

## ON THE MULTIPLICATION OF SPECIES

J. T. Leverich, Cambridge

Evolution is a complex and extremely time-consuming process, which even today continues to affect all existing bird species. Most examples of evolutionary change involve the species as a whole, gradually transforming its entire population in an essentially uniform fashion. This second article in my series is devoted to that minority of evolutionary events that have resulted in speciation, the splitting of one internally cohesive ancestral species into two or more reproductively isolated daughter species.

Although each particular instance of speciation is actually a highly individualized phenomenon, general patterns may be discerned. One classical pattern, which has occurred many times in nature, is this:

### Stage 0: Initial conditions

At the beginning one finds a single species, composed of a fairly homogeneous population of birds breeding in a geographically continuous range. Individual variation within the species is maintained through the normal (Mendelian) processes of particulate inheritance. Indeed, there is a tendency toward increased variability, resulting from the regular occurrence of random mutations, which create new genes. The homogeneity of the species results principally from a free internal gene exchange, that is, from random mating within the population. Concurrently, there is also a tendency toward reduced variability, produced by the pressures of natural selection, eliminating those aberrant individuals (for example, albinistic birds) that deviate too drastically from the general population norms. Yet, all population tendencies stand more or less in balance with one another. The ornithologist says that such a group of birds comprises a single monotypic species.

### Stage 1: Geographic Isolation

The glaciations of the Pleistocene Era were accompanied by severe and prolonged weather changes. Any such traumatic change in external conditions should cause a contraction of the species range. And as a consequence, the species typically separates into two (or more) populations that are geographically isolated from each other. The ornithologist speaks now of allopatric populations, that is, breeding communities occupying non-overlapping ranges.

### Stage 2: Genotypic divergence

Physical isolation interrupts free gene exchange, inhibiting the tendency toward intergroup homogeneity. New genes in either population necessarily remain segregated there. Moreover, natural selection will now favor those genes (new or old) that best adapt each subgroup separately to the peculiar conditions of its own range. The natural and expected result is genotypic divergence: the gene pools of the two populations grow increasingly dissimilar.

Ordinarily, this process is detectable using morphological criteria alone, the two populations come to look different. When this happens, the ornithologist says that there are now two (or more) geographic subspecies. The species as a whole is said to be polytypic.

### Stage 3: Reproductive isolation

As generic divergence continues, certain more severe population differences arise which may serve as mechanisms for maintaining permanently the present (accidental) reproductive isolation of the subspecies. As soon as these isolating mechanisms have evolved, the various populations are technically separate species.

In practice, the ornithologist may find it difficult to decide whether a given pair of populations has reached species rank. Of course, if the populations have re-established contact, then the birds themselves will furnish the necessary evidence (the total absence or limited occurrence of hybridization). However, even when the two populations remain totally isolated, the ornithologist may decide that the two groups have diverged too far morphologically to be classed as a single species. In either case, he says that there are now two species comprising a single superspecies.

Member species of a single superspecies complex usually occupy the same ecological niche;

they depend upon exactly the same environmental resources, and they search for these necessities of life in the same or similar habitats. Thus, they are in competition with each other. Each species will automatically be better adapted to exploit this mutually shared niche within the area in which it evolved. Hence, should the two species come into contact at this point, each would serve as a natural "barrier" to the extension of the range of the other.

Because of this barrier effect, member species of the same superspecies are always allopatric.<sup>3</sup> (If the ranges share a common border, with perhaps a narrow overlap zone, the more precise term is parapatric.) Familiar examples of species pairs at this stage of evolution are the following:

- 1) Rose-breasted Grosbeak (Pheucticus ludovicianus) and Black-headed Grosbeak (P. melanocephalus).
- 2) Indigo Bunting (Passerina cyanea) and Lazuli Bunting (P. amoena).
- 3) Common Redpoll (Acanthis flammea) and Hoary Redpoll (A. hornemanni).

#### Stage 4: Sympatry

As genotypic divergence continues, the various component species of the superspecies frequently come to occupy distinct ecological niches. The barrier effect is eradicated concomitantly. Each species is then free to extend its breeding area into the range previously occupied exclusively by the other.

Ecologically compatible species with broadly overlapping ranges are said to be sympatric. A complex of closely related sympatric species is said to be a species group.

A well-known species group in North America is that composed of the four brown-backed thrushes from the genus Catharus: 1, Gray-cheeked Thrush (C. minimus); 2, Swainson's Thrush (C. ustulatus); 3, Hermit Thrush (C. guttatus); and 4, Veery (C. fuscescens). Their breeding ranges overlap in pairs -- 1 with 2, 2 with 3, and 3 with 4. Only quite locally do three of this species group breed in the same area.

