Introduction

One of the basic questions in ecology is the relationship between species living at the same trophic level, and in particular the relationship between species that may compete for the available resources of food and places to live. One generalization relevant to this problem is known as the com-

---

1 Supported by PHS career development award K3 GM37265 from the National Institute of General Medical Sciences, and by contract AT-(30-1)-3096, U. S. Atomic Energy Commission.
petitive exclusion principle, or Gause's principle. According to this principle, two species competing for the same limited resources cannot coexist in the same locality; that is, one or the other species will sooner or later be eliminated. Considerable disagreement exists among ecologists concerning the validity and the importance of this principle. It is my purpose to show that the principle of competitive exclusion cannot be defended in its generality: two species may compete for limited resources and still coexist. Some of the conditions that allow competitive coexistence are discussed in the latter part of this paper. An investigation of the concepts of ecological niche and competition, which are essential for a precise formulation of the principle of competitive exclusion, precedes the consideration of the principle itself, and of the Volterra equations for species competition, which constitute the mathematical foundation of the principle.

The Ecological Niche

The term *niche* is used in the ecological literature with a variety of meanings, not always well defined. Grinnell (1904, 1917, 1924) was apparently the first naturalist to use the term. For Grinnell, the niche of a species is a subdivision of the habitat; it comprehends all the essential components of the environment in which the organisms live. Elton (1927; also Elton and Miller, 1954) contributed greatly to the popularity of the term, but modified its meaning. For Elton, the niche of an animal is its characteristic role in the ecosystem, especially its energy relations, e.g., the animal's relationships to the food it eats and the significance of this for other organisms in the ecosystem. It has become a commonplace to say that for Grinnell the niche is the "address" of the species, while for Elton the niche is the "function" or role of the organism.

Hutchinson (1957, 1965) gave a formalized definition of niche in terms of set theory. The niche of a species is conceived as a set of points in an abstract hypervolume defined by coordinates each of which represents an environmental factor such as temperature, humidity, kind of food, and so forth. Take two environmental variables, say temperature and relative humidity, measured along rectangular coordinates. The limiting values, within which the species can survive and reproduce, define an area each point of which corresponds to an environmental state permitting the species to exist indefinitely. If the two variables are independent in their action on the species, the area so defined will be a rectangle, but even without such independence the area will exist whatever the shape of its sides. A third variable may now be introduced to define a volume, and then further variables until the ecological factors relevant to the life of the species have all been considered. The $n$-dimensional hypervolume so defined, which contains all the points corresponding to environmental states that permit the species to
exist, is called the fundamental niche of the species. "The fundamental niche of any species will completely define its ecological properties. The fundamental niche defined in this way is merely an abstract formalisation of what is usually meant by an ecological niche" (Hutchinson, 1957, p. 416).

The concept of ecological niche as defined by Hutchinson includes all the ecological relations of the species to the total physical and biotic environment. The limitations of this concept of niche come from the impossibility of being certain that all relevant variables of the environment have been included, and from the difficulty of measuring certain variables (e.g., food quality, food size, and many others) along continuous coordinates. Also, this definition of niche ignores the fact that the probability of survival and reproduction is not the same for all individuals at all points of the hypervolume, nor is it the same for all individuals at any point. It is not at all clear how a distribution of reproductive fitnesses could be incorporated for each point of every variable. Moreover, the set of points defined by the fundamental niche of the species is likely to change with time as the population evolves owing to natural selection. Although of considerable theoretical interest, Hutchinson's concept of ecological niche has, at the present level of knowledge, little operational value.

I suggest using the concept of niche in its maximum generality, to include all the relationships of an organism to the physical and biotic environment. The niche so defined includes the physical conditions of temperature, light, humidity, and so forth, required for the survival of the organism, as well as its requirements of food, place to live, and its relationships to other organisms of the same and other species. It is in this general sense that the term is most frequently used in the biological literature. Heuristically, then, it is possible to speak of the niche of animals in general terms; operationally, however, quantitative or qualitative statements about the niche of an individual or a species can be made only by referring to one (or more) specified component(s) of the ecological niche. For instance, it is possible to measure the survival and the optimal temperature range of organisms of a certain genetic constitution, or of a species; or to compare the food requirements of two species and to conclude that one species has a broader food niche than another, if the diet of the former includes all the foods acceptable to the latter, and in addition some others. Statements such as given in these two examples have a precise meaning subject to empirical verification. Attempts can be made to consider all the components of the niche that are relevant in a specific instance, since obviously not all aspects of the niche are equally significant. General statements can, then, be formulated concerning the niche, such as that the niche of a species $S_1$ is broader than the niche of another species $S_2$. But without explicit or implicit reference to one or several specific components of the niche, general statements concerning the niche of species have no empirical validity.

The concept of niche as defined above is analogous to the accepted usage
of the concept of phenotype. Both concepts include an indefinitely large number of components. They can be used heuristically in general statements and they can also be employed in precise empirical statements by referring to specific components of the generalized concept. The phenotype is the physical makeup of the individual, resulting from the interaction of its genotype with the environment. The niche comprehends all the relationships of the organism to its environment. The niche and the phenotype are both subject to change in the time dimension. For instance, the temperature tolerance and the food requirements of a certain organism may change through its lifetime, as well as its shape and size.

Like the phenotype, the niche refers primarily to the individual organism. Also like the phenotype, the concept of niche can be extended to a population or a species. The niche of the species is described by the significant moments of the frequency distribution of the individuals that make up the species. In a loose sense it is also possible to speak of the niche of a taxon larger than the species, again by specification of the significant moments of the frequency distribution of all the organisms comprised in the taxon. Thus, it is possible to speak of the temperature tolerance and geographic distribution of the species *Drosophila melanogaster*, of the genus *Drosophila*, and of the order *Diptera*.

**The Concept of Competition**

The term competition is applied in biological literature to a variety of phenomena, among them direct struggle among organisms, interactions between organisms trying to secure the same resources, relationships between predator and prey, and others. Birch (1957, p. 6) argued convincingly that "competition" in biology should have the following restricted meaning: "Competition occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or the other in the process."

The "short supply" in the definition may be an *absolute* shortage of a resource, i.e., if there is not enough food for all the animals present, or it may be a *relative* shortage, when the resource is not immediately available to the organisms or they fight over the same morsel, even if the resource is plentiful. Del Solar (1968) and Del Solar and Palomino (1966) have shown that females of *Drosophila pseudoobscura* and *D. melanogaster* have a "gregarious" tendency in oviposition. In the presence of many sites suitable to lay eggs, female *Drosophila* select preferentially the sites in which eggs have been laid by other *Drosophila* females of the same or of a different species. In experimental population cages, the females laid eggs
only in about half of the food cups available, and one cup had 50 percent or more of all the eggs laid. There were considerably more eggs in the cup with the largest number than the number of individuals that could develop from the amount of food in the cup. Competition for food among *Drosophila* larvae occurs in the cup with the largest number of eggs even when plenty of food is available in the surrounding cups. Similarly, competition for food occurs when two birds choose to fight for the same carcass even though there may be enough other carcasses around for both of them.

Two aspects of the process of competition can be distinguished, which have been called by Park (1954) the *exploitation* and the *interference* components of competition. The exploitation component of competition refers to the use of a limited resource by the competing individuals. Interference occurs if the resource is exploited less efficiently when two species or genotypes compete, than when only one is present. Interference between *D. serrata* and *D. pseudoobscura* occurred in the experiments reported below (see p. 125). When only *D. pseudoobscura* AR flies were present in the population, 269 flies emerged per food unit; where only *D. serrata* were present, 535 flies emerged per food unit. When both species competed for food only 133 *serrata* and 105 *pseudoobscura* flies, or a total of 238 flies, emerged per food unit. Weisbrot (1966) found that diffusible metabolites produced by larvae of *D. melanogaster* decreased the survival of *D. pseudoobscura*. Dawood and Strickberger (1969) observed a similar phenomenon in intraspecific competition between *D. melanogaster* larvae: the metabolic wastes of larvae of either one of two genotypes decreased the viability of larvae of any one of three other genotypes.

The exploitation component of competition is illustrated by the careful experiments of Bakker (1961) with *D. melanogaster*. About 0.60 mg of yeast are required by each larva to reach the minimum weight necessary to metamorphose into an adult fly. With 0.30 mg of yeast per larva, no adult flies emerge; with 0.45 mg, 60 percent, and with 0.60 mg, 90 percent, of the larvae become adults. Increasing the amount of food from 0.60 to 2.40 mg per larva does not alter the percentage of larvae becoming adults, but the dry weight of the individual adults increases proportionately to the amount of food (from 0.08 to 0.30 mg per fly). Competition between larvae of *D. melanogaster* and *D. simulans* occurs by exploitation without interference (Miller, 1964). At densities ranging from 10 to 120 larvae per culture, the same number of adults emerge when both species are present in equal numbers as when only *D. melanogaster* or only *D. simulans* is present. Larvae of two species of blowflies, *Lucilia sericata* and *Chrysomya chloropyga*, reared on a limited quantity of meat, gave no evidence of interference, although both competed for the exploitation of the same food (Ullyett, 1950). When larvae of *Lucilia sericata* competed with larvae of *Chrysomyia albiceps* the death rate of *Lucilia* larvae became higher with
increasing larval density. Ullyett observed that the larvae of *C. albiceps* prey on *Lucilia* larvae. This, then, is an example of predation rather than of interference in competition. Predation and parasitism are, doubtless, forms of interference in the nontechnical sense of this word, but predation and parasitism have well-defined meanings in the ecological literature and should not be confused with competition if the latter term is to have a precise and useful meaning in biological discourse.

