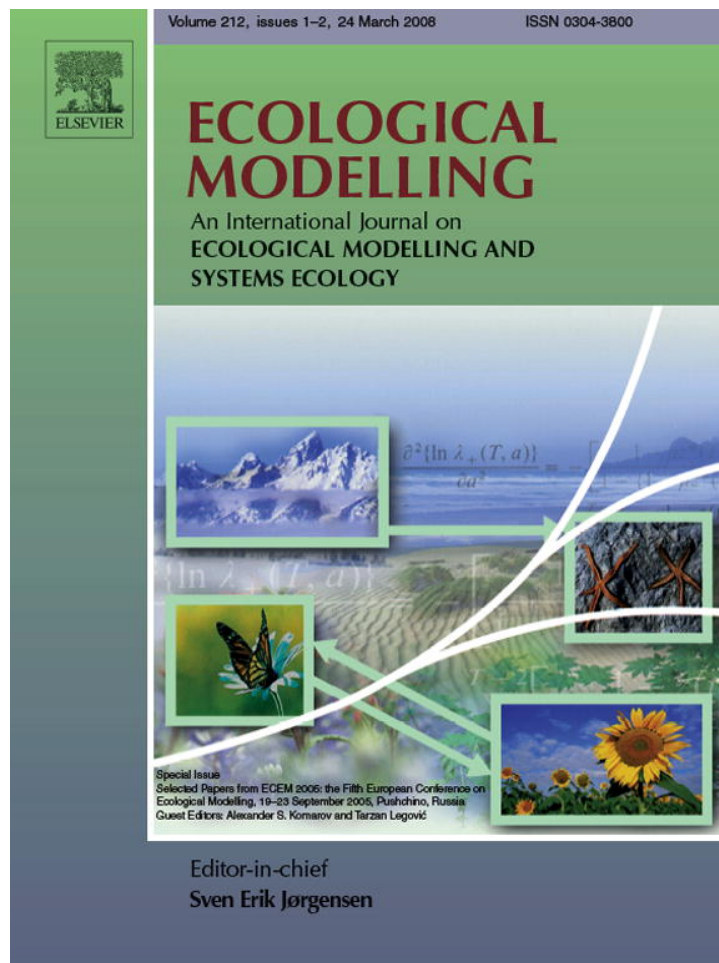


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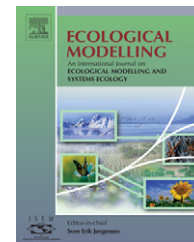
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# The impact of different density stresses on the dynamics of two competitive populations

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## ARTICLE INFO

### Article history:

Published on line 26 November 2007

### Keywords:

Competition

Invasion

Fitness

$r$ -Selection

$R_0$ -selection

$K$ -selection

## ABSTRACT

We compare the asymptotic dynamics of two competitive populations described by a system of two differential equations under different density stresses in order to clarify whether some parameters of the system or a function of them can be interpreted as a fitness criteria which a population should optimise to win the competition. Four types of stress are considered. First, it is an age-independent thinning of individuals that prevents that the common density of two competing populations would be greater than some limit value  $K$ . The second type of stress is a thinning of youngs and the third one is a thinning of adults. These three stresses come into play just when the limit is reached. The fourth stress, like the first one, does not depend on age but, unlike it, begins to take action gradually and increases gradually as density approaches  $K$ . We show that in the first case the population with a greater Malthusian coefficient  $r$  will ultimately supplant the other one. In contrast, in the second and third cases, the greater value of  $r$  does not ensure winning but instead that population whose lifetime reproductive success,  $R_0$ , is higher will supplant the other. And, at last, in the fourth case neither greater  $r$  nor  $R_0$  guarantee the win. Instead, that population whose environmental carrying capacity is greater than the capacity of the other population will supplant the other one.

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## 1. Introduction

The question we try to answer here can be formulated as follows. Let there be two competing populations  $X$  and  $Y$  composed of individuals with phenotypes  $p_x$  and  $p_y$ , correspondingly. Does there exist a phenotype-dependent function or a functional, called fitness criterion, such that the inequality  $F(p_y) > F(p_x)$  implies that the population  $Y$  will inevitably supplant the population  $X$ ? If so,  $F$  may be interpreted as a criterion of evolutionary selection. We will see that, indeed, in some model situations such criteria exist but they can be different for different models. The key role is played by the mechanism of braking or limiting the growth of population density. We consider several types of density-dependent environmental

stress: age-independent thinning, thinning of youngs, thinning of adults, and a model of a steadily increased density stress.

