Galley type for

# Encyclopedia of Evolution

#090

## DENSITY-DEPENDENT SELECTION

Density-dependent selection is a special type of natural selection in which survival and reproduction depend on the population density of other individuals of the same species. Density in this context can be thought of as the number of other individuals nearby. The action of density-dependent selection may be influenced by the varying density of neighbors during different life stages. For instance, insect survival from egg to adult may depend on the density of larvae, whereas the number of eggs laid by females may vary with adult density.

**Development of Logistic Theory.** Robert MacArthur (1962) was the first to develop the mathematical relationship between ecological theories of population growth and the effect of natural selection at different densities. MacArthur accomplished this with the aid of the logistic equation of population growth. This ecological model states that populations at low densities will grow exponentially at the intrinsic rate of population growth (*r*). The logistic model also assumes that, as a population becomes more crowded, the rate of growth declines. The population ceases to grow when it reaches its carrying capacity (*K*), which is the equilibrium population size.

Classical theories of natural selection measured fitness by calculating the intrinsic rate of growth (*r*) of a population. This parameter tends to be maximized by maximizing fertility and survival at low population density. MacArthur extended this idea by suggesting that, at high population density, the population size at carrying capacity (*K*) would be an appropriate measure of fitness. This theory has sometimes been referred to as *r* and *K* selection, drawing from the two parameters of the logistic equation. In 1971, Roughgarden generalized these ideas by suggesting that fitness may be equated with per capita rates of reproduction and population growth. An example of this theory is shown in *Figure* 1.At low population density, natural selection will favor the increase and ultimate fixation of the A1 allele because the A1 homozygotes have highest fitness. However, at high density, natural selection would favor increases in the alternative A2 allele. Most importantly, the outcome of evolution depends on the density of the environment.

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**Trade-offs at Low and High Densities.** A key to this theory is the idea of trade-offs. As illustrated in Figure 1, the genotype that is best at low density has the lowest fitness at high density and vice versa. If these types of trade-offs did not exist, then there would be one best genotype for all environments. Although there are no first principles that can be invoked to prove that trade-offs exist, there are some simple arguments that suggest this is a reasonable assumption. Martin Cody (1966), first developed this idea in the context of life history evolution. Cody argued that all organisms must contend with limited amounts of time and energy. As soon as they devote more of their time and energy to, say, reproduction, they will have less time and energy for other activities, such as competiting for food.

If the trade-off assumption is valid, those populations that have evolved to grow fastest at low density should do poorly at high density and vice versa. These ideas have been tested by maintaining populations of fruit flies (*Drosophila melanogaster*) at very low and very high densities. After eight generations of evolution, the population growth rates of the high- and low-density adapted populations differentiated, and the predicted trade-offs were observed (Figure 2).

These populations of fruit flies have been studied in more detail to determine which traits changed to cause the observed differences in population growth rates. At least three larval behavioral traits become differentiated between the low- and high-density populations. The high-density populations show elevated larval feeding rates compared to the low-density populations. In fruit flies, it is known that high feeding rates translate into increased competitive ability for limited food, which is certainly at a premium in crowded environments. However, larvae with high feeding rates show reduced survival at low density. Feeding rates then explain, at least in part, the trade-offs observed in Figure 2. When populations of fruit flies adapted to high larval densities are moved back to low densities, the flies' feeding rates rapidly evolve to a lower level, presumably as a consequence of the reduced survival of fast feeders at low density. Individuals from populations adapted to high density also move greater distances while foraging compared to individuals from populations adapted to low density. Finally, larvae from populations that have evolved at high densities are less likely to metamorphose into adults (pupate) on the surface of the food and tend to crawl farther from the food surface in search of a pupation site. This altered behavior also improves survival because larvae that pupate on the surface of the food in crowded cultures showed greatly elevated mortality rates.

**Development of Verbal Theory.** At the same time as MacArthur and Roughgarden were developing their quantitative theories of density-dependent natural selection, an extensive verbal theory of $r$ and $K$ selection was developed. A verbal theory is simply one in which the major assumptions and conclusions are argued in words without reliance on formal mathematics. Verbal theories are acceptable ways of developing ideas in biology. However, the logic supporting the conclusions of verbal theories is not always as obvious as it is with mathematical theories. The verbal theories of $r$ and $K$ selection suggested populations that evolved at high density, called $K$-selected, should be composed of individuals with increased competitive ability, larger body size, delayed reproduction, and repeated reproduction over many years, or iteroparity. Populations evolved at low density, or $r$-selected, under this theory would display the opposite set of characteristics: reduced competitive ability, small body size, high levels of reproduction early in life, and survival over fewer reproductive years.

