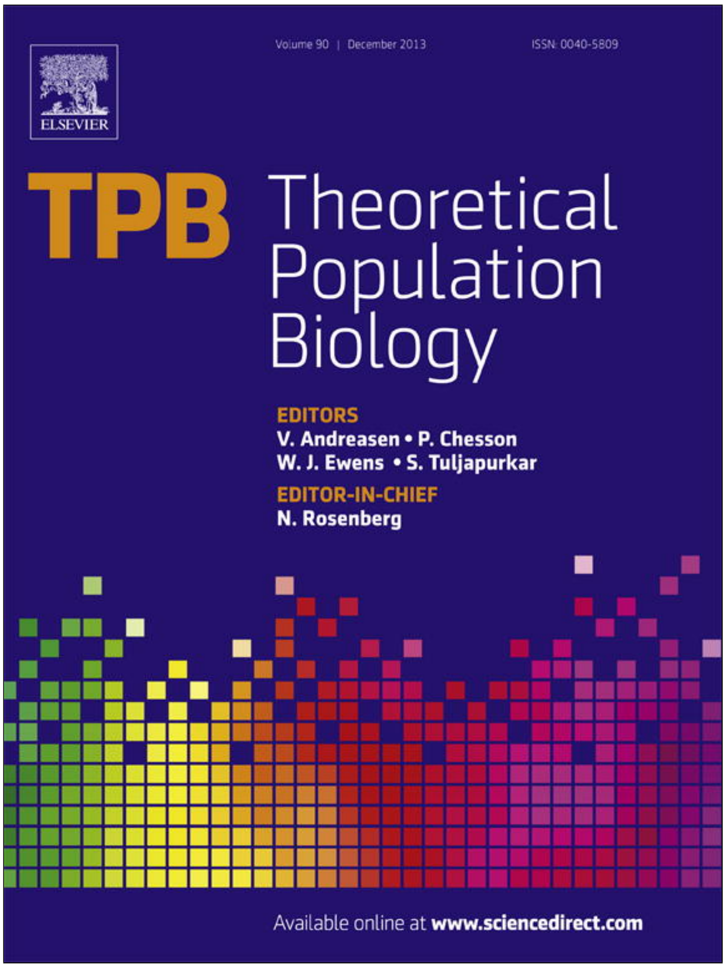
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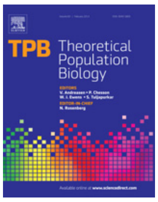

The nest site lottery: How selectively neutral density dependent growth suppression induces frequency dependent selection

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HIGHLIGHTS

- We analyze the population dynamics model.
- We assume selectively neutral density dependent growth suppression.
- At equilibrium size the frequency dependent selection is induced.
- This mechanism can be called nest site lottery.
- Our result suggests existence of the new fitness measure.

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ABSTRACT

Modern developments in population dynamics emphasize the role of the turnover of individuals. In the new approaches stable population size is a dynamic equilibrium between different mortality and fecundity factors instead of an arbitrary fixed carrying capacity. The latest replicator dynamics models assume that regulation of the population size acts through feedback driven by density dependent juvenile mortality. Here, we consider a simplified model to extract the properties of this approach. We show that at the stable population size, the structure of the frequency dependent evolutionary game emerges. Turnover of individuals induces a lottery mechanism where for each nest site released by a dead adult individual a single newborn is drawn from the pool of newborn candidates. This frequency dependent selection leads towards the strategy maximizing the number of newborns per adult death. However, multiple strategies can maximize this value. Among them, the strategy with the greatest mortality (which implies the greatest instantaneous growth rate) is selected. This result is important for the discussion about universal fitness measures and which parameters are maximized by natural selection. This is related to the fitness measures R_0 and r, because the number of newborns per single dead individual equals the lifetime production of newborn R_0 in models without aging. We thus have a two-stage procedure, instead of a single fitness measure, which is a combination of R_0 and r. According to the nest site lottery mechanism, at stable population size, selection favors strategies with the greatest r, i.e. those with the highest turnover, from those with the greatest R_0.

1. Introduction

In the modern theory of evolutionary ecology (Post and Palkovacs, 2009; Pelletier et al., 2009; Morris, 2011; Schoener, 2011) the problem of eco-evolutionary feedback is of special interest. One of the major theoretical problems in the modeling of population dynamics, and in general of evolutionary biology and ecology, is the limit of population growth and its selection consequences. This topic is very important in many disciplines such as evolutionary game theory and life history theory.

The earliest attempt to solve this problem for populations with overlapping generations is the continuous logistic equation introduced by Verhulst in the 19th century (Verhulst, 1838), which can be found in every textbook on ecology and mathematical biology. It inspired the idea of r and K selection (MacArthur and Wilson, 1967), that selection favors different strategies at low densities and near the stable population size, and is still applied in modeling (Cressman et al., 2004; Cressman and Krivan, 2006, 2010). This concept states that there is some arbitrary maximal population size at which growth is suppressed and the population remains stable. However, this approach produces some unusual predictions which provoked a wide discussion (Kozłowski, 1980;

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Łomnicki, 1988; Kuno, 1991; Ginzburg, 1992; Gabriel et al., 2005; Hui, 2006; Argasinski and Kozłowski, 2008) presented in the next section.

The problem of the limits to growth is important not only for ecological population growth models but also for the modeling of natural selection. There is a huge discussion on what is maximized by natural selection and what happens when a population reaches the limit to growth (Metz et al., 1992; Kozłowski, 1993; Mylius and Diekmann, 1995; Brommer, 2000; Dieckmann and Metz, 2006; Metz et al., 2008a,b; Roff, 2008). However in these attempts density dependence is represented by some abstract unspecified factors. Thus the proposed solutions are very general and abstract. A concrete mechanistic interpretation should be helpful in the interpretation of the mathematical notions. In the modification of the logistic equation (Kozłowski, 1980; Hui, 2006) which was applied to game-theoretic modeling (Argasinski and Kozłowski, 2008; Argasinski and Broom, 2012) there is an example of a mechanism responsible for strategically neutral density dependence called in this paper a "nest site lottery". The underlying assumption is that there is a limited number of nest sites in the environment and that every newborn must find a nest site to survive. Thus all newborns produced at some moment in time form a pool of candidates to be drawn from to replace the dead individuals in their nest sites. The difference is that in this case there is an arbitrary maximal population size described by a carrying capacity indicating the number of available nest sites (mechanistically interpreted as nests or holes, where individuals can settle, as in Hui (2006)). However, the stable population size is not the carrying capacity, as in the classical logistic equation, but the dynamic equilibrium between different factors of mortality and fecundity (Kozłowski, 1980; Ginzburg, 1992; Hui, 2006), which can be affected by the dynamics of the population state (Argasinski and Broom, 2012). The advantage of this approach is that it considers a realistic turnover of individuals (Argasinski and Kozłowski, 2008). In this paper we will more rigorously analyze the properties of the nest site lottery mechanism in a simpler model than in the previous papers (Argasinski and Kozłowski, 2008; Argasinski and Broom, 2012).