It is convenient, though not necessary, to imagine  $X$  as a large resident population and  $Y$  as a small population of invaders. The question then is what performances of the invaders can ensure that they supplant the residents.

Or, alternatively, we may consider  $X$  as a large initial population and  $Y$  as a small population of mutants. If a fitness criterion exists and its value is greater for  $Y$  than for  $X$  then  $Y$  will supplant  $X$  and become resident. But another mutant  $Z$  may appear with still greater fitness and then  $Z$  will supplant  $Y$ , and so on. So, with such successive replacements of genotypes, the fitness criterion will grow tending to its maximum.

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doi:10.1016/j.ecolmodel.2007.10.013

This is what is called evolutionary optimization (e.g. Teriokhin and Budilova, 2001; Teriokhin et al., 2003).

Among the firsts, Mylius and Diekmann (1995) drew attention to the importance of taking into account the nature of density stress when considering. They analyzed the situations of different density stresses using the Maynard Smith approach based on the game theory and the notion of evolutionary stable strategy (Maynard Smith, 1982). Here we use a more straightforward and, as we believe, intuitively more perceptible approach, based on the study of the population asymptotic dynamics in different two-populations competition models.

## 2. Models of stopped exponential growth

The model of simple exponential growth is based on the assumption that the rate of growth of population density is proportional to the density (we assume that the common ecotope of two competitive population is fixed so that equations for density and size are equivalent):

$$\begin{cases} \frac{dx}{dt} = r_x x_t \\ \frac{dy}{dt} = r_y y_t \end{cases} \quad (1)$$

where  $x_t$  and  $y_t$  are the densities of X and Y at time  $t$ , and  $r_x$  and  $r_y$  are the so-called intrinsic rates of population growth which can be expressed as differences  $r_x = b_x - d_x$  and  $r_y = b_y - d_y$ , of birth rates  $b_x$  and  $b_y$  and death rates  $d_x$  and  $d_y$  (e.g. May, 2001). Evidently, the model of unlimited exponential growth (1) is unrealistic for very big  $x_t$  and  $y_t$  because of limited environmental resources. Hence it should be modified to take into account such limitations. This can be made in several ways.

Assume that the nature of the environment is such that the sum of densities of X and Y cannot exceed some constant  $K$ , the carrying capacity of the environment. We will suppose that while the condition  $x_t + y_t < K$  is true, the densities  $x_t$  and  $y_t$  grow exponentially in accordance with Eq. (1). But just at the moment when the environment is saturated, i.e. the equality  $x_t + y_t = K$  is attained, some mechanism comes into force which does not allow for the total density to exceed  $K$ . At this moment the populations X and Y begin to compete because the limitation is imposed on their sum so that an increase of one population prevents automatically an increase of another one. Our purpose consists in comparing the dynamics of two populations as dependent on the parameters  $r_x$  and  $r_y$  representing their phenotypes. Especially, we are interested in finding conditions under which Y will supplant X. The mechanism of limiting the sum of densities of X and Y can be realized at least by three ways. First, it is possible to reduce in the same proportion both the density of youngs and the density of adults. Second, only the density of youngs can be reduced. And third, the required limitation can be ensured by reducing only the density of adults.

### 2.1. Age-independent thinning

Rewrite system (1) as follows

$$\begin{cases} x_{t+dt} = x_t + r_x x_t dt \\ y_{t+dt} = y_t + r_y y_t dt \end{cases} \quad (2)$$

and represent the mechanism of proportional reducing the density of youngs and adults as multiplying the right-hand sides of both equations of the system by some coefficient  $\alpha$  (intuitively this process can be imagined as thinning the total population by a factor of  $1/\alpha$  applied with the same intensity to the youngs and to the adults of the both populations X and Y):

$$\begin{cases} x_{t+dt} = \alpha(x_t + r_x x_t dt) \\ y_{t+dt} = \alpha(y_t + r_y y_t dt) \end{cases} \quad (3)$$

The condition that the equality  $x_t + y_t = K$  attained at the moment  $t$  cannot be upset at the following moment  $t + dt$  implies that the following equality:

$$x_{t+dt} + y_{t+dt} = x_t + y_t \quad (4)$$

should be true as soon as the limit  $K$  is attained. Replacing  $x_{t+dt}$  and  $y_{t+dt}$  in (4) with their expressions from (3) we obtain the following equation for calculating  $\alpha$ :

$$\alpha(x_t + r_x x_t dt + y_t + r_y y_t dt) = x_t + y_t$$

from which we get:

$$\alpha = \frac{x_t + y_t}{x_t + r_x x_t dt + y_t + r_y y_t dt} \quad (5)$$

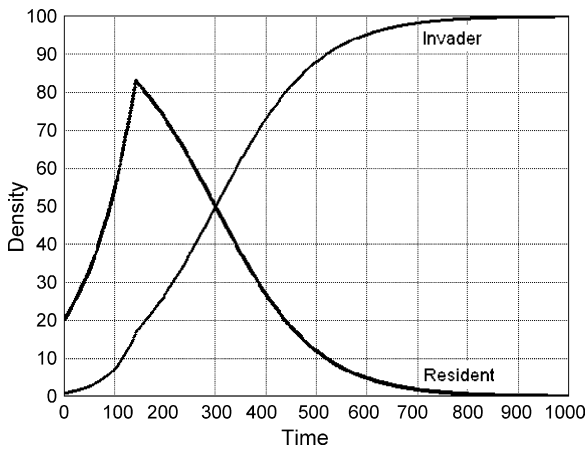
Substituting (5) into (3) and subtracting  $x_t$  and  $y_t$  from the both sides of the first and second equations in (3), we obtain:

$$\begin{cases} x_{t+dt} - x_t = \frac{(x_t + y_t)(x_t + r_x x_t dt)}{x_t + r_x x_t dt + y_t + r_y y_t dt} - x_t \\ y_{t+dt} - y_t = \frac{(x_t + y_t)(y_t + r_y y_t dt)}{x_t + r_x x_t dt + y_t + r_y y_t dt} - y_t \end{cases}$$

from where we obtain under the condition  $dt \rightarrow 0$  the following system of differential equations:

$$\begin{cases} \frac{dx}{dt} = (r_x - r_y) \frac{x_t y_t}{x_t + y_t} \\ \frac{dy}{dt} = (r_y - r_x) \frac{x_t y_t}{x_t + y_t} \end{cases} \quad (6)$$

The above system describes the dynamics of densities of X and Y under their age-independent sum-preserving thinning. We see immediately from (6) that when  $r_y > r_x$ , i.e.  $r_y - r_x > 0$  (and, correspondingly,  $r_x - r_y < 0$ ) the density of Y permanently increases whereas the density of X permanently decreases. This implies that Y will ultimately supplant X. So, a population with greater intrinsic rates of growth,  $r$ , have advantage over that with lesser  $r$  and ultimately supplants it. This means that  $r$  plays the role of fitness criterion when the competition between the resident and mutants is described by system (6). Fig. 1 illustrates this situation for  $r_x = 0.01$  and  $r_y = 0.02$ . We



**Fig. 1 – The dynamics of densities of populations X and Y in the case of age-independent thinning for  $r_x = 0.01$ ,  $r_y = 0.02$ ,  $x_0 = 20$ ,  $y_0 = 1$  and  $K = 100$  (X and Y are marked as resident and invader, correspondingly).**

see that asymptotically the number of X approaches to zero whereas the number of Y tends to the initial common density.

### 2.2. Thinning the youngs

Rewrite now system (1) in another way:

$$\begin{cases} x_{t+dt} = x_t + b_x x_t dt - d_x x_t dt \\ y_{t+dt} = y_t + b_y y_t dt - d_y y_t dt \end{cases} \quad (7)$$

and represent the mechanism of proportional reducing the density of youngs as multiplying the second terms of right-hand sides of both Eq. (7) by some coefficient  $\beta$  (intuitively this process can be imagined as thinning the youngs by a factor of  $1/\beta$ ):

$$\begin{cases} x_{t+dt} = x_t + \beta b_x x_t dt - d_x x_t dt \\ y_{t+dt} = y_t + \beta b_y y_t dt - d_y y_t dt \end{cases}$$

After transformations similar to those made in Section 2.1 we obtain the following system:

$$\begin{cases} \frac{dx}{dt} = \left( \frac{b_x}{d_x} - \frac{b_y}{d_y} \right) \frac{d_x d_y x_t y_t}{b_x x_t + b_y y_t} \\ \frac{dy}{dt} = \left( \frac{b_y}{d_y} - \frac{b_x}{d_x} \right) \frac{d_x d_y x_t y_t}{b_x x_t + b_y y_t} \end{cases} \quad (8)$$

This system describes the dynamics of densities of X and Y under sum-preserving thinning of youngs. We see from (8) that when  $b_y/d_y > b_x/d_x$ , i.e.  $b_y/d_y - b_x/d_x > 0$  (and, correspondingly,  $b_x/d_x - b_y/d_y < 0$ ) the density of Y permanently increases whereas the density of X permanently decreases so that Y will ultimately supplant X.

