CHAPTER 18

Speciation

In this chapter, we turn to the question of how species arise. If we considered species to be merely populations with distinguishing characteristics, the question of how they originate would be easily answered: natural selection or genetic drift can fix novel alleles or characteristics (see Chapters 10–13). But if the permanence of these distinctions depends on reproductive isolation, and if we consider reproductive isolation a defining feature of species, then the central question about speciation must be how genetically based barriers to gene exchange arise. Our description of the forms of reproductive isolation between species must now be complemented by understanding how they evolve.

Sexual selection: A major cause of speciation? Speciation has been most prolific in many groups of animals, such as birds of paradise, in which sexual selection appears to be intense. Here, a male Raggiana bird of paradise (*Paradisaea raggiana*) displays his bounteous plumes to a female. In many such species, only a few males mate with most of the females.

The difficulty this question poses is most readily seen if we consider the postzygotic reproductive barriers discussed in Chapter 17, such as hybrid inviability or sterility. If two populations are fixed for genotypes A_1A_1 and A_2A_2, but the heterozygote A_1A_2 has lower viability or fertility than either homozygous genotype, how could these populations have diverged? Whatever allele the ancestral population may have carried (say, A_1), the low fitness of A_1A_2 would have prevented the alternative allele (A_2) from increasing in frequency and thus forming a reproductively incompatible population.

Suppose, instead, that reproductive isolation between the populations is based on more than one locus. The problem then is that *recombination generates intermediates*. If several loci govern, for example, time of breeding, $A_1A_1B_1B_1C_1C_1$ and $A_2A_2B_2B_2C_2C_2$ might breed early and late in the season, respectively, and so be reproductively isolated. But if mutations A_2, B_2, and C_2 occur in an initially $A_1A_1B_1B_1C_1C_1$ population and increase in frequency, many genotypes with intermediate breeding seasons, such as $A_1A_2B_1B_1C_1C_2$, are formed by recombination, and these genotypes constitute a "bridge" for the flow of genes between the two extreme genotypes.

The problem of speciation, then, is how two different populations can be formed without intermediates. This problem holds, whatever the character that confers prezygotic or postzygotic isolation may be. The many conceivable solutions to this problem are referred to as MODES OF SPECIATION.

Modes of Speciation

The modes of speciation that have been hypothesized can be classified by several criteria (**Table 18.1**), including the geographic origin of barriers to gene exchange, the genetic bases of those barriers, and the causes of evolution of those barriers. These criteria are independent of one another; so, for example, two species may conceivably form by geographic separation (allopatry) of populations, in which reproductive isolation then evolves by either natural selection or genetic drift, which results in few or many genetic differences.

Speciation may occur in three kinds of geographic settings. **Allopatric speciation** is the evolution of reproductive barriers in populations that are prevented by a geographic barrier from exchanging genes at more than a negligible rate. A distinction is often made between allopatric speciation by **vicariance** (divergence of two large populations; **Figure 18.1A**) and **peripatric speciation** (divergence of a small population from a widely distributed ancestral form; **Figure 18.1B**). In **parapatric speciation**, adjacent, spatially distinct populations, between which there is some gene flow, diverge and become reproductively isolated (**Figure 18.1C**). **Sympatric speciation** is the evolution of reproductive barriers within a single, initially randomly mating (panmictic) population (**Figure 18.1D**).

Allopatric, parapatric, and sympatric speciation form a continuum, differing in the initial level of gene flow (m) between diverging populations. Strictly defined, $m = 0$ if speciation is allopatric, and it is maximal ($m = 0.5$) if speciation is sympatric; intermediate cases ($0 < m < 0.5$) represent parapatric speciation (Fitzpatrick et al. 2008). The initial reduction of gene exchange is accomplished by a physical barrier extrinsic to the organisms in allopatric speciation, but by evolutionary change in the biological characteristics of the organisms themselves in sympatric speciation. Allopatric or "nearly allopatric" (with low initial m) speciation is widely acknowledged to be a common mode of speciation; the incidence of sympatric or "nearly sympatric" (with high m) speciation is debated.

From a genetic point of view, the reproductive barriers that arise may be based on genetic divergence (allele differences at, usually, several or many loci), cytoplasmic incompatibility, or cytological divergence (polyploidy or structural rearrangement of chromosomes). We will devote most of this chapter to speciation by genetic divergence.

The causes of the evolution of reproductive barriers, as of any characters, are genetic drift and natural selection of genetic alterations that have arisen by mutation. Peripatric speciation, a hypothetical form of speciation that is also referred to as TRANSILIENCE or FOUNDER EFFECT SPECIATION, requires both genetic drift and natural selection. Both sexual selection and ecological causes of natural selection may result in speciation. In some cases, there may be *selection for reproductive isolation*—that is, to

TABLE 18.1 Modes of speciation

I. Classified by geographic origin of reproductive barriers
  A. Allopatric speciation
    1. Vicariance
    2. Peripatric speciation
  B. Parapatric speciation
  C. Sympatric speciation
II. Classified by genetic and causal bases[a]
  A. Genetic divergence (allele substitutions)
    1. Genetic drift
    2. Peak shift (genetic drift + natural selection)
    3. Natural selection
      a. Ecological selection
        i. Ecological trait causes reproductive isolation
        ii. Pleiotropic genes correlate ecological difference and reproductive isolation
      b. Sexual selection
  B. Cytoplasmic incompatibility
  C. Cytological divergence
    1. Polyploidy
    2. Chromosome rearrangement
  D. Recombinational speciation

[a] Most of the genetic and causal bases might act in an allopatric, parapatric, or sympatric geographic context, and some of the causal bases listed under "Genetic divergence" also apply to cytoplasmic incompatibility, cytological divergence, and recombinational speciation.

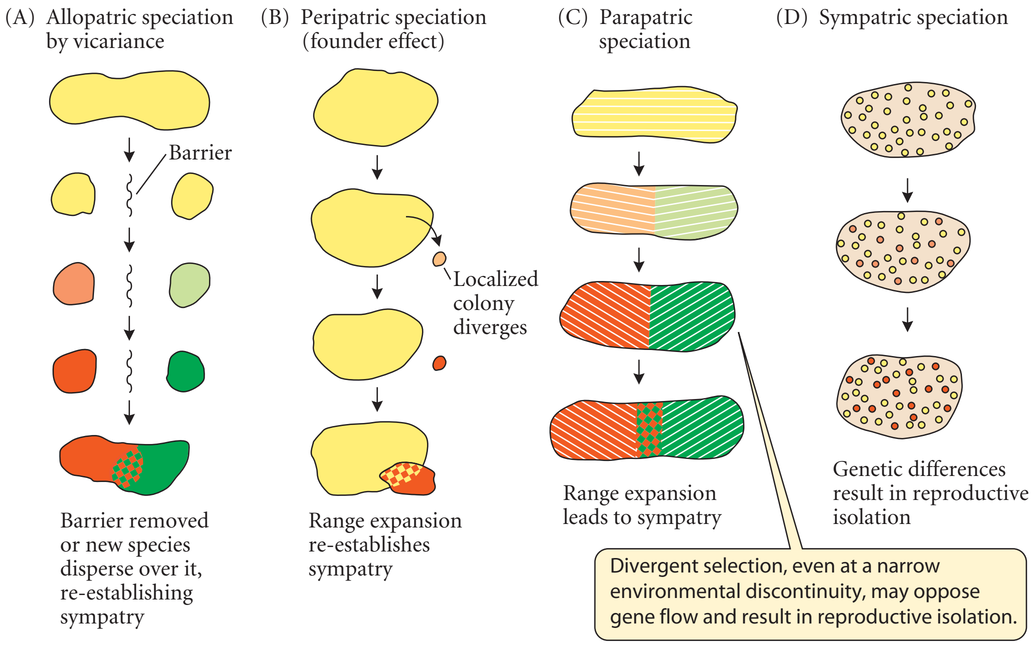


FIGURE 18.1 Schematic diagrams showing the successive stages in models of speciation that differ in their geographic setting. (A) The vicariance model of allopatric speciation. (B) The peripatric, or founder effect, model of allopatric speciation. (C) Parapatric speciation. (D) Sympatric speciation.

prevent hybridization. (Recall the distinction between *selection for* and *selection of* traits, discussed in Chapter 11.) Alternatively, reproductive isolation may arise as a *by-product of genetic changes* that occur for other reasons (Muller 1940; Mayr 1963). In this case, there may be ADAPTIVE DIVERGENCE of the isolating character itself (e.g., climate factors may favor breeding in two different seasons, with the effect that the populations do not interbreed), or the reproductive barrier may arise as a pleiotropic by-product of genes that are selected for their other functions.

Allopatric Speciation

Allopatric speciation is *the evolution of genetic reproductive barriers between populations that are geographically separated* by a physical barrier such as a topographic feature, water (or land), or unfavorable habitat. The physical barrier reduces gene flow enough for sufficient genetic differences to evolve to prevent gene exchange between the populations should they later come into contact (see Figure 18.1A). Although some authors' definitions of allopatric speciation require zero gene flow ($m = 0$) between the populations, in this discussion, we will assume only that m is so low that divergence by very weak selection or even genetic drift is possible. Allopatry is defined by a severe reduction of movement of individuals or their gametes, not by geographic distance. Thus in species that disperse little or are faithful to a particular habitat, populations may be "microgeographically" isolated (e.g., among patches of a favored habitat along a lakeshore). All evolutionary biologists agree that allopatric speciation occurs, and many hold that it is the prevalent mode of speciation, at least in animals (Mayr 1963; Coyne and Orr 2004).

From paleontological and genetic studies (see Chapters 5 and 6), we know that species' geographic ranges change over time, and that populations may become separated and later rejoined. (Consider, for example, the postglacial range expansions portrayed in Figure 6.16.) Thus allopatric populations may expand their range and come into contact. If sufficiently strong isolating barriers have evolved during the period of allopatry, the populations may become sympatric without exchanging genes. If incomplete reproductive isolation has evolved, they will form a hybrid zone (see Chapter 17, where we described the possible fates of hybrid zones). Sympatric sister species that we observe today may well have speciated allopatrically and then expanded their ranges; *current sympatry, in itself, is not evidence that speciation occurred sympatrically.*

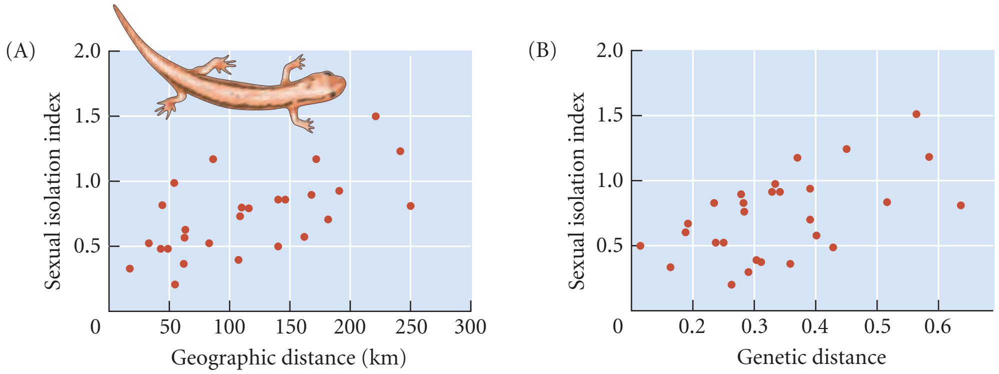


FIGURE 18.2 The strength of sexual isolation between populations of the salamander *Desmognathus ochrophaeus* is correlated with (A) the geographic distance between the populations as well as (B) their genetic distance (Nei's *D*, which measures the difference in allozyme frequencies at several loci). (After Tilley et al. 1990.)

Evidence for allopatric speciation

Because both natural selection and genetic drift cause populations to diverge in genetic composition, it is probably inevitable that if separated long enough, geographically separated populations will become different species. Many species show incipient prezygotic or postzygotic reproductive isolation among geographic populations. For example, Stephen Tilley and colleagues (1990) examined sexual isolation among dusky salamanders (*Desmognathus ochrophaeus*) from various localities in the southern Appalachian Mountains of the eastern United States. They brought males and females from different populations (heterotypic pairs) and from the same population (homotypic pairs) together and scored the proportion of the pairs that mated. Among the various pairs of populations, an index of the strength of sexual isolation varied continuously, from almost no isolation to almost complete failure to mate. The more geographically distant the populations, the more genetically different they were, and the less likely they were to mate (**Figure 18.2**).

Speciation can often be related to the geological history of barriers. For example, the emergence of the Isthmus of Panama in the Pliocene divided many marine organisms into Pacific and Caribbean populations, some of which have diverged into distinct species. Among seven such species pairs of snapping shrimp, only about 1 percent of interspecific matings in the laboratory produced viable offspring (Knowlton et al. 1993).

