

A NOTE ON K-SELECTION

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Since its introduction by MacArthur and Wilson (1967), the distinction between r-selection and K-selection has received a great deal of discussion. This distinction is based on the familiar logistic equation:

$$\frac{dN}{dt} = rN(1-N/K) \quad (1)$$

where N is the population size, r is the intrinsic rate of increase, and K is the equilibrium value of the population (or the "carrying capacity" of the environment for the species of interest). The idea is that in increasing populations selection should favor a higher rate of increase (r-selection), while for populations near their equilibrium value, selection should favor a higher equilibrium value (K-selection).

Pianka (1970) listed a number of ecological and demographic correlates of r- and K-selection. For example, r-selection would be important for short-lived species living in variable or unpredictable climates, subject to density independent mortality. Productivity is favored by r-selection, efficiency is favored by K-selection.

The distinction between r- and K-selection is rich because of the large number of parallel distinctions and it is convenient to have a simple phrase to summarize these distinctions. However, the idea of K-selection described by MacArthur and Wilson is incomplete without considering competition between different phenotypes. In this note an example is given that shows that when competition is considered, selection may favor decreasing K instead of increasing K . It is pointed out that r and K are

not strictly comparable; r being a function of life history parameters while K is not. If life histories are considered, then instead of trying to distinguish between r - and K -selection, one may distinguish between increasing and stable populations. The direction of the force of natural selection will be different for increasing and stable populations, and this difference can lead to different reproductive strategies.

MacArthur's Idea of K-Selection

A careful examination of MacArthur's (1962) model shows that K -selection can favor either increased or decreased K . MacArthur investigated the evolution of carrying capacity, K , by considering a one-locus, two-allele model, where the three genotypes have different values of K . He did not consider competition between genotypes explicitly, but he did assume that K might depend on gene frequency. MacArthur showed that if K for the heterozygote was between those of the homozygotes, then the population would evolve toward the homozygote with the higher K . MacArthur concluded that natural selection should favor that genotype which demands the fewest resources.

The effect of the competition between genotypes may be made precise by considering MacArthur's model:

$$\frac{dn_x}{dt} = n_x (c_{xx} f(p)(K_{xx}(p) - N) + c_{xy} (1-f(p))(K_{xy}(p) - N)) \quad (2)$$

$$\frac{dn_y}{dt} = n_y (c_{xy} g(p)(K_{xy}(p) - N) + c_{yy} (1-g(p))(K_{yy}(p) - N)) \quad (2')$$

where x and y are the two alleles in the population, n_x is the number of x alleles, n_y is the number of y alleles, and p is the proportion of x

alleles. The c 's are constants describing the change in fitness of the corresponding genotypes which accompanies a unit change in N , the total population size. The K 's, which are functions of p , are the values such that, when the combined population of all genotypes equals the K for a particular genotype, then that genotype will have equal birth and death rates. The fact that K depends on gene frequency, p , is important. For any value p , $f(p)$ is the proportion of the x alleles which are combined in the zygote with other x alleles, and $1-f(p)$ is the proportion of x alleles combined with y alleles. Similarly, $g(p)$ is the proportion of y alleles which are combined in the zygote with x alleles and $1-g(p)$ is the proportion of y alleles combined with other y alleles.

Now consider an example:

$$K_{xx}(p) = 250 - 100p,$$

$$K_{xy}(p) = 225 - 100p,$$

$$K_{yy}(p) = 200 - 100p.$$

For all p , we have $K_{xx}(p) > K_{xy}(p) > K_{yy}(p)$; and, therefore, x alleles replace y alleles. However, the equilibrium population size is greater for the yy homozygotes than for the xx . That is, when the whole population consists of genotype xx , we have $p = 1$ and $K_{xx}(1) = 150$, while when the whole population is of genotype yy , we have $p = 0$ and $K_{yy}(0) = 200$. In this example, selection favors the genotype with the lower equilibrium value.

