

Scramble and contest competition, unequal resource allocation, and resource monopolization as determinants of population dynamics

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ABSTRACT

Questions: How do unequal resource allocation, asymmetry, and resource monopolization each affect a population's stability and persistence? How do they differ in their importance to stability and persistence? How may one define precisely the terms 'scramble competition' and 'contest competition'? Might individual-based modelling help us to develop general population theory? Or is it useful only as a method of computer simulation in applied ecology?

Methods: Address the questions with the simplest pre-existing analytical models. Use generation-to-generation difference equations. Define scramble and contest competition according to them. Use models of pure scramble and contest competition and develop and analyse a model of competition in which individuals have abilities to monopolize resources that vary along a continuum. Relate the results to empirical data from field and laboratory studies.

Results: Equal resource allocation among population members prevents population stability and population persistence. If some population members monopolize the resources, both stability and persistence are guaranteed. The generation-to-generation difference equations permit one to define precisely a theoretical gradient of monopolization ranging from complete equality to full monopolization. In some cases, this gradient also permits both stability and persistence.

Keywords: population stability and persistence, resource monopolization, scramble and contest competition, unequal resource allocation.

INTRODUCTION

Individual-based population models allow derivation of a population's properties from the properties of its elements by considering individual differences other than sex and age. For several reasons, such models have not been used in ecology (Łomnicki, 1999). But since

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other natural sciences usually derive the properties of any entities from the properties of their elements, ecology, too, will eventually have to adopt this method. Moreover, the widespread availability of computers makes numerical simulation based on individual properties both feasible and practical (Grimm and Railsback, 2005).

IDEAL SCRAMBLE AND IDEAL CONTEST COMPETITION

Two kinds of competition, first suggested by Nicholson (1954), spring from the way resources are divided among individuals: equal resource allocation (scramble competition) and unequal resource allocation with monopolization (contest competition). Figure 1 translates them into two graphical models. If the competition within a single population affects both survival and reproduction, so that competitive effects carry over to the next generation, then these two models can represent ideal scramble (Fig. 1, top) and ideal contest (Fig. 1, bottom) competition. (I use the adjective ‘ideal’ since these are the cases of pure scramble and pure contest competition.) These two kinds of competition will lead us quickly from individual properties to a simple derivation of difference equations for the population dynamics of the two competitive models (for more detail, see Łomnicki, 1988).

These two models are relevant to real empirical data and exhibit some interesting features. In ideal scramble competition, the appropriate recursion equation for population size, $N_{t+1} = f(N_t)$, depends on the values of four parameters:

- the amount of resources V for the entire population;
- the maximum amount of resources a an individual may take;
- the minimum amount of resources m an individual requires to survive and be able to reproduce;
- the coefficient h of converting resources in excess of m into descendants.

One of three recursion equations holds depending on the relative values of the four parameters. For $N_t \leq V/a$, all individuals have more resources than they can possibly use, so $(a - m)h > 1$. Thus

$$N_{t+1} = (a - m)hN_t. \quad (1)$$

For $V/a < N_t < V/m$,

$$N_{t+1} = (V/N_t - m)hN_t. \quad (2)$$

For $N_t \leq V/m$,

$$N_{t+1} = 0. \quad (3)$$

The upper left and central parts of Fig. 1 depict individual cases of equations (2) and (3). The right-hand part of the figure shows all cases as N_t increases from zero.

Local stability requires that $dN_{t+1}/dN_t > -1$ and it is fulfilled if

$$m < 1/h. \quad (4)$$

Population persistence is assured if the maximum possible value of N_{t+1} is lower than the maximum possible value of N_t . This is the case if

$$m(1 - m/a) < 1/h, \quad (5)$$

where a denotes the maximum amount of resources an individual may obtain. We do not know of any multicellular organism in which the cost of producing a single offspring is higher than the maintenance cost from birth to reproduction. Therefore, inequality (4) is never fulfilled. And, since maximum resource intake a is usually several times higher than the minimum m required for survival, inequality (5) will not be fulfilled either. Consequently, a group of organisms exhibiting ideal scramble competition cannot persist very long.