In some cases, CONTACT ZONES between differentiated forms mark the meeting of formerly allopatric populations. For example, Eldredge Bermingham and John Avise (1986; Avise 1994) analyzed the genealogy of mitochondrial DNA in samples of six fish species from rivers throughout the coastal plain of the southeastern United States. In all six species, DNA sequences form two distinct clades characterizing eastern and western populations, and the two clades make contact in the same region of western Florida (**Figure 18.3**). This pattern implies that gene flow between east and west was reduced at some

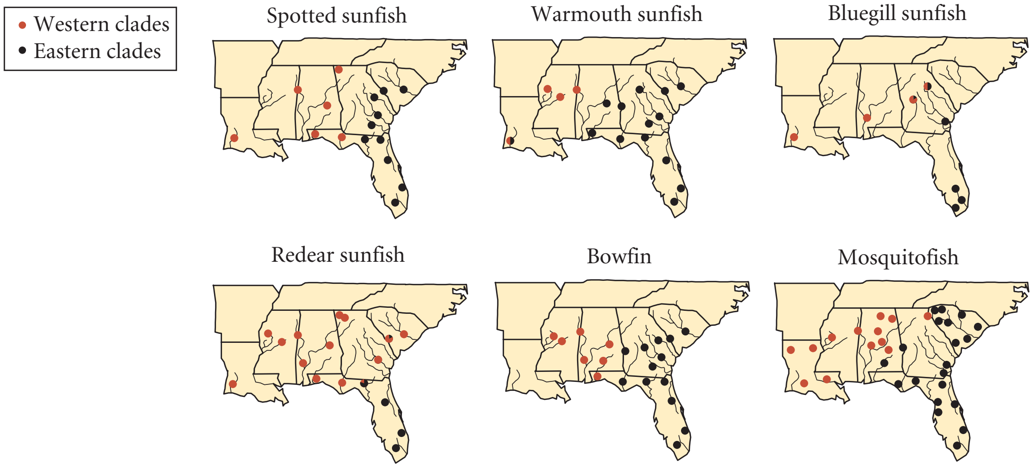
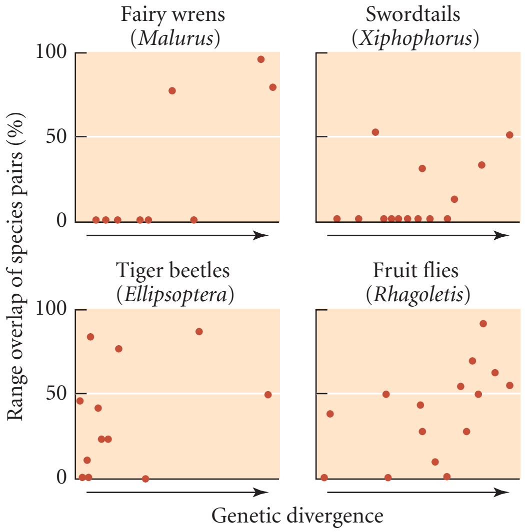


FIGURE 18.3 Evidence for allopatric genetic divergence followed by range expansion and secondary contact. In each of six freshwater fish species of the southeastern United States, mitochondrial DNA sequences fall into two clades, one with a western and one with an eastern distribution. Three families of fishes are represented here: Centrarchidae (sunfishes), Amiidae (bowfin), and Poeciliidae (mosquitofish). (After Avise 1994.)

FIGURE 18.4 The degree of overlap in the geographic ranges of pairs of closely related species, plotted against the genetic divergence between them, which is an index of time since speciation. Overlap increases with time in fairy wrens and swordtail fish, as expected if speciation was allopatric in these groups. There is no correlation between overlap and time since divergence in tiger beetles or *Rhagoletis* fruit flies, a pattern consistent with sympatric speciation. (After Barraclough and Vogler 2000.)

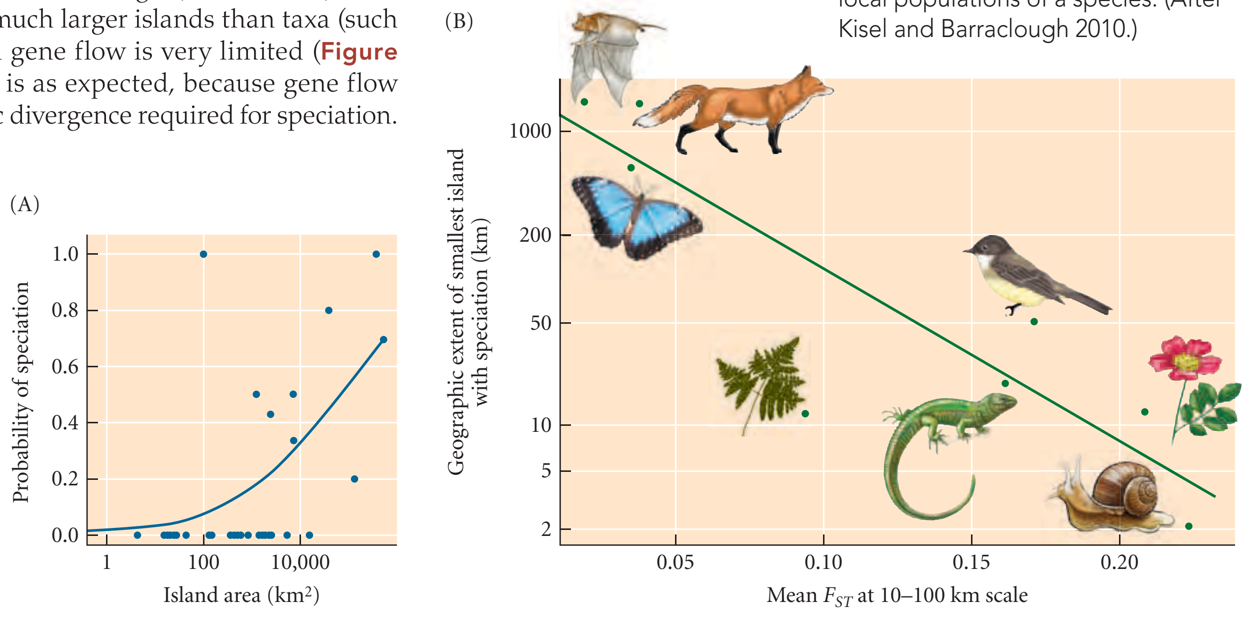


time in the past. The amount of sequence divergence between the two clades suggests that isolation occurred 3 to 4 Mya. At that time, sea level was much higher than it is at present, forming a barrier to dispersal by freshwater fishes.

Tim Barraclough and Alfried Vogler (2000) reasoned that over time, the amount of overlap between the geographic ranges of species that have formed by allopatric speciation can only increase from zero, whereas overlap between species that originated by sympatric speciation should stay the same or decrease. For several clades of closely related birds, insects, and fishes, they plotted degree of range overlap against degree of molecular difference between species, which they used as an index of time since gene exchange was curtailed. Several groups showed increasing overlap with time, as expected in the case of allopatric speciation, whereas two groups of insects displayed a pattern consistent with the possibility of sympatric speciation (**Figure 18.4**).

Species on islands have provided abundant evidence of allopatric speciation. Where two or more closely related species of birds occur together on an island, other islands or a continent can be identified as a source of invading species, and in all cases there is evidence that the ancestors of the several species invaded the island at separate times. For example, many of the islands in the Galápagos archipelago harbor two or more species of Darwin's finches, which evolved on different islands and later became sympatric. But Cocos Island, isolated far to the northeast of the Galápagos, has only one species of finch, which occupies several of the ecological niches that its relatives in the Galápagos Islands fill (Werner and Sherry 1987; see Figure 3.22). In contrast to archipelagoes, no pairs of sister species of birds occur together on any isolated island smaller than 10,000 square kilometers in area. This observation implies that speciation in birds does not occur on land masses that are too small to provide geographic isolation between populations (Coyne and Price 2000). A similar pattern is found in many other taxa (Kisel and Barraclough 2010). Moreover, taxa in which dispersal, and therefore gene flow, over long distances is high (such as bats) have speciated only on much larger islands than taxa (such as snails) in which gene flow is very limited (**Figure 18.5**). This pattern is as expected, because gene flow opposes the genetic divergence required for speciation.

FIGURE 18.5 Speciation is more likely on larger islands. (A) The proportion of lizard lineages that have undergone speciation within isolated oceanic islands is higher on larger islands. (B) For various taxa, the minimum island size allowing speciation is larger in taxa that have higher rates of gene flow (at left). Taxa with low rates of gene flow, such as snails, can speciate within much smaller islands. Gene flow is inversely related to the fixation index (F_{ST}), a measure of the variation in allele frequencies among local populations of a species. (After Kisel and Barraclough 2010.)



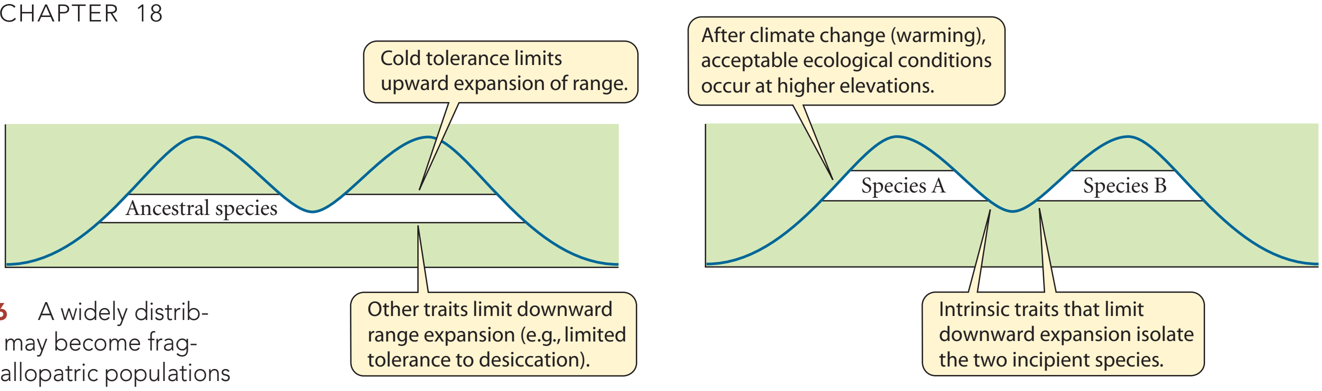


FIGURE 18.6 A widely distributed species may become fragmented into allopatric populations if the habitat on which it depends becomes fragmented by climate change. For example, a species adapted to cool conditions may shift its range to higher altitudes when the climate becomes warmer, and the populations, isolated on different mountains, may become different species. Phylogenetic niche conservatism can therefore contribute to speciation. (After Wiens 2004.)

The role of barriers such as the Isthmus of Panama in curtailing gene flow between populations is obvious, but what kinds of barriers could have produced the great numbers of species, in many taxa, that are found on continents? An important consideration is phylogenetic niche conservatism (see Chapter 6). Geographic distributions may be fragmented if populations maintain dependence on specific environmental conditions, such as climate regimes or habitats. For example, a species that is widely distributed at low elevations in a mountain range when the climate is cool may move upward and form separate populations on different mountains when the climate becomes warmer (**Figure 18.6**). Exactly this pattern has been found for allopatric sister species of salamanders, which are found in locations with similar climate conditions and are absent from intervening regions with different climate conditions (Kozak and Wiens 2006). Populations of a species may also become separated if they become adapted to different habitats that are geographically segregated (Sobel et al. 2010).

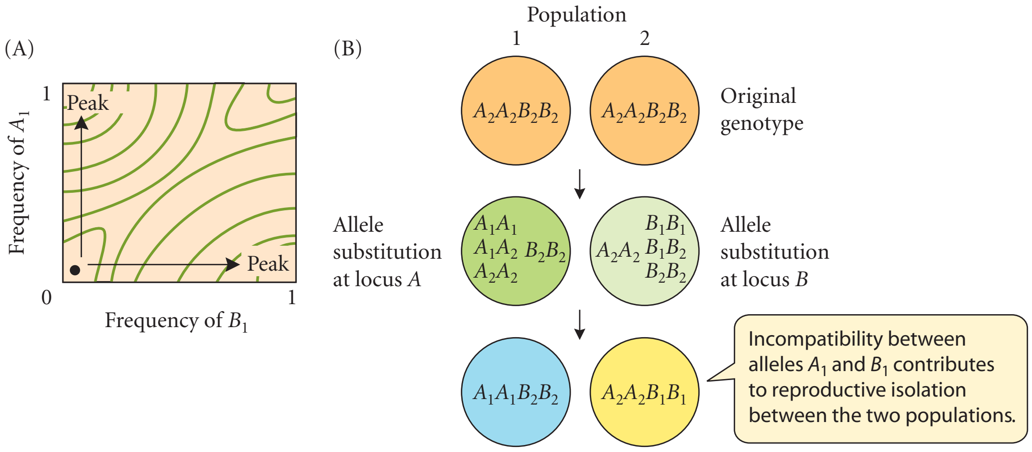
Mechanisms of vicariant allopatric speciation

Models of vicariant allopatric speciation based on genetic drift, natural selection, and a combination of these two factors have been proposed. The combination of genetic drift and selection is discussed later, in relation to peripatric speciation.

