Letters

Further Competitive Exclusion

The perennial battle on what is now known as the "competitive exclusion principle" has again been joined by LaMont Cole [*Science* **132**, 348 (1960)], who minimizes its importance. I will follow L. C. Birch and define competition as occurring "when a number of (organisms) . . . utilize common resources the supply of which is short; or if the resources are not in short supply competition occurs when the (organisms) seeking the resource nevertheless harm one another in the process" [*Am. Naturalist* **101**, 5 (1957)].

The environment of an individual can be partitioned into several areas, as has been done perhaps most clearly by H. G. Andrewartha and L. C. Birch [*Distribution and Abundance of Animals* (Univ. of Chicago Press, Chicago, Ill., 1954)]. It is well known that related allopatric species are often indistinguishable in their requirements for food or "a place in which to live." If only one of these two aspects, which may be called subniches, or an essential part of either of them, is in short supply relative to the needs and behavior of the species, they cannot indefinitely coexist unless (i) they are equally fit in this environment, (ii) immigration replenishes the less fit species, or (iii) the species are prevented by some extrinsic or intrinsic cause from ever reaching the population size where they would compete. It does not matter that the species may differ in many other respects; the possession of identical requirements in one or a part of one of the two subniches, if this is at any season or stage a limiting factor to population size, is enough for the elimination of one species. This restatement of the principle is thus stronger and more testable than the usual one.

Cole cites an example from Skellam purporting to show a case where the principle is false. But they assume "that the species are equally good competitors," so that it is no wonder that both are present indefinitely, and "competitive ability" is used so narrowly that it excludes differences in fertility, which are then brought in to balance the viability component of fitness when the latter differs. But it is certainly rare, and perhaps nonexistent, that two species would have precisely the same total fitness in the same range of environments, although in closely balanced situations either might be eliminated because of, for example, unpredictable individual interactions, which could lead in nature to a fluctuating and patchy distribution of largely pure areas of each species, as in Skellam's model.

Cole's alternative maxim may be rephrased to read, "Species cannot *exist* indefinitely because of the inevitability of random extinction," but, except for individual demes and some rarer (and therefore less fit) species, this is unimportant even over geological time. Most individual species, not to mention life itself, are not likely ever to become extinct by "random" fluctuations, by which I mean simply those for which the causal complex is not adequately known, and which in some cases seem actually to be self-damping.

Competition (in the sense defined) is rare or absent in nature at any one time and place, because of the short time before the elimination of one of the species. Mainly its importance is supported by (i) allopatry of species with apparently identical subniches, (ii) waves of replacement (as in Brown's studies on the ants of the Pacific islands), and (iii) the few nonequilibrium situations now known. Apart from plant successions, which demonstrate the principle beautifully, the latter mainly involve artificially introduced species, such as the gray squirrel in England. Although the importance of competition in these latter cases has been questioned, perhaps justifiably in some, it is usually not clear why the native species should decrease immediately upon the arrival and expansion of the newcomer, except by some form of competition (which may not be aggressive but in the form of higher fertility or some other advantage). Even if exceptions to the principle as now stated could be proved, they would merely add further qualifications to its use and not remove its wide applicability in explaining the distribution of related organisms.

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Leigh Van Valen seems determined to remain entangled in what I referred to as "the semantic difficulties surrounding competitive exclusion." I think I know what he means by a "subniche," but what factors make two species "equally fit" and under what conditions do they "harm one another?" I will concede that the individual organism is "harmed" by the predator that totally consumes it or by the competitor that causes it to starve to death, but this does not necessarily harm the population to which the individual belongs. At this level the activities of other species in holding down numbers may be important influences favoring survival. I do not find myself enlightened by dogmatic assertions containing ambiguous words but, if *Science* is going to print Van Valen's letter, I suppose it merits an answer.

Van Valen's "restatement of the (exclusion) principle" in a "stronger" form is an unsupported assertion that, in the absence of immigration, two species actually limited by competition for the same "subniche" or "part of one" cannot coexist unless "they are equally fit in this environment." Now, most proponents of competitive exclusion believe that species can coexist if there are differences between them and my aim was to present a model in which they can coexist without such differences. In my boiled down version of Skellam's model I (not "they") undoubtedly made the species "equally fit" by assuming no differences whatsoever. This limitation is not an essential part of Skellam's model.

If Van Valen will go to the original he will learn that, with no immigration, two species limited by the same "subniche" ("a place in which to live") can contribute different numbers of potential offspring per individual to the next generation (does this not make them unequally fit?) and can still coexist indefinitely—provided that we neglect the possibility of random extinction, which Van Valen asserts to be unimportant.

My report was not designed to advocate any particular definitions or models of competition but to warn against uncritical acceptance of competitive exclusion as an axiom. I am confident that there remain great possibilities for contributing to our understanding by investigating species interactions under specified conditions in the field, in the laboratory, and in theory. For example, M. H. Williamson [*Nature* **180**, 422 (1957)] has given objective definitions of "controlling factors" and "competition" and has investigated objectively the circumstances under which competing species can and cannot coexist. I doubt that Van Valen will find much comfort in Williamson's conclusions but I commend the paper to him as an example where it is possible to debate the reality of the assumptions [H. G. Andrewartha and T. O. Browning, *Nature* **181**, 1415 (1958); M. H. Williamson, *ibid.*] and where we are left in no doubt about the nature of the conclusions or how they were reached.

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Social Responsibility

The report of the AAAS Committee on Science in the Promotion of Human Welfare, as published in the 8 July issue [*Science* **132**, 68 (1960)], is most interesting; I am writing with regard to three items in this report.

The report mentions, under the heading "Scientists' approaches to their social responsibilities," a third group, "typified by the Society for Social Responsibility in Science, which takes the view that scientists have a moral responsibility to try to limit to ethical uses the applications of science and technology." This statement, while completely correct, may yet give a wrong impression on one point: the members of the society believe that such limitation can be achieved only by a personal commitment. Thus, the members try to decide for themselves what an ethical use is; they try to foresee the applications of their work (and in part, of course, scientists today work directly on applications in any case) and limit their work to tasks which appear ethical to them in the light of the above criteria. They do so for the dual reason that they feel (i) that only so can they fulfill their social responsibilities and (ii) that such personal commitment is the best way of educating the national and international community to the awareness of moral and social implications. In the brief text of the report, the words "try to limit," might be taken to imply such means as strikes which would bring pressure to bear on scientists of opposite views. Such pres-