

## OVERVIEW

# CIRCULAR OVERLAPS: RARE DEMONSTRATIONS OF SPECIATION

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The perfect demonstration of speciation is presented by the situation in which a chain of intergrading subspecies forms a loop or an overlapping circle, of which the terminal forms no longer interbreed, even though they coexist in the same localities. (Mayr 1942:180)

THE SPLITTING OF a single species into two or more is a difficult process to observe, because it can take a great deal of time. Evolutionary biologists have recognized that a solution to this problem is to use geographical variation to infer how change in time might occur. Especially interesting in that regard is the phenomenon of “circular overlaps” (Mayr 1942), or “ring species” (Cain 1954), in which two sympatric and clearly distinct forms are connected by a chain of populations through which the characteristics of one form gradually change into those of the other. The possibility that ring species might exist was first suggested about a century ago by Stejneger (as quoted by Jordan 1905), and since then a number of possible examples have generated intense interest among evolutionary biologists.

One of the most widely known of the proposed examples of ring species is the series of taxa in the Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*L. fuscus*) group (Crochet et al. 2002). Ever since Mayr (1940, 1942) described these gulls as a prime example of circular overlap and geographic speciation, they have figured prominently in university course lectures, textbooks (e.g. Ridley 1993), and popular books on evolution (e.g. Schilthuisen 2001). The usual description follows from Mayr’s writings:

The races of this species are arranged in a circumpolar ring, but *Larus argentatus*, coming from America, invaded western Europe and lives now side by side with *Larus fuscus*, like a good species, although the two “species” are connected by a chain of inter-

mediate forms in Siberia and North America. (Mayr 1940:272)

Those conclusions were based primarily on morphological variation. The two supposedly terminal forms, which overlap in distribution in Europe, differ in size, shape, and plumage color, but those traits gradually change through the chain of forms encircling the Arctic Ocean. In the 60 years since Mayr first popularized that apparent example of ring speciation, evidence has accumulated that the relationships and history of the many taxa within the group are far more complicated than originally believed (reviewed by Mayr 1963, 1970; Grant 1982; Harrison 1985; Burger and Gochfeld 1996). There are many taxa in the group that are outside of the main ring, and there are complex patterns of reproductive isolation and hybridization. According to Burger and Gochfeld (1996:609), “systematics of [*L. argentatus*] and its close relatives represent one of the most complex challenges in ornithology, and typify the discord between evolution, biogeography, reproductive isolation, and taxonomy.”

A number of researchers have examined molecular variation from parts of the *Larus* species complex in the hope of clarifying historical relationships between taxa and current patterns of gene flow (Ryttman et al. 1980, Johnson 1985, Snell 1991, de Knijff et al. 2001, Liebers et al. 2001, Crochet et al. 2002). The study by Crochet et al. (2002) is notable because it is the first molecular study to include samples from all of the taxa that had been considered part of the circumpolar ring species. The mitochondrial DNA variation revealed by Crochet et al. (2002) will be of prime relevance to studies of gull taxonomy, historical biogeography, and speciation. Perhaps most importantly, their results call into question an important element of the standard ring species description of the complex, that the European forms of Herring Gull (including the two taxa *L. argentatus argenteus* in northwestern Europe and *L. argentatus argen-*

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*tatus* in Scandinavia; for taxonomic names we follow Burger and Gochfeld [1996]) are closely related to and derived from the North American form of Herring Gull (*L. argentatus smithsonianus*). Instead, their results suggest that North American *smithsonianus* is more distantly related to the European forms Herring Gull (*L. argentatus argenteus* and *L. argentatus argentatus*) than is the European Lesser Black-backed Gull (*L. fuscus*). It appears that *smithsonianus* is highly related to a group of several other morphologically divergent species, such as Thayer's Gull (*L. thayeri*), Glaucous Gull (*L. hyperboreus*), Iceland Gull (*L. glaucoides*), Slaty-backed Gull (*L. schistisagus*), and California Gull (*L. californicus*), most of which are also found primarily in North America. These results lead Crochet et al. (2002) to suggest that *smithsonianus*, which is usually treated as a subspecies of *L. argentatus* (e.g. Harrison 1985, Burger and Gochfeld 1996), should be treated as its own species, *Larus smithsonianus*. Crochet et al. (2002) caution that this conclusion should be confirmed with higher sample sizes (they included nine *smithsonianus* samples from two sites), but for the time being their results call into question the theory that European *L. argentatus* resulted from a circumpolar expansion and gradual divergence of *L. fuscus*.