*Facilitation* is the antonym of interference in reference to competition. Weisbrot (1966) observed that the presence in the food medium of metabolites produced by *D. pseudoobscura* increased the viability of larvae of *D. melanogaster*, although, as pointed out above, metabolic products of *D. melanogaster* interfered with the development of *D. pseudoobscura*. Facilitation among certain genotypes of *D. melanogaster* was observed by Dawood and Strickberger (1969).

Symbiosis represents the extreme of facilitation. The notion of facilitation, however, should be restricted to situations in which two (or more) species or individuals compete for the same resource. There is facilitation when the effective utilization of the shared resource, i.e., its transformation into biomass, is greater when two species are present than when the same amount of resource is distributed among the two species and exploited separately.

In some cases, facilitation occurs at intermediate densities. The proportion of surviving larvae of *D. busckii* is generally greater when the density of larvae per vial is 32 or 128 than when the density is 2 or 8 larvae per vial (Lewontin and Matsuo, 1963). Facilitation at intermediate densities occurs also in *D. melanogaster* (Lewontin, 1955). In these cases facilitation exists although presumably there is no competition proper since at the lower densities there is no shortage of food.

Nicholson (1954) has distinguished between two types of competition: scramble and contest, which have different effects upon the outcome of the competition. *Scramble* is the kind of competition in which success is usually incomplete; the resource is shared in various proportions by the competing animals. *Contest* occurs when each object of the competition is completely appropriated by one of the competitors (whether the competitor is one individual, as in most cases, or a group of individuals, as in some cases of competition for a territory) so that the competitors are either fully successful or unsuccessful.

In the scramble type of competition some, and at times all, of the requisite secured by the competing animals may not contribute at all to sustaining the population, if it is dissipated by animals that do not obtain sufficient amount of the resource for survival. In the experiments of Bakker (1961), when the initial number of larvae of *D. melanogaster* in a fixed amount of food (120 mg of yeast) was increased from 200 to 400, the proportion of
survivors decreased from 90 percent to nearly zero. At the higher density nearly all food was wasted although there was enough for the development of 180 individuals. On the other hand, in the contest type of competition the object of the competition contributes fully to the maintenance of the population; the successful competitors use it for their own survival while the losers obtain no part of the resource.

Competition for food occurs frequently as scramble, for instance in the competition among Drosophila larvae or among blowfly larvae. Competition for a home territory or for a nesting place occurs usually as contest. Competition for food sometimes takes the form of contest, as in some parasitic wasps; only one wasp larva develops in each prey larva. A wasp approaching a potential prey will not lay any egg on it if the larva already contains a developing wasp.

Competition and natural selection are different concepts, although natural selection occurs in many instances of competition. Natural selection occurs when there is differential reproduction. Natural selection is the result of at least three component processes—differential survival, differential mating success, and differential fecundity. Differential reproduction, and therefore natural selection, can take place without shortage of resources, i.e., without competition in the sense defined above. Genes frequently affect the relative reproductive success of their carriers even when there is no competition. Dobzhansky and Spassky (1953) found that 21 percent of the chromosomes of D. pseudoobscura collected in the field produced complete lethality of the individuals that carried them in homozygous condition; among the nonlethal chromosomes 21 percent decreased the probability of survival of the homozygous carriers, although there was no or little competition.

The reproductive fitness of the carriers of a gene or a genotype may be affected by the intensity of the competition. Birch (1955) found that in D. pseudoobscura, the “Chiricahua” genotype had higher fitness than the “Standard” genotype at low larval densities, while at high larval densities the “Standard” phenotype was superior. Chitty (1965) and Pimentel (1961) have suggested that selection favoring certain genotypes at low densities and others at high densities may be a mechanism contributing to the regulation of animal numbers. The reproductive fitness of a genotype may also be affected by competition with another species. Dawson (1968) found a mutant gene in Tribolium castaneum whose frequency, relative to its wild-type allele, increased gradually when the population competed with T. confusum. As the frequency of the mutant gene increased, the absolute numbers of castaneum in the population decreased gradually until eventually they were completely eliminated by confusum. The most likely explanation of this observation is that the mutant gene had higher intraspecific fitness than its allele but was worse in interspecific competition than the latter.
Genotypes with higher fitness in intraspecific but lower in interspecific competition also occur in *D. willistoni* (Levin, 1967).

**The Principle of Competitive Exclusion**

The notion that two species with similar ecological requirements cannot coexist indefinitely was formulated in modern terms for the first time by Grinnell. In 1904 (p. 375-376) Grinnell wrote, “Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region.” Grinnell drew the conclusion, which follows immediately from that statement: “It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships” (Grinnell, 1917, p. 443). Volterra (1926), Lotka (1932), and also Haldane (1924) concluded from their mathematical investigations of the problem that two species cannot coexist at an equilibrium if they utilize a common resource available in limited amount. This concept was elaborated by Gause (1934; Gause and Witt 1935). In his excellent monograph, *The Struggle for Existence*, Gause reviewed the mathematical investigations and provided experimental and field observations supporting the conclusions derived from them. The notion that two species competing for common resources cannot coexist has come to be referred to as Gause's Principle (Hardin, 1960; Miller, 1967, p. 3) or Gause's Axiom (Slobodkin, 1961, p. 68), and also as the Principle of Competitive Exclusion (Hutchinson, 1965, p. 27; Hardin, 1960), and the Principle of Competitive Displacement (De Bach, 1966).

The British Ecological Society held in 1944 a symposium to examine Gause's contention “that two species with similar ecology cannot live together in the same place, and the bearing of this, if true, on the origin and persistence of species” (Anonymous, 1944). A considerable number of publications dealing with the experimental studies of interspecies competition with various organisms appeared, mostly in British and American journals, during the immediately following years (for instance, Crombie, 1945, 1946, 1947; Elton, 1946; Williams, 1947; Park, 1948, 1954; Bagenal, 1951). Interest on the theoretical and experimental aspects of the principle of competitive exclusion has continued actively to the present day. Examples of recent general treatments are Hutchinson (1965), De Bach (1966) and Miller (1967).

Hardin (1960) stated that ecology stands “at the threshold of a renaissance of understanding, a renaissance made possible by the explicit acceptance of the competitive exclusion principle.” Hutchinson (1965), De Bach (1966), and many others share Hardin's conviction that the principle of competitive exclusion is one of the central and most fertile concepts
in ecological and evolutionary theory. To the contrary, Andrewartha and Birch (1954), and Cole (1960) think that the principle is either invalid or trivial, depending on how it is formulated. According to some other authors (e.g., Patten, 1961; Miller, 1967) competitive exclusion is a useful concept which must, however, be placed within a more general theoretical framework that includes the cooperative as well as the competitive aspects of interspecific relationships.

One source of confusion in the discussions of the competitive exclusion principle is that it means different things to different people. It is perhaps not unfair to include the various formulations in one of two categories, depending on whether the two species are required to be ecologically identical for the principle to apply, or whether competition for at least one limiting resource is taken as sufficient condition for coexistence to be impossible.

The most inclusive formulation states that two species with identical niches cannot coexist. Or, conversely, that two coexisting species must occupy different niches. For instance, Hutchinson (1965, p. 27) states that “in equilibrium communities no two species occupy the same niche,” and according to Slobodkin (1961, p. 122), “if two species persist in a particular region it can be taken as axiomatic that some ecological distinction must exist between them.” Thus formulated, the principle of competitive exclusion is true, but trivial. If niche is understood, in Hutchinson’s broad sense, as including all the ecological relationships of the organism, it is true that no two species occupy the same niche; but two individuals do not occupy the same niche either. The theory of evolution implies unambiguously that two species, whether they coexist or not, will not have exactly the same ecological requirements. Slobodkin’s (1961, p. 123) axiom that some ecological distinction must exist between two species which persist indefinitely at (or close to) a steady state in the same region, can be extended to any two species, whether they coexist or not. The requirement of identical ecological requirements is sometimes relaxed by saying that two species cannot coexist if they have “similar” ecology. Unless it is specified what is meant by “similar” ecology, this formulation is uninformative. Completely circular reasoning occurs when the degree of similarity required is said to be determined empirically: if two species cannot coexist they are considered similar ecologically; if they can coexist they are said not to be sufficiently similar.

A less inclusive formulation of the principle, and therefore more stringent is given by Elton (1927), Lack (1944), Hardin (1960), De Bach (1966), Van Valen (1960) and many others. Although the actual formulations vary, these authors claim that two species cannot coexist if they share one or more resources essential for the survival of the species. Frequently, though not always explicitly, the shared resource is required to exist in
limited supply. That is, according to these authors, two species cannot coexist if they compete for the same essential resource, usually food or a place to live. Competition is here understood in the sense defined above: it occurs when a number of animals share a resource that exists in short supply, or when the animals sharing a resource that is not in short supply harm each other in the process of sharing. Competition for a limited resource, and not necessarily complete ecological identity, is also all that is required in the mathematical investigations of Volterra, Lotka, and Haldane. This is also Gause’s concept: “It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor” (Gause, 1934, p. 19).

