

# Carrying capacity, competition and maintenance of sexuality

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## ABSTRACT

A modification of the logistic equation is critically analysed and its application to competition between sexual and asexual populations presented. Such a model of competition can be a formal representation of the tangled bank hypothesis of the evolution and maintenance of sexuality. It shows that the elimination of asexual individuals by sexual ones is possible only if the size of the habitat or the width of the ecological niche of sexual individuals is twice as large as that of asexual ones. Co-existence of these two forms is theoretically possible under much less rigid conditions. Nevertheless, such co-existence does not imply that the ecological cost of the elimination of asexual individuals by sexual ones is lower than the commonly accepted biological cost of such elimination.

*Keywords:* asexual and sexual reproduction, density dependence, interspecies competition, logistic equation, niche width, population.

## INTRODUCTION

In spite of criticism of the logistic equation (Andrewartha and Birch, 1954; Łomnicki, 1988; Slobodkin, 2001),

$$\dot{N} = rN(1 - N/K) \quad (1)$$

(where  $N$  denotes population size,  $\dot{N}$  its change with respect to time and  $K$  is carrying capacity) is the most popular way of describing limited growth of populations. The logistic equation still plays a central role in theoretical population ecology, as there is no good alternative.

One feature of the logistic equation is an ambiguous definition of carrying capacity,  $K$ . For game managers, carrying capacity is the number of deer that an area can support without visible devastation of plant cover. Carrying capacity is also defined as the number ( $K$ ) of places (e.g. nesting holes) in which a single individual or a pair may live. It implies that, at equilibrium, all available places are occupied, provided the intrinsic rate of increase  $r > 0$ . This means that, after the death of an individual, another one immediately occupies its place. This, in turn, means that there are some individuals seeking empty places, so that the population is divided into established individuals and floaters.

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Another possible definition of carrying capacity is the equilibrium point at which the birth rate equals the death rate, so that  $K$  is determined not only by the size of the habitat or the number of available places, but also by the birth and death rates. The positive dependence of saturation density,  $K$ , on the rate of growth was confirmed in selection experiments on protozoa by Luckinbill (1979). If this is the case, then the relation between the birth rate, death rate and carrying capacity should be clearly determined. This would be of value even if made for a special case only.

A modified form of limited population growth allows for the dependence of equilibrium population size on reproduction and mortality, as shown in my derivation (Łomnicki, 1988) based on the metapopulation model of Levins (1970). A close examination of its applicability and its relation to the classical form of the logistic equation would be useful. It may reveal the mechanism of limited population growth and competition in relation to the evolution of sexuality.

### THE MODEL

Consider a habitat with  $H$  discrete places, each one able to support an individual animal or plant. Instead of considering the number of individuals  $N$ , it is more convenient to think in terms of the proportion of occupied places  $x$ , so that  $N = xH$ . A change in this proportion over time is given by the differential equation

$$\dot{x} = (1 - x)ax - dx \quad (2)$$

Although this model was used to describe the dynamics of a population (Doncaster *et al.*, 2000) or metapopulation (Levins, 1970), its parameters and limitations are rarely clearly articulated. Below I attempt to describe in detail the biological situation related to this model and to define its parameters as precisely as possible. The proportion  $(1 - x)$  of empty places is colonized at rate  $ax$ , while the proportion  $x$  of places occupied by established individuals become empty places with the death of these individuals at death rate  $d$ . The product  $ax$  is the number of propagules or seeds that reach a place, irrespective of whether it is occupied or empty. Parameter  $a$  is the colonization ability of a given population and is linearly related to the birth rate. However, it is neither the colonization rate nor the birth rate. The colonization rate or colonization probability depends on the number of immigrants per place, whether occupied or empty, while this number depends in turn on the proportion  $x$  of occupied places. Parameter  $a$  cannot be defined as the birth rate, since it also includes the ability to reach an appropriate empty place. This is determined not only by physiological and behavioural features of dispersing individuals, but also by the properties of their habitat. If appropriate places are far away from each other within a hostile area with many predators, then  $a$  has much lower values.