Many of the logical flaws with the verbal theory of $r$ and $K$ selection quickly became obvious to many scientists. For instance, the mathematical theories developed by Roughgarden and MacArthur do not have adults of different ages; instead, all reproduction takes place at a single instant in time. The verbal theories mistakenly inferred that the evolution of high carrying capacities would lead to adults surviving and reproducing over many years. The demise of the verbal theory was signaled by a series of review papers by Steven Stearns in 1976 and 1977 that clearly revealed many of the flaws in the verbal theory.

**Studies of Wild Populations.** How important is density-dependent natural selection in wild populations? This has been a difficult question to answer for several reasons. Much of the early empirical work focused on natural populations that were thought to have experienced different density environments. Any difference among these populations in characteristics like fertility and competitive ability was then attributed to density-dependent natural selection. The problem with these types of studies is that historical information on the past density conditions of populations was often anecdotal or incomplete. Likewise, because these natural populations were not under human control, it was often impossible to rule out other factors, such as predation and herbivory, that may have systematically differed between populations. Despite these problems, there are some well-studied natural populations where density-dependent selection is important.

Soay sheep in Scotland, for example, show phenotypic differences in coat color and horn type. Both of these characteristics are under single- or two-locus genetic control. Paul Moorcroft and his colleagues (1996) showed that females with dark coats and small twisted horns survived better at low densities than females with light coats and untwisted horns. However, at high population densities the advantage was reversed. Because population densities vary dramatically in the studied populations, density-dependent selection is probably important for the maintenance of the genetic polymorphisms in horn shape and coat color.

Populations that grow according to the logistic model are expected ultimately to reach an equilibrium size equal to the carrying capacity. However, depending on the characteristics of the population, the approach to this equilibrium can be gradual and smooth, or it may be oscillatory, with the population overshooting and undershooting the carrying capacity by decreasing amounts each generation, or some populations may never settle down to the equilibrium predicted by the logistic equation. These different scenarios reflect different kinds of population stability. Just as density-dependent natural selection may affect population growth rates, it may also affect the stability of population size. Population stability is an important area of biological research because the long-term persistence of populations, especially endangered species, can be affected by their tendency to fluctuate or stabilize. Theoretical work has come up with conflicting predictions. In some cases, density-dependent selection can lead to increased stability of a population, whereas in other cases, stability decreased. There has been one large experiment performed with fruit flies. In this study, fruit flies were placed in an environment that caused the population size to fluctuate. Despite evidence of substantial genetic change in these populations as they adapted to the successive environments, none of these changes appear to have affected the stability of the populations. In this case, the evolution of density-dependent traits did not affect the stability of population size.

[*See also* Fitness; Life History Theory: An Overview; Demography; Genetic Polymorphism; Population Genetics.]

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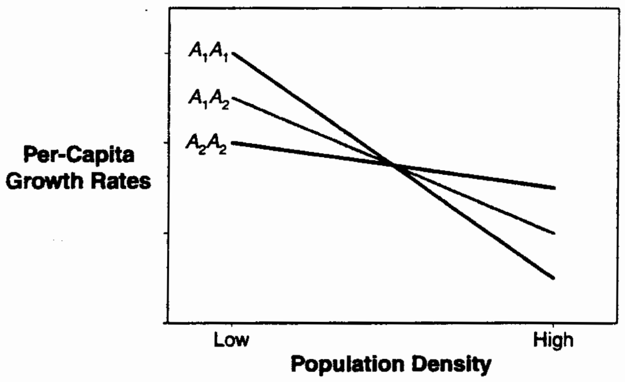
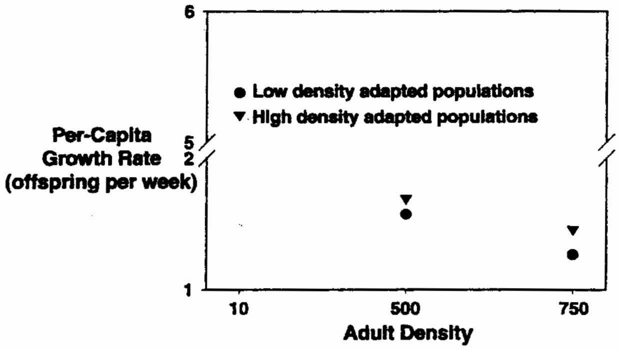
— LAURENCE D. MUELLER



**Density-Dependent Selection.** Figure **1.** Per-capita growth rates (fitness) for three genotypes. At low density, the $A_1A_1$ homozygote has the highest fitness whereas at high density, the $A_2A_2$ homozygote has the highest fitness. The heterozygote has intermediate fitness at all densities. (Laurence D. Mueller).



**Density-Dependent Selection.** Figure **2.** The per-capita growth rates for populations of fruit flies (*Drosophila melanogaster*) that have evolved at either very low density or very high density. The populations that had adapted to low densities for eight generations were tested at one low density (10 adults) and two high densities (500 and 7500 adults). The same tests were carried out simultaneously on the populations that had been maintained at very high densities. (Laurence D. Mueller.)