The Logistic Theory of Population Growth

The logistic theory of population growth was developed independently by Verhulst (1839) and by Pearl and Reed (1920). Pearl (1926), Volterra (1931), Lotka (1932), Gause (1934) and many others have used the logistic theory to describe the growth of populations of various organisms, like man, Drosophila, Paramecium, and yeast. The logistic theory expresses quantitatively the idea that the growth of a population at any time is determined by the interaction between the potential rate of increase of the organisms and some limiting environmental factor. The rate of growth of a population at any time can be described by the differential equation:

$$\frac{dN}{dt} = rN \frac{K-N}{K} = rN \left(1 - \frac{N}{K}\right)$$  \hspace{1cm} (1)

where \( r \) is the capacity of the organisms to increase in numbers under the specified environmental conditions of temperature, humidity, quality of food, and so on, when there are no limiting resources, \( N \) is the density of the population at any time, and \( K \) is the maximum density of the population when the limiting resource is saturated.

The logistic theory assumes that a population has a geometric capacity for increase proportional to the number of individuals present, \( rN \), and that every individual added to the population decreases the capacity to increase per individual by a constant \( c = \frac{1}{K} \). Biologically, this assumption means that every individual added to the population decreases the amount available of the limited resource by a certain quantity; when the resource is saturated the population ceases to grow.
The population is at equilibrium with the environment, that is, it ceases to grow when

$$\frac{dN}{dt} = 0$$ \hspace{1cm} (2)

There are two trivial solutions of (2): when \( r = 0 \) (the organisms have no capacity to reproduce) or \( N = 0 \) (there are no organisms). The nontrivial solution occurs when \( K - N = 0 \), or \( K = N \). \( K \) is then the saturation value, the maximum value that \( N \) can reach given the specified amount of the limiting resource.

The most attractive feature of the logistic theory is its extreme simplicity and, therefore, its mathematical tractability. Simplicity is a desirable quality of any scientific theory, since it helps to make the world comprehensible. Simplicity, however, is no proof of validity. "Our strategy must be to try out simple hypotheses and theories first, but be ready for more complex ones if evidence so indicates" (Dobzhansky, unpublished). Examination of the simplifying assumptions of the logistic theory indicates a number of potential sources of invalidation of the theory. Some of the assumptions are:

1. That the innate rate of increase of the organisms remains constant while the population grows. This assumption implies genetic uniformity of the organisms, or that natural selection is not operative. Yet the relative fitness of genotypes may change as the density of a population changes (Chitty, 1960, 1965; Pimentel, 1961, 1968; Ayala, 1968a, c).

2. That all the organisms in the population have at any time identical demographic properties, that is, that the probability of dying, giving birth, and so on, is the same for all the individuals; or, else, that the age-distribution of the population remains constant.

3. That there is a linear relationship between density and rate of growth, that is, that the rate of growth decreases by a constant amount for each individual added to the population independently of its density. Experiments with a number of insects, particularly Drosophila, have shown that the rate of growth of a population is not linearly related to density (Pearl, 1926; Pearl, Miner, and Parker, 1927; Sang, 1950; and others).

4. That there is no time lag in the response of the organisms to the conditions of the population, that is, that the population responds instantaneously to the addition of each individual. A lag in the response of the organisms leads to oscillations of the population around its saturation point, \( K \), which have been investigated by Utida (1957) and others.

These assumptions are likely to restrict or invalidate the application of the logistic equation to many, if not all, kinds of organisms. For a critical examination of the assumptions of the logistic theory see Andrewartha and
Birch (1954, pp. 362-386). How restrictive the assumptions are depends, of course, on the kinds of organisms being considered. Assumptions 2, and 3, for instance, are more likely to be invalid in organisms with complex life cycles, like insects or man, than in organisms with simple life cycles like yeast or bacteria. Thus, it is not surprising that attempts to fit population growth to the logistic equation have been more nearly successful with unicellular organisms (Loka, 1925; Gause, 1934) than with higher organisms (Andrewartha and Birch, 1954). Yet, even for populations of microorganisms, Feller (1940) has pointed out that other sigmoid equations fit the experimental data as well as, or better than, the logistic curve.

**Volterra’s Equations for Competitive Exclusion**

The logistic equation can readily be extended to two or more species living in a limited universe, that is, two species competing for a limited resource. Competition between two species in the same microcosm was considered theoretically by Volterra (1926) and, independently, by Lotka (1932). Given two species, $S_1$ and $S_2$, living together in a limited microcosm, the rate of growth in numbers of one species, say $S_1$, will be proportional to its innate rate of increase, $r_1$, under the given environmental conditions, and to the number of individuals present, $N_1$. It is assumed, as in the logistic theory, that each individual of $S_1$ added to the population decreases the rate of growth per individual by a constant amount $\frac{1}{K_1}$, where $K_1$ is the saturation density when only $S_1$ is present in the microcosm. It is also assumed that each individual of the competing species, $S_2$, decreases the rate of growth of $S_1$ by a constant amount $\frac{\alpha}{K_1}$. Similarly, each individual of $S_1$ decreases the rate of growth of $S_2$ by a constant amount $\frac{\beta}{K_2}$.

The parameters $\alpha$ and $\beta$, which may be called the coefficients of competition, measure the inhibitory effect of an individual of one species on the rate of growth of the other species.

The instantaneous rate of growth of two species competing for a common limiting resource is expressed by the differential equations

$$\frac{dN_1}{dt} = r_1N_1 \frac{K_1-N_1-\alpha N_2}{K_1};$$

$$\frac{dN_2}{dt} = r_2N_2 \frac{K_2-N_2-\beta N_1}{K_2}$$

(3)
where the symbols represent the parameters just described, and the subscripts 1 and 2 apply respectively to $S_1$ and $S_2$.

The application of equations (3) to actual populations is restricted by the same assumptions as the logistic equation for the growth of a single species, plus the additional assumption that each individual of one species inhibits the growth of the other species by a constant quantity which is independent of the density of either species. Whether these assumptions invalidate or not the application to natural populations of the equations (3) can best be decided by examining whether, as it is sometimes claimed (Slobodkin, 1961, p. 62), the equations and the conclusions derived from them are in good agreement with experimental and field observations. It must be emphasized that the strongest case for the competitive exclusion principle rests on the alleged general validity of certain conclusions derived from the equations (3).

The system described by the equations (3) will be at equilibrium when

$$\frac{dN_1}{dt} = 0, \text{ and } \frac{dN_2}{dt} = 0$$  \hspace{1cm} (4)

Trivial equilibria exist when $r_1, r_2, N_1$, or $N_2 = 0$

A nontrivial solution exists when

$$K_1 - N_1 - \alpha N_2 = 0, \quad \text{and} \quad K_2 - N_2 - \beta N_1 = 0$$  \hspace{1cm} (5)

Equations (5) can be expressed as

$$N_1 = K_1 - \alpha N_2, \quad \text{and} \quad N_2 = K_2 - \beta N_1$$  \hspace{1cm} (6)

which describe the equilibrium density of each species as a linear function of its saturation density, $K$, and the equilibrium density of the competing species. Since equations (6) are algebraic representations of straight lines, the possible outcomes of competition can be best investigated graphically in a plane limited by the rectangular coordinates $N_1$ and $N_2$. By making first $N_1 = 0$, and then $N_2 = 0$, two values that intercept the coordinates are obtained for the first equation (6). The straight line joining these two intercepts contains all the points at which $\frac{dN_1}{dt} = 0$. Inside the area defined by this zero isocline and the two coordinates, $\frac{dN_1}{dt}$ is positive, and either $N_1$ or both $N_1$ and $N_2$ will increase. Outside that area, $\frac{dN_1}{dt}$ is negative and
$N_1, N_2$, or both will decrease. Similarly, by making first $N_1 = 0$, and then $N_2 = 0$ in the second equation (6), the two intercepts with the coordinates of the zero isocline defined by this equation are obtained. All the points at which $\frac{dN_2}{dt} = 0$ are contained in the straight line joining the two intercepts. The simultaneous condition $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$ will occur at the point or points, if they exist, where the two isoclines intercept each other.

Leaving aside the trivial case where $K_1 = K_2$, and $\alpha = \beta$, the outcome of the competition may be investigated by expressing the two coefficients of competition, $\alpha$ and $\beta$, as inequality functions of $K_1$ and $K_2$. There are four possible outcomes, which are represented graphically in Figure 1:

---

**Fig. 1.** Competition between two species. The coordinates $N_1$ and $N_2$ indicate the numbers of the two competing species $S_1$ and $S_2$ respectively. The lines $K_1$, $K_1/\alpha$ and $K_2$, $K_2/\beta$ contain the saturation points for species $S_1$ and $S_2$ respectively. The arrows indicate the change in number of the species; below the saturation line each species will increase; above the saturation line each species will decrease. (a) $S_1$ wins; at equilibrium $N_1 = K_1$, $N_2 = 0$. (b) $S_2$ wins; at equilibrium $N_1 = 0$, $N_2 = K_2$. (c) There is one point of unstable equilibrium at $A$. (d) Stable equilibrium occurs at $B$. 
(a). If \( \alpha < \frac{K_1}{K_2} \) and \( \beta > \frac{K_2}{K_1} \), the system will reach equilibrium only when \( N_1 = K_1 \), and \( N_2 = 0 \). \( S_1 \) is the only survivor.

