1$, where the constant C_1 should be chosen such that: $x_{m_2} = C_1 x_{r_2}^2 \mathrm{e}^{\tau_2} + x_{r_2} c + 1$, $x_{m_2} = \frac{2 + x_{r_2} c}{4} = 1 - \mathrm{e}^{-\tau_2}$. Therefore $C_1 = \frac{(x_{r_2} c - 2)(3 x_{r_2} c + 2)}{16 x_{r_2}^2}$. After that the coordinates: $x_{r_2}^\sigma$, $x_{m_2}^\sigma$ and τ_2^σ can be defined from the following conditions

$$x_{m_2}^\sigma = x_2^\sigma = C_1 (x_{r_2}^\sigma)^2 \mathrm{e}^{\tau_2^\sigma} + x_{r_2}^\sigma c + 1, \quad \tau_2^\sigma = -\log x_{r_2}^\sigma + \frac{2}{x_{r_2}^\sigma c} - \frac{4}{c}. \tag{35}$$
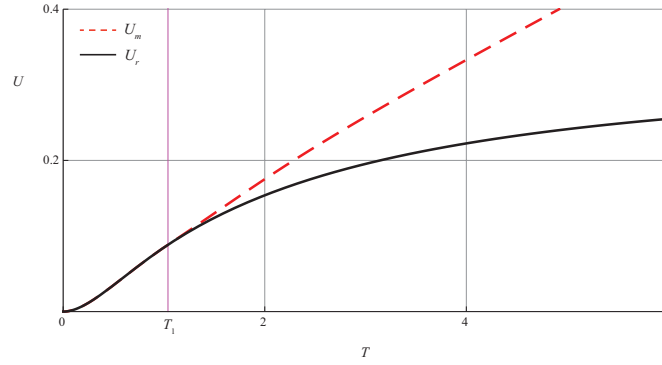
The boundary value T_2 can be obtained from $T_2 = \tau_2^\sigma + \log(x_{r_2}^\sigma(c-1) + 1)/(c-1)$.

Now we compute the value functions $U_r(T)$ and $U_m(T)$ for the region **B** ($T_1 < T \le T_2$), where only the mutant uses bang-bang control. For the resident population we have

$$U_r(T) = U_{r_2} \mathrm{e}^{-c(T - \tau_2)}, \quad U_{r_2} = x_{r_2}(1 - x_{r_2}) + \frac{1 - 2x_{r_2}}{c}, \tag{36}$$

where the point with coordinates $(x_{r_2}, x_{r_2}, \tau_2)$ defines the intersection of the trajectory and surface S_r^σ:

Fig. 8 Difference in the value functions of the resident and the mutant ($c = 3$)

$$\tau_2 = -\log x_{r_2} + \frac{2}{x_{r_2}c} - \frac{4}{c}, \quad x_{r_2} = \frac{e^{(c-1)(T-\tau_2)} - 1}{c - 1}. \tag{37}$$

For the mutant population the value function U_m in the region with $u = \hat{u}$ and $u_m = 1$ satisfies the equation resulting from (33):

$$U_m^{(\hat{u},1)} = x_{m_1}^2 \left(x_r/x_{r_1}\right)^2, \tag{38}$$

where $(x_{r_1}, x_{m_1}, \tau_1)$ is the point of intersection of the trajectory with the curve AB (see Fig. 6). Using (38) and notation from (37), we can write $U_m(T) = U_{m_2} e^{-c(T-\tau_2)}$, $U_{m_2} = x_{m_1}^2 \left(x_{r_2}/x_{r_1}\right)^2$, which is analogous to (36).

In the region **C** the value function for the resident has the same form as in (36), but it has a different form for the mutant. Suppose that the optimal trajectory intersects the surface S^σ at the point with coordinates $(\tilde{x}_{r_2}, \tilde{x}_{m_2}, \tilde{\tau}_2)$. Then the Bellman function at this point is given by

$$\tilde{U}_{m_2} = \tilde{x}_{r_2}^2 \left(\frac{c^2}{16} - \frac{4 + 3\tilde{x}_{r_2}c}{24\tilde{x}_{r_2}^3 c}\right) + \frac{3\tilde{x}_{r_2}c(2\tilde{x}_{r_2}c + 3) + 4}{24\tilde{x}_{r_2}c},$$

which is written using (34) with definition of the constant C_3 from the given boundary conditions.