In contrast to scramble competition, ideal contest competition leads to both local and global stability (lower part of Fig. 1). If $N_t \leq V/a$, then N_{t+1} as a function of N_t is the same as for ideal scramble competition and it is given by (1), while for $N_t > V/a$,

$$N_{t+1} = hV(1 - m/a), \quad (6)$$

and since N_{t+1} is independent of N_t , such dynamics is both locally stable and persistent. Hence, given contest competition, extinction can be brought about only by external factors. After the population attains the density at which competition for resources occurs, population size N_{t+1} does not depend on its size in any previous generation, but only on V , the amount of available resources.

However, the comparison of the two competition models can be misleading. They differ not only by equal and unequal resource allocation but also by resource monopolization. Such monopolization of resources can be defined as independence of individual resource share y from the density of other individuals N , so that the share depends only on an individual's position or rank x in the population and on the amount V of available resources for the entire population. Inequality of resource allocation itself does not ensure population stability and persistence (Łomnicki and Sędziwy, 1989).

A MODEL THAT RANKS INDIVIDUALS BY RESOURCE SHARE

Ideal scramble competition and ideal contest competition rarely occur in the real world. Besides, these two phenomena – inequality and monopolization – are more or less closely related since stronger individuals take disproportionate amounts of resources (a form of asymmetric competition). Therefore, I shall examine a theoretical gradient between ideal scramble and ideal contest competition.

Individual resource share y is described by function $y(x)$ of an individual of rank x . Rank x does not imply a social rank within the population but simply ranks individuals from the highest to lowest resource share. As in the ideal models of competition, I assume that the maximum possible resource intake equals a , while the minimum required for survival to the time of reproduction is m . If $y(x) < m$, an individual of rank x dies without leaving any progeny. But if $y(x) > m$, the individual produces $h(y - m)$ offspring (where $1/h$ is the cost of producing a single offspring).

The amount V of resources (usually food) supplied to the population is now divided among individuals according to three algorithms. All algorithms begin by stipulating that if $N < V/a$, then each individual takes the maximum amount of resources (right-hand graph in Fig. 2). All continue by assuming that if $V/a \leq N \leq 2V/a$, then the individuals of highest rank (lowest x) obtain the maximum resource share a while the remaining ones obtain linearly diminishing amounts (left-hand graph in Fig. 2).

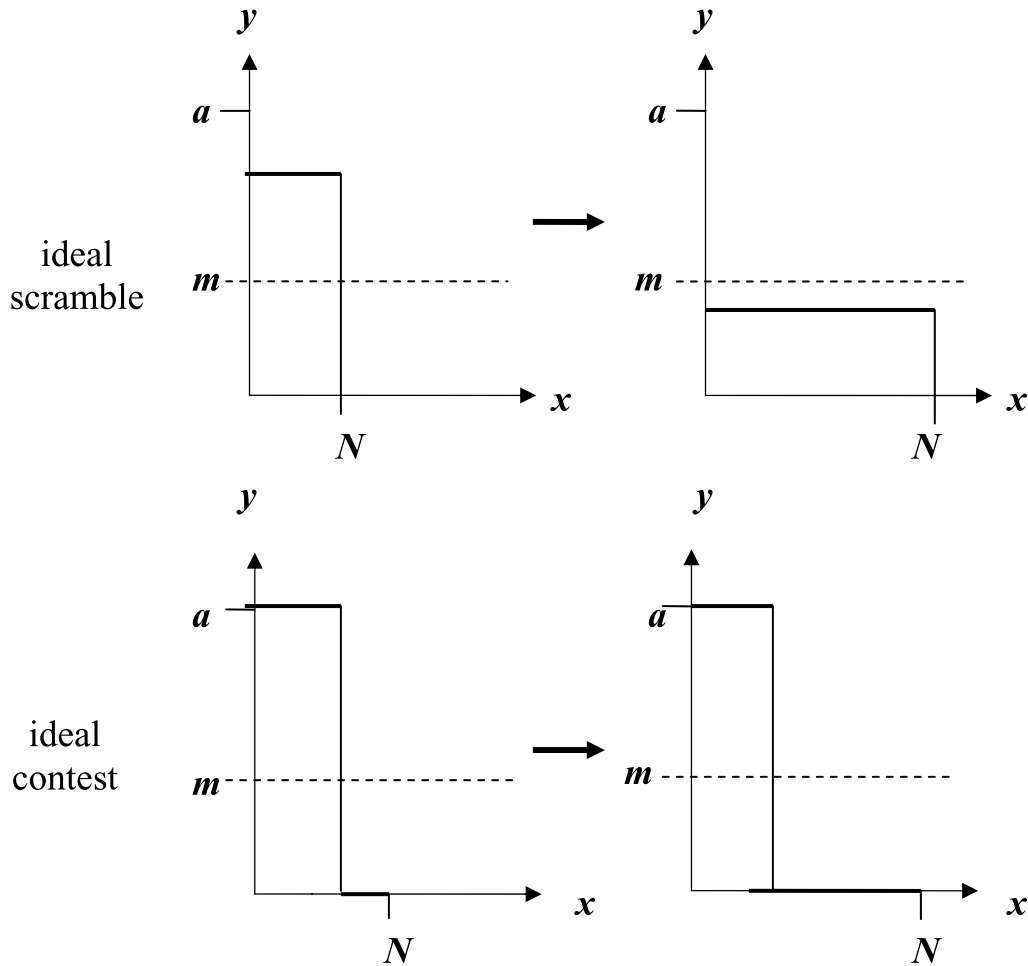
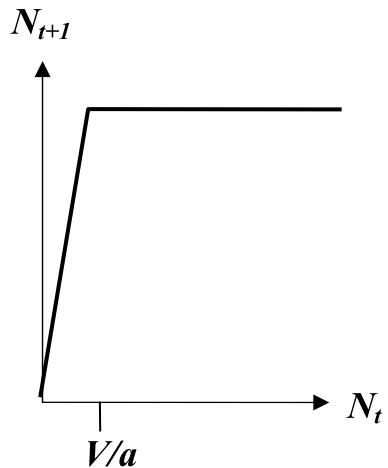
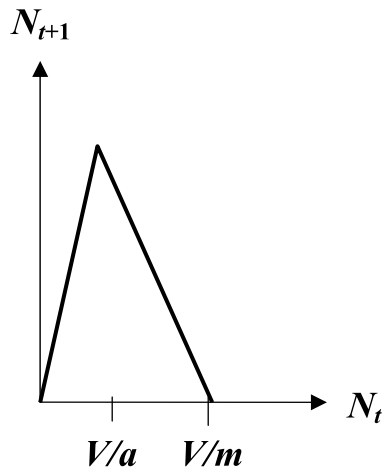