(b). If \( \alpha > \frac{K_1}{K_2} \) and \( \beta < \frac{K_2}{K_1} \), equilibrium is reached only when \( N_2 = K_2 \), and \( N_1 = 0 \). \( S_2 \) is the only survivor.

(c). If \( \alpha > \frac{K_1}{K_2} \) and \( \beta > \frac{K_2}{K_1} \), the zero isoclines intercept at one point (A in the Figure). The outcome of the competition depends on the initial conditions. If \( N_1/N_2 \) is at any time greater than a certain value, equilibrium will be reached when \( N_1 = K_1 \), and \( N_2 = 0 \). If \( N_1/N_2 \) is at any time smaller than that value, equilibrium occurs when \( N_2 = K_2 \) and \( N_1 = 0 \). Thus either \( S_1 \) or \( S_2 \) is the only survivor, depending on the initial conditions. The intercept of the isoclines gives an unstable equilibrium with both species coexisting. Any departure, however small, from the point of equilibrium will lead to fixation with either \( N_1 \) or \( N_2 \) equal to zero.

(d). If \( \alpha < \frac{K_1}{K_2} \) and \( \beta < \frac{K_2}{K_1} \), the two isoclines intercept at one point (B in the Figure), which gives the outcome of the competition if \( N_1 \) and \( N_2 \) are initially greater than zero. (The model is deterministic; stochastic events are ignored.) When

\[
N_1 = \frac{K_1 - \alpha K_2}{1 - \alpha \beta} > 0, \quad \text{and} \quad N_2 = \frac{K_2 - \beta K_1}{1 - \alpha \beta} > 0
\]

(7)

the system reaches equilibrium and \( S_1 \) and \( S_2 \) coexist. The equilibrium given by (7) is stable if \( \alpha < \frac{K_1}{K_2} \) and \( \beta < \frac{K_2}{K_1} \). Any departure from equilibrium will be counteracted by the competition process until the equilibrium is restored. The inequalities \( \alpha < \frac{K_1}{K_2} \) and \( \beta < \frac{K_2}{K_1} \) can be expressed as \( \frac{\alpha}{K_1} < \frac{1}{K_2} \) and \( \frac{\beta}{K_2} < \frac{1}{K_1} \). According to the definitions given above, \( \frac{\alpha}{K_1} \) is the inhibitory effect of one individual of \( S_2 \) on the growth of \( S_1 \), while \( \frac{1}{K_2} \) is the inhibitory effect of one \( S_2 \) individual on the growth of \( S_2 \). Similarly, \( \frac{\beta}{K_2} \) and \( \frac{1}{K_1} \) measure the inhibitory effect of one \( S_1 \) individual on the growth of \( S_2 \) and \( S_1 \), respectively. Thus, the conditions \( \alpha < \frac{K_1}{K_2} \) and \( \beta < \frac{K_2}{K_1} \) mean
that any one organism inhibits the growth of its own species more than it
inhibits the growth of the other species. This is taken to mean that the two
species occupy different niches or, more precisely, that the two species
are not limited by competition for the same shared resource. This argu-
ment constitutes the basis of the competitive exclusion principle: two
species competing for the same limiting resource cannot coexist indefini-
tely; and the reverse formulation: two species coexisting at a stable equilib-
rium are controlled by different limiting resources. The principle can, of course,
be extended by the same argument to more than two species.

Coexistence of Related Species in Nature

Species closely related phylogenetically and ecologically have frequently
been observed to coexist in the same habitat, apparently exploiting the
same resources. Some instances have been recently reviewed by Hutchinson
(1965), and Miller (1967). I shall limit myself to three examples.

Ross (1957) studied a monophyletic group of six species of the leaf-
hopper *Erythroneura* living on sycamores in Illinois. Individuals of up to
five species may occupy the same tree. There are slight differences in
tolerances to dryness among the species. *E. lawsoni* is the only consistent
inhabitant of trees in open, dry, wind-swept situations, while the tolerance
to dryness decreases from *E. arta*, through *E. usitata*, and *E. torella* to *E.
morgani* and *E. bella*. The last five species rarely exist outside humid
valleys or well-protected trees. However, even on trees in sheltered, humid
valleys *E. lawsoni* is also frequently the dominant species. There is little
evidence of competition and Ross suggests that rainfall may be the most
important factor regulating these populations. All the species survive in at
least some favorable foci from which they invade neighboring habitats when
the conditions become favorable.

Fourteen species of the genus *Drosophila* live in the Sierra Nevada Moun-
tains in the Yosemite region of California (Cooper and Dobzhansky, 1956).
Some species, like *D. pseudoobscura*, *D. persimilis*, *D. occidentalis*, and *D.
pinicola* occur at all elevations at which collections have been made ranging
from 850 to 11,000 feet (250 to 3,300m). Some other species are re-
stricted to part of the range. Every species is relatively more abundant in
some altitudinal zones than in others. Within a locality, the relative abun-
dance of different species varies from season to season and from year to
year. There is evidence of competition among *D. pseudoobscura*, *D. per-
similis*, and *D. miranda*, and perhaps also *D. azteca*, whose larvae feed on
the same slime fluxes, mostly of oak trees (Dobzhansky, personal com-
munication). The range of *D. pseudoobscura* includes the range of the
other three species, although it is not the dominant species in all localities.
There is also evidence of competition between *D. occidentalis* and *D. pini-cola*, which feed on fungi.

Dobzhansky and his colleagues have conducted since 1955 extensive studies of the four monophyletic species, *D. willistoni, D. equinoxialis, D. tropicalis*, and *D. paulistorum*, which live in the tropics of the New World.

**TABLE 1**

**Number of Females of Four Sibling Species of *Drosophila* Collected in Various Localities of Central and South America**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Date</th>
<th><em>D. willistoni</em></th>
<th><em>D. tropicalis</em></th>
<th><em>D. equinoxialis</em></th>
<th><em>D. paulistorum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Costa Rica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turrialba</td>
<td>August 1956</td>
<td>14</td>
<td>10</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td>La Lola</td>
<td>August 1956</td>
<td>2</td>
<td>42</td>
<td>89</td>
<td>5</td>
</tr>
<tr>
<td>Panama</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locality not recorded</td>
<td>November 1955</td>
<td>27</td>
<td>17</td>
<td>418</td>
<td>47</td>
</tr>
<tr>
<td>Barro Colorado</td>
<td>August 1956</td>
<td>8</td>
<td>32</td>
<td>22</td>
<td>12</td>
</tr>
<tr>
<td>Cerro Campana</td>
<td>August 1956</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Locality not recorded</td>
<td>February 1958</td>
<td>24</td>
<td>5</td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td>Locality not recorded</td>
<td>August 1959</td>
<td>5</td>
<td>10</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Cerro Campana</td>
<td>September 1961</td>
<td>12</td>
<td>1</td>
<td>11</td>
<td>40</td>
</tr>
<tr>
<td>Barro Colorado</td>
<td>September 1961</td>
<td>4</td>
<td>31</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>Cerro Azul</td>
<td>June 1962</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Darien</td>
<td>December 1962</td>
<td>4</td>
<td>1</td>
<td>72</td>
<td>2</td>
</tr>
<tr>
<td>Colombia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bucaramanga</td>
<td>September 1956</td>
<td>97</td>
<td>2</td>
<td>22</td>
<td>3</td>
</tr>
<tr>
<td>Llanos, Locality 1</td>
<td>March 1958</td>
<td>53</td>
<td>7</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Llanos, Locality 2</td>
<td>March 1958</td>
<td>61</td>
<td>9</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Turbo</td>
<td>February 1967</td>
<td>1</td>
<td>275</td>
<td>31</td>
<td>4</td>
</tr>
<tr>
<td>Leticia</td>
<td>February 1968</td>
<td>29</td>
<td>8</td>
<td>97</td>
<td>102</td>
</tr>
<tr>
<td>Valparaíso</td>
<td>February 1968</td>
<td>228</td>
<td>33</td>
<td>29</td>
<td>89</td>
</tr>
<tr>
<td>La Macarena</td>
<td>February 1968</td>
<td>72</td>
<td>37</td>
<td>177</td>
<td>2</td>
</tr>
<tr>
<td>Mitu</td>
<td>February 1968</td>
<td>116</td>
<td>6</td>
<td>29</td>
<td>121</td>
</tr>
<tr>
<td>Teresita</td>
<td>February 1969</td>
<td>94</td>
<td>240</td>
<td>388</td>
<td>15</td>
</tr>
<tr>
<td>Venezuela</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cumanacoa</td>
<td>November 1956</td>
<td>2</td>
<td>1</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Tuy</td>
<td>January 1963</td>
<td>12</td>
<td>9</td>
<td>88</td>
<td>3</td>
</tr>
<tr>
<td>Sarare</td>
<td>November 1967</td>
<td>12</td>
<td>28</td>
<td>37</td>
<td>2</td>
</tr>
<tr>
<td>Trinidad</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locality not recorded</td>
<td>April 1958</td>
<td>59</td>
<td>2</td>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>British Guyana</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locality not recorded</td>
<td>August 1957</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Brazil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marco</td>
<td>February 1968</td>
<td>16</td>
<td>62</td>
<td>58</td>
<td>14</td>
</tr>
</tbody>
</table>
The species are morphologically indistinguishable, although Spassky (1957) discovered some consistent differences in the genitalia of the males. The species are also ecologically similar: they feed on a variety of tropical fruits, the same fruit frequently containing individuals of two or more species. Nevertheless, the four species coexist over a wide geographic area, from Central America and Trinidad, through Columbia, Venezuela, and Guyana, down to the Matto Grosso in Brazil. Table I has been compiled from the records kept by Mr. Spassky of collections made by several investigators from 1955 to 1968.