THE ORIGIN OF INCOMPATIBILITY How can failure to interbreed, or inability of hybrids to reproduce, arise if they imply fixation of alleles that lower reproductive success? The increase of such alleles to fixation, of course, would be counter to natural selection. Theodosius Dobzhansky (1936) and Hermann Muller (1940) provided a theoretical solution to this problem that does not envision increasing an allele's frequency in opposition to selection. It requires that the reproductive barrier be based on differences at two or more loci that have complementary effects on fitness. In other words, fitness depends on the combined action of the "right" alleles at both loci. The "wrong" combinations of alleles result in Dobzhansky-Muller (DM) incompatibility, as illustrated by the *Drosophila* genes described in Figure 17.14.

Suppose the ancestral genotype in two allopatric populations is $A_2A_2B_2B_2$ (**Figure 18.7**). For some reason, A_1 replaces A_2 in population 1 and B_1 replaces B_2 in population 2, yielding populations monomorphic for $A_1A_1B_2B_2$ and $A_2A_2B_1B_1$, respectively. Both A_1A_2 and A_1A_1 have fitness equal to or greater than A_2A_2 in population 1, as long as the genetic background is B_2B_2; likewise, B_1B_2 and B_1B_1 are equal or superior to B_2B_2, as long as the genetic background is A_2A_2. Therefore these allele substitutions can occur by natural selection (if the fitnesses differ) or by genetic drift (if they do not). However, an epistatic interaction between A_1 and B_1 causes incompatibility, so that either the hybrid $A_1A_2B_1B_2$ has lowered viability or fertility, or $A_1A_1B_2B_2$ and $A_2A_2B_1B_1$ are isolated by a prezygotic barrier, such as different sexual behavior. *The important feature of this model is that neither population has passed through a stage in which inferior heterozygotes existed.* Neither of the incompatible alleles has ever been "tested" against the other within the same population.

This model is supported by genetic data showing that reproductive isolation is based on epistatic interactions among several or many loci (see Chapter 17). It is theoretically possible that the allele substitutions could be caused by either genetic drift or natural selection. However, no convincing examples have been described in which speciation can be



Incompatibility between alleles A_1 and B_1 contributes to reproductive isolation between the two populations.

FIGURE 18.7 The Dobzhansky-Muller theory explains how allele substitution can lead to reproductive isolation. We begin with two populations, both initially composed of genotype $A_2A_2B_2B_2$. (A) The adaptive landscape, in which contour lines represent mean fitness as a function of allele frequencies at both loci, shows how the two populations may move uphill toward different adaptive peaks. (B) Each population undergoes an allele substitution at a different locus (substituting either A_1 or B_1). The hybrid combination $A_1A_2B_1B_2$ has low fitness (as indicated by the "valley" in the center of the landscape) because of prezygotic or postzygotic incompatibility between A_1 and B_1.

attributed entirely to genetic drift (Coyne and Orr 2004). In contrast, natural selection may contribute to the origin of species in several ways.

THE ROLE OF NATURAL SELECTION The most widely held view of vicariant allopatric speciation is that it is caused by *natural selection, which causes the evolution of genetic differences that create prezygotic or postzygotic isolation*. Some—perhaps most—of this reproductive isolation evolves while the populations are allopatric, so that a substantial or complete barrier to gene exchange exists when the populations meet again if their ranges expand (Mayr 1963). Thus speciation is usually an *effect*—a by-product—of natural selection that occurred during allopatry. That selection may be either ecological selection or sexual selection.

The other possibility is that natural selection favors prezygotic (e.g., sexual) reproductive barriers *because of* their isolating function—because they prevent their bearers from having unfit hybrid progeny. Selection would then result in *reinforcement of reproductive isolation*. This reinforcement would occur only when the genetically different populations come into contact and have the opportunity to hybridize. In this scenario, some degree of postzygotic isolation (low hybrid fitness) evolves while the populations are allopatric, but speciation is completed when the incipient species come into contact.

Ecological selection and speciation

Ecological selection might cause speciation in two ways, which have been termed mutation-order speciation and ecological speciation (Schluter 2009). In MUTATION-ORDER SPECIATION, mutations at different genes occur in each population, are selected for the same reason (e.g., they provide adaptation to the same selective factor), and confer DM incompatibility (e.g., mutations A_1 and B_1 in Figure 18.7). The most likely examples of mutation-order speciation described so far are based not on ecological selection, but on genetic conflict, such as that arising from meiotic drive (see Chapter 16). **Ecological speciation** refers to the evolution of barriers to gene flow caused by divergent ecologically based selection (Rundle and Nosil 2005; Schluter 2009; Nosil 2012).

Allopatric populations and species undergo both adaptive divergence and evolution of reproductive isolation, but showing that reproductive isolation is a result of adaptive divergence requires evidence that the two processes are genetically and causally related to each other. The most direct evidence comes from laboratory studies of *Drosophila* and houseflies, in which investigators tested for reproductive isolation among subpopulations drawn from a single base population and subjected to divergent selection for various morphological, behavioral, or physiological characteristics (Rice and Hostert 1993). In many of these studies, partial sexual isolation or postzygotic isolation developed, demonstrating that substantial progress toward speciation can be observed in the laboratory, and that it can be caused by divergent selection. That is, reproductive isolation in these studies was due to pleiotropic effects of genes for the divergently selected character, or closely linked genes.

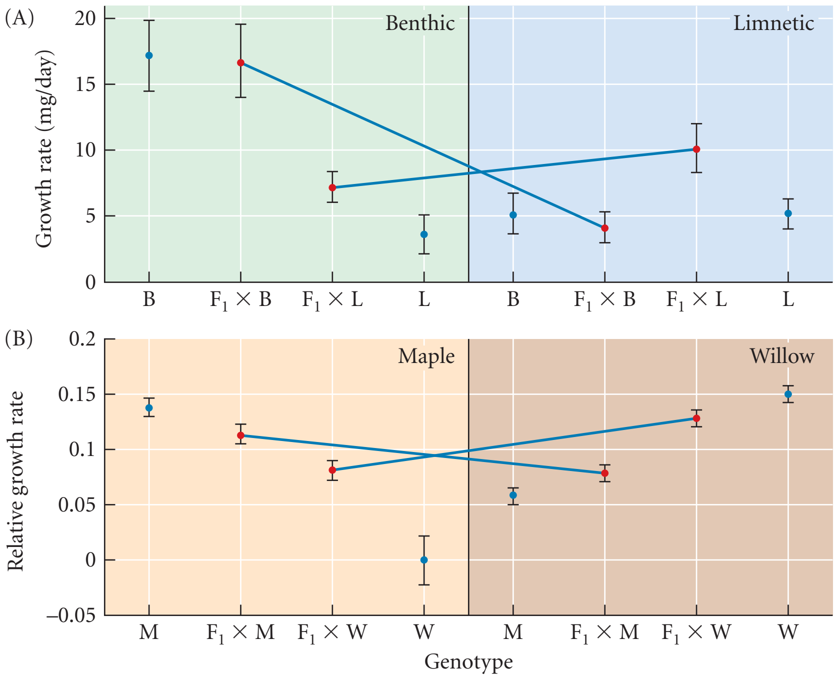


FIGURE 18.8 Postzygotic reproductive isolation, manifested as reduced fitness of hybrids, may depend on environmental context. (A) Blue circles show growth rates of limnetic (open water; L) and benthic (lake bottom; B) forms of the three-spined stickleback when caged in benthic and limnetic habitat. Red circles show growth rates of backcrosses to both parent forms (F_1 × B and F_1 × L). Each backcross type has high fitness in the habitat of its backcross parent and low fitness in the habitat of the other parent type. (B) The same experimental design applied to populations of the leaf beetle *Neochlamisus bebbianae* that are adapted to maple (M; *Acer rubrum*) and willow (W; *Salix bebbiana*). Each backcross hybrid (F_1 × M; F_1 × W) shows highest fitness on the host plant of its "pure" parent type. (A after Rundle 2002; B after Egan and Funk 2009).

In some cases, reproductive isolation is clearly the direct result of ecologically selected character differences. For example, the species of monkeyflowers (*Mimulus*) in Figure 17.6 avoid interbreeding almost entirely by attracting the different pollinators (bees versus hummingbirds) to which their different flowers are adapted. Many incipient species are reproductively isolated by immigrant inviability (Nosil et al. 2005), in which populations are genetically adapted to different environments and have low fitness in each other's environments (see Table 17.2). Examples include stickleback fish that are adapted for foraging in limnetic (open water) versus benthic (lake bottom) habitats (**Figure 18.8A**) and "host races" of insects adapted to different host plants (**Figure 18.8B**). Characters that confer both ecological adaptation and reproductive isolation have been termed "magic traits" by Sergei Gavrilets (2004). Such traits make speciation relatively "easy," and they appear to be fairly common (Servedio et al. 2011).

Alternatively, reproductive isolation can be a by-product of ecological adaptation, presumably because of pleiotropic effects of alleles that affect adaptation. For example, three-spined sticklebacks (*Gasterosteus aculeatus*) have undergone PARALLEL SPECIATION in several Canadian lakes, where a limnetic (open-water) ECOMORPH coexists with a benthic (bottom-feeding) ecomorph that is smaller and differs in shape. These ecomorphs, which are sexually isolated, have evolved independently in each lake; that is, speciation has occurred in parallel (**Figure 18.9A**). Parallel ecological divergence implies that ecological selection has shaped the differences between the ecomorphs. In laboratory trials, fish of the same ecomorph from different lakes mate almost as readily as those from the same lake, but different ecomorphs mate much less frequently (**Figure 18.9B**). Thus features associated with ecological divergence affect sexual isolation (Rundle et al. 2000). Exactly why they do so is not known.

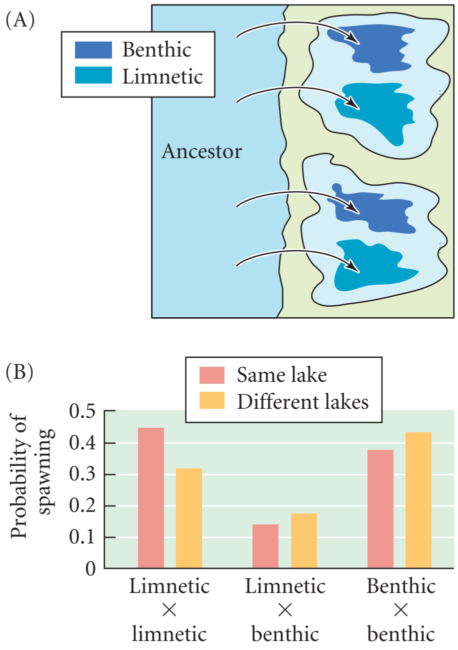


FIGURE 18.9 Parallel speciation in the three-spined stickleback (*Gasterosteus*). (A) Pairs of open-water (limnetic) and bottom-feeding (benthic) ecomorphs have arisen independently in different lakes. (B) Females mate preferentially with males on the basis of their morphology, whether they are from the same or different lakes. This isolating character is evidently adaptive, since it has evolved repeatedly in the same way. (A after Schluter and Nagel 1995; B after Rundle et al. 2000.)

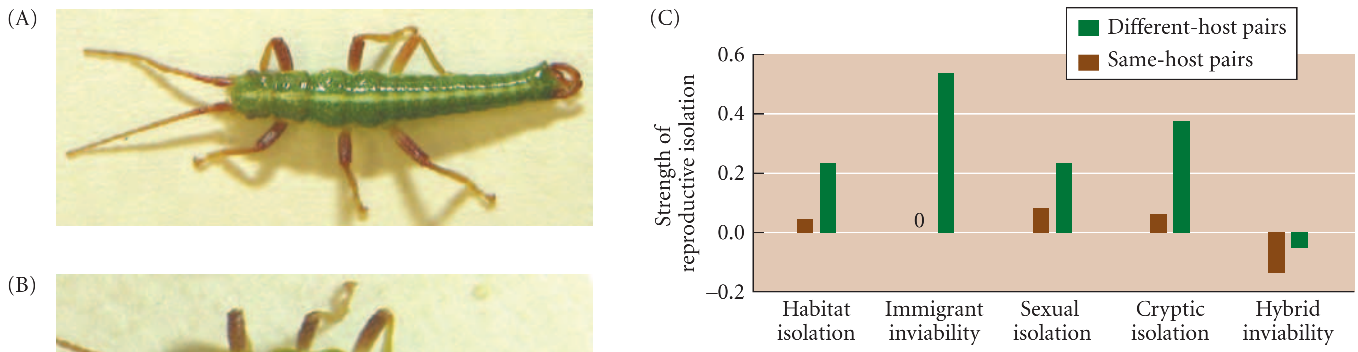


FIGURE 18.10 Ecomorphs of the stick insect *Timema cristinae* found on the shrubs *Adenostoma fasciculatum* (A) and *Ceanothus spinosus* (B) differ in body form and color pattern, closely matching the foliage on which they feed. (C) Pairs of populations from different hosts are more strongly reproductively isolated in several respects than are pairs from the same host. The negative values for hybrid inviability indicate enhanced viability of hybrids, but here these values are not statistically significant. Cryptic isolation refers to reduced fecundity in interpopulation matings. (Photos courtesy of Patrik Nosil; C after Nosil 2007.)

