Reports

Competitive Exclusion

Abstract. It is contended that there is little justification and no necessity for believing in the competitive exclusion principle as usually formulated. There is danger that a trite maxim like this may lead to the neglect of important evidence.

In his usual lucid style, Garrett Hardin (*1*) has made a plea for the "competitive exclusion principle," otherwise known as "Gause's hypothesis," "Grinnell's axiom," and "the Volterra-Lotka law," which seems likely to speed this principle toward the status of dogma. Thus, Hardin joins such influential enthusiasts as Hutchinson and Deevey (*2*), who refer to this principle as "perhaps the most important theoretical development in general ecology" and as "one of the chief foundations of modern ecology."

Some ecologists, including myself, are afraid of dogma and see in this doctrine a device that may be used to avoid Hardin's admonition that "*every* instance of apparent coexistence must be accounted for." It is so easy to dismiss a field observation by merely saying that "they obviously have to occupy different niches or they couldn't coexist." As Hardin notes, the dictum is not susceptible to proof or disproof, so one who cares to use it in this manner is on firm ground. Let me, therefore, present part of the case for keeping an open mind on this matter. My special objections are to the undefined term "competition," to the weaknesses and oversimplifications of the theory that is supposed to support the exclusion principle, and to the summary dismissal of equally good (or bad) theories that lead to the opposite conclusion.

The various meanings that ecologists have attached to the word "competition" have been discussed by Birch (*3*), and I shall not enumerate them here. Usage has been so inconsistent that one could probably make a case for defining competition as "that which eliminates one of two sympatric species occupying the same niche." In this form the exclusion principle makes a neat circular package; it is a law that admits of no exceptions provided that we are sufficiently flexible about the meanings we are willing to attach to the word "niche." I use this example merely to emphasize the semantic problems surrounding competitive exclusion. Hardin is frank about deliberately choosing ambiguous words to state the principle in the form "complete competitors cannot coexist," and I object on the grounds that ecologists are already wasting too much time debating about semantics rather than ecological principles.

As for the so-called theoretical demonstrations of the principle, Hardin's intuitive demonstration is much the simplest. It is undeniable that if a bank pays two depositors different rates of interest and confiscates the excess whenever the sum of the two accounts exceeds a fixed figure, the depositor receiving the lower interest rate is headed for insolvency. However, if we add just a touch of reality to the model by assuming that both men are horse players, it is no longer certain who will go bankrupt first; the situation is now nearer to Park's *Tribolium* experiments. Probability theory tells us that in such a model both men will eventually be ruined and that the probability and imminence of bankruptcy rises very sharply when one's capital happens to be reduced to a low level. If this model has reality for biological situations we may safely assert a principle more general than competitive exclusion, namely, "no two species can remain sympatric indefinitely whether or not they compete."

Volterra and Lotka derived their versions of the principle from extensions of the logistic theory, which has itself become the object of much criticism (*4*). In logistic theory, each added individual reduces the growth capacity of the population by a constant increment, with the result that the number of individuals, N, approaches asymptotically the carrying capacity, K, of the particular habitat. Now, if we mix two species which have asymptotic population levels K_1 and K_2 respectively, and if an individual of either species reduces the growth capacity of both populations, the growth of the mixture can be expressed by differential equations. Let a_1 represent the repressing effect of an individual of species 2 on the growth of species 1 expressed relative to the repression produced by an individual of species 1, and let a_2 represent the corresponding inhibition of species 2 per individual of species 1. Then the outcome of the competition depends on the pair of inequalities $a_1 < K_1/K_2$ and $a_2 < K_2/K_1$.

If the inequality signs are reversed one at a time it will be seen that there are four possible situations to be considered, of which the one shown represents the case where each species inhibits its own population growth more than it inhibits that of the other species. This is also the only case of the four in which the two species do form a stable mixture that will persist indefinitely. Hutchinson and Deevey dismiss this case because they feel that it "*implies that the ecological niches of the two species do not overlap completely.*" Kostitzin (*5*) also dismisses the case, first because coexistence is possible "only in a quarter of the cases which may occur" and second, with a cryptic assertion that for two allied species the internal competition should be less violent than "the struggle between the two groups."

I do not understand the bases for the pronouncements of either Kostitzin or Hutchinson and Deevey. The point at issue is a conclusion of Darwin's coming from Chapter III of the *Origin*, just a few lines ahead of those quoted by Hardin: "But the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers." If Darwin was right the Volterra-Lotka analyses predict not competitive exclusion but coexistence!

Finally, in an important paper (*6*), Skellam has provided a different type of theoretical example in which competitors can coexist. Boiled down to the simplest possible terms the argument is as follows:

Imagine an area A which includes just K "spots," which are small areas suitable for plant growth, and assume that, however many seeds may fall on a "spot," exactly one seedling grows to maturity there and produces B seeds. Of these, a number b (equal to BK/A) will be distributed among the K spots. If at time t there are N_t annual plants on the area, they will yield a mean of bN_t/K seeds per spot. If the seeds are distributed at random over the area, the

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distribution will be of the Poisson form. In this case, $Ke^{-bN_t/K}$ spots will be left vacant and $K(1-e^{-bN_t/K})$ spots will be seeded, so the population in the following year will be

$$N_{t+1}=K(1-e^{-bN_t/K})$$

Skellam shows that this type of difference equation yields a discrete analog of logistic growth.