Let us examine the first pair more carefully. The Gray-cheeked Thrush evolved in the Arctic Zone and inhabits primarily stunted northern fir and spruce forests. As a result, it has become specialized for ground-feeding. Swainson's Thrush evolved in the Boreal Zone, where it inhabits mixed or pure tall coniferous forests. Since it is now an arboreal feeder, it is no longer in competition with the Gray-cheeked Thrush, and the ranges of these two species can and do overlap broadly.

There is, by the way, an obvious moral here. During the May migration, the Massachusetts birder who wishes to find a Swainson's Thrush should watch the trees, at or above eye-level. Gray-cheeked Thrushes will most frequently be seen on or near the ground.

#### Variations in the Evolutionary Pattern

1. Many of our North American subspecies arose during the Pleistocene glaciations, when breeding ranges contracted into isolated glacial refuges. In Australia, a similar contraction accompanied a period of prolonged drought.

Such severe climatic conditions are, however, by no means necessary for new species to evolve. Birds regularly colonize isolated areas on the outer edges of their normal ranges. Any such peripheral isolate bears the potential for becoming a separate species, provided that immigration from the center of the range completely ceases after the initial colonization. Enterprising birds which manage to reach distant islands are even more successful at speciation. If the island should happen to be one of an isolated group, the stage is set for one of nature's finest evolutionary dramas -- spectacular archipelago speciation.

All 14 species of Darwin's finches (genera Geospiza, Camarhynchus, Certhidea) on the Galapagos Islands are presumed to have evolved from a single ancestral species, which invaded this island group from the mainland of South America. The 14 living and 8 extinct species of Hawaiian honeycreepers (Family Drepanididae) are likewise thought to be descended from one (or at most, two) immigrant species.

Biologists are not especially interested in how geographical isolation comes about, but they do insist that this condition is absolutely essential if the speciation process is

to go forward. A single monotypic species may by ordinary evolutionary processes increase its geographic variability, with birds in the south, say, becoming darker and those in the north becoming lighter. It cannot produce two distinct subspecies without spatial isolation of one or more subsidiary populations. Again, if two already differentiated subspecies should re-establish contact before isolating mechanisms are acquired, evolutionary divergence will be arrested at that point. Stage 1 must come first.

2. Biologists agree that Stage 2 must always precede Stage 3. This may seem obvious, since these stages differ mainly as to degree of divergence. Yet, there is a profound truth hidden here.

Until 1940 or so, most evolutionary geneticists believed that a new species came into being by a single drastic mutation (a saltation), which befell a particular individual, who then became the progenitor of the new species. They assumed that isolating mechanisms came first, with the other species differences evolving gradually later. (Saltationists were naturally at some pains to explain where that first individual's mate came from!)

Today's evolutionist regards speciation as a population phenomenon. To him, reproductive isolation (Stage 3) results very gradually and naturally from an accumulation of minor population differences.

3. Stage 4 (ecological compatibility) may occur at any time during the speciation process, or, as we have it, after speciation has been completed. Some pairs of subspecies are already apparently compatible. Should they at some future time acquire isolating mechanisms, these pairs would pass directly from the category of polytypic species to that of species group.

It is not just evolutionary biologists who must make the distinctions discussed above. Each specialist tends to prefer a particular one of these concepts. For most ornithologists (and many bird-watchers), the species is the "biological unit of classification" par excellence. Systematic biologists, however, normally focus on the subspecies; and zoogeographical ornithologists, who specialize in ecological problems, naturally think in terms of superspecies and species groups.

#### Footnotes

1. Mendel's theory of particulate inheritance will probably be familiar to many readers. Two of its principles, which are relevant here, are:
  - a. Offspring inherit each characteristic either from the father or from the mother; the children thus express a composite mixture of parental qualities, not a blend of them. (A "blending" form of inheritance would necessarily do away with half of the population variability in each generation.)
  - b. Offspring carry genes, however, from both parents, and those (recessive) genes which do not express themselves in the first generation may nonetheless "reappear" in subsequent generations.
2. In the first article of this series, What is a Bird Species? (BIRD OBSERVER, Vol. 1, No. 5), it was pointed out that the concept of a species is a "biological" concept, which may be objectively applied to real-life situations. The all-important evidence concerns the actual or potential breeding behavior of the birds themselves.

By contrast, the concept of a subspecies is more old-fashioned, a "morphological" concept, which is more subjective in its application. To justify the naming of a population as a new subspecies, one does not prove that it is distinctive or acts different; one must prove that it "looks different" when examined in the museum tray.

3. This is actually a matter of definition. See Comment 3 of the following section.
4. The words "allopatric" and "sympatric" are widely used in ornithological literature. "Parapatric" is apparently a newer coinage, which has yet to achieve widespread currency. In its place, many authors use various circumlocutions such as "essentially allopatric with a narrow zone of overlap."
5. Lack, D., Darwin's finches, Cambridge University Press, Cambridge, England, 1947.
6. Amadon, D., The Hawaiian honeycreepers (Aves, Drepaniidae [sic]), Bull. Amer. Mus. Nat. History 95: 151-262, 1950.