Those who propose the general validity of the principle of competitive exclusion argue that there is considerable evidence that species drawing upon similar resources exclude one another from the same region. Elton (1946) analyzed published ecological surveys of 55 animal communities and 27 plant communities from a wide range of habitats. Eighty-four to 86 percent of the genera were represented by only one species in any particular community. Surveys for larger regions indicated that the average number of species of the same genus in any community should be greater than the observed number if the species associated at random. Elton concluded that similar species tend to exclude one another from the same community by competition. This analysis by Elton has been convincingly invalidated (Williams, 1947; Bagenal, 1951), but it can still be argued that when two or more species coexist they either do not compete for the same resources, or if they do compete, each species must draw from additional resources so that the coexisting species are not limited by the resources that they share.

It is obvious that no amount of empirical evidence indicating coexistence of competing species obtained from field studies will be a conclusive argument against this sort of argument. The evidence can always be said to be incomplete, with the comment that finer analysis would have indicated significant ecological differences among the coexisting species. "If they seem identical the study is incomplete" (Slobodkin, 1961, p. 123).

Coexistence in the Laboratory

Park (1948) studied the dynamics of mixed populations of the flour beetles, *Tribolium confusum* and *T. castaneum* at 29°C and 65 to 70 percent relative humidity. In some populations *T. confusum*, and in others *castaneum*, was eliminated. Yet both species coexisted for a considerable length of time, dependent on the amount of food provided. With 8 g of flour, the mean number of days to the extinction of one of the species was 548 days; with 80 g of flour, the mean was 1155 days. That is, the two
species coexisted for a mean number of 16 generations with 8 g of flour, and for a mean of 33 generations with 80 g.

The outcome of the competition between *T. confusum* and *T. castaneum* depends on the conditions of temperature and relative humidity (Park, 1954). High temperature and high relative humidity favor *T. castaneum*, while low temperature and humidity favor *T. confusum*. Thus at 34°C and 70 percent relative humidity, *confusum* is always eliminated first, and at 24°C and 30 percent relative humidity, *confusum* always wins. At intermediate temperature and/or relative humidity the outcome is not determined for every population, although the probability of one or the other species winning depends on the specific conditions. At 29°C, *T. castaneum* was the winner species in 86 percent of the populations when the relative humidity was 70 percent; when the relative humidity was 30 percent, *T. castaneum* won in only 13 percent of the populations. It seems that at intermediate temperature and humidity, the two species are nearly equal food competitors, and can coexist for many generations, the final outcome being largely decided by stochastic events. (The indeterminacy of the outcome has been shown by Lerner and Ho, 1961, to be dependent on the genetic constitution of the populations.)

*Drosophila funebris* and *D. melanogaster* can coexist at 20°C for long periods of time. Merrell (1951) found that *D. melanogaster* is favored by the addition of fresh food, while the proportion of *D. funebris* increases with the age of the food. When food is added at regular intervals, a fairly stable equilibrium occurs, with *D. melanogaster* predominating. The two species coexisted until the experiment was terminated after nearly two years or about 30 generations. Although the two species differ ecologically, there is no doubt that they competed for the same basic source of energy.

I have studied competition in the laboratory between *Drosophila serrata* and *D. nebulosa*. At 25°C *D. serrata* is eliminated in a few generations, but at 19°C both species coexist with *nebulosa* predominating (Ayala, 1966a). In another experiment, two populations were started at 19°C with 200 flies of each species. The populations were maintained by the serial transfer technique (Ayala, 1965a). The adult flies were introduced into one-half pint (0.47 liter) bottles with food. Every seven days they were etherized, counted, and transferred to a fresh bottle. When emergence of adult flies began in the containers where the flies had deposited eggs, the newly emerged flies were etherized, counted, and added to the container with the adult population. The adult ovipositing flies were thus in a single container while five other containers for each population had eggs, larvae, pupae, and young adults. This technique allows easy measurement of two parameters, namely, productivity, or number of flies emerging per container, and survival, or average longevity.
Fig. 2. Numbers of Drosophila serrata (solid line) and of D. nebulosa (broken line) in experimental population I.

The process of competition between the two species can be followed in Figures 2 and 3. The means for the number of flies emerging per week ("newborn" flies), the number of flies surviving from the previous week ("old" flies), and the total of both are given in Table II. *D. serrata* and *D.*

Fig. 3. Numbers of Drosophila serrata (solid line) and of D. nebulosa (broken line) in experimental population II.
TABLE II
Mean Number of Flies of *Drosophila serrata* and *D. nebulosa* in Each of Two Experimental Populations

<table>
<thead>
<tr>
<th>Population</th>
<th>Species</th>
<th>Newborn</th>
<th>Old</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td><em>D. serrata</em></td>
<td>126 ± 9</td>
<td>164 ± 9</td>
<td>290 ± 15</td>
</tr>
<tr>
<td></td>
<td><em>D. nebulosa</em></td>
<td>146 ± 13</td>
<td>162 ± 13</td>
<td>308 ± 22</td>
</tr>
<tr>
<td>II</td>
<td><em>D. serrata</em></td>
<td>26 ± 3</td>
<td>49 ± 7</td>
<td>75 ± 10</td>
</tr>
<tr>
<td></td>
<td><em>D. nebulosa</em></td>
<td>267 ± 13</td>
<td>412 ± 17</td>
<td>679 ± 23</td>
</tr>
</tbody>
</table>

*nebulosa* coexisted in both populations for 72 weeks, or about 25 generations.

In population I there were wide oscillations in the numbers of the two species. These oscillations can be interpreted as indications that the equilibrium between the two species is unstable (see below), as due to uncontrolled environmental fluctuations or as the result of changes in the competitive ability of the species by natural selection. The first two hypotheses are unlikely, because populations I and II were treated similarly and simultaneously, and yet, the numbers of the two species remained reasonably constant in population II throughout the experiment. By genetic tests, it was demonstrated that the increase in *D. serrata* in population I, which started around week 22, was due to natural selection of genotypes with improved competitive ability (Ayala, 1969a).

The two species compete in these populations for the available resources of food and space. Clear evidence of competition comes from the inverse relationship between the numbers of the two species. The average number of *D. serrata* is considerably less in population II than in population I, while the reverse is true of *D. nebulosa*. Definite evidence of competition can be obtained from Figure 2; the increase in numbers of *D. serrata* from week 22 to 30 is accompanied by a decrease in *D. nebulosa*. In general, it can be observed from Figures 2 and 3 that when one species increases, the other species living in the same microcosm decreases, indicating that the two species compete for limiting resources.

The competition experiments of *Drosophila* just reported did not include measurement of the saturation levels of each species when growing alone. That is, no attempt was made to measure the parameters $K_1$ and $K_2$ in equations (5), and therefore there is no way to estimate $\alpha$ and $\beta$. To obtain this information, I have studied the competition between *D. serrata* and *D. pseudoobscura* in experiments which will be reported in full elsewhere.
At 19°C *D. pseudoobscura* eliminates *D. serrata* in a few generations and at 25°C *D. pseudoobscura* is rapidly eliminated (Ayala, 1969b). At 23.5°C the two species coexist at relative frequencies that depend on the genetic composition of the particular strains of the two species. Two strains of *D. pseudoobscura* were used, one homokaryotypic for the third chromosome inversion “Chiricahua” (CH), the other homokaryotypic for the third-chromosome inversion “Arrowhead” (AR) (Dobzhansky, 1944). The strain of *D. serrata* was collected in Popondetta, New Guinea (Ayala,

### TABLE III

Mean Number of Flies of *D. serrata* and *D. pseudoobscura* in the Experimental Populations