Below we give the mathematical details of this approach (Sections 2 and 3). Section 4 starts the development of the selection model and in Section 5 the important notion of the turnover coefficient is introduced. Section 6 contains the presentation of the selection dynamics. In Section 7 the relationships between the nest site lottery mechanism and the invasion fitness concept are presented. Section 8 contains the main results which are the Eqs. (14), (15) and their analysis describing the nest site lottery mechanism (intuitively depicted in Fig. 1). We see that, eventually, selection favors the strategy with the highest turnover coefficient out of those with the greatest value of lifetime reproduction. The mechanistic reasoning from Section 8 is completed by Theorem 1 describing the quantitative characterization of the rest points of the system (14), (15). The importance of the obtained results and the general ideas inspired by them is discussed in Section 9 (the last subsection contains a discussion on the two-stage maximization procedure, substituting for the single-step fitness measure, obtained by our results).

2. Density dependence

The cornerstone of mathematical ecology is the Malthusian equation describing exponential population growth,

$$\frac{dn}{dt} = nr = nb - nd = n\left(b - d\right), \tag{1}$$

where b is the birth rate and d is the death rate. However, in Argasinski and Broom (2012, see Appendix 1 there for details) it was shown that with respect to the multiplicative proportionality constant (which can be removed using a change of timescale) acting as the rate of interaction occurrence, these parameters can be interpreted as demographic parameters describing the outcomes of the average interaction with elements of the environment or other individuals. Then $b \in [0, \infty)$ can be interpreted as the number of newborns produced during an interaction event and $d \in [0, 1]$ as the probability of death during an interaction event. We will assume this mechanistic interpretation in our model. Thus the Malthusian coefficient r can be interpreted as the balance between mortality d and fertility b. The above model is not realistic, because it allows for infinite population growth. The classical solution of this problem is the use of the logistic equation, which is Eq. (2),

$$\frac{dn}{dt} = nr\left(1 - \frac{n}{K}\right). \tag{2}$$

However, this relies on a problematic assumption which has very serious consequences. Eq. (2) produces artifacts in population growth models (Kuno, 1991; Gabriel et al., 2005) and selection models related to replicator dynamics (Argasinski and Kozłowski, 2008). For example, it suppresses the selection dynamics in the replicator dynamics by setting the right hand sides of the strategy dynamics equations to 0 (Argasinski and Kozłowski, 2008), the trajectory escapes to infinity for $r < 0$ (i.e. $b < d$) and initial population size greater than K (known as Levins' paradox, Gabriel et al., 2005) or the trajectory decreases with increasing rate for $r < 0$ and initial population size slightly smaller than K (Kuno, 1991). This is caused by the fact that the term r is multiplied by the suppression coefficient, which implies that with population growth, both mortality and fertility decrease, and mortality decreasing with increasing population size and reaching zero at equilibrium is biologically counterintuitive. Mortality should not decrease with population growth and individuals cannot be immortal at equilibrium. The above problems suggest that models should rely on clear and mechanistic assumptions (Geritz and Kisdi, 2012). Thus, density dependent suppression should act only on the number of juveniles recruited to the population (Kozłowski, 1980; Ginzburg, 1992) and the initial population size should be smaller than the carrying capacity (Hui, 2006; Argasinski and Kozłowski, 2008; Argasinski and Broom, 2012) leading to

$$\dot{n} = n\left(b\left(1 - \frac{n}{K}\right) - d\right), \tag{3}$$

where the suppression term $(1 - n/K)$ describes newborns' survival probability. This provides an important distinction between newborn candidates introduced to the environment (described by per capita number b) and recruited newborns, survivors of the density dependent stage (described by $b\left(1 - \frac{n}{K}\right)$).

This problem was emphasized by Kozłowski (1980) for the first time, but surprisingly this paper did not get as wide an appreciation as it deserved. This problem was also mentioned in the classical book "Population Ecology of Individuals" (Łomnicki, 1988). Then it was reinvented by Ginzburg (1992), but (3) was rejected there as it "disagrees with our intuition about unchanging equilibrium". Hui (2006) argued, against Ginsburg's claim, that (3) is the proper approach and should be substituted for (2). The discussion started by Ginzburg also did not receive much attention. Argasinski and Kozłowski (2008) then applied Eq. (3) to avoid the suppression of selection that occurs after the equilibrium size is reached caused by Eq. (2) without knowledge of this discussion, and (3) is a cornerstone of the ecologically realistic approach to dynamic evolutionary games (Argasinski and Broom, 2012). Then (3) was mentioned as an example of the proper mechanistic approach (Geritz and Kisdi, 2012), but not as the general alternative to (2). However, we believe that (3) deserves much stronger attention from a general audience.

Although (3) has been applied in complex selection models (Argasinski and Kozłowski, 2008; Zhang and Hui, 2011; Argasinski and Broom, 2012), the selection consequences of this approach have not been rigorously analyzed, since previous papers (Kuno, 1991; Ginzburg, 1992; Gabriel et al., 2005; Hui, 2006) focused on population density dynamics and ecological aspects. This distinction between adults and newborn candidates is very important for ecological and evolutionary reasoning, because differences between juvenile and adult mortality can have serious selection consequences. For example, a lack of mortality differences means that a small fecundity advantage can favor evolution of semelparity over iteroparity (this problem is known as Coles Paradox, Cole, 1954), while mortality differences can significantly change the situation (Charnov and Schaffer, 1973). The selection mechanism induced by (3) is thus very interesting and will be analyzed in later sections.

3. The population in equilibrium

We can calculate equilibrium size, by setting the right hand side of Eq. (3) to be equal to 0, which gives either $n = 0$ or

$$\tilde{n} = \left(1 - \frac{d}{b}\right) K. \tag{4}$$

Note that for positive $\tilde{n}$, the condition $b > d$ should be satisfied. After substitution of $\tilde{n}$ into the logistic coefficient $(1 - n/K)$, we obtain the equilibrium newborn survival probability d/b. This is reasonable; due to the turnover of individuals, in any short time interval for every nb newborns we have nd dead individuals. Thus nd/nb describes the number of newborns competing for each single nest site vacated by a dead individual. Only one newborn can settle in a single place, thus each newborn can survive with probability d/b. This newborn survival should be valid for any density dependent mortality acting on juveniles, not only for logistic suppression, because only in this case does fertility equal overall mortality.