The apparent downfall of one of the best known cases of a ring species is an appropriate occasion to ask just what a ring species is and how many examples are known. In this overview, we provide a brief history of the ring species concept, summarize the proposed cases, and conclude with some comments regarding the *Larus* complex.

#### THE RING SPECIES CONCEPT

When different biologists use the term "ring species," they may actually have different ideas in mind (Irwin et al. 2001a). The term can actually refer to a series of three related but distinct concepts. First, the presence of a series of intermediate forms between two species shows that variation between species is qualitatively similar, though different in degree, as variation within a species (Ridley 1993). Ring species can thus provide important evidence for evolution, demonstrating that small changes can eventually accumulate into the differences between distinct species. It is primarily this basic aspect

of ring species that has made them such important systems in the teaching of evolutionary principles.

Second, ring species may be used to reconstruct the history and causes of divergence during speciation (Wake 2001). If an ancestral species expands around both sides of an ecological barrier, the expanding fronts might diverge to the level of species by the time they meet on the other side of the barrier. If a ring species arose in that way, variation around the ring might represent variation in time, allowing the observation of the traits of two species as well as their common ancestor.

Third, ring species potentially show that speciation between the terminal forms can occur despite substantial gene flow around the ring. Such a demonstration would show that speciation does not require geographic isolation, something that has often been considered an essential condition for speciation (Mayr 1970). Genetic exchange between populations generally inhibits divergence, but recent theoretical and empirical studies have shown that substantial divergence can occur even with gene flow, especially when there is natural selection for local adaptation (e.g. Kondrashov et al. 1998, Dieckmann and Doebeli 1999, Danley et al. 2000, Gavrillets 2000, Smith et al. 2001). These studies suggest that there is no theoretical reason why ring species with extensive gene flow through the ring cannot exist.

Different researchers have placed differing emphasis on these potential characteristics of ring species. For example, Mayr (1942) emphasized the historical aspect of circular overlaps. Many of the examples of circular overlaps that he cited had clear breaks in gene flow at several places around the ring (Mayr 1970), but they nonetheless showed a clear gradient in forms between the two terminal forms. Mayr (1970) wrote that in circular overlaps "the process of geographic speciation can be followed step by step. A more dramatic demonstration of geographic speciation... cannot be imagined." On the other hand, Dobzhansky and his collaborators emphasized the role of gene flow through the transitional forms in limiting divergence of the terminal forms (Dobzhansky 1958, Dobzhansky and Spassky 1959, Dobzhansky and Pavlovsky 1967). They argued that the chain of populations was a "genetic bridge" that enabled genes to be exchanged be-

TABLE 1. A summary of avian groups that have been described as “circular overlaps” or “ring species”. For more information on specific cases, and for nonavian examples, see Irwin et al. (2001a) and references therein. Few if any cases have all the characteristics of ideal ring species, and more research is needed to evaluate many of them.