In this example, the fact that $K_{xx}(p) > K_{xy}(p) > K_{yy}(p)$ means that the xx genotypes are more resistant to the effects of competition than the xy genotypes, which are, in turn, more resistant than the yy genotypes.

The $-100p$ term means that the bearers of the x alleles inflict more competitive damage. This is not simply a pathological example. Such a case could arise if the xx genotype is larger than the yy genotype, with the xy intermediate, and if the larger genotypes are more efficient. Efficiency could mean greater resistance to the effects of competition, while larger size could mean causing more competitive damage.

Cope's rule says that in a number of groups there has been a phylogenetic tendency for animals to increase in size. If the environment can support fewer of the larger animals than it can of the smaller, then, insofar as Cope's rule is true, evolution has tended to decrease K .

In MacArthur's model of K -selection, intraspecific competition is introduced implicitly, by letting K depend on the gene frequency, p . Christiansen and Fenchel (1977) describe a model of Poulson (1975) that considers intraspecific competition explicitly. Poulson's model also shows that K -selection may favor decreased K . As biological evidence, Christiansen and Fenchel (1977) cite the work of Strandgaard (1972), who showed that in a population of roe deer the presence of very dominating males decreased the population density below the level that the productivity of the environment allowed. While this example demonstrates interference competition, it is not, in principle, necessary that intraspecific competition be due to interference.

Gill (1974) has emphasized the importance of competition in evolutionary models. He suggests considering α -selection, as well as r -selection and K -selection. Gill defines competition to include intraspecific as well as interspecific competition, but an example he uses suggests that he is

mainly concerned with interspecific competition. The point is that intraspecific competition must be considered as well as interspecific competition.

Life History Selection for Increasing or Stable Populations

Many of the ideas about r- and K-selection are discussed in Stearns' (1976, 1977) reviews of life history strategies. As Stearns (1977) points out, "Unlike r, K cannot be realistically expressed as a function of life history traits Thus r and K cannot be reduced to units of common currency" (p. 155). This is certainly true if we use the same narrow idea of K-selection as introduced by MacArthur (1962). However, if we use a broader idea of K-selection, including such things as interspecific competitive ability and predator avoidance, as well as certain life history traits, we may find axes along which we may usefully distinguish r- and K-selection. For life history strategies, the most important distinction is whether the population is increasing or is stable. It is this distinction which will be considered here.

Of course, populations cannot always increase. Populations that show rapid increases, such as in colonizing species, must also decrease. Populations that show wide fluctuations usually exist in varying environments and the individuals' strategy must take account of decreases as well as increases. I do not intend to discuss overall strategy, but rather to look at the difference between selection in increasing and in stable populations.

The force of natural selection acts on life history parameters in a particular direction, much as a physical force acts on a body in a particular direction. Other things being equal, natural selection favors

increased fecundity, increased juvenile survival and increased adult survival. Other things are not equal, however, and it is important to know the relative importance of the various life history parameters. Stearns (1976, Table 2) presents evidence that there is a trade off between fecundity and adult survival. That is, an increase in fecundity results in decreased adult survival. Whether it is advantageous to exchange some adult survival for increased fecundity depends both on how much fecundity is gained per unit adult survival lost, and on the direction of natural selection.

This may be illustrated by considering a simple special case of the model for birds considered by Ricklefs (1977). For birds that breed at age one, the annual rate of increase λ (note that $r = \ln\lambda$) will be given by

$$\lambda = l_1 B + (1-M) \quad (3)$$

where l_1 is the probability of surviving from fledging to breeding; B , the fecundity, is the average number of daughters fledged per breeding female each year, and M is the annual adult mortality. Assume that juvenile survival, l_1 , is influenced by the environment, but is beyond the control of the parents. The question is: What is the relative importance of fecundity and adult mortality?

