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11 February 1974

Solar Energy by Photosynthesis: Manganese Complex Photolysis

In a recent article (*1*) a reference was made to the photolysis of a binuclear manganese complex [reference 20 in (*1*)] in which oxygen evolution was measured by a Teflon-coated silver-gold electrode [figure 7 in (*1*)]. In an attempt to quantify this effect it has become apparent that most, if not all, of the change in slope of the apparent oxygen concentration is the result of a small temperature change (0.4°C) on the oxygen permeability of the membrane. Upon illumination in a visible band the thermostated sample solution is warmed slightly by thermal de-excitation of the excited state of the complex. This in turn increases the diffusion rate of atmospheric oxygen across the Teflon membrane, causing a change in the apparent oxygen concentration as sensed by the electrode.

In light of these results, we are seeking alternate evidence for oxygen evolution by the binuclear manganese complex.

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17 June 1974

Ecological Genetics and Natural Selection in Mollusks

Jones (*1*) has raised again the controversial question as to whether polymorphism in shell color and pattern in the land snail *Cepaea* is correlated with climate. He provides evidence suggesting that in *C. nemoralis* there is a correlation between gene frequencies at the shell color locus and mean summer temperature, but he could find no correlation with climate for other loci. Following earlier workers, Jones acknowledges that there is a correlation between polymorphism and habitat in some (but not all) English populations of *C. nemoralis*, and that there are situations in which frequency-dependent selection by predators occurs. The possibility of heterozygote advantage is also entertained. There remain, however, many inexplicable variations in the frequency of the phenotypes that are not correlated with obvious environmental features. These "area effects" occur over what are claimed to be ecologically similar environments, and thus far have defied explanation.

There is an extensive literature on polymorphism in *Cepaea*, some of it cited by Jones (*1*), but two features of the ecology of the snails, population size and population density, both potentially important in the interpretation of genetic diversity, have been neglected by most workers. Estimates of population size would seem desirable if genetic drift is to be accepted or rejected as a major factor affecting gene frequencies, and estimates of population density would seem relevant in view of the correlations that have already been established between density and polymorphism in other species of molluscs.

Thus in *Donax rugosus*, a common bivalve of the sandy shore in West Africa, polymorphism correlates well with population density, the diversity of phenotypes being greater at high as compared to low densities (*2*). In the African land snail *Limicolaria martensiana*, polymorphism also increases with density, and in the Kampala area of Uganda there is little or no polymorphism where the snails exist at densities of less than 1 per square meters; but where they occur at densities in excess of 100 per square meter, polymorphism is maximal (*3*).

The association of genetic diversity with population density in *Donax* and *Limicolaria* can be interpreted theoretically in terms of frequency-dependent apostatic selection by predators like birds. Such predators are likely to acquire search images of their prey; and at high densities where predation is heavy, phenotypes that stand out or contrast may be at a selective advantage.

That there are variations in population density in *Cepaea nemoralis*, even in an apparently uniform environment, has been demonstrated (*4*). If, then, density can vary, why should not the genetic diversity also be affected? Perhaps, too, what appears to us as a uniform environment is to a snail immensely varied; this would certainly explain variations in density over quite small areas. I do not mean to imply that variation in population density (and indeed in population size) are necessarily of profound importance in understanding polymorphism in *Cepaea*, but it would certainly be worth looking to see if there are density effects.

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1 February 1974; revised 27 March 1974

Owen suggests that population density may have an effect in controlling gene frequencies in populations of *Cepaea* and of other mollusks. In the light of the recent important theoretical work (*1*) on possible relations between density and the genetic structure of populations this suggestion is an interesting one. Some information is already available on population density in *C. nemoralis* (*2*), and it is clear even to the casual collector that this species shows enormous local variations in abundance. However, it is difficult to estimate real population densities in many land mollusks (including *Cepaea*) by simply making collections because very frequently a large proportion of the population is buried beneath the surface of the ground (*2*). Accurate estimates can therefore be made only by capture-recapture experiments. Another practical difficulty that may arise is that samples upon which apparent associations of gene frequency with density are based are not independent of each other, so that intensive sampling of one region with a high population density and, quite coincidentally, with a characteristic gene frequency may give rise to a spurious appearance of density dependence.