4. The case of multiple individual strategies

Assume that there are different individual phenotypes $i = 1, \ldots, H$ each characterized by per capita reproduction b_i and mortality d_i. Thus every strategy is described by a two dimensional vector $v_i = [b_i, d_i] \in ([0, \infty) \times [0, 1])$ describing demographic parameters interpreted as in (1). Note that K describes the number of nest sites and is the same for all phenotypes. Denoting $n = \sum_i n_i$ and $q_i = \frac{n_i}{n}$, we can describe the following dynamics:

$$\frac{dn_i}{dt} = n_i \left(b_i \left(1 - \frac{n}{K}\right) - d_i\right). \tag{5}$$

The value n_i increases with time if

$$n < \left(1 - \frac{d_i}{b_i}\right) K \tag{6}$$

and decreases in the opposite case. Thus for every strategy there is a critical population size which is a threshold between regions of growth and decline. Above the population size critical for a particular strategy, the effective fertility $b_i \left(1 - \frac{n}{K}\right)$ will be smaller than the mortality d_i. Thus the dynamics of the population size plays an important role, which is described by the equation

$$\begin{aligned}\frac{dn}{dt} &= \sum_i \dot{n}_i = \sum_i n_i \left(b_i \left(1 - \frac{n}{K}\right) - d_i\right) \\ &= n \left(\left(1 - \frac{n}{K}\right) \sum_i q_i b_i - \sum_i q_i d_i\right),\end{aligned}$$

giving

$$\frac{dn}{dt} = n \left(\left(1 - \frac{n}{K}\right) \bar{b} - \bar{d}\right), \tag{7}$$

where $\bar{b}(q) = \sum_i q_i b_i$ and $\bar{d}(q) = \sum_i q_i d_i$. We can easily calculate that in this case, instead of reaching the stable equilibrium, the population size converges to the stationary density manifold (Cressman et al., 2001; Cressman and Garay, 2003a,b)

$$\tilde{n} = \left(1 - \frac{\bar{d}}{\bar{b}}\right) K, \tag{8}$$

the form of which is conditional on the strategy frequencies. Thus we introduced diversity among individual strategies to our model. In our model, in the general case, newborn survival $\left(1 - \frac{n}{K}\right)$ is a phenomenological function, linear with respect to the fraction of free nest sites. Thus in this approach the recruitment probability equals the probability of finding a free nest site in a single trial. This is a very specific mechanism which will not be suitable for many species. However, similar mechanisms will work for any density dependent factor $u(n)$ acting on births that is monotonically decreasing with respect to n. Then for growth rate $b_i u(n) - d_i$, the critical population size will be $n = u^{-1}\left(\frac{d_i}{b_i}\right)$. The newly produced offspring of the carriers of the different strategies form a pool of candidates from which randomly drawn individuals will be recruited to settle in the available nest sites. This is the core of the "nest site lottery" mechanism which will be analyzed in the following sections. Note that Eqs. (5) and (7) suggest the importance of the factors $\frac{d_i}{b_i}$ and $\frac{\bar{d}}{\bar{b}}$. This will be analyzed in the next section.

5. The turnover coefficient *L*

Here we will introduce an important characterization of population dynamics. We shall define the function $L(v) = b/d$ for a single strategy v. L describes the number of newborns per single dead individual, which we shall refer to as the turnover coefficient (for the relationship of the turnover coefficient with lifetime reproduction, see the Discussion). Surprisingly, a similar coefficient describing the energy allocated to reproduction divided by mortality can be found in life history papers (Taylor and Williams, 1984, Kozłowski, 1992, 1996, Werner and Anholt, 1993, Perrin and Sibly, 1993, for an overview see Kozłowski, 2006). Analogously, for a mixture of strategies where $\bar{v}(q) = \sum_i q_i v_i = [\bar{b}, \bar{d}]$ is the average strategy contained in the convex hull of the strategies v_i (see Fig. 1), we define $L(\bar{v}(q)) = \bar{b}/\bar{d}$. Thus

$$\begin{aligned}L(\bar{v}(q)) &= \frac{\bar{b}}{\bar{d}} = \frac{\sum\limits_i q_i b_i}{\sum\limits_i q_i d_i} = \frac{\sum\limits_i q_i d_i L(v_i)}{\sum\limits_i q_i d_i} \\ &= \sum_i \frac{q_i d_i}{\sum\limits_j q_j d_j} L(v_i) = \sum_i y_i L(v_i),\end{aligned} \tag{9}$$

which is a weighted average of the $L(v_i)$s and $y_i = q_i d_i / \sum_j q_j d_j$ describes the fraction of i strategists among individuals dying during a small time interval Δt (according to Appendix A, (A.2)). $L(\bar{v}(q))$ is thus the average L among dead adult individuals. The L-function can be useful in describing the multiplicative newborn survival (recruitment probability) because after substitution of the stable population size $\tilde{n}$ into the logistic suppression coefficient we obtain:

$$\left(1 - \frac{\tilde{n}}{K}\right) = \bar{d}/\bar{b}, \tag{10}$$

which can be denoted as $1/L(\bar{v}(q))$.

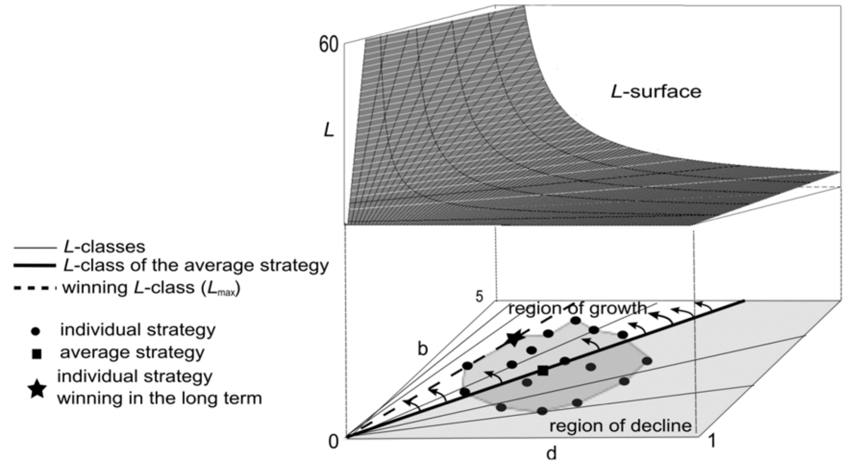

Fig. 1. The figure shows the plot of the *L*-surface over the strategy space. The individual strategies and *L*-classes are shown on the strategy space. The *L*-class of the populations average strategy is the border between regions of growth and decline. The growth of the frequencies of the strategies from the growth area induce counterclockwise movement of the *L*-class of the average strategy, leading to the selection of *L*-maximizing strategies. However, among *L*-maximizers, selection for greater mortality *d* can be induced by the introduction of suboptimal mutants. In this case the strategy lying on the maximal *L*-class line, farthest from zero, wins.

If there is any variation in the $L(v_i)$s, then we have that $\bar{b}/\bar{d}$ lies strictly between the smallest and largest values of L, $L_{\min} < \bar{b}/\bar{d} < L_{\max}$. $L(v)$ describes the number of newborn candidates produced per single dead individual for the strategy $v = [b, d]$, during Δt. When the strategic argument is the averaged vector, describing a population with a mixture of strategies, then the value of L is the average number of newborn candidates produced per single dead individual in this population. When the population is in size equilibrium (at the stationary density manifold), then the newborn survival component can be described by the value of L of the average population strategy; thus it becomes frequency dependent.

