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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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 saltatory locomotion in the adult but also provides space for reproductive organs. Because of the extreme morphological differences between the tadpole and the frog, anuran species that retain a larval stage are mechanically obligated to metamorphose.

Both ecologically and morphologically, a paedogenetic tadpole is evolutionarily implausible. Presumably, in jointly perfecting the suspension-feeding, herbivorous tadpole and the saltatory, carnivorous frog, canalization has made the paedogenetic tadpole genetically unlikely.

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6. As an extreme example of feeding efficiency, tadpoles of *Xenopus laevis* can clear a volume of water in excess of eight times their body volume per minute [calculated from data in (*5*)].
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8. Wilbur and Collins (*1*) define dW/dt as the growth rate for a tadpole and g as a threshold value for dw/dt above which a tadpole large enough to metamorphose nevertheless continues to gain weight, but below which metamorphosis is immediately initiated.

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Wassersug raises the obvious and interesting question why there are no paedogenetic anurans. We chose to restrict our discussion to models useful in explaining the observed diversity of amphibian life cycles. Wassersug attempts to define the limits of diversity possible for anuran evolution, a far more ambitious task. I do not believe it is possible to determine the limits of evolutionary change, except for restrictions imposed by the laws of the physical sciences. The essence of evolution is the attainment of the intuitively improbable; consider the remarkable convergence in function yet difference in phylogeny of the vertebrate and cephalopod eyes. Haldane once commented that the universe is not only queerer than we suppose, but queerer than we can suppose.

Wassersug seeks an answer to his question in morphological arguments. Although it may not be easy to visualize how maturation of the gonads might be completed in the larval state, elongation of the ilial bars or morphological specializations for suspension feeding can hardly be constraints on the evolutionary possibilities for anurans. Sex differentiation occurs before metamorphosis and the gonads begin to develop within the body cavity of the growing tadpole (*1*).

The fossil record does not add insights. The earliest known frogs are from the Jurassic and, except for having ribs, are not very different morphologically from modern frogs of the families Ascaphidae and Discoglossidae. Estes and Reig (*2*) point out that elongation of the ilium and tarsal elements are present in several primitive Paleozoic amphibians as an adaptation for swimming and are only incidentally a preadaptation for saltation. *Triadobatrachus* from the Early Triassic of Madagascar is the only clue to the possible proanuran condition. This form has a tail and elongate hind limb elements. It presumably was an aquatic form and the fossil specimen is probably a young animal, but it is difficult to ascertain if it had a metamorphosis as complete as in later anurans.

Clearly frogs have been committed for a long time to a complex life cycle in which temporary aquatic habitats are exploited by a larval form specialized for rapid growth. Some anuran lines have shortened the larval stage as an adaptation to terrestriality and have direct development. Other lines have become aquatic, not by becoming paedogenetic but by retaining the adult form, which is a very suitable design for the aquatic mode of living. Paedogenetic frogs as well as viviparous turtles and birds are perhaps evolutionary possibilities but ecological impracticalities.

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A Chondrule: Evidence of Energetic Impact Unlikely

Lange and Larimer (*1*) conclude that the morphology and mineralogy of an unusual chondrule from the Ngawi meteorite are the results of a highly energetic impact within the solar nebula. Enclosed within the chondrule's fragmented olivine crust is an embedded magnetite grain which, according to their calculations, impacted with a velocity between 1 and 10 km/sec. The lower and upper velocity limits are determined by the possible range of chondrule temperatures at the time of impact and the melting temperature of glass and sulfide.

The evidence given for an energetic collision is inconsistent with laboratory impact data. In an experiment simulating the destruction in space of tektites by micrometeoroid impact, Gault and Wedekind (*2*) found that 1 joule/g of projectile kinetic energy per unit mass of a spherical target completely ruptures the sphere and less than 0.1 joule/g results in a crater. Spallation, caused by the reflection of shock waves from the surface, generates about as much damage in the antipodal region as around the impact site on the sphere. From the values given for the mass ratio of the magnetite grain to the remainder of the chondrule of 1/50 and the calculated range of impact velocities of 1 to 10 km/sec (*1*), the kinetic energy per unit mass values are 10 to 1000 joule/g, far in excess of the amount required to completely disintegrate the chondrule. Moreover, for the upper limit, complete melting of the magnetite grain would occur. Even if it had not shattered, there are no fractures about the magnetite grain or near the opposite surface that are characteristic of the spallation process. A velocity of 0.1 km/sec would correspond to the kinetic energy per unit mass required for cratering. Although this velocity is below the experimental range of velocities, noticeable damage should still occur. Lange and Larimer propose a cushioning effect by the outer layer of the chondrule as a mechanism to preserve the chondrule from shattering. Experiments on a centimeter scale (*3*) and micrometer scale (*4*) show that thin, less cohesive layers attenuate the effects on a massive substrate but that the protective layer is cleared away