An important feature of this model is continuous time, so that the value of the product  $ax$  can be very low and therefore equal to the probability of colonization within a time unit, or the rate of colonization. However, when dispersion and colonization are seasonal phenomena, a discrete model of population growth has to be applied. One can then expect a high number of propagules per place for every time unit. From the Poisson distribution, the probability that at least one individual is able to reach a place is given by  $1 - e^{-ax}$ , and equation (2) takes the form

$$x_{t+1} = x_t + (1 - x_t)[1 - \exp(-ax_t)] - dx_t \quad (3)$$

The two models given by equations (2) and (3) describe a population for which the number of available places is fixed; that is, it does not depend on population density or the density of dispersing propagules. The linear negative dependence of the increase in the number of established individuals is due to the shortage of available places, and it is the only density-dependent process allowed by this model, since the mortality,  $d$ , of established individuals is constant and density-independent. There is no Allee effect, and a propagule arriving at an occupied place cannot search for another one but dies without establishing itself. Therefore, parameter  $d$  is not the death rate, as usually defined, since it does not include the mortality of propagules searching for places to establish themselves; it only includes the death rate of established individuals. One may call parameter  $a$  the birth rate and parameter  $d$  the death rate, but their meanings are different from those commonly accepted in theoretical ecology.

The population dynamics described by equation (2) have two equilibria: a trivial one at  $x = 0$  and a locally and globally stable one at  $x = k$ , defined by

$$k = 1 - d/a \quad (4)$$

This is the population size at equilibrium expressed as the proportion of occupied places. Since the population size  $N = xH$ , where  $H$  is the number of available places, then the population size at equilibrium  $L$  is given by  $L = kH$  or, from equation (4),

$$L = H(1 - d/a) \quad (5)$$

After multiplying equation (2) by  $H$ , so that the population dynamics are expressed as the number  $N$  of individuals, and substituting  $H$  into it as defined by (5), one obtains

$$\dot{N} = (a - d)N(1 - N/L) \quad (6)$$

which is exactly the logistic equation but the parameters have a slightly different meaning. I deliberately apply  $L$  instead of  $K$  to show that the equilibrium point  $L$  is not the carrying capacity and that it is determined not only by the size of the habitat  $H$ , but also by parameters related to the birth and death rates,  $a$  and  $d$  respectively.

### INTERSPECIFIC COMPETITION

The classical Lotka-Volterra application of the logistic equation to interspecific competition for population  $i$  competing with population  $j$  is given by

$$\dot{N}_i = r_i(K_i - N_i - \alpha_{ij}N_j)/K_i \quad (7)$$

where  $\alpha_{ij}$  denotes the inhibitory effect of an individual of population  $j$  on population  $i$ . Providing the intrinsic rates of growth  $r_i$  and  $r_j$  are positive, the outcome of interspecies competition is independent of the birth and death rates, as shown in ecology textbooks (e.g. Begon *et al.*, 1986). Such independence appears not only counterintuitive but also very unlikely. This outcome depends only on the respective carrying capacities (the higher  $K$  wins) and the very abstract and difficult-to-estimate parameter  $\alpha_{ij}$ . This parameter can measure differences and overlaps in the diets of two competitors, but it is difficult to imagine how it can measure differences in birth and death rates or differences in other characters that determine the outcome of competition.

The importance of birth and death rates in interspecies competition can be taken into account by modifying equation (2) into the form

$$\dot{x} = (h_x - x - y)a_x x - d_x x \tag{8}$$

where  $h_x$  denotes the fraction of the places available to population  $X$ , which may overlap more or less with the fraction available to population  $Y$ . The introduction of parameter  $\alpha_{XY}$  does not make sense within this model, since an individual either does or does not occupy an appropriate place but does not compete with another individual in the same place.