So, populations with greater ratios  $R_0 = b/d$  have advantage over those with smaller  $R_0$  that implies that in this model  $R_0$  plays the role of fitness criterion. This result contrasts with the situation considered in the previous paragraph where the fitness criterion was not the ratio  $R_0 = b/d$  of birth rate to death rate but their difference  $r = b - d$ .

The parameter  $R_0$  can be interpreted as lifetime reproductive success of an individual because it can be viewed as a product of the birth rate  $b$  by the inverse of death rate  $1/d$  which, in its turn, is equal to the expected lifespan,  $L$ . Though the both criterions,  $r$  and  $R_0$ , increase with increasing  $b$  and decreasing  $d$  their maximum values as functions of  $b$  and  $d$  are attained at different values of these arguments. Hence we may expect that, for some combinations of  $b$  and  $d$ , an invader Y capable to supplant the resident X in the case of age-independent thinning will be ousted by the resident in the case of thinning the youngs, and vice versa.

A typical situation when an invader is more advantageous from the point of view of the criterion  $r$  as compared with  $R_0$ , arises when great values of  $r$  are due to great values of birth rates. For example, if  $b_y = 0.10$ ,  $d_y = 0.03$ ,  $b_x = 0.05$  and  $d_x = 0.01$  then  $r_y - r_x = (0.10 - 0.03) - (0.05 - 0.01) = 0.03$  but  $R_{0y} - R_{0x} = (0.10/0.03) - (0.05/0.01) = -1.67$ . This means that, in the case of an age-independent thinning, Y will inevitably supplant X because  $r_y > r_x$  but if the density press acts only on the youngs then, on the contrary, Y will be supplanted by X because  $R_{0y} < R_{0x}$ . That is an invader with a high birth rate but in the same time with a relatively high mortality will win under age-independent thinning and will lose under youngs-aimed thinning. We will see in the next paragraph that such an invader will lose in the case of adults-aimed thinning too.

### 2.3. Thinning the adults

The thinning of adults can be considered as increasing their death rate in the same proportion both for residents and mutants. To embed this mechanism into the system (7) we will modify it by increasing the death rates in the both equations a factor of  $\delta$

$$\begin{cases} x_{t+dt} = x_t + b_x x_t dt - \delta d_x x_t dt \\ y_{t+dt} = y_t + b_y y_t dt - \delta d_y y_t dt \end{cases}$$

After transformations similar to those made in Section 2.1 we obtain:

$$\begin{cases} \frac{dx}{dt} = \left( \frac{b_x}{d_x} - \frac{b_y}{d_y} \right) \frac{d_x d_y x_t y_t}{d_x x_t + d_y y_t} \\ \frac{dy}{dt} = \left( \frac{b_y}{d_y} - \frac{b_x}{d_x} \right) \frac{d_x d_y x_t y_t}{d_x x_t + d_y y_t} \end{cases} \quad (9)$$

This system describes the dynamics of densities of X and Y under sum-preserving thinning of adults. Though system (9) slightly differs from (8), we can see that it leads to the same conclusions as (8). Namely, when  $b_y/d_y > b_x/d_x$ , i.e.  $b_y/d_y - b_x/d_x > 0$  (and, correspondingly,  $b_x/d_x - b_y/d_y < 0$ ) the density of Y permanently increases whereas the density of X permanently decreases so that ultimately Y will supplant X. Thus in the situation of thinning adults just as in the previously considered situation of thinning youngs the fitness criterion is the same,  $R_0$ .

## 3. Logistic limitation

In the models of stopped exponential growth we considered rather rigid ways of preserving the summary population

density after having attained the carrying capacity  $K$ . The well-known model of two-population competition (Lotka, 1925; Volterra, 1926; May, 2001) assume a more soft mechanism of stabilizing the summary population density near the carrying capacity  $K$ . It looks as follows

$$\begin{cases} \frac{dx}{dt} = r_x x_t \left(1 - \frac{x_t + y_t}{K}\right) \\ \frac{dy}{dt} = r_y y_t \left(1 - \frac{x_t + y_t}{K}\right) \end{cases} \quad (10)$$

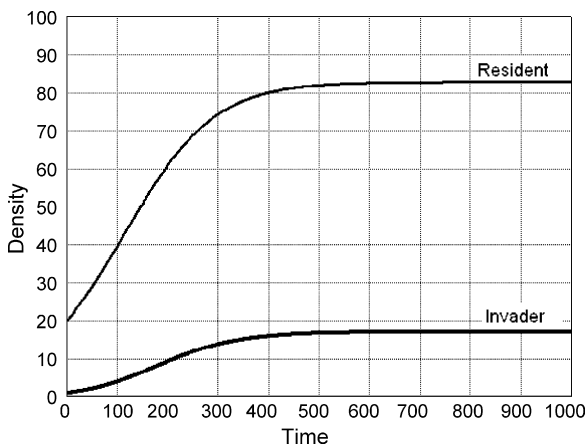
We may call it model of logistic growth because system (10) is a straightforward generalization of well-known model of logistic growth of one population for the case of two populations.