Proposed cases of avian ring species	Comments
Crested Honey-buzzard ( <i>Pernis ptilorhynchus</i> ) and Barred Honey-buzzard ( <i>P. celebensis</i> )	Two forms coexist in the Philippines, whereas islands to the southwest have intermediate forms.
Herring Gull ( <i>Larus argentatus</i> ) and Lesser Black-backed Gull ( <i>L. fuscus</i> )	See text.
Common Ringed Plover ( <i>Charadrius hiaticula</i> ) and Semipalmated Plover ( <i>C. semipalmatus</i> )	It was thought that two species coexisted on Baffin Island and were connected by continuous circumpolar variation. It is now thought that forms on either side of the Bering Strait are distinct species.
Crimson Rosella ( <i>Platycercus elegans</i> ), Adelaide Rosella ( <i>P. adelaidae</i> ), and Yellow Rosella ( <i>P. flaveolus</i> )	In southeast Australia, <i>elegans</i> and <i>flaveolus</i> were once thought to coexist without hybridization and <i>adelaidae</i> appeared intermediate. It now appears that all three forms hybridize where they meet.
Mangrove Kingfisher ( <i>Halcyon chloris</i> ) and Micronesian Kingfisher ( <i>H. cinnamomina</i> )	Two species coexist on the island of Palau, but on other islands only one form occurs. If not for their coexistence, the two forms might be considered a single species.
Sky Lark ( <i>Alauda arvensis</i> ), Japanese Sky Lark ( <i>A. japonica</i> ), and Oriental Sky Lark ( <i>A. gulgula</i> )	Both <i>arvensis</i> and <i>gulgula</i> occur in central Asia without interbreeding. They are separated by a gap in distribution in northern China. An intermediate form, <i>japonica</i> , occurs in Japan.
Greenish Warbler ( <i>Phylloscopus trochiloides</i> )	See text.
Chiffchaff ( <i>Phylloscopus collybita</i> ) and Mountain Chiffchaff ( <i>P. sindianus</i> )	Two forms coexist in the Caucasus mountains, but the chain connecting them through possibly intermediate forms in central Asia and western Russia has a major gap and possibly one or two species boundaries.
Sulawesi Triller ( <i>Lalage leucopygialis</i> ), Pied Triller ( <i>Lalage nigra</i> ), and White-shouldered Triller ( <i>L. sueurii</i> )	On Sulawesi Island, <i>leucopygialis</i> and <i>sueurii</i> coexist, while an intermediate form, <i>nigra</i> , occurs on other islands.
Brown Thornbill ( <i>Acanthiza pusilla</i> ) and Tasmanian Thornbill ( <i>A. ewingii</i> )	Two forms coexist in Tasmania, but each resembles <i>A. pusilla</i> , on Australian mainland.
Great Tit ( <i>Parus major</i> )	A complex situation in which four groups of taxa form two continuous rings in Asia, with hybridization where different groups meet. Two distinctive forms occur in the Russian Far East, but it is now known that there is some hybridization between them.
Large Tree-finch ( <i>Camarhynchus psittacula</i> ) and Medium Tree-finch ( <i>C. pauper</i> )	Two forms occur on one Galápagos Island, with a series of intermediates occurring on other islands.

tween forms that are otherwise reproductively isolated.

#### PROPOSED CASES OF RING SPECIES

Given those different ideas of the important aspects of ring species, proposed cases come in wide variety. At least 23 taxa (reviewed by Irwin et al. 2001a) have been proposed as ring species (18 of those were listed by Mayr 1963), although additional examination have called many of them into question. Birds have figured

prominently as examples, with 12 proposed cases (Table 1). There are also proposed circular overlaps of amphibians (2), rodents (3), arthropods (5), and plants (1).

The most ideal example of a ring species would have three characteristics. First, two distinctive forms would coexist while being reproductively isolated in the same area. Second, there would be a chain of intermediate forms connecting them through a continuous geographic ring. Third, there would be no breaks in gene flow except between the terminal

forms. But as our discussion of the ring species concept above shows, biologists might consider a system to be a ring species even if it did not have all of those characteristics.

In fact, few if any of the proposed examples have all the characteristics of ideal ring species (Wake and Schneider 1998, Irwin et al. 2001a). For example, most of the proposed cases have major gaps in distribution, making significant gene flow throughout the chain of populations unlikely. In fact, seven of the cases that Mayr (1963) mentioned were cases in which an island was colonized twice by a single species and the two colonizing groups diverged into sympatrically coexisting forms. In those cases, gene flow through the ancestral forms is unlikely to play an important role. There are many additional examples of double invasions that Mayr did not list (Coyne and Price 2000). Also, in many proposed ring species there is either hybridization between the supposed terminal forms of the ring or locations around the ring where there is sudden change between forms that are reproductively isolated to some degree.

Given these complications, why did Mayr call those cases "the perfect demonstration of speciation"? Mayr (1963) felt that all of the cases he cited had one characteristic in common: two distinct forms coexisted, but forms elsewhere had intermediate characteristics. For example, in the Galápagos Islands, the Medium Tree-finch (*Camarhynchus pauper*) and the Large Tree-finch (*C. psittacula psittacula*) coexist on Floreana, but a series of intermediate forms occur on nearby islands (*C. psittacula affinis* on Isabela, *affinis/psittacula* intergrades on Duncan, *C. psittacula psittacula* on Santa Cruz; Lack 1947, Grant 1986). The progressive morphological differences in those finches through the chain of islands, with the most divergent forms coexisting as separate species on the same island, illustrates how small changes can accumulate into differences between species. This link between microevolution and speciation (Irwin et al. 2001a) is particularly clear when the history of range expansion can be reconstructed, in which case we can use variation in space to infer variation in time.