Fig. 1. Resource allocation for the two extreme cases: ideal scramble competition (top row) and ideal contest competition (bottom row). In the left-hand and middle graphs (of both rows), the x -axis shows the rank of the N individuals in a population. Individuals are arranged in order, from those that obtain the most resources (on the left-hand side of the axis) to those that get the least (on the right). The y -axis shows the amount of resources garnered by each individual. There are V available resources. An individual may use no more than a units of resource, but it must obtain at least m units or else die without leaving progeny. So V/a individuals is the largest number of individuals that can each obtain a full share of resources; and V/m individuals is the largest number of individuals that can each obtain a share of resources adequate to survive. In the ideal scramble case, all N individuals get the same amount of resource, i.e. V/N units. In the ideal contest case, the top V/a individuals all get the maximum amount (a units)

If $N > 2V/a$, there are not enough resources to supply all individuals. The three cases diverge. For the sake of simplicity, assume that from the top individual to the one with the lowest resource share, an individual's resource share, y , diminishes linearly with its rank x in the population. One may now consider the three different cases.



but the others get nothing. The graphs in the left-hand column (of both rows) show resource allocation when $V/a < N < V/m$. The two middle diagrams describe the allocations in a larger population, $N > V/m$. In the ideal scramble model, all individuals get less than m resources, and the entire population becomes extinct. In the ideal contest, as before, the top V/a individuals take all the resources. The right-hand graphs (of both rows) display the recursion relationship for the population dynamics of the models. Here the axes are population sizes. See equations (2), (3), and (6) in the text. Beginning from small population sizes, N grows until there are V/a individuals. Beyond that N , in the scramble model, as N grows, the ratio N_{t+1}/N_t declines. Analysis of this model (equations 4 and 5) shows that it will not be locally stable and is most unlikely to be globally stable. In the contest model, however, N stops growing at V/a individuals and is maintained at that size in perpetuity.