When the optimal trajectory moving along the surface S^σ intersects the curve AD at some point with coordinates $(\tilde{x}_{r_2}^\sigma, \tilde{x}_{m_2}^\sigma, \tilde{\tau}_2^\sigma)$ (see Fig. 6), the Bellman function can be expressed as follows: $\tilde{U}_{m_2}^\sigma = \tilde{U}_{m_2} \tilde{x}_{r_2}^\sigma / \tilde{x}_{r_2}$. Thus $U_m(T) = \tilde{U}_{m_2}^\sigma e^{-c(T-\tau_2^\sigma)}$.

The difference in the values functions (number of offspring per mature individual) of the mutant and optimally behaving resident is presented in Fig. 8. It is shown that as soon as the season length is longer than T_1, residents may be out-competed by selfish "free riding" mutants (see also Fig. 7). Let us notice, that otherwise the payoff functions of the mutants and residents are the same. Therefore the optimal strategy for the resident population is *evolutionary stable*.

3.5 Generalization to sufficiently small but non-zero values of ε

In this section we consider the case of non-zero ε such that the condition (24) remains fulfilled. This means that the trajectory intersecting the singular surface S_r^{σ} does not cross it, but moves along it due to the residents who make it invariant through the behavior $\hat{u}_r$ (23).

In this case, the phase space can also be divided into two regions: according to whether x_r is smaller or larger than on S_r^{σ}. In both of these regions the structure of the solution has similar properties to the case considered above when ε is arbitrarily small. On the surface S_r^{σ} the optimal behavior is also similar to that of the previous case.

In the region with larger x_r values than the ones on the surface S_r^{σ}, there is a part of the switching surface S_m and a singular arc S_1^{σ} where the mutant uses an intermediate strategy. The surface S_1^{σ} can be defined using the expression (22). In the other region, we also have a part of S_m and a singular arc S_2^{σ} which is different from S_1^{σ} and may not exist for some values of the parameters c and ε.

To identify the values for which the surface S_2^{σ} is a part of the solution let us, write the necessary conditions as in (31-32): $\mathscr{H}\big|_{u_r=1} = 0$, $\mathscr{A}_m = 0$, $\mathscr{A}_m' = \{\mathscr{A}_m\mathscr{H}\} = 0$. Using these equations, we are able to obtain the values of λ_r, λ_m and ν on the surface S_2^{σ} and substitute them into the second derivative $\mathscr{A}_m'' = \{\{\mathscr{A}_m\mathscr{H}\}\mathscr{H}\} = 0$ to derive the expression for the singular control applied by the mutant on this surface:

$$u_m = \frac{2x_m - (1-\varepsilon)c(1+x_m)}{2 - (1-\varepsilon)c + x_m\varepsilon c}\ . \tag{39}$$

There are several conditions which must be satisfied. First of all, the control (39) should be between zero and one

$$0 \leq \frac{2x_m - (1-\varepsilon)c(1+x_m)}{2 - (1-\varepsilon)c + x_m\varepsilon c} \leq 1\ . \tag{40}$$

Second, the Kelley condition should also be fulfilled [11, p. 200]:

$$\frac{\partial}{\partial u_m}\frac{d^2}{dt^2}\frac{\partial\mathscr{H}}{\partial u_m} = \{\mathscr{A}_m\{\mathscr{A}_m\mathscr{H}\}\} \leq 0\ .$$

This leads to the inequality

$$2 - (1-\varepsilon) + x_m\varepsilon c \geq 0\ . \tag{41}$$

In particular, conditions (40) and (41) together give $x_m \leq 2/(2-c)$.