Two ecomorphs of the stick insect *Timema cristinae* are associated with different host plants in the chaparral vegetation of California, and they differ in several morphological features that make each ecomorph better camouflaged on its own host plant than on the other. Patrik Nosil (2007) has studied several components of reproductive isolation between multiple pairs of different-host populations of this species (**Figure 18.10**). He concluded that ecological divergence directly reduces gene flow in two ways. First, habitat isolation reduces gene flow because large patches of chaparral vegetation are dominated by one or the other plant. Second, immigrant inviability results from the high mortality the insects suffer if they disperse to the "wrong" host, where they are easy targets for birds. Indirect effects of ecological divergence include sexual isolation, which is greater between different-host than same-host populations, and reduced fertility in cross-matings: females that mate with the other ecomorph lay fewer eggs.

Daniel Funk and colleagues (2006) provided evidence that divergent ecological adaptation commonly contributes to speciation by compiling data from the literature on reproductive isolation, indicators of ecological divergence among species, and genetic distances among species in several groups of plants, insects, fishes, frogs, and birds. Genetic distance was used as an index of time since pairs of species had diverged from their common ancestor. By statistically controlling for time, the investigators showed that the level of reproductive isolation achieved at any time is correlated with the degree of ecological divergence between species (**Figure 18.11**).

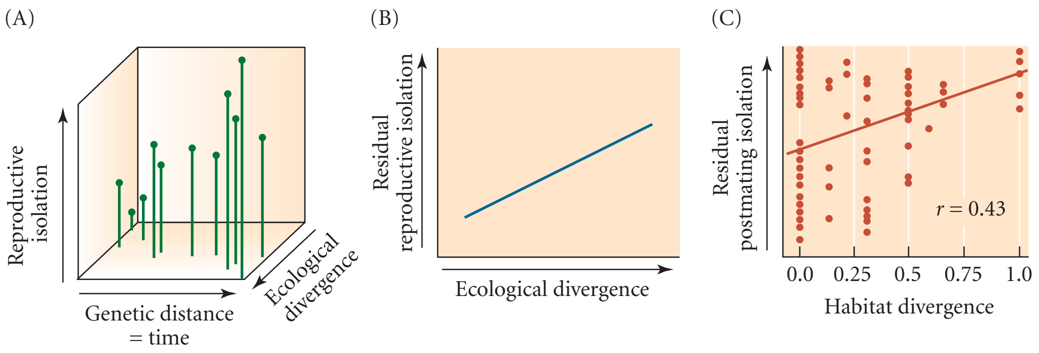


FIGURE 18.11 A method for testing the hypothesis that reproductive isolation evolves as a by-product of ecological divergence. (A) For several pairs of species, experimental estimates of reproductive isolation are plotted against both the time since common ancestry (estimated by genetic distance, as in Figure 17.9) and a measure of ecological difference. (B) The amount of "residual" reproductive isolation that is not accounted for by time since common ancestry is plotted against ecological divergence and tested for correlation. (C) An example of real data, showing that postzygotic isolation between pairs of flowering plant species is significantly correlated with difference in habitat use. (After Funk et al. 2006.)

Sexual selection and speciation

Closely related species of animals are often sexually isolated by female preferences for features of conspecific males. In fact, many authors consider sexual isolation to be the most important reproductive barrier, although this view is controversial (Coyne and Orr 2004). One hypothesis proposed to explain the differences between species in these characteristics is that they enable individuals to recognize conspecific mates and avoid hybridization, which would be disadvantageous if hybrid offspring have low fitness. An alternative hypothesis is that divergent sexual selection in different geographic populations of a species results in different male display traits and female preferences (Fisher 1930; West-Eberhard 1983). This hypothesis has been supported by mathematical models (Lande 1981; Pomiankowski and Iwasa 1998; Turelli et al. 2001).

It is very likely that sexual selection has been an important cause of speciation, especially in highly diverse groups such as Hawaiian *Drosophila*, birds of paradise, and hummingbirds (see Figure 17.5), in which males are often highly (and diversely) colored or ornamented (Panhuis et al. 2001). The male color patterns of some closely related African lake cichlids act as reproductive barriers between species, and it is likely that sexual selection has contributed to the extraordinarily high species diversity of these fishes (Seehausen et al. 1999). Some comparisons of the species diversity of sister groups of birds suggest that sexual selection has enhanced diversity (**Figure 18.12**). Groups of birds with promiscuous mating systems have higher diversity than sister clades in which pair-bonds are formed and the variance in male mating success is presumably lower—resulting in weaker sexual selection (Mitra et al. 1996).

The role of sexual selection in speciation has been extensively studied in orthopteran insects (e.g., crickets) and frogs, in which males produce fairly simple acoustic mating signals that can be simulated and varied electronically. For example, two sister species of crickets (*Gryllus texensis* and *G. rubens*) in the southern United States differ in the pulse rate of the male song, and females of both species show a much stronger response to

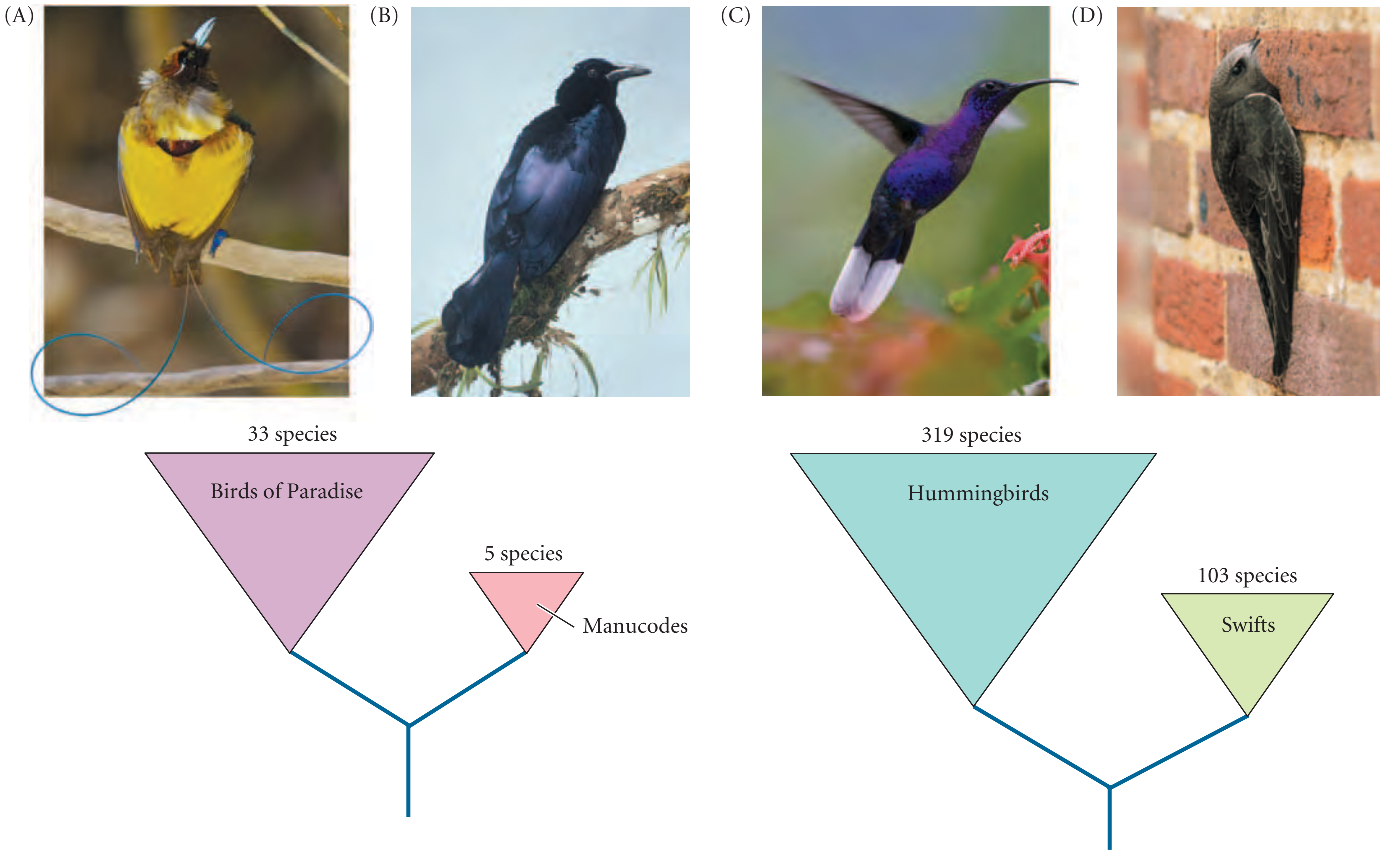


FIGURE 18.12 In sister clades of birds that differ in their mating system, those clades that mate promiscuously and do not form a pair-bond (A, C) tend to have more species than nonpromiscuous clades that do form pair-bonds (B, D). The promiscuously mating clades are thought to experience stronger sexual selection. (A) A promiscuous male magnificant bird of paradise (*Cicinnurus magnificus*) and (B) a nonpromiscuous manucode (*Manucodia comrii*). (C) A male violet sabrewing hummingbird (*Campylopterus hemileucurus*) and (D) a common swift (*Apus apus*), a member of a sister clade that forms pair-bonds.

synthesized songs with pulse rates characteristic of their own species (Gray and Cade 2000). Hybrids produced in the laboratory are viable and fully fertile, and there is no evidence that the differences in male song or female preference have evolved to reduce hybridization, because distant allopatric populations of the two species, which have no opportunity to hybridize, are just as different as sympatric populations. Among populations of a Hawaiian cricket (*Laupala cerasina*), male calls also vary in pulse rate, and female preferences are strongly correlated with the rates of conspecific males (**Figure 18.13**; Grace and Shaw 2011). In crosses between two other species of *Laupala*, male pulse rate and female pulse preference were genetically correlated and possibly controlled by the same genes. Such correlation that would facilitate divergence by sexual selection (see Chapter 17).

There has been little research on why sexual selection varies among populations, leading to divergence and sexual isolation. In some cases, visual signals (e.g., coloration) and acoustic signals have been shaped in part by selection for more effective transmission and reception, which can be affected by the environment (Endler and Basolo 1998). For example, the songs of birds that live in the undergrowth of Amazonian forests have higher frequencies ("pitch") than those of close relatives that inhabit stands of bamboo, a difference that corresponds to the most effectively transmitted signal in each environment (Tobias et al. 2010a). It is also likely that the course of runaway sexual selection, or of selection for condition-dependent indicators of fitness, comes to differ between populations, but whether natural selection or genetic drift causes such changes in course is a problem for future research. Sexual conflict (see Chapter 15) can easily lead to the evolution of reproductive isolation caused by different male features that reduce female fitness, and different female countermeasures, in different populations (Gavrilets 2000). Göran Arnqvist et al. (2000) found that among 25 pairs of sister clades, species richness was greater in those with polygamous females, in which sperm of multiple males may compete, than in those with monogamous females.

Sexual selection also probably plays a role in the evolution of gametic isolation, a major barrier to gene flow between species of broadcast-spawning marine invertebrates (**Figure 18.14A**; Palumbi 2009). In some cases, as in abalones and related snails, both a sperm-surface protein and the egg protein with which it interacts during fertilization have diverged rapidly by natural selection (**Figure**

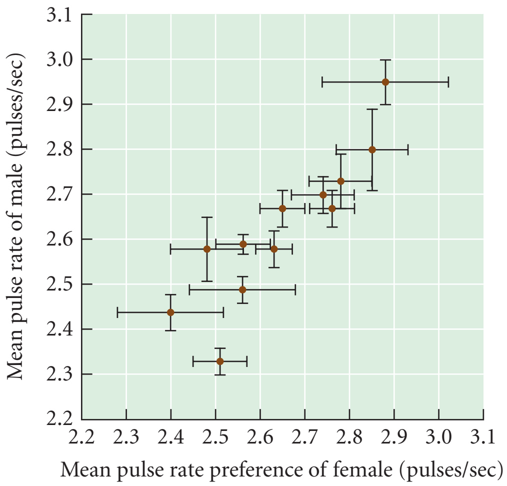


FIGURE 18.13 The pulse rate of the mating call of male crickets (*Laupala cerasina*) and the pulse rate preferred by females both vary among local populations. These differences are genetically based. The confidence intervals around each point show that females of the most widely different populations would not readily mate with males at the other extreme. (After Grace and Shaw 2011.)