Such a historical approach has been used to study speciation in two ring species, the *Ensatina* salamanders and the Greenish Warblers (*Phylloscopus trochiloides*). Based on studies of geographic variation in morphological charac-

ters, Stebbins (1949) concluded that *Ensatina* expanded southward from northern California along two mountain ranges that are separated by the Central Valley of California, and molecular analysis have generally supported that view (Wake and Yanev 1986, Moritz et al. 1992, Jackman and Wake 1994, Wake and Schneider 1998). Now, two forms of *Ensatina* that differ dramatically in color patterns coexist in the mountains of southern California, where they hybridize only occasionally (Brown 1974). The patterns of variation in *Ensatina* beautifully illustrate the gradual divergence of two forms from their common ancestor. A complicating factor is that there appear to be several breaks in current gene flow around the ring, including a major gap in distribution in southern California (Wake and Yanev 1986, Highton 1998, Wake and Schneider 1998).

A group that perhaps comes closest to meeting all the requirements of an ideal ring species is the Greenish Warblers (Irwin et al. 2001b, Wake 2001, Wood 2001), which inhabit temperate forests of Asia and eastern Europe. Ticehurst (1938) observed that two forms coexisted in central Siberia, apparently without interbreeding, and that those two forms are connected by gradual variation through a chain of populations encircling the uninhabited Tibetan Plateau to the south. Ticehurst (1938) and Mayr (1942) proposed that this situation arose when an ancestral species in the Himalayas expanded northward along two pathways. Variation in mitochondrial DNA has confirmed the separate origins of the two Siberian forms and the reproductive isolation between them (Irwin et al. 2001b). Other traits, such as songs, song recognition, and plumage color, differ distinctly between the Siberian forms but change gradually around the ring. There is one major gap in distribution in northeastern China, but that may be the result of recent habitat destruction, and Greenish Warblers on either side of the gap are similar relative to the variation throughout the complex (Irwin 2000, Irwin et al. 2001b).

Knowledge of the history of the Greenish Warblers has allowed a reconstruction of the evolution of traits associated with reproductive isolation. During the northward expansions, ecological traits have evolved in parallel, and songs have become longer and more complex in both west and east Siberia. However, songs have also diverged in structure, resulting in a

lack of recognition where the reproductively isolated forms have come into contact in Siberia. It is likely that parallel shifts in ecological traits during the northward expansions have caused parallel changes in the form and intensity of sexual selection on songs. But because there are many ways that complex songs can evolve from simple ones, songs have diverged in structure (Irwin 2000, Irwin et al. 2001a, b). These insights regarding interactions between ecological changes, sexual selection, behavioral evolution, and speciation are only possible because of the ring of populations connecting the Siberian forms. If presented with only the two Siberian forms, we would have little understanding of how the differences between them had arisen.

Because we can learn so much from ring species, it is unfortunate that there are so few examples that come close to the ideal. They are rare for several reasons. Their formation requires unusual geographic circumstances (Wake 2001), when a species can expand around a geographic barrier through a continuous ring of suitable habitat. The size of the barrier must be large compared to the distances that individuals disperse, and the range expansion must occur at a rate that is slow enough for differentiation to occur before the two fronts meet on the other side of the barrier. Taxonomic rules of classification, which force biological variation into specific, hierarchical categories, create a bias against recognizing ring species (Irwin et al. 2001a, Wake 2001). Generally, a ring species must be classified either as a single species, a treatment that conceals the species-level divergence, or as two or more species, a treatment that conceals the presence of gradual variation between reproductively isolated forms. It is conceivable that many taxa that are already well sampled in museum collections are in fact ring species. Discoveries of more examples are most likely in groups that are relatively little studied and that have low dispersal distances.

Ring species, once they have formed, might be short-lived. Extinctions or habitat changes in a portion of the ring might reduce gene flow and increase local adaptation, possibly leading to the formation of multiple species boundaries around the ring. However, cases that are made up of a series of reproductively isolated forms may still provide examples of stepwise varia-

tion in traits, allowing for the reconstruction of divergence and the causes of speciation. We advocate that such cases, which are no longer ideal ring species, be considered “circular overlaps,” a term that is devoid of taxonomic implications but refers to the process of gradual expansion and stepwise divergence.

