



# Nest site lottery revisited: towards a mechanistic model of population growth suppressed by the availability of nest sites



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## ABSTRACT

In the “nest site lottery” mechanism, newborns form a pool of candidates and randomly drawn candidates replace the dead adults in their nest sites. However, the selection process has only been analyzed under the assumption of an equilibrium population size. In this study, we extend this model to cases where the population size is not at an equilibrium, which yields a simplified (but fully mechanistic) biphasic population growth model, where the suppression of growth is driven only by the availability of free nest sites for newborns. This new model is free of the inconsistency found in the classical single phase models (such as the logistic model), where the number of recruited newborns can exceed the number of free nest sites. We analyzed the stability of the stationary density surfaces and the selection mechanisms for individual strategies described by different vital rates, which are implied by the new model.

## 1. Introduction

### 1.1. Problem of growth limitation

The problem of limited population growth is a crucial question in theoretical ecology. The first attempt to provide a mathematical description of this problem (and the main theoretical approach found in current textbooks) was the logistic equation introduced by Verhulst (1838), but this approach was criticized for producing paradoxical predictions (e.g., the possibility of escape to infinity for negative growth rates, called Levin's paradox (Kuno, 1991; Ginzburg, 1992)). Density-dependent growth suppression is related to a crucial question in evolutionary biology regarding the definition of fitness and its measures (Metz, 2008; Kozłowski, 1993; Mylius and Diekmann, 1995; Brommer, 2000; Dieckmann and Metz, 2006; Roff, 2008; Metz et al., 2008a, 2008b). The first model of the selective properties of limited population growth, which was inspired by the logistic model, was the influential concept of  $r$  and  $K$  selection introduced by MacArthur and Wilson (1967). Later, this concept was criticized for being too simplified and for producing incorrect predictions (Barbault, 1987; Getz, 1993; Stearns, 1977), it was replaced by the more detailed and precise life history theory (Stearns, 1992; Roff, 1992). In addition, it was shown that the classical logistic model also yields paradoxical and misleading predictions in selection models (Argasinski, 2008). However, similar to the concepts underlying the  $r$  and  $K$  selection

theory, the intuition that the selection rules are different for suppressed and unsuppressed growth still seems to be reasonable. However, it should be described using a more precise and mechanistic conceptual framework instead of an abstract phenomenological logistic model. The disadvantage of the logistic model is that this approach does not consider the turnover of individuals. An approach that is free of the disadvantages of the classical logistic growth was given by Kozłowski (1980), Łomnicki (1988); Ginzburg (1992) and Gabriel et al. (2005). This approach was applied to derive a more realistic evolutionary game theoretic framework (Argasinski and Broom, 2013a), where payoffs are expressed as demographic parameters. In this model, only the birth rate is under suppression, which leads to the following equation:

$$\dot{n} = n[b(1 - n/K) - d]. \quad (1)$$

We can also consider the discrete version

$$n(t+1) - n(t) = n(t)[b(1 - n/K) - d], \quad (2)$$

where  $n(t)$  is the population size (or concentration) at time  $t$ ,  $b$  and  $d$  are the birth and death rates, and  $K$  is the maximal population load (Hui, 2006, 2015), which can be interpreted as the number of nest sites in the environment. This implies that  $n \in [0, K]$ . In addition, instead of an arbitrarily selected carrying capacity, the dynamics converge to a dynamic equilibrium between mortality and fertility  $\tilde{n} = (1 - d/b)K$ . This is similar to the emerging carrying capacity concept found in epidemiological models (Bowers et al., 2003; Sieber et al., 2014). Thus,

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in the framework presented above, the term  $(1 - n/K)$  can be clearly interpreted as juvenile survival, which depends on the number of available nest sites. Therefore, a question arises regarding the form of juvenile survival  $(1 - n/K)$  if we assume that nest sites for newborns are the limiting factor. Should this be a simple linear function of the fraction of free nest sites  $(1 - n/K)$ , or something more complicated? The function  $(1 - n/K)$  causes problems in the discrete model (2), e.g., the trajectory can escape from the interval  $[0, K]$ .

Therefore, the present study provides a mechanistic derivation of a function to describe how juvenile survival is determined by the availability of nest sites for newborns. This more realistic function can replace the term  $(1 - n/K)$  in (2). The underlying basic principles are explained in the “nest site lottery” selection model Argasinski and Broom (2013b).

### 1.2. “Nest site lottery” model of Argasinski and Broom

The general selective properties of (1) were analyzed by Argasinski and Broom (2013b). The model is based on the following system of differential equations describing the selection of strategies with fertilities  $b_i$  and mortalities  $d_i$ .

$$\dot{n}_i = n_i[b_i(1 - n/K) - d_i]. \tag{3}$$

It has been shown that the system above converges to a stable density surface (Cressman et al., 2001; Cressman and Garay, 2003):

$$n = \left(1 - \frac{\bar{d}(q)}{\bar{b}(q)}\right)K, \tag{4}$$

where  $q_i = n_i/\sum_j n_j$ ,  $\bar{d}(q) = \sum_i q_i d_i$ , and  $\bar{b}(q) = \sum_i q_i b_i$ . When this occurs, the growth limitation driven by juvenile recruitment survival induces the “nest site lottery” mechanism.

