

# A Frog Model of Geographic Speciation



**Alan R. P. Journet** is an associate professor at Southeast Missouri State Univ., Cape Girardeau, MO 63701, where for five years he has been coordinating the General Biology program. Journet has experience in teaching and research in Britain, Canada, Australia, Texas and Missouri. His publications include articles on technical writing, teaching techniques in general biology and research in various aspects of plant/herbivore ecology and the numerical analysis of medieval manuscripts.

Alan R.P. Journet

Because the topic of speciation is poorly treated in many introductory biology texts, many students perceive that one population of organisms is divided by a barrier into two groups. Time and genetic divergence influence the two separate populations. The barrier is then removed and the two populations cannot (or do not) interbreed. They are, therefore, good biological species, and we have two species where there was one before. This absurd oversimplification of the process does scant justice to our understanding of the genetics of speciation, and encourages the notion that speciation, with the requirement of complete separation and extensive time, must be a rare event indeed.

The following model, involving frogs, illustrates to students, through question and discussion, how speciation may occur and leads to the generalization that any environmental event that reduced reproductive success in matings between groups or organisms will promote speciation.

## The Frog Model

Let us consider a population of frogs that occurs from Quebec, in Canada, down the east coast of the U.S. to Florida. Would we expect any differences between the far northern and far southern frogs? Clearly, climates are different. We would predict adaptations of frogs to local climates, particularly in relation to time of breeding. We would see a cline in this and other characteristics associated with climatic adaptation. But, since we have one continuous population throughout the range, with gene flow possible throughout, extensive divergence and local adaptations would be swamped by mating and migration of alleles between local groups. Even if the population were broken up into a number of local sub-populations, frog migration would prevent complete adaptation to local conditions and would act as a unifying force on the total frog gene pool from north to south.

Now, we suggest, a mountain range erupts from the east coast back up the Potomac through Washington D.C. to the Mississippi completely separating the population into two. We now have two populations (A to the north, B to the south) with no migration, mating or gene flow between them. Would local adaptation occur under these circumstances? With the barrier in place, considerable genetic divergence between populations, as they adapt to local conditions, is possible. A review of mutation, variation, reproduction, genetic recombination and natural selection illustrates how this divergence may occur.

Now, what would we expect to happen if the mountain erodes? Gradually the northern population would move south and equally gradually the southern population would move north. Eventually there would be a zone of overlap where individuals from A and B coexist. In this region of overlap, what do we expect to happen; would we see one species, two species or three species? Students commonly offer the last choice.

We need to consider some assumptions. Matings between  $A \times A$  individuals are 100 percent successful, as are matings between  $B \times B$  individuals. Predictions concerning the outcome depend on the success of  $A \times B$  encounters. Let us consider four possibilities and explore each.

1. A and B individuals might have diverged so much (requires a long period of separation) that they fail even to recognize one another as potential mates. The  $A \times B$  mating, therefore, never occurs and we already have two perfect biological species. This is probably the least frequent means of geographic speciation, but it is the trivial condition that many texts seem to leave students understanding.
2. A and B individuals cannot discriminate, they mate and the outcome is as successful as within population matings ( $A \times B = 100\%$ ). This, it seems obvious to me, will lead to the reunifi-

cation of one good species from the two populations. Many students, however, predict that this condition will lead to three species, which leads to some discussion about student misunderstandings.

3. A and B individuals cannot discriminate and, consequently, mate. But the outcome is completely unsuccessful; mating success  $A \times B = 0\%$ . Now, the problem is that frogs cannot discriminate, but each time they mate between rather than within populations they are completely unsuccessful. To be anthropomorphic, they have wasted their time. It is not a reproductively successful behavior. But, there is no way for the frogs to avoid making the error, so they continue to mate with members of the other population. Since we have discussed evolution as a change in allele frequency that occurs, through natural selection, as a consequence of the reproductive superiority of individuals bearing certain alleles as opposed to others, we must identify an allele that would be reproductively superior in this system. Clearly, we have an environment in which there is an incredibly strong selection pressure favoring any characteristic that would cause frogs to avoid making the error. Selection, therefore, will favor any allele (or series of alleles) which:
  - a. makes frogs in population A and B different;
  - b. allows frogs to discriminate between members of the two populations; and
  - c. leads them to mate preferentially with members of their own population.We can see that there is a series of steps, not necessarily one allele, simultaneously causing the total change in behavior. Since frogs that avoid the error would be 100 percent successful, while those making the error would be 0 percent successful, such a set of alleles would be tremendously adaptive. Once the set of alleles had become firmly entrenched in the two populations such that no mistaken matings between populations occurred, we would have two good species. The reproductive isolating mechanisms evolve in a situation where interpopulation mating occurs but is disadvantageous. Reproductive isolating mechanisms do not develop during periods of separation when there is no contact between populations since such mechanisms would have no selective advantage.
4. Again, here, we have the two populations unable to discriminate. As a result, mating between them occurs. Mating within populations is still 100 percent, but between populations is it  $100\% > ? > 0\%$ . What happens now? Clearly there is gene flow between populations, and mating continues. But those individuals which

mate with the other population do not contribute as extensively to the next generation as those who mate with members of their own population. Again, there is selection pressure favoring differences, discrimination and preferential mating. Since  $A \times B = >0\%$  the pressure is weaker than in case 3 above. In fact, the pressure favoring discrimination is inversely proportional to the probability of reproductive success in cross-population mating. Again, then reproductive isolating mechanisms have adaptive value in reducing error.