6. Selection dynamics

The behavior of Eq. (5) suggests frequency dependent self-regulation of the population state. Eq. (7) shows attraction to the stable size manifold (8), which suggests that the dynamics on this manifold should be analyzed. To describe the frequency dependent selection associated with the system we have presented, tools appropriate to game dynamics are required. Thus we should describe the population in terms of the strategy frequencies q_i and the population size n. However, at the stable size manifold the population size is given by (10). We can assume that the strategies are close enough to each other that a separation of timescales between fast n dynamics and q dynamics occurs. Then we can assume that selection occurs on the stationary size manifold. Now we can describe the selection process realized by the "nest site lottery" mechanism. Thus using (10), we can write the selection dynamics from (5) as

$$\frac{dn_i}{dt} = n_i\left(b_i\frac{\bar{d}(q)}{\bar{b}(q)} - d_i\right). \tag{11}$$

Because the average growth rate on the stable size manifold is zero then the Eq. (11) can be replaced by the replicator dynamics (see Appendix A)

$$\frac{dq_i}{dt} = q_i\left(b_i\frac{\bar{d}(q)}{\bar{b}(q)} - d_i\right) = q_i d_i\left(\frac{L(v_i)}{L(\bar{v}(q))} - 1\right). \tag{12}$$

Therefore the growth rate of the i-th strategy becomes a function of the strategy frequencies q (frequency dependent):

$$M(v_i, q) = b_i\frac{\bar{d}(q)}{\bar{b}(q)} - d_i = d_i\left(\frac{L(v_i)}{L(\bar{v}(q))} - 1\right),$$

and by Eqs. (7) and (8) the stationary population size manifold is described by

$$\tilde{n} = \left(1 - \frac{\bar{d}(q)}{\bar{b}(q)}\right)K = \left(1 - \frac{1}{L(\bar{v}(q))}\right)K.$$

Note that the growth rate function M describes a mixture of all mortality and fecundity components, not only the density independent mortality d and fecundity b as in the Malthusian parameter r. The growth rate is positive when $L(v_i) > L(\bar{v}(q))$, which implies that

$$\frac{b_i}{d_i} > \frac{\sum_j q_j b_j}{\sum_j q_j d_j}. \tag{13}$$

Thus there is a threshold between regions of growth (strategies with reproductive surplus) and reduction (strategies with death rate exceeding birth rate) which has the linear form $b_i = L(\sum_j q_j v_j)d_i$ (see Fig. 1). The threshold describes the set of strategies for which the growth rate $M(v_i, q)$ equals 0. Frequencies q_i of strategies v_i with a greater value of L than the average strategy $\sum_j q_j v_j$ will increase under the replicator dynamics. In effect the averaged strategy shifts towards those strategies because it is a linear combination of the strategies present in the population. This implies an increase of L of the average strategy (see Fig. 1). However, among growing strategies, the greatest growth rate is by the strategy with the greatest growth rate $M(v_i, q)$. Because in this case the dynamics is on the stationary density manifold, the current population size is very close to (8) and (13) is equivalent to satisfying inequality (6) (passing the critical population size). Thus at the stationary size manifold the threshold between the growth and decline of the strategy frequency is equivalent to the threshold between the growth and decline of the number of carriers of that strategy (this may not be satisfied far from the stationary size manifold). Frequency dependence induces an increase of the slope of the threshold which eventually leads to the selection of the strategy with the greatest L, which confirms the result of Mylius and Diekmann (1995). Note that their second result, that density dependent adult mortality leads simply to r maximization as in unlimited growth models, directly comes from the independence of the replicator dynamics from background fitness.

7. The monomorphic resident–mutant case

We can simplify the above model by assuming a monomorphic population invaded by a rare mutant; thus this resembles the classical ESS approach (Maynard Smith, 1982) in the context of life history evolution (Charlesworth and Leon, 1976; Mylius and Diekmann, 1995). In the limiting case where the strategy trait tends to zero, we approach the method known as invasion analysis which is the cornerstone of adaptive dynamics (Dieckmann and Law, 1996; Metz et al., 1996; Geritz et al., 1998; Dercole and Rinaldi, 2008). Using Eq. (12), the resident growth rate is zero and the rare mutant growth rate function M is $b_{\mathrm{mut}}(d_{\mathrm{res}}/b_{\mathrm{res}}) - d_{\mathrm{mut}}$ which must be positive to invade the population. Thus the equilibrium population size increases.

To be an ESS itself, the "mutant" population should be stable against the previous resident, and thus:

$$b_{\mathrm{res}}\frac{d_{\mathrm{mut}}}{b_{\mathrm{mut}}} - d_{\mathrm{res}} < 0 \Rightarrow \frac{b_{\mathrm{res}}}{d_{\mathrm{res}}} < \frac{b_{\mathrm{mut}}}{d_{\mathrm{mut}}},$$

which is the same condition. Thus in both cases we obtain $L_{\mathrm{res}} < L_{\mathrm{mut}}$.

Note that, when we consider only the death component of the Malthusian equation then we obtain the equation $\dot{n} = -nd$; thus this is an exponential decay with decay constant d, and so the average lifetime of the individual is $\kappa = 1/d$. In any short time interval of length Δt, for every nb newborns we have nd dead individuals. We can change the timescale to set Δt as the new time unit. Then initial rates, and thus respective births and deaths numbers, should be multiplied by some timescale specific constant. However this constant cancels out in $L(\upsilon)$. Thus $L(\upsilon)$ is the lifetime reproduction R_0. Therefore we have obtained for the "nest site lottery" mechanism, the classical result that under limited growth only lifetime reproduction is maximized and there is no selection pressure on the lifespan. However this occurs only in a monomorphic resident–mutant model. The case of a population composed of an arbitrary number of individual strategies is more interesting.

8. Multiple strategies with $L = L_{\max}$

We have seen that evolution leads to the fixation of the strategy with the largest value of L, $L_{\max}$. What if there is more than one such strategy? The following question arises: is there selection between strategies with the same L? We can show this by applying a multipopulation game-theoretic approach (Appendix A and Argasinski, 2006) and divide strategies present in the population among subpopulations with the same L, but different ds (Appendix B). Assume than we have m such classes with H_j different strategies in the j-th L-class (then the lower strategy index describes the number within the particular L-class and the upper strategy index describes the L-class). Then for all strategies (for all i) from the same L-class $L(\upsilon_i^j) = L^j$. When we assume that the dynamics is on the stable density manifold, we obtain the following equations

$$\frac{dq_i^j}{dt} = q_i^j\left(\frac{L^j}{L(\bar{\upsilon}(q))} - 1\right)\left(d_i^j - \sum_w q_w^j d_w^j\right), \tag{14}$$

$$\frac{dg_j}{dt} = g_j\left(\frac{L^j}{L(\bar{\upsilon}(q))} - 1\right)\sum_w q_w^j d_w^j, \tag{15}$$

describing the changes of the proportion of the i-th strategy within the j-th L-class (Eq. (14)) described by q_i^j and related frequencies between L-classes (15) described by g_j. Thus selection between L-classes is driven by the first bracketed term from Eq. (14) and affects both intra- and inter-group dynamics. However, there is selection inside each L-class towards greater d. When suboptimal L-classes are outcompeted, the intrinsic selection driven by the bracket $\left(d_i^j - \sum q_w^j d_w^j\right)$ is also suppressed. The form of Eq. (15) shows that among growing L-classes, those with smaller L can grow faster than those with larger, due to a greater $\sum q_w^j d_w^j$, until they fall under the L-selection threshold.