From (3) we can see that the relative effect on λ of small changes in fecundity and mortality will be given by

$$(\partial\lambda/\partial B)/(\partial\lambda/\partial M) = - l_1 \quad (4)$$

That is, since first year survival, l_1 , is less than 1 -- usually much

less than 1 -- the effect of a small increase in fecundity is less important -- usually much less important -- than an equal small decrease in adult mortality. For a stable population $\lambda = 1$ and $l_1 = M/B$. For stable populations, this relative importance of small equal changes in fecundity and adult mortality will equal M/B .

What if, in fact, $l_1 = 2M/B$, say? In this case, juvenile survival is twice that necessary for a stable population; the population will increase; and from (4) we can see that the relative importance of small changes in B compared with small changes in M will now be twice as great as for a stable population. Here 2 is the net reproductive rate, R_0 . In this model, for given values of B and M , the relative importance of small changes in fecundity compared to small changes in adult mortality will be R_0 times as great as it would be if the population actually were stable ($R_0 = 1$). One might say, with this model in mind, that the relative importance of fecundity is greater for increasing populations than for stable ones.

Birds might be expected to adjust their reproductive effort according to whether their population is stable or increasing. This idea may apply in the case of a population with moderate fluctuations from year to year, when there is a fairly strict limitation on the breeding population due to territorial behavior or a limitation in nest sites. If this means that the chance of this year's young being recruited into next year's breeding population is greater when this year's population is low than when it is high, then juvenile survival is effectively higher from low breeding densities than from high. Greater reproductive effort might then be expected when density is lower.

Lack (1966, Chapt. 2) has shown that, for great tits, clutch sizes are higher when density is lower. One explanation is that more food is available at low breeding densities, but another, suggested here, is that adults should risk some of their survival chances for the sake of increased fecundity. Thus we might expect birds to produce larger clutches at low densities than at high densities even if density does not affect the effort needed to produce a given size clutch. If this is part of the explanation of the fact that clutch size is higher when breeding density is lower then we might expect lower adult survival after breeding under less crowded conditions.

It may be that the influence of Cole's seminal paper (1954) on the population consequences of life history phenomena has led to an over-emphasis on increasing populations and the question of how the growth rate may be maximized. For increasing populations, selection favors increased fecundity and decreased development time. Lewontin (1965), considering drosophila, has compared the relative importance of increasing fecundity and decreasing development time and concludes that, roughly, a 10% decrease in development time is equivalent to a 100% increase in fecundity. The relative value of decreasing development time and increasing fecundity have been shown by MacArthur and Wilson (1967, p. 88) and Green and Painter (1975) to depend on the net reproductive rate, R_0 . Mertz (1971), considering the California condor, has shown that for decreasing populations selection favors later reproduction.

It is useful to bear in mind that many animal populations are quite stable. For stable populations, selection favors increasing the net

reproductive rate, R_0 , but does not affect development time, except insofar as development time affects the net reproductive rate. Adult survival is more important for species whose populations are stable. An example has been well described by Goodman (1974) whose study of the Red-footed Booby (Sula sula) revealed a reproductive strategy characterized by small clutch size, slow growth and low intensity reproductive effort. Goodman's impression is that when it comes to reproduction, "the birds are not trying very hard." He shows that, for his birds, keeping adult mortality low is much more important than fecundity. What matters to these birds is how many young they can produce, not how fast they can produce them.

Summary

The distinction between r- and K-selection is convenient as a loose summary of a number of related distinctions, but it should not be taken literally. A close look reveals that there are difficulties with the idea of K-selection. As described by MacArthur and Wilson (1967), the idea is incomplete without explicitly considering competition between genotypes. When competition is considered it is no longer clear whether evolution would tend to increase or decrease K. Furthermore, r and K are not comparable. When life history parameters are considered the distinction between r-selection and K-selection corresponds to the distinction between increasing and stable populations. The force of natural selection acts in different directions for increasing and stable populations. Thus, for animals capable of a range of reproductive strategies, we might expect to see different strategies used under different environmental conditions.

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