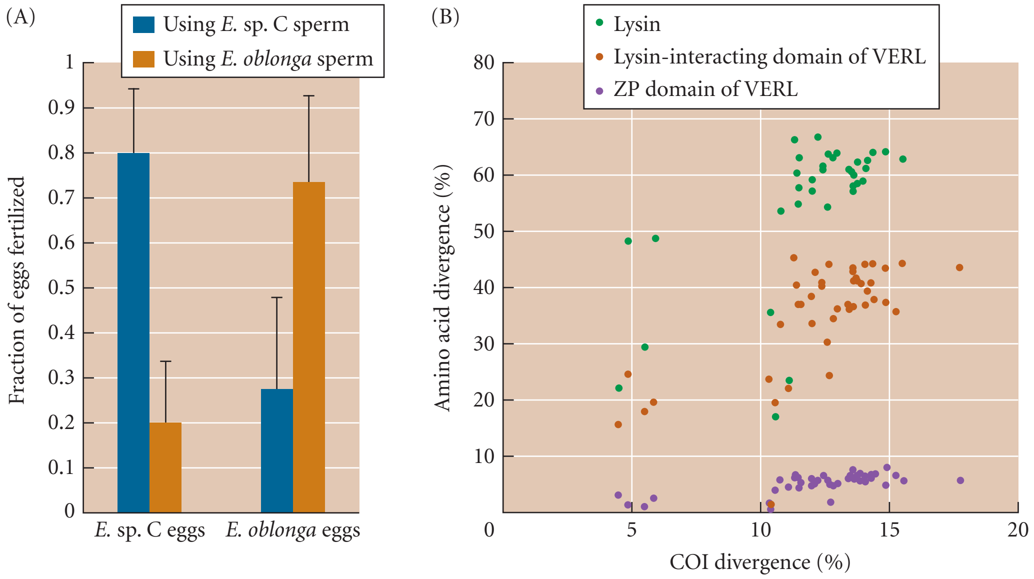


FIGURE 18.14 Gametic isolation based on protein differences. (A) When eggs from two closely related sea urchin species, *Echinometra oblonga* and *E.* species C, are exposed to a mixture of sperm of both species, conspecific sperm are much more successful in fertilization. (B) Fertilization in the marine snail genus *Tegula* is partly based on the ability of the sperm protein lysin to dissolve the vitelline envelope, a species-specific reaction that depends on the binding of lysin to an envelope protein called VERL (vitelline envelope receptor for lysin). Among species of *Tegula*, sequence divergence of lysin and the domain of VERL with which lysin interacts is high and has increased with time since speciation, as measured by divergence of a mitochondrial gene (COI). The ZP domain of VERL, which does not interact with lysin, has diverged more slowly. (A after Palumbi 2009; B after Hellberg et al. 2012.)

18.14B), resulting in a block to crossing between species. How natural selection has caused this divergence is unclear. One possibility is that egg surface proteins evolve to prevent infection by pathogens, and that sperm proteins must adjust. Sexual conflict is perhaps a more likely answer: changes in the egg surface that slow down sperm entry are advantageous because fertilization by more than one sperm kills the egg. Any such changes in the egg will impose selection for sperm that can beat their competitors by penetrating more quickly.

Reinforcement of reproductive isolation

We have seen that reproductive isolation can arise as a *side effect* of genetic divergence due to natural selection. However, many biologists have supposed that reproductive isolation evolves, at least in part, as an *adaptation to prevent the production of unfit hybrids*. The champion of this viewpoint was Theodosius Dobzhansky, who expressed the hypothesis this way:

> Assume that incipient species, A and B, are in contact in a certain territory. Mutations arise in either or in both species which make their carriers less likely to mate with the other species. The nonmutant individuals of A which cross to B will produce a progeny which is adaptively inferior to the pure species. Since the mutants breed only or mostly within the species, their progeny will be adaptively superior to that of the nonmutants. Consequently, natural selection will favor the spread and establishment of the mutant condition. (Dobzhansky 1951, p. 208)

Dobzhansky introduced the term “isolating mechanisms” to designate reproductive barriers, which he believed were indeed mechanisms designed to isolate. In contrast, Ernst Mayr (1963), among others, held that although natural selection might enhance reproductive isolation, reproductive barriers arise mostly as side effects of allopatric divergence, whatever its cause may be. Mayr cited several lines of evidence: sexual isolation exists among fully allopatric forms; it has failed to evolve in some hybrid zones that are thought to be thousands of years old; features that promote sexual isolation between species are usually not limited to regions where the species are sympatric and face the “threat” of hybridization. It is now generally agreed that natural selection can enhance prezygotic reproductive isolation between hybridizing populations, but how often this process plays a role in speciation is not known (Servedio and Noor 2003; Butlin et al. 2012).

The enhancement of prezygotic barriers that Dobzhansky envisioned is often called **reinforcement** of prezygotic isolation.

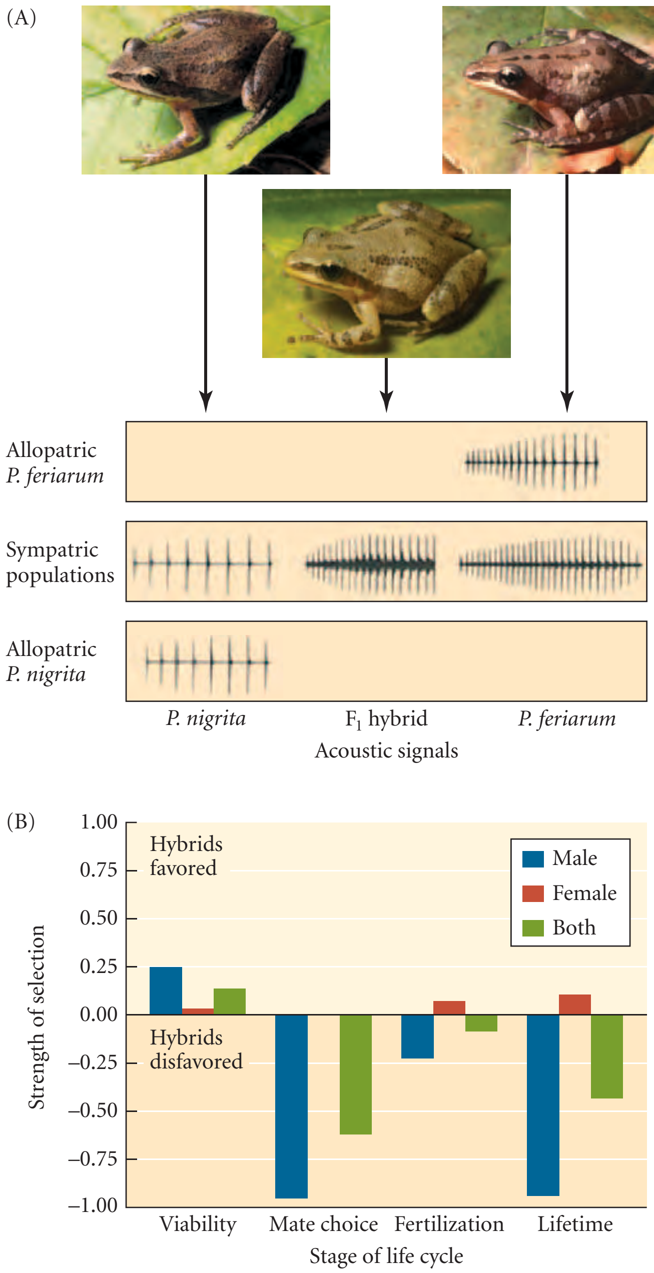


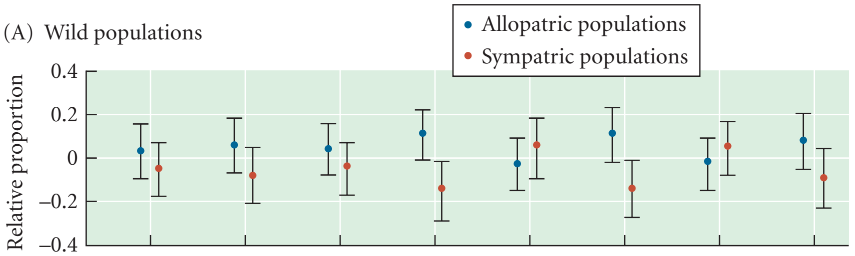
FIGURE 18.15 Character displacement and reinforcement of sexual isolation. (A) The range of the chorus frog *Pseudacris feriarum* in the eastern United States partly overlaps that of the more southern *P. nigrita*. The oscillograms (displaying amplitude plotted against time) show that male calls differ more in pulse rate between sympatric populations of the two species than between allopatric populations. The call of the F_1 hybrid is also shown. (B) The geographic pattern of character displacement in these frogs was probably caused by reinforcement of prezygotic isolation. Hybrid males have reduced fitness both because they are less preferred by nonhybrid females (mate choice) and because they have lower average success in fertilizing eggs. (After Lemmon and Lemmon 2010; photos courtesy of Emily Lemmon.)

Reinforcement has been cited as a cause of **reproductive character displacement**, meaning a *pattern* whereby characters differ more where two taxa are sympatric than where they are allopatric (Brown and Wilson 1956). Population genetic models have shown that reinforcement can evolve: alleles that reduce the likelihood of interbreeding can increase in frequency because they are more likely to be inherited by viable nonhybrid offspring than are alleles that permit random mating—which will decline in frequency if they are inherited by unfit hybrids (Servedio and Noor 2003).

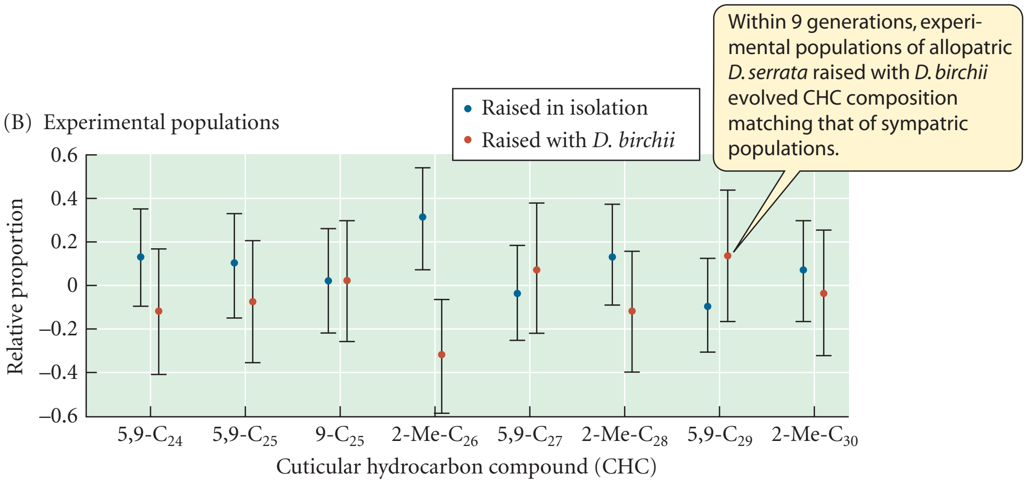
Reinforcement of prezygotic isolation appears to occur fairly often (Noor 1999). For example, the pulse rate and pulse number of the male mating call of the chorus frog *Pseudacris feriarum*, of eastern North America, are higher in populations that are sympatric with a more southern species, *Pseudacris nigrita*, and females have likewise shifted their preference for male calls (**Figure 18.15A**). Male hybrids have lower fertility than nonhybrids, and female *P. feriarum* discriminate against hybrid male calls (**Figure 18.15B**). This pattern of character displacement is the expected consequence of reinforcement. Similarly, *Drosophila serrata* and its close relative *D. birchii* are sympatric in northern Australia, but *D. serrata* extends much farther south than *D. birchii* does. Females of both species choose males based on their relative proportions of several hydrocarbon compounds in the cuticle (CHCs). There is an abrupt difference in male CHCs between allopatric and sympatric populations of *D. serrata* (**Figure 18.16A**). When Megan Higgie and Mark Blows (2007) confined allopatric *D. serrata* with *D. birchii* in laboratory populations, the composition of male CHCs evolved within nine generations toward the composition found in sympatric *D. serrata* (**Figure 18.16B**), showing that reinforcement was not only predictable, but could occur very rapidly. In another experiment, Higgie and Blows (2008) found that in laboratory populations formed by crossing sympatric and allopatric populations of *D. serrata*, male CHCs evolved toward the natural allopatric composition, and female preference evolved toward the CHC composition found in allopatric populations. Sexual selection alone, then, favors a different CHC composition than selection for reinforcement.

When Jerry Coyne and Allen Orr (1989) compiled experimental data on reproductive isolation in *Drosophila*, they found that sexual (but not postzygotic) isolation was stronger between sympatric pairs of species (or populations) than between allopatric populations

(A) Wild populations



(B) Experimental populations



Within 9 generations, experimental populations of allopatric *D. serrata* raised with *D. birchii* evolved CHC composition matching that of sympatric populations.

FIGURE 18.16 Evidence of reinforcement of differences in hydrocarbon composition of the male cuticle (CHC) in two species of *Drosophila*. Female mate choice is mediated by the relative proportions of cuticular hydrocarbons. (A) The relative proportions of eight CHCs in populations of *D. serrata* that are allopatric and sympatric with *D. birchii*. (B) The relative proportions of these CHCs in *D. serrata* from allopatric populations differed between stocks kept in the same cages as *D. birchii* for nine generations and those kept isolated from *D. birchii*. (After Higgie and Blows 2007.)

of the same estimated age (see Figure 17.10). They suggested that this pattern was a consequence of reinforcement. The evidence for this interpretation has grown. For example, Roman Yukilevich (2012), in an analysis of a similar but larger data set, compared asymmetry in both sexual isolation and postzygotic isolation in reciprocal crosses between species or populations of *Drosophila*. That is, the hybrid offspring of the cross female A × male B may have lower viability or fertility (indicating a stronger postzygotic barrier) than the offspring of female B × male A. Yukilevich found that for almost every sympatric pair, the cross that produces lower hybrid fitness also shows stronger sexual isolation than the reciprocal cross. Allopatric pairs, in contrast, showed no correlation between sexual and postzygotic isolation. This pattern is predicted by the hypothesis that selection for reinforcement of sexual isolation is stronger if the fitness penalty for cross-mating is greater.

