Letters

Oxygen Transport

I found Scholander's article on O_2 transport [*Science* **131**, 585 (1960)] very interesting, and I think I can lend support to it since similar conclusions were drawn (though not published) by myself and J. P. Baumberger some years ago in a completely different experimental situation [*J. Gen. Physiol.* **36**, 255 (1952)].

We found that the polarographic diffusion current for O_2 given by whole blood was six times greater than that given by plasma when both were measured at O_2 tension of 100 mm-Hg at 37°C. This excess diffusion current depends not only on red cell concentration but on factors which increase the rate of dissociation of HbO_2: degree of O_2 saturation, pCO_2, pH, and temperature. The readiness with which HbO_2 releases O_2 determines (i) the rate at which O_2 is replaced in the immediate vicinity of the "consuming" cathode and (ii) the rate at which Scholander's "bucket-brigade" operates, at a greater distance from the cathode. (The rate of "passing the bucket" obviously depends on the dissociation rate.) The driving force behind this steady-state flow is the constant rate of O_2 "consumption" of the cathode, which maintains a constant pO_2 gradient in its vicinity.

The resultant of this situation is that, at a pO_2 of 100 mm-Hg, the cathode receives O_2 from whole blood at a rate at which it could receive O_2 from plasma only at a pO_2 of 600 mm-Hg. If we now substitute rapidly metabolizing cells for the cathode, the conclusion follows that in the presence of oxygenated red blood cells the effective rate of diffusion of O_2 to the consuming cells at a given pO_2 will be much greater than could be expected on the basis of the O_2 tension difference alone.

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Competitive Exclusion

As an economist, I have been delighted with the recent revival of the earlier view that ecology and economics are closely related. Hardin's article ["The competitive exclusion principle," *Science* **131**, 1292 (29 Apr. 1960)] is an excellent example of this revival, as would be expected in view of his previous work. Unfortunately, it contains an error in economics. From the principle that complete competitors cannot coexist he deduces the development of monopolies. The principle, however, applies to species, not individuals. Park's experiments did not show that one individual flour beetle grew so large that it eliminated all the others, only that one species grew so numerous that it eliminated the other. If the principle has any application to economics at all, it would indicate that one type of economic enterprise might, by multiplication of its members, replace another, but this would not lead to monopoly. The problem of monopoly is a real one, and an important one, but it has nothing to do with the competitive exclusion principle.

I rather dislike attacking an article which is, in general, as superior as Hardin's, but in this one area he is wrong.

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Garrett Hardin points out that the "competitive exclusion principle"—that is, that "complete competitors cannot coexist"—is essentially a theoretical concept unlikely of direct proof in the field. I believe this conclusion is strengthened if it is considered that at least three common conditions, not mentioned by Hardin, must be *absent* if the replacement of one species by its complete competitor is to proceed in a direct fashion. However, at least two of these conditions are likely to be *present* in the field unless the replacement process is quite rapid.

If there exist two complete competitors, species A and B; if species A is slowly replacing species B; and if this process is to continue directly to the point of (local) extinction of species B; then the following possibilities must *not* occur:

1) A decrease in the genetically determined competitive ability of species A below the level of that of species B.

2) An increase in the genetically determined competitive ability of species B above the level of that of species A.

3) A change in the environment sufficient to shift the competitive superiority from species A to species B.

The first possibility is somewhat unlikely, on evolutionary grounds; the second is fairly likely if the replacement process is quite slow, a condition which also implies that the difference in competitive abilities of the two species is small and hence likely to be easily changed by genetic variation. The third possibility would appear to be quite likely under many conditions. If the particular environmental factor is one which oscillates between the condition favoring one species at one time and the other at another time, and if the rate of oscillation is sufficiently fast as com-