<table>
<thead>
<tr>
<th>Population</th>
<th>Species</th>
<th>Newborn</th>
<th>Old</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>44</td>
<td><em>D. serrata</em></td>
<td>125 ± 14</td>
<td>137 ± 14</td>
<td>262 ± 25</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>105 ± 10</td>
<td>149 ± 16</td>
<td>255 ± 24</td>
</tr>
<tr>
<td>45</td>
<td><em>D. serrata</em></td>
<td>101 ± 8</td>
<td>87 ± 7</td>
<td>187 ± 11</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>119 ± 8</td>
<td>169 ± 11</td>
<td>288 ± 17</td>
</tr>
<tr>
<td>46</td>
<td><em>D. serrata</em></td>
<td>162 ± 15</td>
<td>168 ± 16</td>
<td>331 ± 27</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>92 ± 9</td>
<td>115 ± 14</td>
<td>207 ± 20</td>
</tr>
<tr>
<td>47</td>
<td><em>D. serrata</em></td>
<td>131 ± 8</td>
<td>161 ± 10</td>
<td>292 ± 14</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>108 ± 8</td>
<td>171 ± 12</td>
<td>279 ± 18</td>
</tr>
<tr>
<td>48</td>
<td><em>D. serrata</em></td>
<td>129 ± 9</td>
<td>160 ± 13</td>
<td>289 ± 18</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>107 ± 8</td>
<td>154 ± 11</td>
<td>261 ± 17</td>
</tr>
<tr>
<td>49</td>
<td><em>D. serrata</em></td>
<td>149 ± 9</td>
<td>155 ± 11</td>
<td>304 ± 13</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>97 ± 8</td>
<td>127 ± 10</td>
<td>223 ± 16</td>
</tr>
<tr>
<td>Average</td>
<td><em>D. serrata</em></td>
<td>133.0 ± 7.5</td>
<td>144.5 ± 9.1</td>
<td>277.6 ± 12.8</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> AR</td>
<td>104.6 ± 7.1</td>
<td>147.4 ± 11.0</td>
<td>252.0 ± 16.8</td>
</tr>
<tr>
<td>64</td>
<td><em>D. serrata</em></td>
<td>268 ± 15</td>
<td>278 ± 17</td>
<td>547 ± 27</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>61 ± 8</td>
<td>69 ± 8</td>
<td>129 ± 15</td>
</tr>
<tr>
<td>66</td>
<td><em>D. serrata</em></td>
<td>245 ± 18</td>
<td>295 ± 23</td>
<td>539 ± 33</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>78 ± 10</td>
<td>66 ± 9</td>
<td>145 ± 17</td>
</tr>
<tr>
<td>67</td>
<td><em>D. serrata</em></td>
<td>269 ± 20</td>
<td>319 ± 21</td>
<td>588 ± 33</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>74 ± 7</td>
<td>75 ± 8</td>
<td>149 ± 14</td>
</tr>
<tr>
<td>68</td>
<td><em>D. serrata</em></td>
<td>248 ± 19</td>
<td>314 ± 25</td>
<td>562 ± 38</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>55 ± 7</td>
<td>70 ± 8</td>
<td>125 ± 13</td>
</tr>
<tr>
<td>69</td>
<td><em>D. serrata</em></td>
<td>254 ± 19</td>
<td>254 ± 21</td>
<td>508 ± 36</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>49 ± 12</td>
<td>61 ± 9</td>
<td>110 ± 20</td>
</tr>
<tr>
<td>Average</td>
<td><em>D. serrata</em></td>
<td>257.0 ± 13.5</td>
<td>292.0 ± 16.0</td>
<td>549.1 ± 25.6</td>
</tr>
<tr>
<td></td>
<td><em>D. pseudoobscura</em> CH</td>
<td>63.3 ± 6.2</td>
<td>68.3 ± 7.4</td>
<td>131.7 ± 13.1</td>
</tr>
</tbody>
</table>
Six replicate populations were started where *D. serrata* competed with *D. pseudoobscura* AR, and five replicates in which it competed with *D. pseudoobscura* CH. Every population was started with 300 flies of each species. The populations were maintained by the serial transfer technique described above.

In six weeks, the two species reached equilibria at levels dependent on the genetic composition of *D. pseudoobscura*. The populations were studied for 40 weeks, or about 15 generations. Table III gives the means and standard errors of each species for the following parameters: number of flies emerging per week ("newborn"); number of flies surviving from the previous week ("old"); and the total of both. The total count of each species in two populations, one of each type, chosen at random are represented in Figures 4 and 5. At equilibrium, *D. pseudoobscura* flies were 18 percent of the total number in the CH populations and 45 percent in the AR populations. Homozygous AR/AR flies are better competitors with *D. serrata* than flies CH/CH. The increase of *D. pseudoobscura* in the AR compared to the CH populations occurs at the expense of a decrease in the number of *D. serrata*.

After the populations reached equilibria, flies of each species were sampled from every population. With the *F₁* progenies of these samples, the following "single-species" populations were established: three *D. pseudo-

![Population 67](image)

*Fig. 4. Numbers of Drosophila serrata (solid line) and of D. pseudoobscura CH (broken line) in experimental population 67.*
Fig. 5. Numbers of Drosophila serrata (solid line) and of D. pseudoobscura AR (broken line) in experimental population 47.

*obscura* CH and three AR populations; six *D. serrata* populations. Every population was started with 600 adult flies and maintained at 23.5°C by serial transfer. The mean numbers of flies after equilibrium and the standard errors are given in Table IV. The number of flies of one species is more than double in the single-species than in the two-species populations.

Equations (3) can now be solved for $\alpha$ and $\beta$:

**TABLE IV**

Mean Number of Flies in the Single-Species Populations

<table>
<thead>
<tr>
<th>Population</th>
<th>Newborn</th>
<th>Old</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. pseudoobscura</em> AR, 40</td>
<td>272 ± 13</td>
<td>418 ± 14</td>
<td>690 ± 18</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> AR, 41</td>
<td>262 ± 25</td>
<td>378 ± 29</td>
<td>640 ± 27</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> AR, 42</td>
<td>274 ± 17</td>
<td>388 ± 42</td>
<td>662 ± 43</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> AR, average</td>
<td>269.3</td>
<td>394.9</td>
<td>664.1</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> CH, 60</td>
<td>208 ± 32</td>
<td>271 ± 35</td>
<td>480 ± 35</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> CH, 61</td>
<td>281 ± 32</td>
<td>373 ± 50</td>
<td>654 ± 60</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> CH, 62</td>
<td>300 ± 29</td>
<td>374 ± 55</td>
<td>674 ± 69</td>
</tr>
<tr>
<td><em>D. pseudoobscura</em> CH, average</td>
<td>263.2</td>
<td>339.4</td>
<td>602.7</td>
</tr>
<tr>
<td><em>D. serrata</em>, 40</td>
<td>508 ± 46</td>
<td>682 ± 59</td>
<td>1190 ± 63</td>
</tr>
<tr>
<td><em>D. serrata</em>, 41</td>
<td>566 ± 51</td>
<td>669 ± 87</td>
<td>1235 ± 74</td>
</tr>
<tr>
<td><em>D. serrata</em>, 42</td>
<td>530 ± 37</td>
<td>692 ± 100</td>
<td>1222 ± 93</td>
</tr>
<tr>
<td><em>D. serrata</em>, 60</td>
<td>524 ± 40</td>
<td>689 ± 70</td>
<td>1213 ± 49</td>
</tr>
<tr>
<td><em>D. serrata</em>, 61</td>
<td>530 ± 76</td>
<td>821 ± 97</td>
<td>1351 ± 104</td>
</tr>
<tr>
<td><em>D. serrata</em>, 62</td>
<td>563 ± 42</td>
<td>730 ± 108</td>
<td>1294 ± 101</td>
</tr>
<tr>
<td><em>D. serrata</em>, average</td>
<td>536.8</td>
<td>713.9</td>
<td>1250.7</td>
</tr>
</tbody>
</table>
\[ \alpha = \frac{K_1 - N_1 - \frac{dN_1}{dt} \left( \frac{K_1}{r_1 N_1} \right)}{N_2} \]
\[ \beta = \frac{K_2 - N_2 - \frac{dN_2}{dt} \left( \frac{K_2}{r_2 N_2} \right)}{N_1} \]

At equilibrium, \( \frac{dN_1}{dt} = \frac{dN_2}{dt} = 0 \), and therefore

\[ \alpha = \frac{K_1 - N_1}{N_2} \quad \beta = \frac{K_2 - N_2}{N_1} \]

Designating *D. pseudoobscura* as \( S_1 \) and *D. serrata* as \( S_2 \) we obtain for the CH populations: \( K_1 = 602.7, \ K_2 = 1250.7, \ N_1 = 131.7, \ N_2 = 549.1 \). Therefore:

\[ \alpha_{\text{CH}} = \frac{602.7 - 131.7}{549.1} = 0.858 \]
\[ \beta_{\text{CH}} = \frac{1250.7 - 549.1}{131.7} = 5.327 \]

\[ \frac{K_1}{K_2} = \frac{602.7}{1250.7} = 0.482 \]
\[ \frac{K_2}{K_1} = \frac{1250.7}{602.7} = 2.075 \]

For the AR populations: \( K_1 = 664.1, \ K_2 = 1250.7, \ N_1 = 252.0, \ N_2 = 277.6 \). Therefore:

\[ \alpha_{\text{AR}} = \frac{664.1 - 252.0}{277.6} = 1.485 \]
\[ \beta_{\text{AR}} = \frac{1250.7 - 277.6}{252.0} = 3.861 \]

\[ \frac{K_1}{K_2} = \frac{664.1}{1250.7} = 0.531 \]
\[ \frac{K_2}{K_1} = \frac{1250.7}{664.1} = 1.883 \]
The $\alpha$'s and $\beta$'s are, in both populations, greater than $K_1/K_2$ and $K_2/K_1$, respectively, giving evidence of competition. However, the conditions for coexistence according to the Volterra equations are $\alpha < \frac{K_1}{K_2}$ and $\beta < \frac{K_2}{K_1}$. The Volterra equations, then, are not necessarily valid for all instances of competition between species. Two species competing for limiting resources may coexist.

**Conditions for Competitive Coexistence**

The widespread acceptance of the principle of competitive exclusion has led to considerable neglect in the exploration of the conditions that may allow coexistence of competing species. I shall now consider briefly some of the mechanisms that may lead to competitive coexistence.