To construct the singular arc S_2^{σ}, we should substitute the singular control u_m from (40) and $u_r = 1$ into the equation describing the dynamics (13): $x_m' = x_m(1 - c((1-\varepsilon)u_r + \varepsilon u_m)) - u_m$, with the boundary conditions obtained from the tangency condition for the optimal trajectory from the domain $u_m = u_r = 1$ intersecting the switching surface S_m:
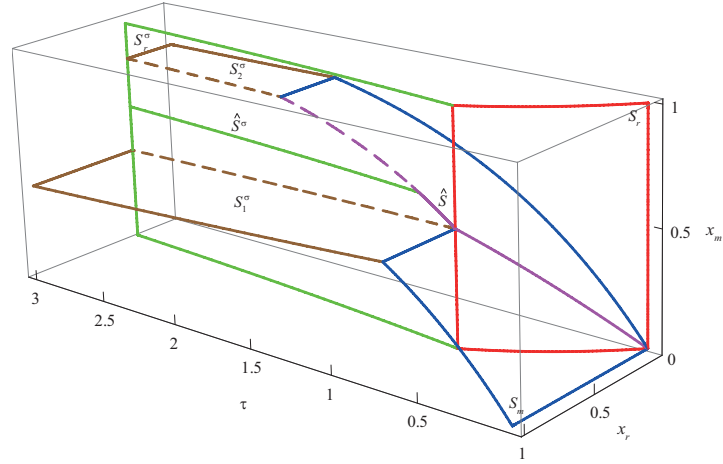
**Fig. 9** Structure of the optimal behavioral pattern for $c = 1.25$ and $\varepsilon = 0.35$

$$x_m\left(-\log\left(1 - \frac{1}{2 - c(1-\varepsilon)}\right)\right) = \frac{1}{2 - c(1-\varepsilon)}.$$

Such tangency occurs only if $0 \leq \frac{1}{2-c(1-\varepsilon)} \leq 1$, which that comes from the condition that a singular surface S_m exists only for $0 \leq x_m < 1$. This gives the following inequality: $1 - c(1-\varepsilon) \geq 0$ for the existence of the surface S_2^{σ}. One can check that the inequalities (40-41) are fulfilled as well. The optimal behavioral pattern for a particular case is shown in Fig. 9.

4 Long-term evolution of the system

Model (2) was introduced in [1] as the intra-seasonal part of a more complex multi-seasonal model of population dynamics in which consumers and resources live for one season only. It was assumed that the (immature) offspring produced by the consumers and resources in season i and defined by the system of equations (3), mature during the inter-season to form the initial consumer and resource populations of season $(i+1)$, up to some overwintering mortality. The consumer and resource population densities at the beginning of season $i+1$ is thus $c_{i+1} = \mu_c J_i$, $n_{i+1}(t=0) = \mu_n J_{n,i}$, with J_i and $J_{n,i}$ defined in (3) ($\mu_n, \mu_c < 1$ allow for overwintering mortality).

In the presence of a mutant invasion, things differ slightly as the total consumer population is structured into $c_{r_i} = (1 - \varepsilon_i)c_i$ residents and $c_{m_i} = \varepsilon_i c_i$ mutants that have different reproduction strategies. Assuming that reproduction is asexual and an offspring simply inherits the strategy of their parent, the inter-seasonal dynamics are as follows: $c_{r_{i+1}} = \alpha \tilde{U}_r(c_i, \varepsilon_i, n_i, T) = (1 - \varepsilon_{i+1})c_{i+1}$, $c_{m_{i+1}} = \alpha \tilde{U}_m(c_i, \varepsilon_i, n_i, T) =$
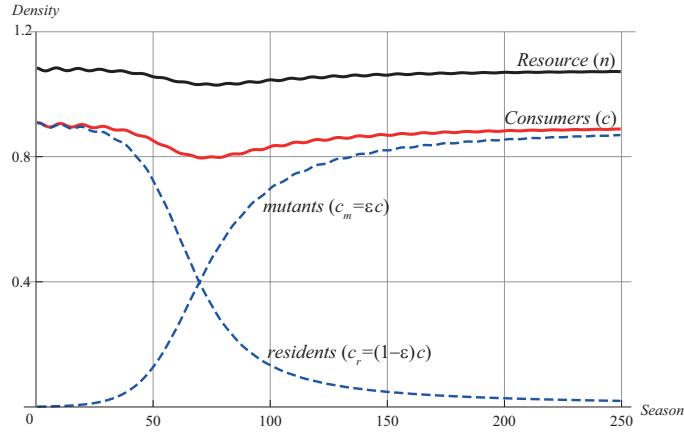
Fig. 10 Effect of an invasion by mutants on the system