Case 1

The first case is close to the ideal scramble (Fig. 3A). The top individual cannot obtain the maximum amount of resources a , and even the weakest one gets a share of the resources. This implies that the resource share of individuals depends not only on the amount, V ,

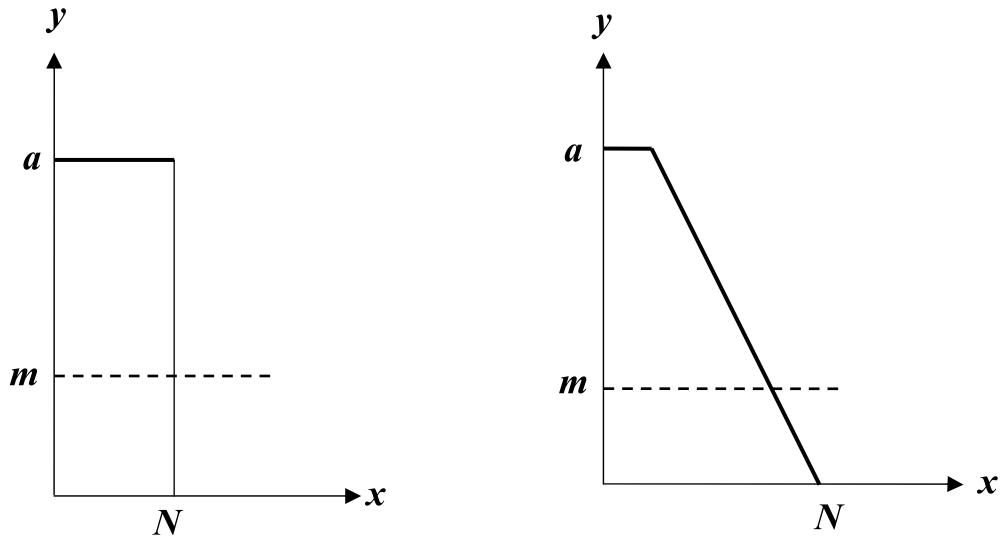


Fig. 2. Distribution of resource share y as a function of individual rank x for population size N if $N \leq V/a$ (left-hand panel) and if $V/a < N \leq 2V/a$ (right-hand panel) for all three cases of the gradient in competitive strength among individuals. The distributions of y for $N > 2V/a$ are given in Fig. 3. For further explanation, see Fig. 1.

of available resources, but also on the population size N . The population dynamics of non-overlapping generations for this model is given by:

$$N_{t+1} = h\{V - mN_t[1 - mN_t/(4V)]\}. \quad (7)$$

The condition for local stability is less restrictive than in the ideal scramble case (inequality 4), since it is the same as inequality (5) for persistence [i.e. $1/h > m(1 - m/a)$] in the ideal scramble case. Nevertheless, with a low cost of production of a single individual $1/h$ and high maintenance cost m , population density is locally unstable.

The condition for persistence of the first case is given by

$$1/h > m(1 - m/a)/2. \quad (8)$$

Inequality (8) is only a little less restrictive than inequality (5) (from the ideal contest case). So the gradient of resource allocation in Case 1 makes for only a small decrease in the restrictive conditions for stability and persistence compared with the ideal contest case.

Case 2

In the second case (Fig. 3B), I assume that with lower amounts of resources V , both the number of individuals, N , that receive some resource share and the maximum resource share, a , are reduced by the same fraction to match the value of V . Some of the weaker competitors get nothing. These dynamics are described by equation (9):

$$N_{t+1} = h\{V - mN_t[\sqrt{2V/(aN_t)} - m/(2a)]\}. \quad (9)$$

Here, local stability depends on:

$$1/h > m[\sqrt{V/(2aN_t)} - m/(2a)]. \quad (10)$$

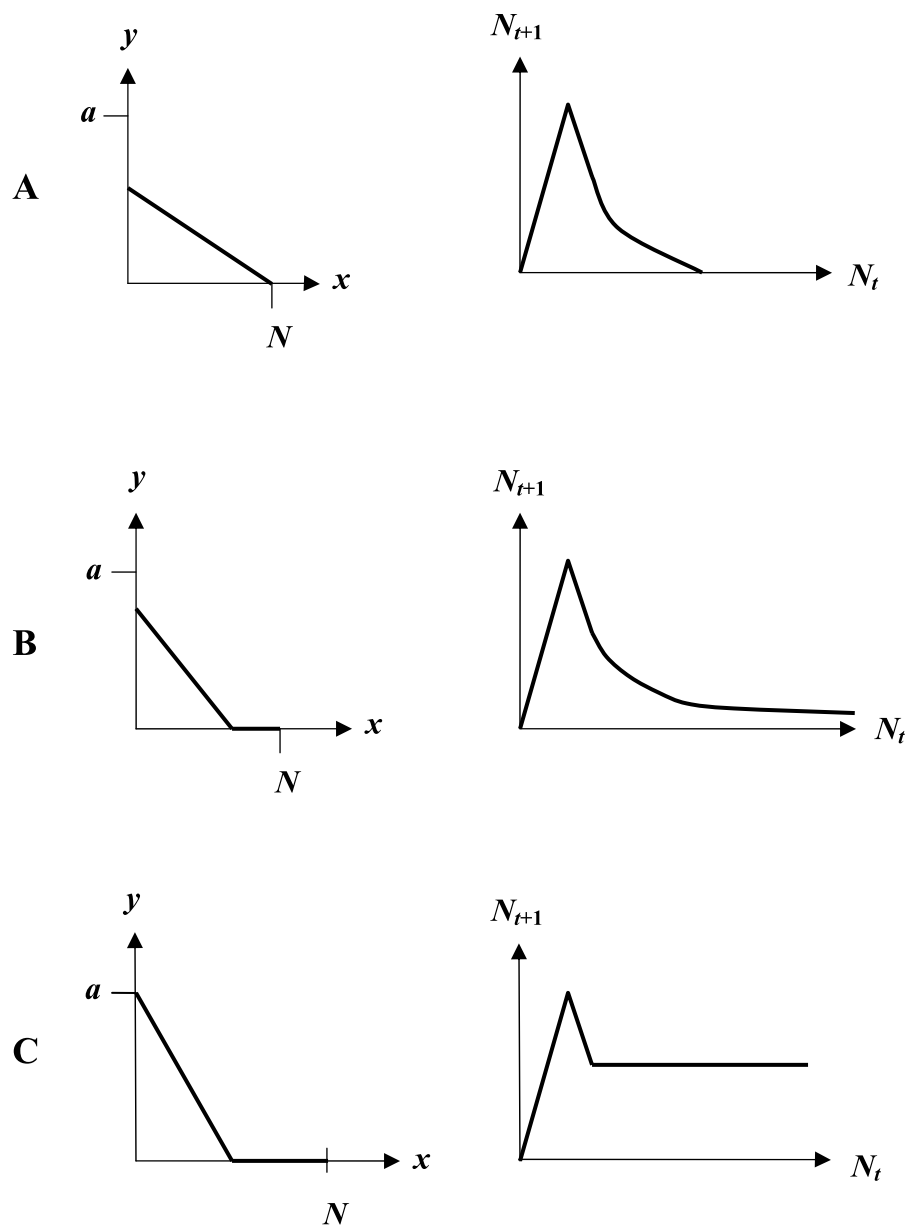


Fig. 3. Left-hand diagrams: the three cases of distribution of resource share y as a function of individual rank x for population size $N > 2V/a$. Right-hand diagrams: dynamics (N_{t+1} as a function of N_t). For further explanation, see Fig. 1 and text.

Persistence requires:

$$1/h > m(1 - ma)/(2a). \tag{11}$$

Both inequalities (10) and (11) are less restrictive than for an ideal scramble. Nevertheless, stability and persistence are still endangered by very high values of the parameters h and m .

Case 3

In the third case (Fig. 3C), the strongest competitor gets the greatest share of resources, but many more of the weaker competitors get nothing. The dynamics of this case are given by

$$N_{t+1} = hV(1 - m/a)^2. \quad (12)$$

Since N_{t+1} is independent of N_t , the population always persists and, at least for $N_t > 2V/a$, it is locally stable.

DISCUSSION

The models in the real world

One may find ideal scramble and ideal contest cases in the real world. For example, cultivated plants selected for synchronous germination time and planted in a homogeneous habitat can maintain stable and persistent populations due to external control of their densities. But they correspond to an ideal scramble case. Thus, when planted at high density, such cultivated plants may not be able to produce any seeds; that is equivalent to population extinction. The same may be true for other plants and animals kept in artificial, very homogeneous habitats without any possibility of some monopolization of available resources.

The best candidate for an ideal contest case with resource monopolization seems to be territoriality. However, as shown theoretically by Lopez-Sepulcre and Kokko (2005), territory size may depend also on population size. That dependence may interfere with ideal contest competition. On the other hand, the competition of terrestrial plants for light (but not for water and minerals) does lead to contest competition because the light reaching taller individuals is not limited by the number of shorter ones (Weiner 1990, 1995).