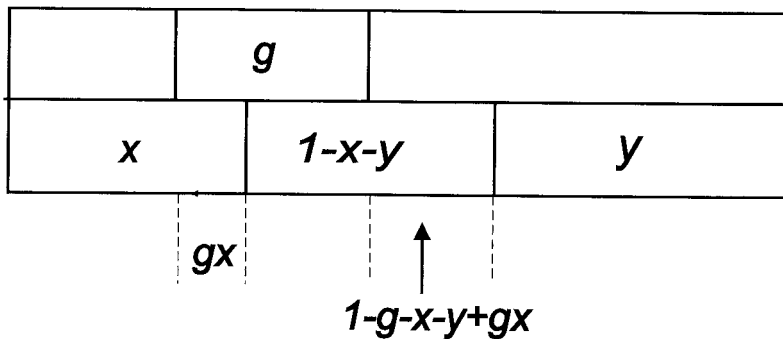
**COMPETITION BETWEEN SEXUAL AND ASEQUAL INDIVIDUALS**

Assuming that sexual and asexual individuals do not interbreed (for an exception, see Bell, 1982), they can be considered as populations of two different species competing with each other in the same habitat. The tangled bank hypothesis postulates that sexual forms, because they are more variable, are able to use resources and places not available to asexual ones, as suggested by some empirical studies (Vrijenhoek and Pfeiler, 1997; Cullum, 2000). Let us assume that asexual forms produce twice the progeny and therefore their colonization ability is twice the colonization ability,  $a$ , of sexual ones, and that asexual individuals are not able to live and reproduce in the fraction  $g$  of places open to sexual ones. Applying the model described by equation (2) to the dynamics of sexual ( $X$ ) and asexual ( $Y$ ) populations yields the following set of equations:

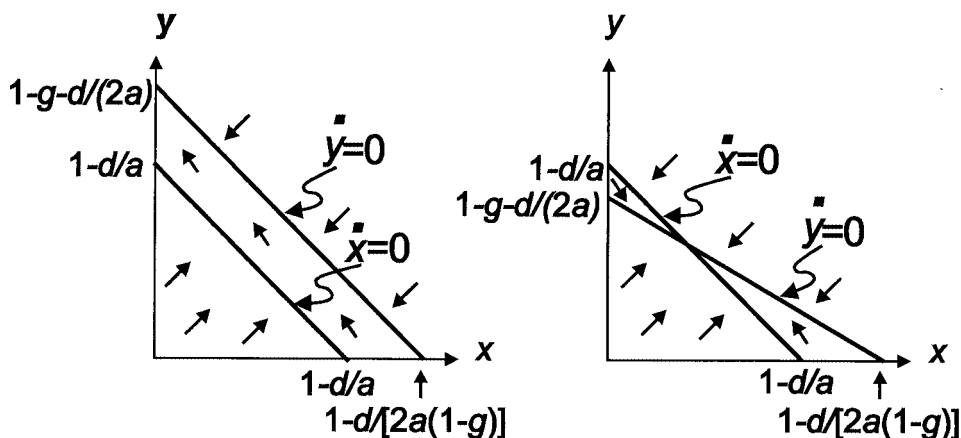
$$\dot{x} = ax(1 - x - y) - dx \tag{9a}$$

$$\dot{y} = 2ay(1 - g - x + gx - y) - dy \tag{9b}$$

Note that the colonization ability  $2a$  of asexual forms is twice the rate  $a$  of sexual ones. Empty places that can be colonized are limited by the proportion  $g$  of places not available for asexual individuals and the proportions  $x$  and  $y$  already occupied. The proportion  $x$  of the established sexual individuals that limits available places is in turn reduced by  $g$ ; that is, the proportion  $gx$  of sexual forms that find places in the part of the habitat not available for asexual forms (Fig. 1).



**Fig. 1.** The proportions of places unavailable ( $g$ ) and available ( $1 - g$ ) for asexual individuals (upper part), and the proportions of places that are occupied by sexual individuals ( $x$ ) and asexual individuals ( $y$ ) or are empty ( $1 - x - y$ ). As shown in the lower part of the figure, colonization by asexual individuals is limited by the number of places occupied ( $x + y$ ) and by the proportion  $g(1 - x)$  but not by the proportion  $gx$ .



**Fig. 2.** Changes in the proportions  $x$  and  $y$  of places occupied by sexual and asexual individuals, respectively, as described by equation (9). Two possible outcomes of competition are presented here: the elimination of sexual individuals by asexual ones (left) and the co-existence of both forms (right). See text for further explanation.

The isoclines  $\dot{x} = 0$  and  $\dot{y} = 0$  are straight lines on the phase surface (Fig. 2) with coordinates  $x$  and  $y$ . The isocline  $\dot{x} = 0$  cuts both the  $x$  and  $y$  axes at  $k_x = 1 - d/a$ . The isocline  $\dot{y} = 0$  cuts the  $x$  axis at  $1 - d/[2a(1 - g)]$  and the  $y$  axis at  $k_y = 1 - g - d/(2a)$ . Asexual forms are eliminated by the sexual ones if, at the  $x$ -axis,  $k_x > 1 - d/[2a(1 - g)]$ , which implies that

$$g > 1/2 \quad (10)$$

Sexual form cannot be eliminated if, on the  $y$ -axis,  $k_y > k_x$ , which implies that

$$g > d/(2a) \quad (11)$$

The proportion  $x_E$  of sexual individuals at the point where the isoclines  $\dot{x} = 0$  and  $\dot{y} = 0$  intersect is given by

$$x_E = 1 - d/(2ga) \quad (12)$$

from which conditions (10) and (11) can also be derived.