Peripatric speciation

THE PERIPATRIC SPECIATION HYPOTHESIS One of Ernst Mayr's most influential and controversial hypotheses was founder effect speciation (1954), which he later termed peripatric speciation (1982b). He based this hypothesis on the observation that, in many birds and other animals, isolated populations with restricted distributions, in locations peripheral to the distribution of a probable "parent" species, are often highly divergent from those parent species, to the point of being classified as different species or even genera. For example, the paradise-kingfisher varies little throughout the large island of New Guinea, but has differentiated into several distinctly different forms on small islands along its coast (**Figure 18.17**).

Mayr proposed that genetic change could be very rapid in localized populations founded by a few individuals and cut off from gene exchange with the main body of the species. He reasoned that in such populations, allele frequencies at some loci would differ from those in the parent population because of accidents of sampling (i.e., genetic drift), simply because a small number of colonists would carry only some of the alleles from the source population, and at different frequencies. (He termed this initial alteration of allele frequencies the FOUNDER EFFECT; see Chapter 10.) Because epistatic interactions among genes affect fitness, this initial change in allele frequencies at some loci would alter the selective value of genotypes at other, interacting loci. Hence selection would alter allele frequencies at these loci, and this in turn might select for

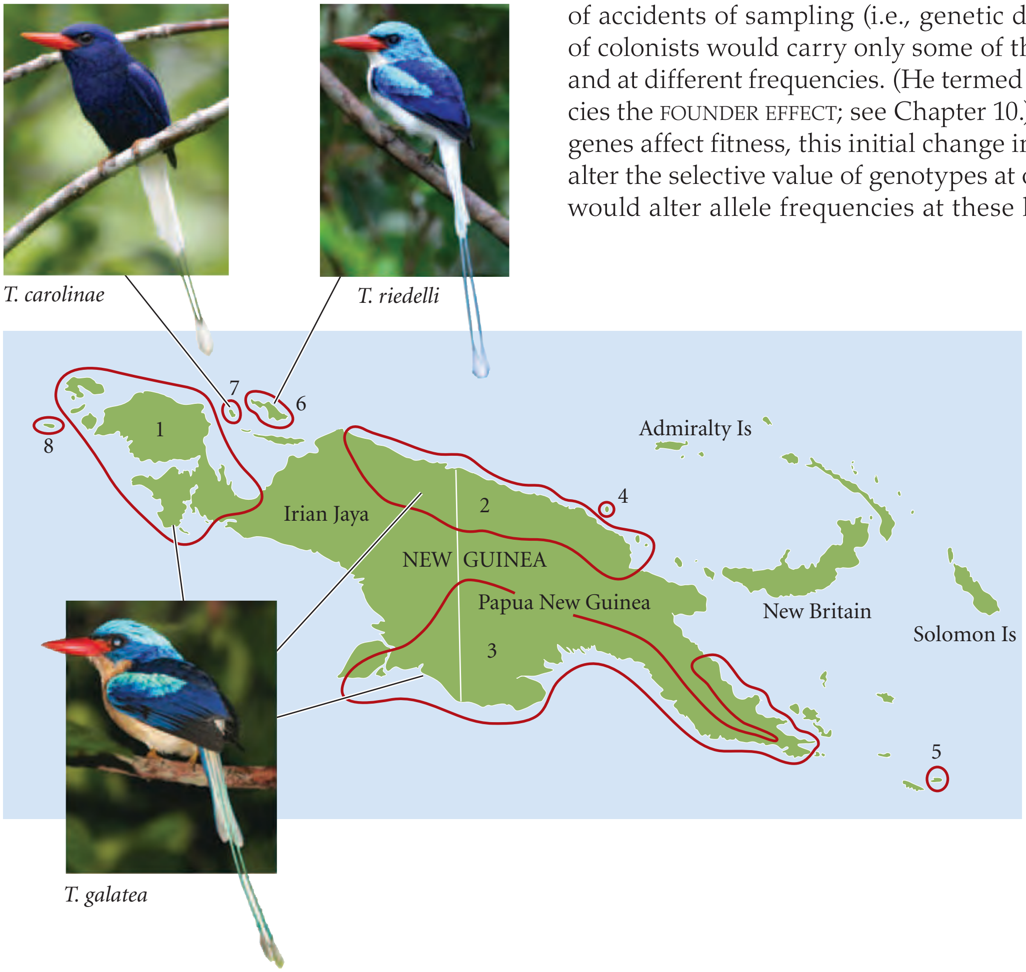


FIGURE 18.17 Variation among paradise-kingfishers in New Guinea. *Tanysiptera galatea* is distributed throughout the New Guinea lowlands (regions 1, 2, 3) and some satellite islands (4, 5), whereas the very localized forms *T. riedelii* on Biak Island (6) and *T. carolinae* on Numfor Island (7) are now recognized as distinct species. (After Mayr 1954; *T. galatea* photo courtesy of Rob Hutchinson/Birdtour Asia; *T. riedelii* and *T. carolinae* courtesy of Mehd Halaouate.)

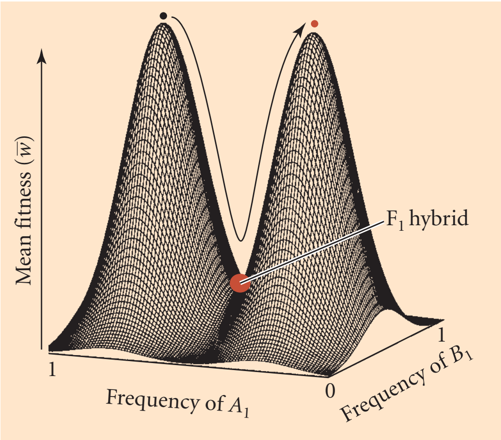
changes at still other epistatically interacting loci. The “snowballing” genetic change that might result would incidentally yield reproductive isolation.

As Mayr (1954) pointed out, this hypothesis implies that substantial evolution would occur so rapidly, and on so localized a geographic scale, that it would probably not be documented in the fossil record. If such a new species expanded its range, it would appear suddenly in the fossil record, without evidence of the intermediate phenotypic changes that had occurred. Thus this hypothesis, he said, might help to explain the rarity of fossilized transitional forms among species and genera. Mayr thus anticipated, and provided the theoretical foundation for, the idea of PUNCTUATED EQUILIBRIUM (see Chapters 4 and 22) advanced by Niles Eldredge and Stephen Jay Gould (1972). Hampton Carson (1975) and Alan Templeton (1980) later advanced a related hypothesis, which they called **founder-flush speciation**, in which they emphasized that during the rapid initial population growth (“flush”) of such a colony, advantageous combinations of rare alleles at different loci might be more likely to arise and be fixed than in a stable population. These genetic changes might affect characteristics that contribute to reproductive isolation.

One interpretation of these hypotheses employs the metaphor of an adaptive landscape (see Figure 12.21). According to this interpretation, the colony undergoes a PEAK SHIFT from one adaptive (coadapted) combination of genes (that of the parent population) through a less adaptive genetic constitution (an adaptive valley) to a new adaptive equilibrium (**Figure 18.18A**). The process begins when genetic drift in the small, newly founded population shifts allele frequencies from the vicinity of one adaptive peak (with high frequency of, say, genotype $A_1A_1B_1B_1$) to the slope of another adaptive peak (at which genotype $A_2A_2B_2B_2$ has high frequency). This stage can be accomplished by genetic drift, but not by natural selection, since selection cannot reduce mean fitness. However, selection can move the allele frequencies up the slope away from the valley toward the new peak. Some population geneticists consider peak shifts unlikely because genetic drift is unlikely to move a population’s genetic composition across an adaptive valley in opposition to natural selection (Charlesworth and Rouhani 1988; Turelli et al. 2001). However, speciation can occur by genetic drift if an isolated population moves along an “adaptive ridge” to the other side of an adaptive valley from the parent population (**Figure 18.18B**; Gavrilets 2004). Moreover, as Montgomery Slatkin (1996) pointed out, genetic drift is actually weak during rapid population growth because the average number of offspring per capita is greater than in a stable population. Therefore rare combinations of advantageous alleles are more likely to increase in frequency, enabling a population to ascend a new fitness peak. This theory, together with evidence that epistatic interactions among genes are very common (Phillips 2008; Zwarts et al. 2011), makes founder effect speciation a plausible possibility.

EVIDENCE FOR PERIPATRIC SPECIATION Several investigators have passed laboratory populations through repeated bottlenecks to see whether reproductive isolation can evolve in this way. Some investigators interpret these experiments as providing little evidence of reproductive isolation (Rundle 2003; Coyne and Orr 2004); others argue that although incipient reproductive isolation may have evolved in only a fraction of experimental populations, it happens often enough to support the founder-flush hypothesis (Templeton 2008). For example, Agustí Galiana and colleagues (1993) passed 45 laboratory populations of *Drosophila pseudoobscura* through repeated phases of rapid population growth and bottlenecks of a few (1–9) pairs, then tested the populations for sexual isolation from one another. Almost half the experimental populations, especially those passed through more severe bottlenecks, displayed some evidence of sexual isolation.

(A) Peak shift across an adaptive valley



(B) Genetic drift along an adaptive ridge

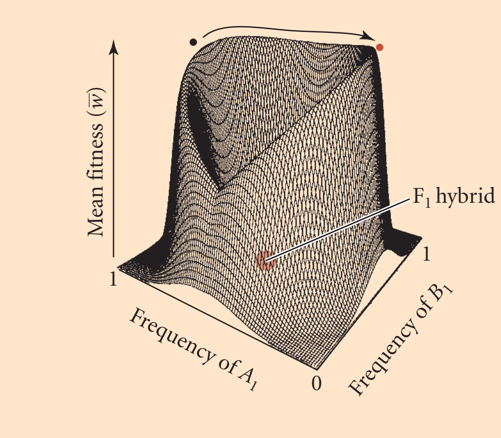


FIGURE 18.18 Two adaptive landscapes show how peripatric speciation might occur. The height of a point on the three-dimensional landscape represents the mean fitness of a population ($\overline{w}$). The mean fitness is a function of allele frequencies at loci *A* and *B*. (A) In a peak shift, a population evolves from one adaptive peak to another by moving downhill (lowering fitness) and then uphill. The F$_1$ hybrid of a cross between populations on the two peaks lies in the valley; that is, it has low fitness, which causes some reproductive isolation between the populations. (B) Genetic drift along an adaptive ridge, in which genetic constitutions with the same fitness connect the beginning and end states of a population. The F$_1$ hybrid between populations with these genetic constitutions lies inside the crater. (After Gavrilets and Hastings 1996.)

Many species do originate, as Mayr said, as localized “buds” from a widespread parent species. This is shown by gene trees such as that of the *Greya* moths in Figure 17.3, in which a geographically localized species is more closely related to certain populations of a more widespread species than the populations of the widespread species are to one another (Avise 1994). But this pattern, in itself, does not tell us whether the population experienced a bottleneck that might have triggered the evolution of reproductive isolation. Evidence on this last point can be provided by the pattern of DNA sequence variation. We saw in Chapter 10 (p. 275) that the effective size (N_e) of a population—the measure of a population’s size that is most affected by bottlenecks in its history—can be estimated from the proportion of neutral polymorphic sites in its DNA sequences. Extension of the same coalescent theory makes it possible to estimate N_e for the ancestral population that split into two populations or species (Wakeley and Hey 1997). High levels of shared polymorphism (indicating incomplete lineage sorting; see Figure 2.25) indicate that the populations have not suffered drastic reduction in size since they became separated.