Now let us assume that we have two species with numbers N_1 and N_2 "struggling" for the K spots and, to be certain that we do not introduce anything that can be called a niche difference, we will assume that individuals of the two species produce the same number of seeds. Both species would be expected to miss seeding $Ke^{-b(N_1+N_2)/K}$ of the spots, species 1 should occur alone on

$$Ke^{-bN_2/K}(1-e^{-bN_1/K})$$

spots, species 2 should occur alone on

$$Ke^{-bN_1/K}(1-e^{-bN_2/K})$$

spots, and both species should fall on

$$K(1-e^{-bN_1/K})\,(1-e^{-bN_2/K})$$

spots.

If we assume that the species are equally good competitors, so that each "wins" on one-half of the spots seeded by both, it is easy to see that both species can be expected to persist. For example, the proportion of species 1 in the $(t+1)$st year is given by the formula

$$\tfrac{1}{2}+\frac{e^{-bN_2/K}-e^{-bN_1/K}}{2(1-e^{-b(N_1+N_2)/K})}$$

so that, if at some point, $N_1=N_2$, the species will continue indefinitely to be equally abundant.

If one objects to the assumption of random distribution of the seeds, he should note that the nonrandom spatial distributions which are typical in natural situations are usually of the type in which the number of occupied spots is smaller than predicted from the Poisson theory, thus increasing the opportunity for even an inefficient competitor to persist by seeding vacant spots. Skellam considers ecologically more interesting cases in which one of the competing species always loses on the spots seeded by both, and he shows that even in these cases the species can coexist, provided that the poorer competitor produces more seeds than the other species. He also shows that in a "good" habitat (where K/A is large) the inefficient competitor will be driven out, but that in a poor habitat greater fertility may outweigh competitive ability. I submit that it would be very unfortunate if ecologists should be persuaded by a doctrine that such matters are not worthy of consideration.

It has been suggested (*7*) that Skellam's model "is primarily applicable to annual plants with a definite breeding season, . . ." but it could doubtless be applied almost without change to, for example, woodducks or other hole-nesting birds, where the availability of "spots" suitable for reproduction limits population size. I am confident that such an approach can be applied to perennial species with modifications that leave it still at least as biologically realistic as the logistic model of competition.

Why, then, do empirical data seem to support the competitive exclusion principle? First, because, by definition, no two species are identical, so that if one looks closely enough he is bound to find something that can be considered a difference in the ecological niches. Second, because survival and reproduction are processes that always contain chance elements and have finite probabilities of failure. Hardin seems to believe that if Park could control environmental conditions accurately enough the competition between the two species of *Tribolium* would give "an invariable result." It is more probable, in fact I regard it as certain, that Park is correct in believing that he has discovered environmental conditions under which the two species are so nearly evenly matched that the stochastic elements take over and mediate the outcome. No amount of tinkering with temperature and relative humidity is going to cause the little ball always to hop into the same slot of a roulette wheel. Third, if a population is being held below the carrying capacity of its habitat by the necessity of sharing some limited environmental resource with another species, it should be self-evident that there will be a selective advantage for any new gene that reduces or eliminates this sharing. I consider that Darwin's finches have differentiated not because *"Ecological differentiation is the necessary condition for coexistence"* but simply because natural selection will promote the spread of genes that permit a population to enlarge by exploiting an unfilled ecological niche.

If we really must have a competitive exclusion principle for pedagogic purposes, I am willing to subscribe to something like: "Species cannot coexist indefinitely because of the inevitability of random extinction, but, for species that conform to certain rather restrictive rules, competition may speed the process of species elimination." Each ecologist can decide for himself whether or not such a principle should become one of the foundations for a branch of science.

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Pupil Size as Related to Interest Value of Visual Stimuli

Abstract. Increases in the size of the pupil of the eye have been found to accompany the viewing of emotionally toned or interesting visual stimuli. A technique for recording such changes has been developed, and preliminary results with cats and human beings are reported with attention being given to differences between the sexes in response to particular types of material.

Qualities which have nothing to do with vision as such have long been attributed to the eyes. Perhaps the most poetical expression of this is found in the lines of Guillaume de Salluste: "These lovely lamps, these windows of the soul." Even if the eyes are not the "windows of the soul," there is an increasing amount of evidence that the eyes, more specifically the pupils, register directly certain activities of the nervous system, including, but not restricted to, the effects of visual stimulation.

Kuntz (*1*) discusses the control of the constriction and dilation of the pupil by the sympathetic and parasympathetic divisions of the autonomic nervous system. The light reflex, which is a change in pupil size due to changes in environmental light conditions, is controlled by the parasympathetic division through the action of the ciliary ganglion. The role of the sympathetic division in determining the size of the pupil is more complex, but Kuntz points out that "strong emotional states are accompanied by general sympathetic stimulation" and that "deep emotions of pleasure as well as fear are commonly accompanied by pupillary dilation."

Evidence that control of pupillary dilation by the sympathetic division of the autonomic nervous system is governed by hypothalamic centers is discussed by Gellhorn (*2*), who concludes that "pupillary dilation is one of the most constant symptoms observed on stimulation of the hypothalamus." Furthermore, Gibbs and Gibbs (*3*) report that hypothalamic stimulation will elicit purring in cats, which is generally con-