$\varepsilon_{i+1}c_{i+1}$ and $n_{i+1} = \beta\tilde{V}(c_i, \varepsilon_i, n_i, T)$, where $\alpha = \mu_c\theta$, $\beta = \mu_n\gamma$, and the functions $\tilde{U}_r = (1-\varepsilon_i)c_i\int_0^T (1-u_r(t))p_r(t)\,dt$, $\tilde{U}_m = \varepsilon_i c_i\int_0^T (1-u_m(t))p_m(t)\,dt$, $\tilde{V} = \int_0^T n(t)\,dt$ can be computed from the solution of the optimal control problem (10) with the dynamics given by (9). As stated earlier, the energies of both the mutants and residents are zero at the beginning of each season ($p_r(0) = p_m(0) = 0$). For the particular case $\varepsilon = 0$, the values $\tilde{U}_r$ and $\tilde{U}_m$ were derived analytically in subsection 3.4, but these are not useful in a multi-season study where the frequency of mutants is bound to evolve. In the following, we therefore resorted to a numerical investigation, in order to decipher the long-term fate of the mutants' invasion.

Here, we follow an adaptive dynamics type approach and assume that, among all possible behaviors [1], the resident consumer and the resource population are at a (globally stable) equilibrium. We investigate what happens when a small fraction of mutants appear in the resident consumer population. We actually assume that resident consumers are "naive" in the sense that even if the mutant population becomes large through the season-to-season reproduction process, the resident consumers keep their collective optimal strategy and treat mutants as cooperators, even if they do not cooperate.

The case that we investigated is characterized by $\alpha = 2$, $\beta = 0.5$ and $T = 4$. Initially, the system is near the all-residents long-term stable equilibrium point $c = 0.9055$ and $n = 1.0848$. At the beginning of some season, a mutant population of small size $c_m = 0.001$ then appears ($\varepsilon \approx 1.1\ 10^{-3} < 1/c$). We see in Fig. 10 that the mutant population increases its frequency within the consumer population and modifies the dynamics of the system. Despite this drastic increase, it is however noteworthy to underline that $c_i < 1$ in all seasons, so that $\varepsilon < 1/c_i$ is true verified and the analysis presented in this paper is valid for all seasons.

The naive behavior of the consumers is detrimental to their progeny: as the seasons pass, mutant consumers progressively take the place of the collectively optimal residents and even replace them in the long run (Fig. 10), making the mutation suc-

cessful. We should however point out that the mutants' strategy, as described in (10), is also a kind of "collective" optimum: in some sense, it is assumed that mutants cooperate with other mutants. If the course of evolution drives the resident population to 0 and only mutants survive in the long run, this means that the former mutants become the new residents, with exactly the same strategy as the one of the former residents they replaced. Hence, they are also prone to being invaded by non-cooperating mutants. The evolutionary dynamics of this naive resident-selfish mutant-resource thus appears to be a never-ending process: selfish mutants can invade and replace collectively optimal consumers, but at the end transform into collectively optimal consumers as well, and a new selfish mutant invasion can start again. We are actually not in a "Red Queen Dynamics" context, since we focused on the evolution of one species only, and not co-evolution [18]. Yet, what the Red Queen said to Alice seems to fit the situation we have just described very well: "here, you see, it takes all the running you can do to keep in the same place" [5].

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