We are interested in analyzing which strategy (strategies) will dominate the population in the long term. In particular, $\dot{q}_i$ in Eq. (12) is always positive if strategy i has $L(\upsilon_i) = L_{\max}$, whenever there is variation in the L values in the population. Thus the proportions of such strategies increase; but also, following Eq. (14), the strategies out of these with the largest values of d_i increase the fastest. Thus if there is either repeated small mutations involving strategies with $L(\upsilon_i) < L_{\max}$ or a constant low level of mutation involving a mix of strategies making $L(\bar{\upsilon}(q)) < L_{\max}$, the population will evolve to the strategy out of those with $L(\upsilon_i) = L_{\max}$ such that d_i takes the largest value. Thus repeated mutations or invasions of suboptimal strategies induce selection towards maximal d among $L_{\max}$ strategists. It is easy to show that in the absence of density dependent suppression, this strategy has the greatest r but only among $L_{\max}$ strategies, since $b_i = d_i L_{\max}$. The strategies from other L-classes can have even greater r, but they will be outcompeted by the mechanism described by the bracketed term in Eq. (12). In the case when the population consists only of the $L_{\max}$ individuals, the same outcome can be caused by repeated ecological catastrophes leading to a decrease of the population size. Then the strategy with the greatest d_i will have the greatest growth rate during the growth phase of the population.

However, let us focus on the evolution of the system under the replicator dynamics in a single particular "turn", during which no mutation occurs. Suppose that there are precisely I strategies in the $L_{\max}$-class, and assume that the initial state of the $L_{\max}$-class is described by vector $q = (q_1^{\max}(0), \ldots, q_I^{\max}(0))$ and initial relative size $g_{\max}$.

Theorem 1. *The replicator dynamics converges to the vector*

$$q = (q_1^{\max}(0) g_{\max}(0)\lambda^{d_1}, \ldots, q_I^{\max}(0) g_{\max}(0)\lambda^{d_I}),$$

where λ is a constant that satisfies the equation $g_{\max}(0)\sum_{i=1}^{I} q_i(0)\lambda^{d_i} = 1$.

For the proof see Appendix C.

Theorem 1 shows that the rest point describing the frequencies among $L_{\max}$ strategists is fully determined by the initial state of the $L_{\max}$-class and its initial relative size $q_1^{\max}(0)$. Despite frequency dependence, this occurs independently of the initial frequencies of the other strategies (note that in our model there are no direct interactions between individuals). Thus calculation of q reduces to the finding of the appropriate value of λ. Note that the rest point q can be interpreted as the state of the whole population in general coordinates and the final state of the $L_{\max}$-class (then $g_{\max} = 1$). Note that if initially $g_{\max}(0) = 1$, then obviously $\lambda = 1$. The parameter λ can be described as the inflation coefficient because it inflates the frequencies to sum them to one and compensate for the impact of $g_{\max}(0)$.

9. Discussion

9.1. How the nest site lottery works?

We started from the basic population growth equation which is the cornerstone of the framework underlying evolutionary game theory and replicator dynamics (Maynard Smith, 1982; Cressman, 1992; Hofbauer and Sigmund, 1988, 1998) and its more ecologically realistic extensions Cressman and Garay, 2003a,b, Argasinski, 2006, Argasinski and Kozłowski, 2008, Argasinski and Broom, 2012). We presented an analysis of the dynamics of the mechanism inducing frequency dependent selection towards the strategy maximizing the turnover coefficient $L(\upsilon_i)$.

This phenomenon can be explained mechanistically. All newborns introduced into the population at the same moment in time form a pool of candidates. Each newborn has an equal probability of surviving (find a nest place), thus the strategy maximizing the number of newborns (trials) maximizes the fraction in the pool of candidates and in effect the amount of survivors. However, every dead adult can be substituted by an individual with any other strategy, thus each death is an additional free place in the lottery. Thus it is profitable for the strategy carried by some subpopulation to maximize the number of trials (newborns) per single offered place (dead adult). In addition, we have shown that among strategies with the largest value of the turnover coefficient $L_{\max}$ there is a selection pressure towards the strategy with the greatest d. This is intuitive from Eq. (12), because for strategies with the maximal number of newborn candidates produced per dead adult (i.e. maximizing the bracketed term in Eq. (12)), the growth rate will increase with the number of dead adults (described by the fraction $q_i d_i$ in Eq. (12)) since each of them will be exchanged for $L_{\max}$ newborns in the pool of candidates. Note that this provides a gene centered mechanistic explanation of the phenomenon which can be naively interpreted in terms of group selection and an altruistic "sacrifice" of adults, to release the nest sites for juveniles. However, our model shows that it is an outcome of "selfish" fitness maximization at the individual level. In addition our model suggests a possible tradeoff in resource allocation between maximization of the number of candidates in the nest site lottery and survival of the parental individual.

9.2. Importance of the nest site lottery mechanism

The model presented in this paper is as simple as possible, to emphasize the mechanistic aspects of the analyzed phenomenon. For example, there are no direct interactions between individuals as in game-theoretic models. Our model has an extremely simplified age structure consisting only of juveniles and adults (more on the limitations of pure age-dependent models can be found in Metz and Diekmann (1986)). However, it was shown that the impact of density dependent factors (thus also the mechanism described in this paper and its generalizations) can significantly affect and alter the outcomes of game-theoretic models (Argasinski and Kozłowski, 2008; Argasinski and Broom, 2012). This is caused by the feedback driven by the fact that when population size is on the stable size manifold every newborn should find a new nest site vacated by a dead adult. Our model is the simple case example of a one-dimensional monotone density dependence acting on the effective birth rate (more on this and other general cases can be found in Metz et al. (2008a,b)). However, as was shown at the end of Section 4, our results can be extrapolated to other factors that are monotonically decreasing with respect to the population size, acting like juvenile survival. It is possible that other environmental feedback loops of the same type to those in our model may induce similar selection mechanisms.

The mechanism shown in this paper supports the intuition underlying r and K selection theory (MacArthur and Wilson, 1967), that natural selection favors different strategies in growing populations than in populations with suppressed growth. The theoretical and methodological aspects of this approach were criticized (Barbault, 1987; Getz, 1993; Stearns, 1977), however as an intuition it still seems to be relevant (for modern approaches see for example Metz et al., 2008a,b). An alternative to the r and K approach is life history theory (Roff, 1992; Stearns, 1992), where the problem of different selection mechanisms in limited and unlimited populations also exists. Maybe phenomena similar to those revealed by our simple model can be found in other, more general or different specific models related to general population dynamics, life history evolution, adaptive dynamics or population genetics. This can be the subject of future research.