Bearing in mind these important reservations, I would point out that there are no clear associations between gene frequency and population density (as measured by sample size) in *C. nemoralis* on the Marlborough Downs (*3*) or in *C. vindobonensis* in the Velebit Mountains of Yugoslavia (*4*). An extensive survey of population density by means of capture-recapture methods in *C. nemoralis* and *C. hortensis* in Somerset has also revealed no associations of gene frequency or degree of polymorphism with density (*5*). Clarke and Murray (*6*) have taken 250 samples of *Partula* (which has the advantage that population size can be estimated by sampling because the snails do not bury themselves) on the island of Moorea, and find no relationship between the genetic structure of populations and their density.

There exists considerable information on density-dependent selection in laboratory populations (*7*). Any extension of this data to natural populations is clearly very desirable. I therefore concur with Owen's suggestion that further research should be carried out on the possible effects of population density on polymorphism in *Cepaea*.

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6 May 1974

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Evolution of Anuran Life Cycles

Although Wilbur and Collins (*1*) make a valuable contribution to our understanding of the biology of amphibian larvae, they skirt the interesting question of why there are no paedogenetic anuran larvae. They state that "Species that live in constant aquatic habitats surrounded by hostile environments (desert ponds, caves, high-altitude lakes) may evolve permanent larvae genetically incapable of metamorphosis." Yet frogs breed in a diversity of habitats and none have paedogenetic tendencies; all must metamorphose. I believe that a close look at the adaptive zone of the generalized anuran larva offers a partial answer to this problem and helps refine the Wilbur-Collins model.

Anatomically, a frog larva is grossly different from a frog, salamander, or salamander larva (*2*). Tadpoles have unique chondrocrania which relate to a suspension-feeding way of life, with the ceratohyal serving as the piston of a buccal pump (*3*). Stomach contents show that tadpoles, whether they have hard mouthparts or not, can be indiscriminate suspension feeders on phytoplankton (*4*). Tadpoles have an efficient mucus entrapment system that allows them to extract particles less than a micron in size from their feeding currents (*5, 6*). Salamander larvae, on the other hand, are basically active carnivores, hunting large, individual prey items.

In comparison with most vertebrates, tadpoles have poorly developed and nonfunctional appendicular structures. Reproductive organs are absent. Tadpoles apparently have sacrificed or delayed much somatic and reproductive differentiation in favor of tissues directly related to ingestion, digestion, or food storage (the tail); at any one time almost 50 percent of the dry weight of a tadpole may be stomach contents (*7*).

The result of all this specialization in morphology (*3, 5*) and feeding behavior (*4, 5, 7*) is that tadpoles have very rapid growth rates but are especially vulnerable to predation. Tadpoles can survive to metamorphosis in environments such as temporary or semipermanent pools, which show rapid rises in aquatic primary production, but time lags in the appearance of aquatic predators. These should be the most common habitats for tadpoles and, indeed, they are.

Rather than being paedogenetic in "constant aquatic habitats" (*1*), tadpoles are rare in these environments. Wilbur and Collins refer to a "highly predictable aquatic habitat" as an environment favoring paedogenesis. The predictability of an environment can be a hazard to tadpoles which are relatively defenseless herbivores, if potential predators can "predict" as accurately as the frogs. A few genera have evolved tadpoles that can live in permanent, more or less predictable environments. Their larvae make use of structural complexity to hide from predators (for example, between rocks in streams, or among macrophytes in lakes). These environments are not likely to have as explosive rises in aquatic primary production as are smaller, more temporary bodies of water. In permanent ponds and lakes, tadpoles must spend a longer time reaching the minimum size at which they can metamorphose; "dW/dt" and "g" are likely to be lower than for larvae in temporary pools (*8*). While it may be more difficult for predators to find individual tadpoles in these habitats, the predators have a longer time to hunt. Given this situation, it is not surprising that only a handful of anuran species take more than 1 year to reach metamorphosis, and these are all temperate forms in regions with a short growing season.

In regions with highly predictable environments, frogs are more likely to evolve terrestrial development than extended aquatic life. The greatest numbers of species with nonaquatic, direct development are found in the relatively aseasonal wet tropics of the New World (for example, species of the genus *Eleutherodactylus*).

Finally, part of the area where the adult urogenital system differentiates in a frog is topographically outside the body cavity of a tadpole. In order for the organism to become reproductive, some major morphological reorganization—a metamorphosis—is necessary. Elongation of the ilial bars at metamorphosis not only is essential for