The condition given by inequality (10) is very unlikely to be met, since it requires that more than half of the habitat is not available for asexual individuals, while the entire habitat is available for sexual ones. Condition (11) is less rigid and, if met without meeting condition (10), it leads to co-existence. This requires very low mortality,  $d$ , of established individuals and high colonization ability,  $a$ . Under such circumstances, the right-hand side of inequality (10) can be low and, therefore, a small fraction of places available for sexual but not for asexual individuals may allow for co-existence of both forms. Since large differences in the size of habitats or ecological niches, as postulated by condition (10), are unknown from empirical data, the tangled bank hypothesis as presented by this model does not explain elimination of asexual by sexual reproduction.

Modification of this model for discrete time units, by applying the colonization probability given by  $(1 - e^{-ax})$  instead of  $ax$ , does not allow for an analytical solution. Under

very low numbers of immigrants per place, the discrete model does not differ from the continuous one, while under very large numbers of immigrants, the probability of colonization approaches unity. Assuming that  $(1 - e^{-ax}) = 1$ , or in other words that in every time unit each place is colonized, a modification for discrete time units will allow an analytical solution. The probability that an individual which establishes itself comes from a given population is proportional to the fraction of migrants from this population. Therefore, the probability that a sexual individual establishes itself is  $ax/(ax + 2ay) = x/(x + 2y)$ , while the probability that an asexual one does is  $2y/(x + 2y)$ . Changes in the proportion of occupied places,  $\Delta x$  and  $\Delta y$ , are therefore given by

$$x_{t+1} = x_t + (1 - x_t - y_t)x_t/(x_t + 2y_t) - dx_t \quad (13a)$$

$$y_{t+1} = y_t + 2[1 - g - x_t(1 - g) - y_t]y_t/(x_t + 2y_t) - dy_t \quad (13b)$$

The outcome of competition as described by these equations is similar to that described by the continuous model (equations 9a, 9b). The sexual forms outcompete asexual ones only if  $g > 1/2$ , which is identical to condition (10), and if

$$g > d/(1 + 2d) \quad (14)$$

Inequality (14) replaces condition (11) in the discrete model, which allows for co-existence when inequality (10) is not met. As in the former model, it is more likely to be fulfilled if the death rate,  $d$ , of established individuals is very low.

## DISCUSSION

The model presented above does not allow for the maintenance of sexuality through the mechanisms postulated by the tangled bank hypothesis. This is because there are no empirical data to show that niche width or the number of available places for sexual individuals is double that of asexual ones. Nevertheless, co-existence of both forms is possible theoretically, and this model formalizes analytically the arguments of the tangled bank hypothesis. In an asexual population, if the death rate,  $d$ , is low in relation to the birth rate and colonization ability,  $a$ , then almost all places available for asexual individuals are occupied. Therefore, an extension of the habitat by a small proportion  $g$ , available for sexual individuals only, gives them a chance to survive and co-exist. But if  $g$  is small, then the proportion  $x$  of sexual individuals co-existing with asexual ones is also small. Co-existence in sympatry of both sexual and asexual forms is a rare phenomenon. Of 106 insect species reproducing without sex listed by Bell (1982), sympatric occurrence of both forms of reproduction is known for only six of them. There may be other reasons for this rare occurrence of co-existence in spite of the predictions of the model presented here. If the size of the habitat for sexual individuals is only slightly wider, the proportion of sexual individuals predicted by the model is very small, and a very low density of partners for reproduction may not allow for their persistence.

The model presented above, while very different from the numerical simulations of the tangled bank hypothesis by Bell (1982), yields rather similar results: with a two-fold advantage of a single clone, competition between sexual and asexual individuals cannot eliminate the latter. Only after some additional complications introduced by Bell can asexual reproduction be eliminated: a lower than two-fold cost of sex or the co-existence of many clones and their stochastic extinction when they are very rare.