The models herein that assign a continuous share of resources to individuals based on their rank is not based on an innate rate of population growth or some assumed natality and mortality coefficients, but instead on some physiological parameters, i.e. maximum a and minimum m resource share and the number of offspring per unit of resources h . The assumptions concerning these parameters are also simplified but the basic physiological properties of plant and animals are retained. For population stability and persistence, the most important criterion is a low value of the product mh . This product is more important for determining stability and persistence than the structure of those versions of the model in which N_{t+1} depends on N_t . With very high values of the product mh , stability and persistence are hardly possible. On the other hand, in the third scramble case of the gradient (Fig. 3C) and in the ideal contest case as well, it is the structure of the model (i.e. making N_{t+1} independent of N_t) that ensures population stability and persistence irrespective of the parameters m and h . In these two scenarios, population dynamics itself is of minor importance, since population density is determined by habitat quality or some density-independent processes. Perhaps that explains why botanists were, for a long time, not very interested in population dynamics but rather in habitat qualities: terrestrial plants that compete for light generate contest competition.

The rules of dividing V resources among N individuals presented here may seem very artificial, but the distribution of body weights of many plants and animals, when ordered from the heaviest to the lightest, exhibit patterns that suggest these rules (Uchmanski, 1985). With excess resources, the individual body weights of both plants and animals show little

variance, and presumably little variance in their individual resource shares. With increasing population size, the variance and skewness of the distribution increase but can be concealed by high mortality of the weakest individuals.

The straight-line rule also appears artificial. But adding a small curvature does not alter the main idea of this model, which is that in some populations, an increasing population size can alter the resource share of all individuals, whereas in other models monopolization by the strongest individuals occurs and their resource shares cannot be altered by increasing population size.

The importance of individual-based models

The most popular recent applications of individual-based models are computer simulations of population dynamics on the basis of some known or assumed properties of individuals (Grimm and Railsback, 2005). This approach is very useful and fruitful for solving some applied problems of ecology, conservation, and environmental protection. However, it is difficult or impossible to obtain knowledge of all properties of all individuals even in small populations in the field. Interrelations between individuals are even more difficult to estimate. So individual-based models require one to assume some unlikely knowledge, especially that concerning individual interrelations. If management decisions based on individual-based models succeed, we will be justified in suspecting that the assumptions were the correct ones.

The application of individual-based models to basic ecological theory faces similar difficulties. We infer distribution of body weights from theoretical models (e.g. Kimmel, 1986) and from distributions of body weights (e.g. Uchmanski, 1985). We can assume interrelations among individuals based on knowledge of animal behaviour and the mechanisms of plant growth. Nevertheless, variation in body size and its distribution is the easiest to obtain. And so many researchers concentrate on inequality among individuals (Filin and Ovardia, 2007; Vindenes *et al.*, 2008), not taking into account the importance of monopolization for population stability and persistence.

The importance of monopolization is often ignored because these two phenomena – inequality and monopolization – are often strongly correlated, and monopolization cannot exist without inequality. The exponential growth of plants and animals with strong competition for resources can amplify small differences among individuals and lead to monopolization. On the other hand, one can imagine situations (e.g. the inability of some insects and birds to grow above an optimum body size) that prevent the development of large differences among individuals and consequently attenuate or eliminate some kinds of monopolization. In spite of the close relation between them, these two phenomena have to be clearly distinguished. In the model presented here, Case 3 is such an intermediate situation, where for some value of N_t , population size N_{t+1} in the next generation depends on N_t , whereas for higher value of N_t , the size of N_{t+1} is independent of N_t . Therefore, Case 3 is an example of contest competition, but not ideal contest competition.

Some important population phenomena cannot be understood from the point of view of evolutionary theory without taking into account individual differences and monopolization. These include regulation of population densities by emigration from optimal local habitats into hostile environments – in other words, movements of animals from source to sink environments (Pulliam, 1988). Some kinds of despotic distribution, as defined by Fretwell (1972), can be understood when monopolization of resources by some individuals is taken into account.

General models of population dynamics that include individual properties and interrelations among individuals within a single population may be extremely useful, especially if these interrelations lead to resource monopolization by some population members.

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