Several investigators have used this approach to judge whether or not divergent, peripheral populations have undergone severe bottlenecks that could have induced founder-flush speciation. The web-toed salamander *Hydromantes brunus*, which occupies a small geographic range on the periphery of that of the more broadly distributed *H. platycephalus*, clearly evolved as a localized population of their common ancestor (**Figure 18.19A**). The lower level of sequence variation in *H. brunus* implies that it may have been founded by about 1500 individuals (**Figure 18.19B**)—a small number relative to the ancestor of *H. platycephalus*, but probably too large to have enabled speciation by the founder-flush mechanism (Rovito 2010). A similar analysis has been applied to the zebra finch (*Taeniopygia guttata*), which consists of morphologically and behaviorally different populations in Australia, where it is very abundant, and in the Lesser Sunda Islands to the northwest (Balakrishnan and Edwards 2009). The Lesser Sunda

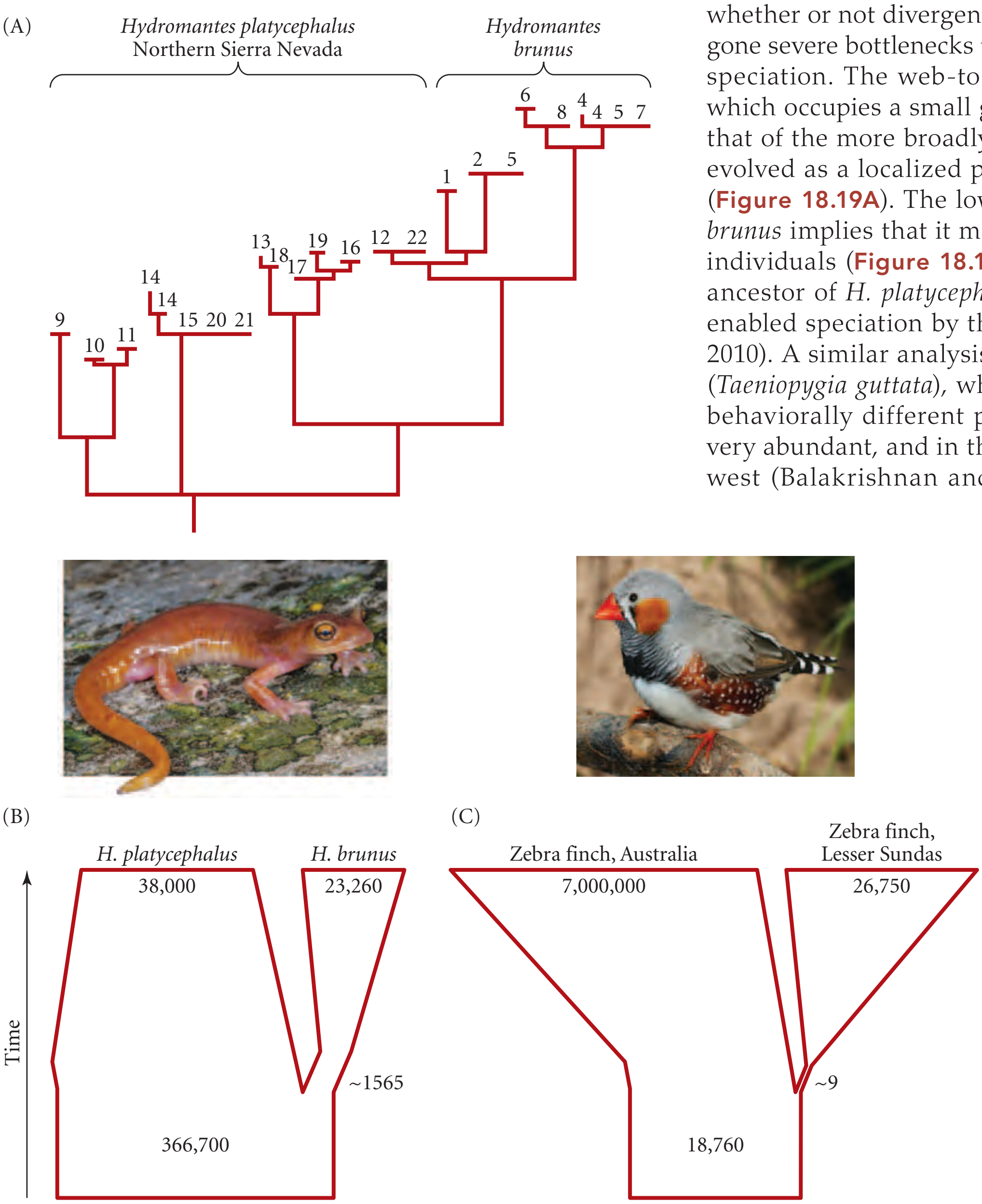


FIGURE 18.19 Tests for a population bottleneck in recent or incipient speciation. (A) A gene tree shows that the salamander *Hydromantes brunus* is nested within the more widespread species *H. platycephalus*. (B) Estimates of the effective population sizes of these species at present, in their common ancestor, and during the origin of *H. brunus*. (C) A similar estimate of effective population sizes for the zebra finch *Taeniopygia guttata*. Unlike the salamander *H. brunus*, the Lesser Sunda population of the zebra finch, which appears to be an incipient species, has undergone a strong reduction of population size, suggesting that it is a candidate for founder effect or founder-flush speciation. (A after Rovito 2010; B, data from Rovito 2010; C, data from Balakrishnan and Edwards 2009.)

subspecies may have been founded by as few as 9 individuals, from which it increased to a current N_e estimated at more than 26,000 (**Figure 18.19C**). In most analyses of recently derived sister species (see Figure 17.16), however, incomplete sorting of shared gene lineages provides evidence that both species have had large effective population sizes and have not experienced severe bottlenecks.

Alternatives to Allopatric Speciation: Speciation with Gene Flow

Allopatric, parapatric, and sympatric speciation form a continuum, from little to more to much gene flow between the diverging groups that eventually evolve biological barriers to gene exchange. The higher the rate of gene flow between two populations, the stronger divergent selection must be for their allele frequencies to differ (see Figure 12.10). Even in allopatric speciation, there may be some gene flow between populations, but it is very low compared with the divergent action of natural selection or genetic drift. Parapatric speciation is essentially the same process, but since the rate of gene flow is higher, the force of selection must be correspondingly stronger to engender genetic differences that create reproductive isolation, and it must be stronger still to produce the genetic discontinuities required for sympatric speciation.

SPECIATION WITH GENE FLOW occurs if reproductive isolation evolves while the incipient species are exchanging genes (Pinho and Hey 2010). This term includes parapatric and sympatric speciation, as well as cases in which incipient reproductive isolation between formerly allopatric populations is reinforced (as described above). An important feature of speciation with gene flow is the existence of substantial genetic difference in genomic regions that harbor divergently selected loci, but little genetic difference in regions that are not divergently selected. In these latter regions, gene flow between the populations opposes differentiation (see Figure 17.17). Thus there may exist ISLANDS OF DIVERGENCE between otherwise undifferentiated genomes, a pattern that is being revealed in many closely related species pairs by studies of multiple genetic markers.

We have seen that reproductive isolation between populations is almost always based on a combination of allele differences at two or more loci (the Dobzhansky-Muller model). In Figure 18.7, for example, the gene combinations A_1B_2 and A_2B_1 are incompatible (they display at least partial pre- or postzygotic isolation). Thus, for any substantial reproductive isolation to occur, *the alleles at these loci must be in strong linkage disequilibrium* (i.e., there must be a strong association between A_1 and B_2, and between A_2 and B_1). Recombination tends to break down associations between alleles (see Figure 9.20). Unless the reproductive incompatibility between carriers of these gene combinations is very strong, they will produce some hybrid offspring (A_1B_2/A_2B_1), in which recombination will give rise to the other allele combinations, reducing linkage disequilibrium. Importantly, recombination strongly opposes the evolution of a new incompatible gene combination in an initially randomly mating population. In order for two partly incompatible subpopulations to form when there is an initially predominant genotype (say, A_2B_2, as in Figure 18.7), the rare mutations A_1 and B_1 must increase in frequency and become associated with their complementary partners (B_2 and A_2, respectively); but recombination continually breaks down these initially uncommon gene combinations. Recombination opposes the formation of reproductively isolated gene combinations whenever there is gene flow. In allopatric populations, in contrast, the substitution of different alleles in each population, resulting in incompatible combinations (as in Figure 18.7), is not opposed by the recombination that stems from gene flow. *The breakdown of different combinations of genes in linkage disequilibrium, due to gene flow and recombination, is the most powerful obstacle to speciation with gene flow* (Felsenstein 1981; Gavrilets 2004). The more genes are needed to establish reproductive isolation, the more serious this obstacle is. We now consider how speciation with gene flow might occur despite this obstacle.

Genomic studies of speciation with gene flow

Recent investigations have used GENOME SCANS, employing large numbers of markers such as SNPs, to characterize the extent and pattern of genetic difference during speciation (Nosil and Feder 2012). Frequency differences (calculated as indexes such as F_{ST}; see Chapter 10) between the populations are calculated for all such markers. The theory of selection versus gene flow leads us to expect islands of strong genetic divergence near selected loci, standing above the "sea" of slight or modest differentiation at neutral loci (**Figure 18.20A**). When many nearby sites have been selected, larger islands or "continents" of divergence might be observed (**Figure 18.20B**). These will be indicated by neutral genetic markers (such as SNPs) in genomic regions that have undergone selective sweeps (see Chapter 12, p. 336). Many of the differences between populations and species, however, including those that underlie DM incompatibility and other components of reproductive isolation, are genetically variable within the populations, so evolution based on standing variation is likely (Cutter 2012). For this reason, among others, the selective sweeps around some selected differences may be too short to include any genetic markers and may not be detected (Strasburg et al. 2012). Hence the number of genomic islands is likely to underestimate the number of selected differences between populations.

The number of genomic islands detected between recently diverged populations and species varies among the organisms studied so far (Nosil and Feder 2012). In some cases, genomic divergence has been greater in genome regions with reduced recombination rates, as theory predicts. For example, the genomic difference between the closely related species *Drosophila pseudoobscura* and *D. persimilis* is greater within than outside the several chromosome inversions that distinguish these species (McGaugh and Noor 2012). (Recall that recombination is greatly reduced between chromosomes that differ by an inversion; see Chapter 9). Genome studies have shown that some gene flow often occurs even between some readily distinguished species, despite considerable reproductive isolation. For example, even though the sunflower species *Helianthus annuus* and *H. petiolaris* are strongly reproductively isolated, they are differentiated only by small genomic islands, the

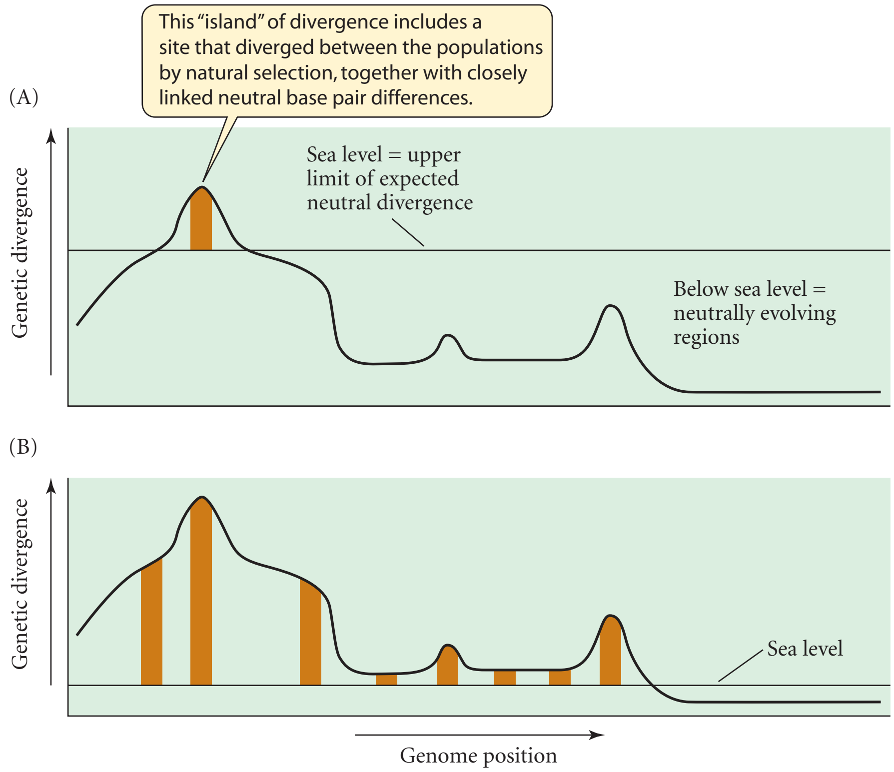


FIGURE 18.20 Hypothetical "islands" and "continents" of genetic divergence between populations. The amount of divergence (DNA sequence difference) is plotted along a region of the genome. (A) Above the horizontal line ("sea level"), the degree of divergence is statistically distinguishable (has "outlier status") from the expected level of divergence by random genetic drift. (B) If many selected loci have diverged, they and their closely linked neutral variants may form divergent genomic "continents." (After Nosil and Feder 2012.)

nearby genes having been largely homogenized by gene flow and recombination (Sambatti et al. 2012). In some cases, islands of divergence include genes known to contribute to reproductive isolation. For example, DNA sequence divergence among hybridizing populations of *Heliconius* butterflies (see Figure 12.20) was greatest at the loci that determine differences in the pattern of warning coloration (Nadeau et al. 2012). These color patterns are subject to strong positive frequency-dependent selection (see Figure 12.16B), and also contribute to behavioral isolation between some species.