What happens if  $r_y > r_x$ ? Will  $Y$  supplant  $X$  as it was the case in the situation of age-dependent thinning? As we see from Fig. 2 illustrating the dynamics of densities of  $X$  and  $Y$ , obtained by integrating (10) for  $r_x = 0.01$ ,  $r_y = 0.02$ , it is not so. In contrast to Fig. 1,  $Y$  does not supplant  $X$  though  $r_y > r_x$  (note, however, that nor  $Y$  supplants  $X$ ).

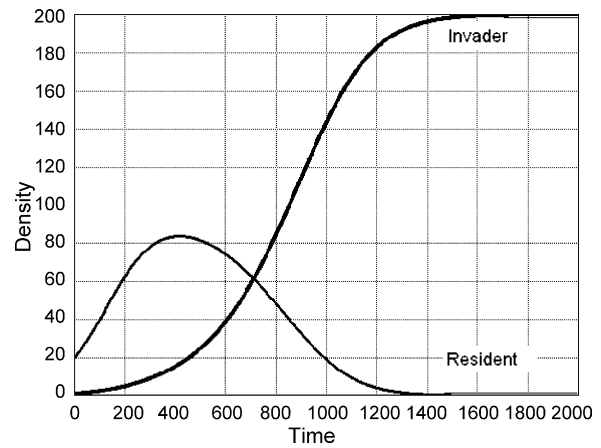
Thus we may conclude that in the case of logistic model described by system (10) the value of  $r$  does not change crucially the fitness of population. But this model has one more phenotypic parameter, the carrying capacity  $K$ . If we suppose that this parameter differs for  $X$  and  $Y$  then we will obtain the following model:

$$\begin{cases} \frac{dx}{dt} = r_x x_t \left(1 - \frac{x_t + y_t}{K_x}\right) \\ \frac{dy}{dt} = r_y y_t \left(1 - \frac{x_t + y_t}{K_y}\right) \end{cases} \quad (11)$$

An example of dynamics of  $X$  and  $Y$ , obtained by integrating (11) for  $K_y = 200$  and  $K_x = 100$  for equal intrinsic rates of growth  $r_x = r_y = 0.01$ , is given in Fig. 3. We see that now  $Y$  supplants  $X$ . The reason is that  $X$ , having lesser environment capacity, is more sensible to density stress: as soon as the limit  $K_x$  is surpassed the rate of growth of  $X$  (determined by the right-hand side of the first equation in (11)) becomes negative whereas the rate of growth of  $Y$  remains positive.



**Fig. 2 – The dynamics of densities of populations  $X$  and  $Y$  in the case described by system (10) for  $r_x = 0.01$ ,  $r_y = 0.02$ ,  $x_0 = 20$ ,  $y_0 = 1$  and  $K = 100$  ( $X$  and  $Y$  are marked as resident and invader, correspondingly).**



**Fig. 3 – The dynamics of populations  $X$  and  $Y$  in the case described by (11) for  $r_x = r_y = 0.01$ ,  $x_0 = 20$ ,  $y_0 = 1$ ,  $K_x = 100$  и  $K_y = 200$  ( $X$  and  $Y$  are marked as resident and invader, correspondingly).**

So we conclude that in the case of logistic environmental press the role of fitness criterion is played by  $K$ .

#### 4. Conclusion

Thus we showed that any population formed of invaders or mutants, even very small, that surpasses the resident population in  $r$  in the case of age-independent thinning, in  $R_0$  in the cases of thinning of only youngs or of only adults, and in  $K$  in the case of age-independent steadily increased density press, will ultimately supplant the resident population. Particularly, in the case of recurring mutations this implies that, depending on the type of environmental density stress, successful mutants will have correspondingly higher values of  $r$ ,  $R_0$  or  $K$ . So, these characteristics may be considered as criteria of evolutionary fitness for corresponding environmental situations. We may also figuratively say that, depending on the type of environmental density stress,  $r$ -,  $R_0$ - or  $K$ -strategy of evolutionary selection should be realized.

#### Acknowledgements

The authors are grateful to anonymous referees for helpful suggestions. The work was supported by a grant from the Russian Foundation for Basic Research (07-04-00521).

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