#### THE *LARUS* COMPLEX

Given the findings of Crochet et al. (2002), should we despair that the *Larus* group is not such a simple and clear case of ring speciation as had been thought? We think not. The *Larus* group remains a fascinating system for evolutionary biologists. Because of the group's contrasting patterns of morphological and molecular variation, complex patterns of reproductive isolation and hybridization, and large number of taxa spread over most of the world, many important insights regarding evolution are sure to emerge from further study of the gulls. In particular, we think that a full analysis of variation in the different types of molecular markers studied by different research groups (e.g. allozymes—Ryttman et al. 1980, Johnson 1985, Snell 1991; AFLP markers—de Knijff et al. 2001; and mitochondrial DNA—Liebers et al. 2001, Crochet et al. 2002) will be very informative. All of those markers show little differentiation throughout *Larus*, suggesting that the entire complex diversified recently. However, mitochondrial DNA, which is maternally inherited, differs much more between taxa than nuclear markers, which are biparentally inherited. That pattern might be explained by greater male-mediated gene flow, either because males disperse farther or because hybrid males have higher fitness than hybrid females (i.e. Haldane's [1922] rule). Another factor that might contribute to the greater differentiation in mitochondrial DNA is its lower effective population size compared to nuclear genes (Palumbi et al. 2001). As Crochet et al. (2002) point out, it appears that hybridization causes introgression of genes between the various *Larus* taxa. As research on another complex group of highly related taxa—Darwin's finches—has shown, introgressive hybridization can play an important role in evolution (Grant and Grant 2002). In light of the potential for hybridization to result in introgression of genet-

ic markers between taxa with different histories, we agree with Crochet et al. (2002) that some caution should be used in inferring historical relationships from a single inherited unit such as mitochondrial DNA. We also note that the mitochondrial DNA data seem consistent with a very rapid circumpolar expansion of the *fuscus-smithsonianus-argentatus* group (a "star-like" radiation) and subsequent mitochondrial divergence because of isolation by distance. If that occurred, the group might in fact be a ring species, although the mitochondrial DNA would not show it.

Those caveats aside, the mitochondrial patterns as presently understood do not support the hypothesis that the *fuscus-smithsonianus-argentatus* circumpolar ring arose by a simple history of gradual expansion and divergence. But exactly what did happen remains unclear. Morphologically, the gulls still show a remarkable pattern, with stepwise changes through the chain of forms and two clearly distinct forms living together in Europe. If the morphological similarity between European *argentatus* and North American *smithsonianus* did not arise as a result of recent shared ancestry, it must have arisen through convergence or from morphological stasis while other related groups speciated and diverged morphologically. The low amount of molecular variation and the lack of a strong link between molecular relationships and morphological patterns in the *Larus* group suggest that phenotypic evolution can occur quickly in these gulls. The relative importance of natural selection, sexual selection, and drift in driving those changes remains to be seen. Further study of the *Larus* gulls could reveal much about the interactions between natural selection, sexual selection, hybridization, and reproductive isolation in speciation.

#### ACKNOWLEDGMENTS

We thank T. Price for comments and discussion and the National Science Foundation for financial support.

#### LITERATURE CITED

- BROWN, C. W. 1974. Hybridization Among the Subspecies of the Plethodontid Salamander *Ensatina eschscholtzii*. University of California Press, Berkeley.
- BURGER, J., AND M. GOCHFELD. 1996. Family Laridae (Gulls). Pages 572–623 in Handbook of the Birds of the World. Vol. 3, Hoatzin to Auks (J. del Hoyo, A. Elliottand, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.
- CAIN, A. J. 1954. Animal Species and their Evolution. Hutchinson House, London.
- COYNE, J., AND T. PRICE. 2000. Little evidence for sympatric speciation in island birds. *Evolution* 54:2166–2171.
- CROCHET, P.-A., J.-D. LEBRETON, AND F. BONHOMME. 2002. Systematics of the large white-headed gulls: Patterns of mitochondrial DNA variation in western European taxa. *Auk* 119:603–620.
- DANLEY, P. D., J. A. MARKERT, M. E. ARNEGARD, AND T. D. KOCHER. 2000. Divergence with gene flow in the rock-dwelling cichlids of Lake Malawi. *Evolution* 54:1725–1737.
- DE KNIJFF, P., F. DENKERS, N. D. VAN SWELM, AND M. KUIPER. 2001. Genetic affinities within the Herring Gull *Larus argentatus* assemblage revealed by AFLP genotyping. *Journal of Molecular Evolution* 52:85–93.
- DIECKMANN, U., AND M. DOEBELI. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–357.
- DOBZHANSKY, T. 1958. Species after Darwin. Pages 19–55 in *A Century of Darwin* (S. A. Barnett, Ed.). Heinemann, London.
- DOBZHANSKY, T., AND O. PAVLOVSKY. 1967. Experiments on the incipient species of the *Drosophila paulistorum* complex. *Genetics* 55:141–156.
- DOBZHANSKY, T., AND B. SPASSKY. 1959. *Drosophila paulistorum*, a cluster of species *in statu nascendi*. *Proceedings of the National Academy of Sciences USA* 45:419–428.
- GAVRILETS, S. 2000. Waiting time to parapatric speciation. *Proceedings of the Royal Society of London, Series B* 267:2483–2492.
- GRANT, P. J. 1982. *Gulls: A Guide to Identification*. T. and A. D. Poyser, London.
- GRANT, P. R. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, New Jersey.
- GRANT, P. R., AND B. R. GRANT. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- HALDANE, J. B. S. 1922. Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics* 12: 101–109.
- HARRISON, P. 1985. *Seabirds: An Identification Guide*. Houghton Mifflin, Boston.
- HIGHTON, R. 1998. Is *Ensatina eschscholtzii* a ring-species? *Herpetologica* 54:254–278.
- IRWIN, D. E. 2000. Song variation in an avian ring species. *Evolution* 54:998–1010.
- IRWIN, D. E., J. H. IRWIN, AND T. D. PRICE. 2001a. Ring species as bridges between microevolution and speciation. *Genetica* 112–113:223–243.