Thus, when the population reaches the stable density surface, the manifold where there is a balance between mortality and fertility (Cressman et al., 2001; Cressman and Garay, 2003), then all of the newborns introduced into the population at the same time will form the pool of candidates for recruitment. Recruited newborns that will replace adult individuals dying within a short time interval in the nest sites released by them are drawn from the pool of candidates. We note that by adding to the nest site lottery mechanism's assumption that mortalities  $d_i = \xi$  do not differ for all strategies and that they are sufficiently low to allow the separation of timescales between fertility and mortality, then we obtain the assumptions that underlie the derivation of the Moran process. In this special limiting case, the newborn candidates will compete for a single nest site released by a dead adult. However, for the general case described by Argasinski and Broom (2013b), it has been shown that the selection of strategies can be described by the following replicator dynamics model derived from system (3) and expressed as the relative frequencies  $q_i$ :

$$\dot{q}_i = q_i \left( b_i \frac{\bar{d}(q)}{\bar{b}(q)} - d_i \right). \tag{5}$$

System (5) can be presented in terms of the turnover coefficient  $L_i = b_i/d_i$  and  $L(q) = \bar{b}(q)/\bar{d}(q)$  (Argasinski and Broom, 2013b). The parameter  $L$  describes the number of newborns that replace a single dead adult individual, which leads to the following form of (5):

$$\dot{q}_i = q_i d_i \left( \frac{L_i}{L(q)} - 1 \right). \tag{6}$$

From the bracketed term  $(L_i/L(q) - 1)$ , we find that  $q_i$  increases when  $L_i > L(q)$ . Thus, the system above shows that the “nest site lottery” leads to the fixation of the individuals with the maximal parameter  $L_i$ , which is caused by the bracketed term  $(L_i/L(q) - 1)$ . In a monomorphic population, the mutant with a greater value of  $L_i$  will win, which is equivalent to maximizing the lifetime reproductive success  $R_0$ , a well-known fitness measure in life history theory (Stearns, 1992; Roff,

1992). However, if we assume a polymorphic population, the same value of  $L_i$  can be obtained for different values of  $d_i$  and  $b_i$ . Thus, it is possible that several different strategies with the maximal  $L_i$  will be present at the rest point of (6). However, they are not equivalent because they will have different values for  $d_i$ , which appears on the right-hand side of equation (6).  $L$ -maximizing individuals will have the same value for the term  $(L_i/L(q) - 1)$ , and thus, those with the greatest growth rate will also have the highest mortality rate  $d_i$ . Then, every perturbation of the system (a decrease in the population size or invasion by mutants with a smaller value for  $L_i$ ) will lead to a significant increase in the frequency of the  $d$ -maximizing strategy from the class of  $L$ -maximizers (so the model will describe a single round of selection between perturbation events). Thus, in the long term with many perturbations, this strategy will outcompete the other  $L$ -maximizing strategies. Therefore, those with the shortest life-span will win among the life history strategies with the maximal  $L_i$ . These results suggest that the growth-limiting mechanism based on juvenile recruitment survival will affect the selection process because it transforms the maximization of the growth rate into a double staged process comprising the maximization of  $L_i$  and the maximization of  $d_i$  among the strategies with the maximal  $L_i$  (Argasinski and Broom, 2013b).

### 1.3. Universality and independence of the underlying suppression factors in the “nest site lottery” mechanism

However, the model presented by Argasinski and Broom (2013b) provides a clear mechanistic explanation only in the case where the population state is close to equilibrium (4). The problem is that system (5) was obtained based on a system of equations of type (1), where juvenile survival is described by the term  $(1 - n/K)$ . Deviation from the population size equilibrium changes juvenile survival from  $\bar{d}(q)/\bar{b}(q)$  into the abstract phenomenological factor  $(1 - n(t)/K)$ . However, the equality of this factor to the fraction of free nest sites is not justified by any interpretation. In Argasinski and Broom (2013b), it was shown that the mechanism described by system (5) is universal for all decreasing juvenile survival functions  $u(n)$ . For every system of equations of type  $\dot{n}_i = n_i[b_i u(n) - d_i]$ , the general population size can be described by the equation  $\dot{n} = n[\bar{b}(q)u(n) - \bar{d}(q)]$  leading to the stable density manifold  $\tilde{n} = u^{-1}(\bar{d}(q)/\bar{b}(q))$ , which can differ significantly from (4) depending on the form of  $u(n)$ . Thus, at equilibrium manifold, juvenile survival will be equal to  $\bar{d}(q)/\bar{b}(q)$ , which is the basis of system (5). Therefore, we can obtain the recruitment lottery mechanism for every decreasing juvenile survival function  $u(n)$ , regardless of the form of  $u(n)$ . We note that since  $r_i = b_i u(n) - d_i = d_i(L_i u(n) - 1)$ , then reduction of the population size caused by periodic disasters leads to the long term  $d_i$  maximization among  $L$ -maximizers. Possible errors in the factor  $u(n)$  will only affect the equilibrium population size  $\tilde{n} = u^{-1}(\bar{d}(q)/\bar{b}(q))$ . Thus, a question arises regarding the situations where the assumption about the balance between mortality and fertility does not hold, but a shortage of nest sites occurs. To answer this question, we need a mechanistic juvenile survival function that accurately describes the impact of the shortage of nest sites. Based on the nest site lottery, this should depend on the number of newborn candidates rather than only the adults. This problem is the focus of the current paper.

## 2. Results

Let us introduce an alternative population growth model where density-dependent suppression is driven by the availability of free nest sites for newborns introduced into the environment. The new model is biphasic and suppression starts when the number of newborns exceeds the number of free nest sites. For simplicity, we assume that no other mortality factors affect juvenile recruitment. We demonstrate the dynamic stability and selective properties of our model. We use a discrete approach because it is easier to interpret the parameters. Table 1 contains the list of important symbols.

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