Condition 4 is, probably, by far the most common condition. It is this situation that will favor alleles conferring upon their bearers the ability to discriminate and exhibit nonrandom mating since such matings will have a higher probability of reproductive success. We may envisage, in our frog population, changes in color pattern, mating calls, location of mating, timing of mating etc.

This example of speciation, developed in relation to a geographic barrier, leads to a generalization: speciation will be likely whenever one population of organisms is divided into two sub-units (demes) such that reproductive success is lower in matings between than in matings within units. Thus, speciation through polyploidy (common in plants) or through ecological separation can be seen as further examples of this general principle.

This discussion leads to the realization that the biological species concept is flawed in that we will expect to find, at any time, populations of organisms various stages of speciation, from interbreeding populations to complete separation.

The emphasis in this discussion is on the process of speciation and the principles of selection that drive it. The emphasis is not on a list of terms and definitions of various reproductive isolation mechanisms and various barriers. While such are useful as examples, they are not the end in themselves. Reference, throughout the discussion, to the frog example has proven a useful way of illustrating the process through a concrete model that the students can readily understand. Nonetheless, the entire process of speciation cannot be dealt with rapidly without leaving many students confused.

### Some Examples

The existence of variation among populations of individuals of the same species has been documented for several decades at least. The presence of clearly identified geographic races or sub-species has been described in rat snake color patterns (Conant 1958), the shape of the crests of drongos (Mayr and Vaurie 1948) and the coloration of grackles (Yang and Selander 1968). Relatively continuous variation, as in a

cline, is present in the cyanide concentration of clover, *Trifolium* (Jones 1973) from north to south in North America. Ecotypes, the existence of certain genotypes associated with particular environmental conditions, has been reported for *Potentilla* in the Sierras (Clausen *et al.* 1940) and *Agrostis* in relation to mine tailings (Antonovics, Bradshaw & Turner 1971).

Mayr (1963) has discussed the role of geographic isolation in speciation, with consideration to the role of peripheral isolated populations in the process. The multiple invasions of islands, such as Darwin's Finches in the Galapagos, and the Australian bird *Acanthiza pusilla* (Mayr 1942) are examples of this phenomenon.

The specific nature of isolating mechanisms is discussed in Mayr (1963), where pre-mating and post-mating mechanisms are identified. Futuyma (1979) points out that the collective term *isolating mechanism* should be clearly separated into pre- and post-mating mechanisms. Post-mating barriers generally (except in maternal care) are not increased in consequence of natural selection since genes (alleles) conferring sterility cannot increase; rather, those conferring fertility would increase. Post-mating barriers, thus, are those which have evolved during a period of genetic separation. Effective post-mating barriers will induce, through selection, effective pre-mating barriers since such will prevent ineffective use of resources on low probability or low fertility reproductive activities.

Wilson (1965), also discussed in Futuyma (1979), illustrates the likelihood of speciation versus fusion in the event of the overlap of two previously isolated populations. If the frequency of mating between populations is relatively low, and the fitness of the product of such a mating is low, this serves as selection pressure favoring any gene that allows and encourages discrimination such that there will ultimately be a cessation of interbreeding. If the fitness of the hybrid is low (effective post-mating barrier), speciation can occur with a relatively high degree of interbreeding (ineffective pre-mating barrier). The existence of high fertility among naturally separated species (genetically) illustrates effective pre-mating isolation with in-effective post-mating isolation. This situation is found in orchids (Adams and Anderson 1958) and cichlids (Fryer and Iles 1972).

Examples of pre-mating mechanisms that have evolved include the firefly flash patterns (Lloyd 1966) and color patterns allowing species discrimination. Secondary sexual characteristics of birds, such as hummingbirds (Skutch 1973), allow the selection of appropriate mates. In ducks, Pough (1951) noted that the males were not conspicuously different from females or, indeed, one another, in areas of nonoverlap. This is an example of character displacement in sexual patterns.

An excellent discussion of color variation in local populations and the results of hybridization experiments in admiral butterflies can be found in Platt (1983). Further examples of geographic variation, speciation and the consequences of hybridization can be found in Endler (1977).

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