- IRWIN, D. E., S. BENSCH, AND T. D. PRICE. 2001b. Speciation in a ring. *Nature* 409:333–337.
- JACKMAN, T. R., AND D. B. WAKE. 1994. Evolutionary and historical analysis of protein variation in the blotched forms of salamanders of the *Ensatina* complex (Amphibia: Plethodontidae). *Evolution* 48:876–897.
- JOHNSON, C. 1985. Biochemical genetic variation in populations of *Larus argentatus* and *Larus fuscus* in northwestern Europe. *Biological Journal of the Linnean Society* 24:349–363.
- JORDAN, D. S. 1905. The origin of species through isolation. *Science* 22:545–562.
- KONDRASHOV, A., L. YAMPOLSKY, AND S. SHABALINA. 1998. On the sympatric origin of species by means of natural selection. Pages 90–98 in *Endless Forms: Species and Speciation* (D. J. Howard and S. H. Berlocher, Eds.). Oxford University Press, Oxford.
- LACK, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge, United Kingdom.
- LIEBERS, D., A. J. HELBIG, AND P. DE KNIFF. 2001. Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadriiformes). *Molecular Ecology* 10:2447–2462.
- MAYR, E. 1940. Speciation phenomena in birds. *American Naturalist* 74:249–278.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.
- MAYR, E. 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- MAYR, E. 1970. *Populations, Species, and Evolution: An Abridgment of Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- MORITZ, C., C. J. SCHNEIDER, AND D. B. WAKE. 1992. Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Systematic Biology* 41:273–291.
- PALUMBI, S. R., F. CIPRIANO, AND M. P. HARE. 2001. Predicting nuclear gene coalescence from mitochondrial data: The three-times rule. *Evolution* 55:859–868.
- RIDLEY, M. 1993. *Evolution*. Blackwell Scientific Publications, Boston, Massachusetts.
- RYTTMAN, H., H. TEGELSTRÖM, AND H. JANSSON. 1980. Isozyme differences in three related *Larus* species (Aves). *Hereditas* 92:117–122.
- SCHILTHUIZEN, M. 2001. *Frogs, Flies, and Dandelions. Speciation—The Evolution of New Species*. Oxford University Press, Oxford.
- SMITH, T. B., C. J. SCHNEIDER, AND K. HOLDER. 2001. Refugial isolation versus ecological gradients. *Genetica* 112–113:383–398.
- SNELL, R. R. 1991. Interspecific allozyme differentiation among North Atlantic white-headed larid gulls. *Auk* 108:319–328.
- STEBBINS, R. C. 1949. *Speciation in salamanders of the plethodontid genus Ensatina*. University of California Publications in Zoology 48:377–526.
- TICEHURST, C. B. 1938. *A Systematic Review of the Genus Phylloscopus*. Trustees of the British Museum, London.
- WAKE, D. B. 2001. Speciation in the round. *Nature* 409:299–300.
- WAKE, D. B., AND C. J. SCHNEIDER. 1998. Taxonomy of the plethodontid salamander genus *Ensatina*. *Herpetologica* 54:279–298.
- WAKE, D. B., AND K. P. YANEV. 1986. Geographic variation in allozymes in a “ring species,” the plethodontid salamander *Ensatina eschscholtzii* of western North America. *Evolution* 40:702–715.
- WOOD, H. 2001. Ringing the changes. *Nature Reviews Neuroscience* 2:1.