9.3. What is maximized by natural selection, and when?

The exact meaning of "fitness" is a subject of endless discussion (Metz et al., 1992; Kozłowski, 1993; Mylius and Diekmann, 1995; Brommer, 2000; Dieckmann and Metz, 2006; Metz et al., 2008a,b; Roff, 2008). Basically "fitness" can be defined as the instantaneous growth rate or invasion exponent (Metz, 2008). However, if eco-evolutionary feedback is of a particularly simple kind, the optimization approach can be applied (Metz et al., 2008a,b; Gyllenberg et al., 2011) where some "fitness measures" or "proxies" are maximized. There is a widely known fact in life history theory that in a population with unlimited growth, the Malthusian growth rate r is a proper fitness measure, while on the stable size manifold, lifetime production of newborns (before juvenile mortality selection) R_0 is the correct measure. In Mylius and Diekmann (1995) there is a statement that the invasion fitness method (Metz et al., 1992) suggests that R_0 and r are necessarily both maximal at the ESS (although this statement is unclear since some strategies can maximize R_0 and others can maximize r). Our results support this claim, and show that an analogous mechanism can act in population dynamic and game-theoretic models.

Here an important claim is that of Brommer and Kokko (2002), who say that R_0 is a rate independent reproductive measure which does not depend on the timing of reproductive events. This is because R_0 is described on the lifespan timescale, not the population dynamic timescale like r. Despite its simplified form our model can be a useful illustrative example for this problem. How can we use a lifespan perspective in our approach? At first, assume that population growth is unlimited (every newborn candidate can find a nest site). Then demographic parameters b and d describing strategy v, are constant and the average lifetime of the individual is $\kappa(v) = 1/d$ (as in Section 7). Then $r(v) = b - d = (L(v) - 1)/\kappa(v)$ and $L(v)$ is the lifetime reproduction R_0 (or the average R_0 among individuals dying during Δt in a population described by v). Therefore, the formula $r = (L - 1)/\kappa$ shows how the growth rate is affected by lifetime reproduction in the case of a non-age structured population with unlimited growth. It shows that an individual should basically replace itself, but for the strategy growth rate to be positive requires a reproductive surplus during a lifetime. Now introduce the limitation of the nest sites causing density dependent selection. Our results show that under density dependence, the growth rates of the strategies are affected by the frequency dependent surplus reducing mechanism, described by newborn survival $1/L(\bar{v})$ which is the function of the other strategies present in the population. In effect $r(v)$ is replaced by density dependent growth rate $M(v, q) = (L(v)/L(\bar{v}) - 1)/\kappa(v)$ and $R_0 = L(v)/L(\bar{v})$. Thus the strategies maximizing the lifetime production of newborn candidates $L(v)$ will maximize R_0 and the bracketed term of $r(v)$. However among $L(v)$ maximizers, the strategy with smallest $\kappa(v)$ will have greatest $r(v)$.

9.4. Conclusion

Our simple model suggests an insight into the mechanistic nature of selection under limited growth and has serious interpretational consequences. It clearly shows that this problem should not be formulated as the alternative: evolution maximizes r OR R_0. In our simple model, when the population reaches a stable size manifold, then a mechanism that modifies the r's of competing strategies, which are no longer constants, emerges to select the strategy with maximal R_0, or with maximal r, among multiple strategies with maximal R_0. Thus, our model suggests the existence of another fitness measure which is the combination of R_0 and r, if our reasoning holds in age structured and other more complex models. However, it will be not a function which should be maximized, but a two staged procedure. The first stage should identify the strategies maximizing the turnover coefficient, while the second stage should find strategies with the greatest r from strategies chosen in the first stage. We note that our analysis is a simplification, and whereas $R_0 = L(v_i)$ in the models without age structure as presented in this paper, this is not necessarily satisfied in age structured models. This should be the subject of future research.

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Appendix A. Multipopulation replicator dynamics

Assume that we have H individual strategies. Standard replicator dynamics can be derived by rescaling the growth equation $\frac{dn_i}{dt} = n_i M_i$ to the related frequencies $q_i = n_i / \sum_j n_j$ which leads to the equation $\frac{dq_i}{dt} = q_i \left[M_i - \bar{M}\right]$ (where $\bar{M} = \sum_j q_j M_j$). This equation describes the evolution of strategy frequencies in the unstructured population. However, we might be interested in the modeling of the structured population divided into subpopulations such as different sexes, species etc. Assume that we want to decompose an entire population into z subpopulations. Define

$$k^j = [k^j_1, \dots, k^j_{H_j}] \tag{A.1}$$

as a vector of indices of strategies exhibited by individuals from the j-th subpopulation ($k^j_i \in \{1, \dots, H\}$, and H_j is the number of strategies in the j-th subpopulation). For example the notation $k^2 = [1, 3, 5]$ means that, in the second subpopulation there are (only) individuals with strategies 1, 3 and 5. Every strategy should belong to a single unique subpopulation. Then according to Argasinski (2006), by the following change of coordinates

$$q^j = [q^j_1, \dots, q^j_{H_i}] = \left[\frac{q_{k^j_1}}{\sum_{i=1}^{H_j} q_{k^j_i}}, \dots, \frac{q_{k^j_{H_j}}}{\sum_{i=1}^{H_j} q_{k^j_i}}\right] \quad j = 1, \dots, z \tag{A.2}$$

we obtain a distribution of relative frequencies of strategies in the j-th subpopulation. The distribution of proportions between subpopulations has the form

$$g = [g_1, \dots, g_z] = \left[\sum_{i=1}^{H_1} q_{k^1_i}, \dots, \sum_{i=1}^{H_z} q_{k^z_i}\right], \tag{A.3}$$

where g_j is the proportion of the j-th subpopulation. Every decomposition into subpopulations can be reduced again to a single population model by the opposite change of coordinates $q(g, q^1, \dots, q^z)$ where

$$q_{k^j_i} = g_j q^j_i. \tag{A.4}$$

When we apply the above transformations to the replicator equations, we obtain a set of equations that describes the dynamics inside the subpopulations (intraspecific dynamics). When the set of strategies in each subpopulation is characterized by the vector of indices k^j, then the system of replicator equations will be:

$$\frac{dq^j_i}{dt} = q^j_i \left[M^j_i - \bar{M}^j\right] \quad i = 1, \dots, H_j - 1,\ j = 1, \dots, z \tag{A.5}$$

$$\frac{dg_s}{dt} = g_s \left[\bar{M}^s - \bar{M}\right] \quad s = 1, \dots, z - 1 \tag{A.6}$$

where $\bar{M}^s = \sum_{i=1}^{H_s} q^s_i M^s_i$ is the mean fitness in the s-th subpopulation and $\bar{M} = \sum_{s=1}^{z} g_s \bar{M}^s$. In practical applications of this method to the modeling of biological problems, the replicator equations can be defined on the decomposed population. This will simplify the formulation of the model, because when strategies are initially assigned to subpopulations, there is then no need to change their indices. The choice of subpopulations is arbitrary and depends on the biological assumptions underlying the analyzed problem. For example, the entire population may be divided into two competing subpopulations of hosts and parasites or prey and predators. On the other hand, it may be divided into two subpopulations of males and females, when interspecific dynamics will describe the evolution of the secondary sex ratio, and intraspecific dynamics will describe changes of the frequencies of strategies inside the male and female subpopulations. The subpopulations can be divided into subsubpopulations, and the entire population may be transformed into a complex multilevel cluster structure. However, all these structures are equivalent to a single population replicator dynamics model.