**Selection and Life Cycles**

Among insects and other organisms with complex life cycles survival and reproduction may depend on different resources at different stages of development. The larvae of certain mosquitoes are aquatic and have a different diet from that of the terrestrial adults. Larval survival depends on the availability of certain plants and microorganisms; the fecundity of the adult females depends instead on their ability to obtain a protein meal from vertebrate blood. (The possibility that wild mosquitoes substitute hemolymph from larvae of other insects for vertebrate blood has been suggested recently by Harris, Riordan, and Cooke, 1969.) Butterfly larvae feed on leaves and other soft parts of their food plants, while the imagoes feed on flower sap. Food shortages may limit the survival of larvae; adults, however, are frequently controlled by predators (Kettlewell, 1955; Ford, 1964).

In laboratory experiments with the sheep-blowfly *Lucilia cuprina*, Nicholson (1954, 1957) has shown that two limiting factors, one operating at the larval and the other at the adult stage, may interact and regulate jointly the density of the population. Sloboedkin (1954, 1957) showed that two limiting factors, food and predation, may jointly determine population size in *Daphnia*. In serial transfer populations of *Drosophila serrata* Ayala (1966b) found that the number of flies emerging per food unit was determined by the amount of food. In these very crowded populations, the adults competed for living space. Population size was controlled by the interaction between the competition for food among the larvae and the competition for living space among the adults. When space was kept constant an increase of 50 percent in the amount of food resulted in an increase of 39 percent in the number of adults emerging per time unit,
yet the average adult population increased only by 17 percent. Similar results were obtained in experiments with D. pseudoobscura, D. melanogaster, and D. birchii (Ayala, 1967, 1968b). The interaction between food and space in the regulation of the size of the Drosophila populations was further investigated in an experiment in which the amount of food and the amount of space were both varied (Ayala, unpublished). When space was kept constant an increase of 50 percent in the amount of food resulted in an increase of 36 percent in the average population size; when food was constant an increase of 100 percent in the amount of space produced an increase of 20 percent in the average population numbers (Ayala, 1968c).

If the survival of larvae and adults is limited by different factors, it is possible that one species may be a better competitor than the other species at one stage of the life cycle but worse at some other stage. This seems to be the case in the competition between D. serrata and D. nebulosa, and between D. serrata and D. pseudoobscura. For instance, in Table II it can be observed that in population I the average number of adults emerging per week is greater for D. nebulosa than it is for D. serrata. Yet the average number of "old" flies is about the same for the two species, indicating that the average longevity of adult flies is greater for D. serrata than it is for D. nebulosa. Similarly (Table III) more D. serrata flies emerge per unit food than D. pseudoobscura AR, yet this difference is neutralized by the greater average longevity of the D. pseudoobscura flies.

A simple theoretical model can be constructed that allows the coexistence of two competing species if the relative fitness of one species is lower at one stage of development but higher at another than the relative fitness of the competing species. Assume that the fitness of one species, $S_1$, relative to another species, $S_2$, is $W_1$ for survival from zygote to adult; and that the fitness of $S_2$ relative to $S_1$ is $W_2$ for the adults (fecundity included). Let $P = \frac{N_1}{N_2}$ be the proportion of $S_1$ to $S_2$ zygotes at a certain time, $t_0$. We have:

\[
\begin{array}{c|c|c|c}
&S_1 & S_2 \\
\hline
P & 1 & P \\
W_1 & 1 & W_1 \\
PW_1 & 1 & PW_1 \\
W_2 & 1 & W_2 \\
\end{array}
\]

After one generation of competition the proportion of $S_1$ to $S_2$ will be $PW_1$ to $W_2$ or $N_1W_1/W_2$ to $N_2$. If $W_1 > W_2$ the proportion of $S_1$ zygotes will increase after each generation of competition; if $W_1 < W_2$ the proportion of $S_1$ will decrease; and if $W_1 = W_2$ the proportion of $S_1$ to $S_2$ will remain constant from one generation to the next.
Frequency-Dependent Selection

The condition $W_1 = W_2$ leads to an unstable equilibrium. The equilibrium between the two species remains at the proportion determined by the initial conditions. If the ratio of $N_1$ to $N_2$ changes for whatever reason, the original equilibrium will not be restored but rather a new equilibrium will be established at the ratio of $N_1$ to $N_2$ determined by the change. Stochastic events will ultimately lead to the elimination of one or the other species. An unstable equilibrium probably occurred in the experiments by Park (1948, 1954) with Tribolium. One or the other species was eliminated in every experiment, although the probability of elimination of each species was determined by the conditions of temperature and moisture. Indication that competition at the larval stage between D. melanogaster and D. simulans may lead to an unstable equilibrium has been obtained by Miller (1964, 1967).

The condition $W_1 = W_2$ appears also to be highly restrictive. It seems unlikely that the relative advantage of one species over the other at one stage of development will be compensated exactly by its disadvantage at some other stage. However, $W_1 = W_2$ will be less unlikely if the relative

![Graph](image)

Fig. 6. Relative fitness, $W_1$ and $W_{2'}$, of species $S_1$ and $S_2$ respectively. The fitnesses are linear functions of the relative numbers of the two species. $W_1$ is the fitness of $S_1$ after selection. $P$ gives the ratio of $N_1$ to $N_2$ at which a stable equilibrium is reached. $P'$ is the equilibrium point after selection.
Fig. 7. The relative fitnesses are nonlinear functions of the relative numbers of the two species. See Fig. 6 for meaning of the symbols.

fitnesses of the two species are in some fashion inversely related to their relative numbers. This requirement of frequency-dependent relative fitness has the additional interest of adding to the equilibrium in (9) the property of stability. Let $W_1$ in (9) be inversely related, and $W_2$ be directly related to $N_1/N_2$. The two species will reach a stable equilibrium at $P = N_1/N_2$ if there is a $P$ at which $W_1 = W_2$. This relationship is illustrated in Figure 6 and 7. In Figure 6, the $W$'s are linear functions of $N_1/N_2$; in Figure 7 the $W$'s are related to $N_1/N_2$ by some unspecified nonlinear function. If the $W$ function is of the type $W = a + bN$, where $a$ and $b$ are constants, the fitness curve will be linear; a nonlinear fitness curve will be given, for instance, by the function $W = a + \frac{b}{N}$.

The only necessary condition for an equilibrium to exist in this case is that the two fitness curves intersect at least at one point. If the relative fitnesses of the two species are inversely related to their relative numbers the equilibrium determined by the intersection of the two fitness curves will be stable. This inverse relationship between relative numbers and fitness implies that $W_1 > W_2$ to the left of $P$, and $W_1 < W_2$ to the right of $P$. Thus, whenever $N_1/N_2 > P$, $W_2$ will be greater than $W_1$ and $N_1/N_2$ will decrease until $N_1/N_2 = P$. Similarly, if $N_1/N_2 < P$, then $W_1 > W_2$ and
$N_1/N_2$ will increase until $N_1/N_2 = P$. Mathematical models of frequency-dependent fitness for intraspecific competition have been discussed by Lewontin and White (1960), Clarke (1964), and Anderson (1969).

Variations in the relative fitness of alternative genotypes as a function of the frequency of the genotypes have been observed, particularly in *Drosophila* studies (L'Heritier and Teissier, 1937; Levene, Pavlovsky, and Dobzhansky, 1954; Petit, 1966; Kojima and Yarbrough, 1967). For a recent review see Petit and Ehrman (1969). In the competition between *Drosophila melanogaster* and *D. simulans*, Narise (1965) observed that the competitive ability of a species increased as the relative number of its parents increased. Pimentel et al. (1965) studied competition between the housefly and the blowfly and observed that natural selection increased the competitive fitness of the rare species. Ayala (1966a, 1969a) observed the same phenomenon in the competition between *Drosophila* species.

Frequency dependent selection has been scarcely investigated in the field. Of great interest is Clarke's (1962) observation that bird predators learn to search for prey of a certain appearance, and therefore kill a disproportionately high percentage of the common varieties of certain snails and a low percentage of the rare ones. As the frequency of a certain snail type increases, its relative fitness decreases. This mechanism may lead to a stable equilibrium between two competing species. The selective advantage of one species over another in the exploitation of food or other resources may be upset by its being preyed on disproportionately more than the other species. How common the phenomenon of frequency dependent selection is in nature remains to be investigated.

*Niche Heterogeneity and Temporal Variations*

The $W_1$ and $W_2$ curves in Figures 6 and 7 may represent the mean overall fitnesses of the two competing species when all the stages of the life cycle are considered. Frequency-dependent selection may then lead to an equilibrium between competing species in other cases besides the situation where the disadvantage of one species at some stage of development is compensated by an advantage at some other stage. Moreover, the model developed by (9) can easily be modified to apply to a variety of situations. Assume, for instance, that the two competing species draw from two (or more) resources that exist in different amounts and are exploited by the species with different efficiency. For instance, $S_1$ may exploit food $A$ more efficiently than $S_2$, but $S_2$ may be more efficient than $S_1$ in the exploitation of food $B$. $W_1$ and $W_2$ in (9) may be taken now to represent the relative efficiency of $S_1$ and $S_2$ in the exploitation of $A$ and $B$. If the two resources exist in different amounts, $W_1$ and $W_2$ are each multiplied by a factor determined by the relative abundance of the two resources. An equilibrium may be
reached at a frequency of $S_1$ and $S_2$ determined by the magnitude of $W_1$ and $W_2$ and of the two resources. The equilibrium proportion of the two species may be stable if the amount of the two resources remains constant, but a new equilibrium may be obtained if the proportion of $A$ and $B$ changes. Mathematical models leading to stable equilibrium among competing genotypes when several resources exist have been developed by Levene (1953) and Prout (1968).