Two models (Case and Taper, 1986; Doncaster *et al.*, 2000), similar to that described here, have claimed quite different results. Doncaster *et al.* (2000) stated that their model allows asexual individuals to be outcompeted by sexual ones. Based on their own assumptions and within the framework of their model, it is impossible to prove their claim that a sexual population may drive out asexual invaders altogether. According to these authors, it is possible if  $k_1 > k_2/\alpha_{21}$ , where  $k_1$  and  $k_2$  are states of equilibrium for single sexual and single asexual populations respectively, and  $\alpha_{21}$  is the inhibitory effect of a sexual population on an asexual one and is assumed to be smaller than unity. By applying the definitions of all these parameters as given in their paper, it is clear that elimination of asexual individuals by sexual ones is possible only if the reproductive disadvantage of sexual individuals is balanced with equally high mortality. West and Peters (2000) did not notice this mistake in their critique of the paper by Doncaster *et al.* (2000).

Doncaster *et al.* (2000) also showed that the proportion of sexual individuals increases with an increase in  $R_0$  (equal to the ratio  $a/d$  in my terminology) and they suggested that it confers an advantage to sexual reproduction. This result, based on numerical calculations, can also be seen in my equation (12), which shows that the proportion of sexual individuals co-existing with asexual ones is an increasing function of the ratio  $a/d$ . Nevertheless, it does not imply that asexual individuals can be eliminated by sexual ones, unless the size of the habitat of the sexual forms is twice that of asexual ones.

Case and Taper (1986) suggested the elimination of asexual forms by sexual forms under less rigid conditions than those proposed here. Their model is much more complicated than mine, but with the similar assumption of the niche width of the sexual individuals being larger than that of the asexual ones. Their numerical simulations allow for the sexual forms to win the competition even if the standard deviation of their niche width is only 10% higher than that of asexual forms. Some features of the model of Case and Taper (1986) are very different from those of the model presented here. The shape of the niche is given by a Gaussian distribution and the elimination of asexual individuals requires that the means of the distribution are identical or almost identical for both sexual and asexual individuals. The peaks for the density functions for both sexual and asexual niches are identical, which implies that a wider niche contains more resources. The dynamics of the resources is determined by a logistic equation with additional mortality introduced by the asexual and sexual consumers. A shortage of resources affects both the reproduction and mortality of these consumers. While their reproduction is a linearly increasing function of the amount of resources with no upper limit set by consumer physiology, their mortality is an exponentially decreasing function of the resources.

In my model, one point may appear insignificant but it is of crucial importance for the results obtained. Since the sexual individuals are able to use the fraction  $g$  of resources not available to asexual ones, they do not compete with the asexual individuals for this fraction of resources. This is introduced to the model by the term  $gx$  in equations (9b) and (13b). This term shows that fraction  $g$  of the proportion  $x$  of sexual forms do not compete with asexual ones (Fig. 2). When dropping this term from equation (9b), the condition (10) for the elimination of the asexual individuals, namely that  $g > 1/2$  changes to  $g > d/(2a)$ , is exactly the condition (11) for co-existence in the original model, with the term  $gx$  included. In the same way, when dropping the term  $gx$  from equation (13b), condition (10) changes into condition (14),  $g > d/(1 + 2d)$ , which is also the condition for co-existence in the original model. The conditions for co-existence are much less rigid than the conditions for the elimination of asexual individuals. If the death rate,  $d$ , of established individuals is low

or low in relation to colonization abilities, and if the term  $gx$  is ignored, elimination of the asexual forms is possible, even if the niche of the sexual ones is only a little bit wider, as in the model of Case and Taper (1986).

Since the numerical model of Case and Taper (1986) is very complicated, it is difficult to determine whether they included the phenomenon described by the term  $gx$ . Their equation (7) suggests that they did not. For this reason, I doubt their conclusion that a small increase in niche width may allow the elimination of asexual individuals by sexual ones. Two other theoretical modes of the tangled bank hypothesis (Bell, 1982; Doncaster *et al.*, 2000) do not consider the sizes of habitats or the width of ecological niches explicitly, applying instead a very abstract inhibitory effect,  $\alpha$ , of one kind of individuals on another. Therefore, it is impossible to determine whether the phenomenon described here by the term  $gx$  is of importance in their model.

In conclusion, the co-existence of sexual and asexual individuals within the same population, a rather rare phenomenon, can easily be explained by the models of inter-specific competition. This is the case if the asexual forms are not able to use resources available to sexual ones only or, as shown in many ecology textbooks, the inhibitory effects of one population on another are smaller than unity. On the other hand, the complete elimination of asexual individuals by sexual ones is not possible without the amount of resources for the sexual population being twice that for the asexual one.

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