Appendix B. Derivation of Eqs. (14) and (15) describing selection strategies inside *L*-classes and change of sizes of *L*-classes

Let us assume than we have m such classes with H_j different strategies in the j-th L-class. In addition, assume that the dynamics is on the stable size manifold. Then the initial system of the replicator equations can be transformed into two sets of differential equations. Firstly, the within L-class dynamics (according to (A.5)):

$$\frac{dq^j_i}{dt} = q^j_i \left(M(v^j_i) - \bar{M}^j\right), \tag{B.1}$$

where q^j_i is the proportion of the i-th strategy in the j-th L-class and $\bar{M}^j = \sum_w q^j_w M(v^j_w) = \sum_w q^j_w d^j_w \left(L(v^j_w)/L(\bar{v}(q)) - 1\right)$. Secondly, the between L-class dynamics (according to (A.6)):

$$\frac{dg^j}{dt} = g^j \left(\bar{M}^j - \bar{M}\right), \tag{B.2}$$

where g^j is the proportion of the j-th L-class and $\bar{M} = 0$, since the population is on the stable size manifold. Since for all strategies (for all i) from the same L-class $L(v^j_i) = L^j$, after substitution of the respective formulae into Eqs. (B.1) and (B.2), we obtain the Eqs. (14) and (15):

$$\frac{dq^j_i}{dt} = q^j_i \left(d^j_i \left(\frac{L(v^j_i)}{L(\bar{v}(q))} - 1\right) - \sum_w q^j_w d^j_w \left(\frac{L(v^j_w)}{L(\bar{v}(q))} - 1\right)\right) \tag{B.3}$$

$$= q^j_i \left(\frac{L^j}{L(\bar{v}(q))} - 1\right)\left(d^j_i - \sum_w q^j_w d^j_w\right), \tag{B.4}$$

$$\frac{dg_j}{dt} = g_j \left(\frac{L^j}{L(\bar{v}(q))} - 1\right) \sum_w q^j_w d^j_w. \tag{B.5}$$

Appendix C. Proof of Theorem 1

From (12) we have that

$$\frac{dq_i}{dt} = d_i q_i \left(\frac{L(v_i)}{L(\bar{v}(q))} - 1\right)$$

and so

$$\left(\frac{L(v_i)}{L(\bar{v}(q))} - 1\right) = \frac{1}{d_i q_i}\frac{dq_i}{dt}. \tag{C.1}$$

Consider any pair of strategies $v_i = [b_i, d_i]$ and $v_j = [b_j, d_j]$ from the same L-class (i.e. $L(v_i) = L(v_j)$). Using (C.1) we obtain

$$\begin{aligned}\frac{1}{d_i q_i}\frac{dq_i}{dt} &= \frac{1}{d_j q_j}\frac{dq_j}{dt}\\ &\Rightarrow \int \frac{1}{d_j q_j} dq_i = \int \frac{1}{d_j q_j} dq_j + C\\ &\Rightarrow \frac{\ln q_i(t)}{d_i} = \frac{\ln q_j(t)}{d_j} + C. \end{aligned} \tag{C.2}$$

Considering $t = 0$ in Eq. (C.2) we obtain

$$C = \frac{\ln q_i(0)}{d_i} - \frac{\ln q_j(0)}{d_j}. \tag{C.3}$$

Combining (C.3) with (C.2) we obtain

$$\begin{aligned}\frac{\ln q_i(t) - \ln q_i(0)}{d_i} &= \frac{\ln q_j(t) - \ln q_j(0)}{d_j}\\ &\Rightarrow \left(\frac{q_i(t)}{q_0(t)}\right)^{1/d_i} = \left(\frac{q_j(t)}{q_0(t)}\right)^{1/d_j}. \end{aligned} \tag{C.4}$$

Eq. (C.4) holds for any pair i, j from the same L-class, so that

$$\begin{aligned}\left(\frac{q_i(t)}{q_0(t)}\right)^{1/d_i} &= \lambda(t)\\ &\Rightarrow q_i(t) = q_i(0)\lambda(t)^{d_i},\end{aligned}$$

for some L-class specific $\lambda(t)$. It is clear from Eq. (12) and the fact that $L(\bar{v}(q))$ is increasing whenever there is heterogeneity of L values within the population that for the $L_{\max}$-class the corresponding value $\lambda(t)$ is always increasing and for any other class it is either always decreasing, or starts by increasing and then eventually switches to decreasing, when the population size passes the corresponding threshold (6). Since $\lambda(t)$ is bounded above and below, and a monotonic function (decreasing or increasing) then it converges. Letting $\lambda = \lim_{t\to\infty} \lambda(t)$ gives

$$q_i = \lim_{t\to\infty} q_i(t) = q_i(0)\lambda^{d_i}. \tag{C.5}$$

We know that $\sum_i q_i = 1$, thus for at least one L-class the corresponding $\lambda(t)$ should not converge to 0. The system (14), (15) shows that it will be $L_{\max}$-class. However, the above reasoning used coordinates describing the strategy frequencies in the whole population (a metasimplex coordinates, Argasinski, 2006). According to (A.4), $q_i(0)$ can be described in the coordinates of the system (14) and (15) and after change of the indices $i = k_a^l$ where l is the index of the L-class and a is the index of the strategy within this L-class, we have $q_{k_a^l} = g_l q_a^l$. Thus the rest-point will contain only the L-maximizing strategies, so that the state of the $L_{\max}$-class will be equivalent to the state of the whole population (i.e. according to (A.4) $g_{\max} = 1$ and $q_{k_i^{\max}} = q_i^{\max}$), but frequencies $q_{k_i^{\max}}(0)$ will not sum to 1. However, from (A.4) we have $q_{k_a^{\max}}(0) = g_{\max}(0)q_a^{\max}(0)$. Then (C.5) for the $L_{\max}$-class can be presented as:

$$q_a^{\max} = q_a^{\max}(0)g_{\max}(0)\lambda^{d_a}. \tag{16}$$

References

Argasinski, K., 2006. Dynamic multipopulation and density dependent evolutionary games related to replicator dynamics. A metasimplex concept. Math. Biosci. 202, 88–114.

Argasinski, K., Broom, M., 2012. Ecological theatre and the evolutionary game: how environmental and demographic factors determine payoffs in evolutionary games. J. Math. Biol. http://dx.doi.org/10.1007/s00285-012-0573-2. Open access.