Oscillations in the competitive ability of the species from one generation to another may also lead to competitive coexistence. The diurnal cycle may modify from one generation to the next the competitive fitness of species with a generation time smaller or somewhat larger than one day. Seasonal changes will affect the fitness of species whose generations last several weeks. Cycles of several years of amplitude in the weather pattern or food availability are also known to occur. Haldane and Jayakar (1963) have given mathematical models leading to stable equilibria among genotypes when their relative fitnesses oscillate in time. Of considerable interest is their observation, which can readily be extended to two competing species, that two genotypes can coexist when the arithmetic mean of the fitnesses is greater (even much greater) for one of the genotypes, if their geometric mean is smaller than that of the other genotype.

Migration between populations, and still other mechanisms, may also lead to competitive coexistence. It is not my purpose to explore these mechanisms in detail, but rather to emphasize that under a variety of circumstances two species may compete for limited resources and yet coexist.

The Role of Natural Selection

In the foregoing discussion I have largely ignored the genetic composition of the competing species. Populations have been treated as if they were genetically homogeneous. Yet natural populations of sexual outbreeding organisms are known to be highly polymorphic genetically.

Moore (1952a), studying competition between *Drosophila melanogaster* and *D. simulans*, has shown that populations with improved competitive ability can be developed by selection, and that this can be done in relatively few generations. Pimentel (1961) and Pimentel et al. (1965) have investigated theoretically and experimentally the operation of natural selection on populations of competing species, and have concluded that natural selection may contribute to the stability of the system and lead to competitive coexistence. When two species compete with each other for a number of generations, the dominant species is at an evolutionary disadvantage in the sense that intraspecific competition is the main selective force acting on it, while the sparse species is being selected for interspecific
competitive ability. Individuals of the rare species compete mostly with individuals of the abundant species, while the individuals of the abundant species compete primarily among themselves. In the rare species selection will favor genotypes with high interspecific competitive fitness, while in the dominant species selection favors genotypes with high intraspecific fitness. As the interspecific competitive fitness of the sparse species evolves, this species may increase in relative numbers and become the dominant one. Selection will now favor the other species. Oscillations in the dominance of the species may occur; given enough time a genetic adjustment between the competing species should result.

Pimentel et al. (1965) observed reversal of dominance in an experimental study of competition between the housefly, *Musca domestica*, and the blowfly, *Phaenicia sericata*. In a 16-cell population system, the housefly was dominant during the first 50 weeks of the experiment. From week 50 on, the blowfly increased sharply in numbers, and it became clearly dominant from week 57 until week 65 when the housefly became extinct. It was shown that selection had enhanced the genetic competitive ability of the blowfly.

Ayala (1966a) studied competition of *Drosophila serrata* with *D. pseudoobscura, D. nebulosa*, and *D. melanogaster*. In each case, *D. serrata* was initially at a disadvantage but eventually it became dominant in each of the three combinations. In another experiment, represented in Figure 2, the competition between *D. serrata* and *D. nebulosa* reached an equilibrium early in the experiment, with a frequency of *D. serrata* around 30 percent. On week 22 *D. serrata* started a gradual increase in absolute and relative numbers, reaching a frequency of 90 percent by week 31. No reversal of dominance occurred in the parallel experiment (population II) represented in Figure 3, which was carried out simultaneously. Between weeks 31 and 33 flies of both species were sampled from populations I and II. With the *F₁* progenies of these samples five types of test populations were established (Ayala, 1969a): (1) *D. serrata* from population I and *D. nebulosa* from the stocks; (2) *serrata* from population II with *nebulosa* from the stocks; (3) *serrata* from the stocks with *nebulosa* from the stocks; (4) *serrata* from the stocks with *nebulosa* from population I; (5) *serrata* from the stocks with *nebulosa* from population II. Four replicate populations of each type were made; all started with 300 flies of each species. The process of competition in these “test” populations was studied for 12 weeks or three to four generations. Comparison among the first three types of populations showed that the competitive ability of *D. serrata* flies from population I was greater than that of *D. serrata* from population II or from the stocks. Comparison among the last three types of populations indicated that the competitive ability of *D. nebulosa* had increased through selection in both populations I and II.
The selection in population 1 of genotypes of *D. serrata* with greatly enhanced competitive ability did not result in the extinction of *D. nebulosa*. This is consistent with the hypothesis advanced earlier that competitive fitness may be frequency dependent. The effect of natural selection may then be interpreted as a displacement of the fitness curve in Figures 6 and 7. The fitness curve after selection (represented by the broken line in the figures) intercepts now the fitness curve of the competing species at a point to the right of the previous intercept. A new equilibrium is established at $P' > P$, with the relative numbers of $N_1$ greater than at the previous equilibrium.

The reversals of dominance observed in the competition between *Drosophila* species appear to be in agreement with Pimentel's (1961, 1968) postulate that natural selection favors the sparse species. Pimentel's explanation, however, cannot be accepted without modification. If two species coexist in a limited environment both may share some of the available resources of food and space, while each species may also exploit resources that the other species is not able to use, or does not exploit efficiently. In the *Drosophila* populations both species may share some food resources, like carbohydrates and certain yeast species, and they also share the available space. But it is likely that larvae of one species eat some yeast or mold species that are not exploited by the other species, and vice versa (Da Cunha et al., 1951; Merrell, 1951). Similarly, adult flies of the two species may utilize differentially certain components of the available space, and show preference for certain oviposition sites (Moore, 1952b; Del Solar, 1968). It is also possible for one species to utilize catabolites produced by, and useless to, the other species. In the extreme situation, each species may live on the metabolites of the other species, as in the phenomenon of symbiotic mutualism.

Selection for interspecific competitive ability may, then, occur in two different ways. First, selection may improve the ability of one species to exploit the resources also exploited by the second species. This may be called selection for “positive competitive ability” or, simply, selection for competitive ability proper. Second, genotypes may be selectively favored that allow the population to exploit resources not utilized by the competing species. This second process may be called selection for “avoidance of competition” since it tends toward decreasing the intensity of the competition. Obviously, intermediate situations can exist, such as the case of improvement of the ability of one species to exploit one resource that the other species exploits inefficiently or to a limited extent.

If two coexisting species exploit mostly the same limited resources, it is likely that one or the other species will eventually become extinct. However, selection for avoidance of competition increases the probability of coexistence by leading the two species towards ecological differentiation.
Therefore, selection for avoidance of competition operates as a positive feedback mechanism. The longer it proceeds the more likely are the two species to coexist, and therefore the greater the probability that the selection will continue. From the evolutionary point of view only selection for avoidance of competition is likely to continue for a large number of generations. If this reasoning is correct, one can make the prediction that populations of two species in localities where the two species coexist will be ecologically more divergent than populations of the two species in localities where they do not coexist. The accentuation of differences between species wherever they are sympatric has been named "character displacement" (Brown and Wilson, 1956).

Selection for competitive ability, i.e., selection for exploitation of the resources utilized by both species, will affect the two species independent of their relative frequencies. If the same yeast species is equally eaten by larvae of two Drosophila species, selection for intraspecific competition will be equivalent to selection for interspecific competition. The intensity of the selection will depend on the absolute numbers of both species together and not on their relative frequencies. On the contrary, selection towards avoidance of competition will preferentially occur in the sparse species. If one species is more efficient in the exploitation of the resources shared by both, those genotypes of the other species will be favored that allow the flies to exploit resources not utilized by the dominant species. Reversals of dominance are likely to be the result of selection for avoidance of competition.

Levin (1967) has investigated theoretically the role of natural selection in interspecies competition. The addition of genetic variability and selection to the Volterra equations makes possible the coexistence of two competing species. Oscillations in species dominance occur when at least at one of the loci controlling competitive performance one of the homozygotes has maximum interspecific competitive ability, but minimum intraspecific fitness, or vice versa.

Summary

The Volterra equations for competition between species and the principle of competitive exclusion are based on oversimplified assumptions about the nature of the competition process between species. Experiments with Drosophila species show that two species can compete for limited resources and yet coexist. Some of the biological mechanisms leading to competitive coexistence are frequency-dependent fitness, fitness interactions between stages of the life cycle, and temporal oscillations of relative fitness. Natural selection leads towards ecological differentiation of competing species and, therefore, promotes the stability of the ecosystems.
References


LEVENE, H. 1953. Genetic equilibrium when more than one ecological niche is available. Amer. Natural., 87:331-333.

O. PAVLOVSKY, and TH. DOBZHANSKY. 1954. Interaction of the adaptive values
in polymorphic experimental populations of *Drosophila pseudoobscura*. Evolution, 8:335-349.


**Merrell, D. J. 1951.** Interspecific competition between *Drosophila funebris* and *Drosophila melanogaster*. Amer. Natural., 85:159-169.