Argasinski, K., Kozłowski, J., 2008. How can we model selectively neutral density dependence in evolutionary games. Theor. Popul. Biol. 73, 250–256.

Barbault, R., 1987. Are still r-selection and K-selection operative concepts? Acta Oecol.-Oecol. Gen. 8, 63–70.

Brommer, J., 2000. The evolution of fitness in life-history theory. Biol. Rev. 75, 377–404.

Brommer, J., Kokko, H., 2002. Reproductive timing and individual fitness. Ecol. Lett. 5, 802–810.

Charlesworth, B., Leon, J.A., 1976. The relation of reproductive effort to age. Am. Nat. 110, 449–459.

Charnov, E.L., Schaffer, W.M., 1973. Life history consequences of natural selection: Cole's result revisited. Am. Nat. 107, 791–793.

Cole, L.C., 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29, 103–137.

Cressman, R., 1992. The Stability Concept of Evolutionary Game Theory. Springer.

Cressman, R., Garay, J., 2003a. Evolutionary stability in Lotka–Volterra systems. J. Theoret. Biol. 222, 233.

Cressman, R., Garay, J., 2003b. Stability in N-species coevolutionary systems. Theor. Popul. Biol. 64, 519–533.

Cressman, R., Garay, J., Hofbauer, J., 2001. Evolutionary stability concepts for N-species frequency-dependent interactions. J. Theoret. Biol. 211, 1–10.

Cressman, R., Krivan, V., 2006. Migration dynamics for the ideal free distribution. Am. Nat. 168, 384–397.

Cressman, R., Krivan, V., 2010. The ideal free distribution as an evolutionarily stable state in density-dependent population games. Oikos 119, 1231–1242.

Cressman, R., Krivan, V., Garay, J., 2004. Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. Am. Nat. 164, 473–489.

Dercole, F., Rinaldi, S., 2008. Analysis of Evolutionary Processes. Princeton University Press.

Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. 34, 579–612.

Dieckmann, U., Metz, J.A.J., 2006. Surprising evolutionary predictions from enhanced ecological realism. Theor. Popul. Biol. 69, 263–281.

Gabriel, J.P., Saucy, F., Bersier, L.F., 2005. Paradoxes in the logistic equation? Ecol. Model. 185, 147–151.

Geritz, S.A.H., Kisdi, É., 2012. Mathematical ecology: why mechanistic models? J. Math. Biol. 65 (6), 1411–1415.

Geritz, S.A.H., Kisdi, É., Meszéna, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12, 35–57.

Getz, W.M., 1993. Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources—r-K selection revisited. Evol. Ecol. 7 (3), 287–305.

Ginzburg, L.R., 1992. Evolutionary consequences of basic growth equations. Trends Ecol. Evol. 7, 133.

Gyllenberg, M., Metz, J.A.J., Service, R., 2011. When do optimisation arguments make evolutionary sense? In: Chalub, F.A.C.C., Rodrigues, J.F. (Eds.), The Mathematics of Darwin's Legacy. Birkhäuser, pp. 233–268.

Hofbauer, J., Sigmund, K., 1988. The Theory of Evolution and Dynamical Systems. Cambridge University Press.

Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press.

Hui, C., 2006. Carrying capacity, population equilibrium, and environment's maximal load. Ecol. Model. 192 (1–2), 317–320.

Kozłowski, J., 1980. Density dependence, the logistic equation, and r- and K-selection: a critique and an alternative approach. Evol. Theory 5, 89–101.

Kozłowski, J., 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends Ecol. Evol. 7, 15–19.

Kozłowski, J., 1993. Measuring fitness in life-history studies. Trends Ecol. Evol. 8, 84–85.

Kozłowski, J., 1996. Optimal initial size and adult size of animals: consequences for macroevolution and community structure. Am. Nat. 147, 101–114.

Kozłowski, J., 2006. Why life histories are diverse. Pol. J. Ecol. 54 (4), 585–604.

Kuno, E., 1991. Some strange properties of the logistic equation defined with r and K–inherent defects or artifacts. Res. Popul. Ecol. 33, 33–39.

Łomnicki, A., 1988. Population Ecology of Individuals. Princeton University Press.

MacArthur, R.H., Wilson, E.O, 1967. The Theory of Island Biogeography. Princeton University Press.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press.

Metz, J.A.J., 2008. Fitness. In: Jørgensen, S.E., Fath, B.D. (Eds.), Evolutionary Ecology. In: Encyclopedia of Ecology, vol. 2. Elsevier, pp. 1599–1612.

Metz, J.A.J., Diekmann, O., 1986. The Dynamics of Physiologically Structured Populations. In: Lecture Notes in Biomathematics, vol. 68. Springer Verlag (Chapter IV), Section 1.2.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., van Heerwaarden, J.S., 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M. (Eds.), Stochastic and Spatial Structures of Dynamical Systems. North-Holland, pp. 183–231.

Metz, J.A.J., Mylius, S.D., Diekmann, O., 2008a. When does evolution optimize? Evol. Ecol. Res. 10, 629–654.

Metz, J.A.J., Mylius, S.M., Diekmann, O., 2008b. Even in the odd cases when evolution optimizes, unrelated population dynamical details may shine through in the ESS. Evol. Ecol. Res. 10, 655–666.

Metz, J.A.J., Nisbet, R.M., Geritz, S.A.H., 1992. How should we define 'fitness' for general ecological scenarios? Trends Ecol. Evol. 7 (6), 198–202.

Morris, D.W., 2011. Adaptation and habitat selection in the eco-evolutionary process. Proc. R. Soc. B 278 (1717), 2401–2411.

Mylius, S.D., Diekmann, O., 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos 74, 218–224.
Pelletier, F., Garant, D., Hendry, A.P., 2009. Eco-evolutionary dynamics. Philos. Trans. R. Soc. B 364, 1483–1489.
Perrin, N., Sibly, R.M., 1993. Dynamic models of energy allocation and investment. Annu. Rev. Ecol. Syst. 7, 576–592.
Post, D.M., Palkovacs, E.P., 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 1629–1640.
Roff, D.A., 1992. The Evolution of Life Histories, Theory and Analyses. Chapman & Hall.
Roff, D.A., 2008. Defining fitness in evolutionary models. J. Genet. 87, 339–348.
Schoener, T.W., 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331, 426.
Stearns, S.C., 1977. Evolution of life-history traits–critique of theory and a review of data. Ann. Rev. Ecol. Syst. 8, 145–171.
Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press.
Taylor, P.D., Williams, G.C., 1984. Demographic parameters at evolutionary equilibrium. Can. J. Zool. 62, 2264–2271.
Verhulst, P.F., 1838. Notice sur la loi que la population pursuit dans son accroissement. Corresp. Math. Phys. 10, 113–121.
Werner, E.E., Anholt, B.R., 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. Am. Nat. 142, 242–272.
Zhang, F., Hui, C., 2011. Eco-evolutionary feedback and the invasion of cooperation in Prisoner's dilemma games. PLoS One 6 (11), e27523. http://dx.doi.org/10.1371/journal.pone.0027523.