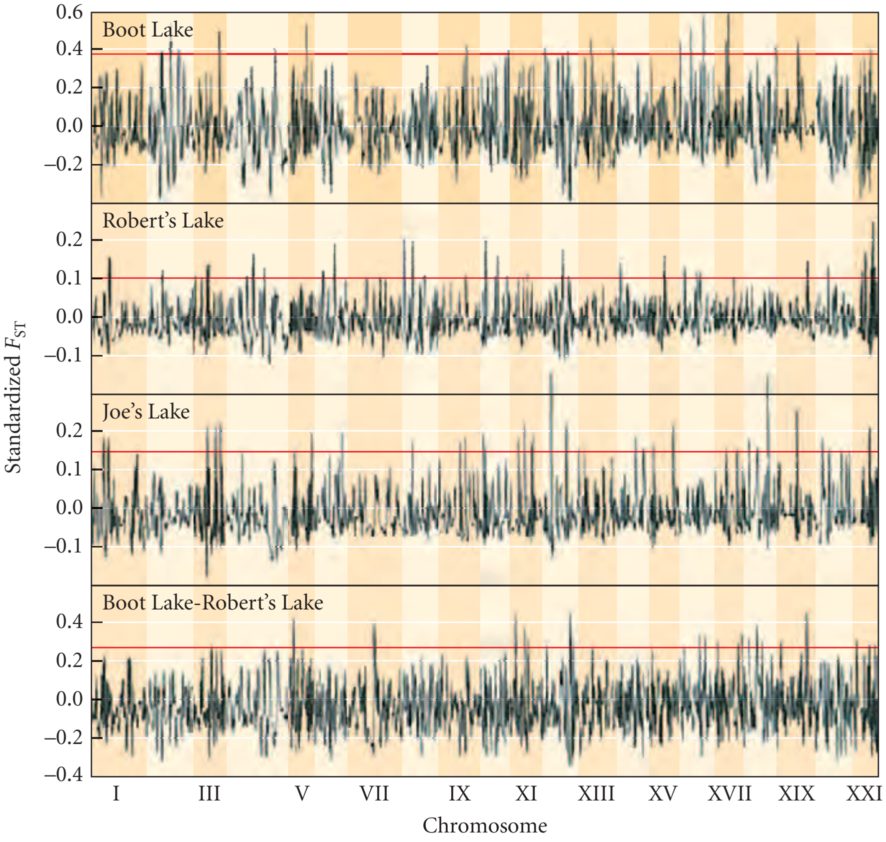
Parapatric speciation

Parapatric speciation can theoretically occur if gene flow between populations that occupy adjacent regions with different selective pressures is weaker than divergent selection for different gene combinations (Endler 1977; Gavrilets 2004). Hybrids may have low fitness, and individuals with the "wrong" genotype or phenotype that migrate across the border may fail to survive and reproduce (Nosil et al. 2005). Consequently, clines at various loci may tend to develop at the same location, resulting in a primary hybrid zone that has developed in situ, but may look like a secondary hybrid zone (Endler 1977; Barton and Hewitt 1985). Steady genetic divergence may eventually result in complete reproductive isolation.

Another possibility is that populations separated by distance can evolve reproductive incompatibility, even though the species is distributed throughout the intervening region. Divergent features that arise at widely separated sites in the species' distribution may spread, supplanting ancestral features as they travel and preventing gene exchange when they eventually meet. Russell Lande (1982) has theorized that prezygotic isolation could arise in this way as a result of divergent sexual selection.

Parapatric speciation undoubtedly occurs and may even be common, but it has been difficult to demonstrate that it provides a better explanation than allopatric speciation for real cases (Coyne and Orr 2004). An example of parapatric divergence is provided by three-spined sticklebacks (*Gasterosteus aculeatus*) in four lakes, each with an outlet stream, on Vancouver Island in western Canada (Roesti et al. 2012). Even though there is no external barrier to movement between lake and stream subpopulations, the subpopulations differ adaptively in several morphological features. (Studies of other populations of sticklebacks have shown that morphologically different forms are often sexually isolated to some degree; see Figure 18.9.) A genome scan revealed that genetic differences between lake and stream populations were most pronounced in central chromosome regions where the recombination rate is low, and that, even taking this into account, the lake/stream pairs were highly divergent at many genomic sites (**Figure 18.21**). Thus there exists extensive genetic divergence, despite gene flow, caused by selection at many sites. It is difficult to determine whether the divergence occurred in the face of gene flow, or in allopatric populations that subsequently met and interbred.

FIGURE 18.21 Genomic differentiation among parapatric and allopatric populations of sticklebacks. Each of the four panels shows differentiation between two samples along all 21 chromosomes. The vertical marks indicate values of F_{ST}, a measure of the difference in frequency of SNPs, at each variable site found on a chromosome. (These values were standardized to correct for differences in F_{ST} caused by location within a chromosome.) In each panel, marks that rise above the horizontal red line are sites with significantly different frequencies between the samples. The upper three panels show genomic differences between parapatric pairs of populations in three lakes and their connected streams. The lowest panel contrasts allopatric populations, in two lakes. Despite gene flow, the parapatric populations show about as many genetic differences as the allopatric populations. (After Roesti et al. 2012.)



Sympatric speciation

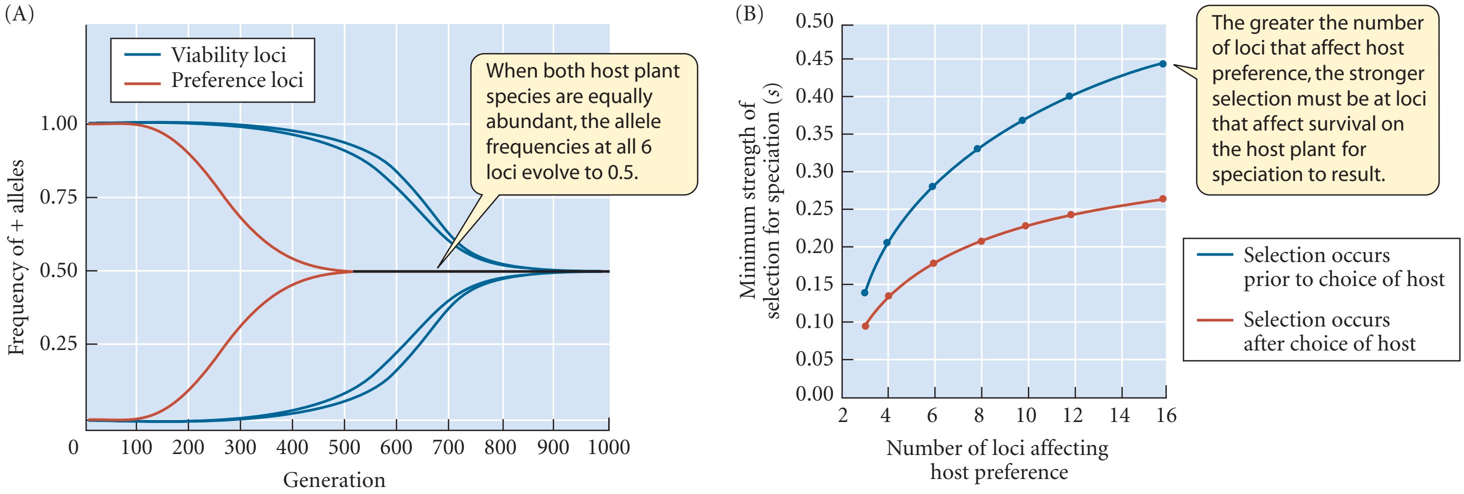
Sympatric speciation is a highly controversial subject. Speciation would be sympatric if a biological barrier to gene exchange arose within an initially randomly mating population without any spatial segregation of the incipient species—that is, if speciation occurred despite high initial gene flow. The difficulty any model of sympatric speciation must overcome is how to establish linkage disequilibrium among a set of genes that together confer reproductive isolation: in other words, how to reduce the frequency of the intermediate genotypes that would act as a conduit of gene exchange between the incipient species. Ernst Mayr (1942, 1963), the most vigorous and influential critic of the sympatric speciation hypothesis, showed that many supposed cases are unconvincing and that the hypothesis must overcome severe theoretical difficulties. Under certain special circumstances, however, these difficulties are not all that severe (Turelli et al. 2001; Gavrilets 2004; Bolnick and Fitzpatrick 2007).

MODELS OF SYMPATRIC SPECIATION Most models of sympatric speciation postulate disruptive (diversifying) ecological selection (see Chapter 12) at one or several loci at which different alleles confer adaptation to two distinct resources. For example, different homozygous genotypes (say, A_1A_1 and A_2A_2) might have high fitness on one or the other of two resources, and intermediate (heterozygous A_1A_2) phenotypes might have lower fitness because they are not as well adapted to either resource. In some cases (Servedio et al. 2011), the selected ecological trait is a "magic trait" (Gavrilets 2004) that also creates reproductive isolation. For example, differences in the color or form of flowers that serve to attract different pollinators (as in the monkeyflowers shown in Figure 17.6) are adaptations that may also cause reproductive isolation. Similarly, if a species of herbivorous insect has the habit of finding mates on its preferred host plant, different genotypes that prefer different host plants will tend to be reproductively isolated (Bush 1969).

Alternatively, selection may favor not only ecologically adaptive alleles (such as A_1 and A_2), but also alleles, at different loci, that tend to make their carriers mate nonrandomly, if this would result in their having fewer poorly adapted heterozygous offspring. (This model is somewhat similar to reinforcement.) If such alleles increased in frequency, and if an association (linkage disequilibrium) between alleles at the ecological trait loci and the mating locus (say, M_1 and M_2) were to develop, the result would be two partially reproductively isolated populations (say, $A_1A_1M_1M_1$ and $A_2A_2M_2M_2$) that are adapted to different resources. This would be a step toward speciation (but only a step, because the single M locus would provide only partial premating isolation, and more such loci would be required to complete the process.) Two models of nonrandom mating have been considered: (1) **assortative mating**, in which individuals prefer mates that match their own phenotype, and (2) trait-preference, in which different genes control a female preference and a male trait (as in most sexual selection models; see Chapter 15).

Progress toward sympatric speciation is theoretically somewhat more likely if there is divergence in a "magic trait" that affects ecological divergence and automatically restricts interbreeding. In computer simulations of an insect in which some loci affect host plant preference and others affect physiological adaptation to the different plants, the frequencies of both kinds of alleles may rapidly increase (**Figure 18.22A**), and gene flow may be strongly reduced, so that the population divides into two host-associated, ecologically isolated incipient species. However, if host preference is a continuous, polygenic trait, reproductive isolation will not evolve unless selection is strong (**Figure 18.22B**). Somewhat similar models describe sympatric speciation by adaptation to a continuously distributed resource, such as prey size (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). Some authors have questioned how realistic these models are (Coyne and Orr 2004; Gavrilets 2004).

EVIDENCE FOR SYMPATRIC SPECIATION The conditions required for sympatric speciation to occur are theoretically more limited than those for allopatric speciation, and



When both host plant species are equally abundant, the allele frequencies at all 6 loci evolve to 0.5.

The greater the number of loci that affect host preference, the stronger selection must be at loci that affect survival on the host plant for speciation to result.

FIGURE 18.22 Some results of a computer simulation of sympatric speciation in an insect that mates on its host plant. (A) Alleles that enhance survival on or preference for one host plant species are referred to as "+ alleles"; those that have the complementary effect are called "– alleles." The simulation shows changes in the frequency of the + allele at four loci that affect survival (viability loci) and two loci that affect host preference (preference loci) when the + allele at each locus begins with a frequency near 0 or 1. Eventually, half the population prefers and survives better on one host and half on the other, representing progress toward reproductive isolation. (B) These curves show how strong selection at viability loci has to be to result in speciation when preference is controlled by multiple loci. The strength of selection at each viability locus is *s* (the coefficient of selection; see Chapter 12). The two curves model life histories in which selection occurs before and after the choice of host occurs. (After Fry 2003.)

sympatric speciation does not occur easily (Gavrilets 2004). Ecological and genetic research can help to determine whether or not conditions are favorable for sympatric speciation in specific groups of organisms (Bolnick and Fitzpatrick 2007). However, because there is so much evidence for allopatric speciation, sympatric speciation must be demonstrated, rather than assumed, for most groups of organisms. Demonstrating sympatric speciation is quite difficult because evidence must show that a past allopatric phase of genetic differentiation is very unlikely (Coyne and Orr 2004). However, many possible examples, supported by varying degrees of evidence, have been proposed.

Just as allopatric speciation results from division in space, ALLOCHRONIC speciation might result from division in time (i.e., if the breeding season of a population becomes divided). For example, in Japanese sites with mild winters, the moth *Inurois punctigera* breeds throughout the winter, and moths breeding from November to March show little difference in genetic composition. In contrast, populations in sites with very cold winters consist of genetically different subpopulations that mate in early winter and in late winter (Yamamoto and Sota 2009).

"Host races" of specialized herbivorous insects—partially reproductively isolated subpopulations that feed on different host plants—have often been proposed to represent sympatric speciation in progress, although the evidence for this is limited (Futuyma 2008). The most renowned case, studied first by Guy Bush (1969) and later by Jeffrey Feder and colleagues (2005), is that of the apple maggot fly (*Rhagoletis pomonella*). The larvae develop in ripe fruits and overwinter in the ground as pupae; adult flies emerge in July and August and mate on the host plant. The major ancestral host plants throughout eastern North America were hawthorns (*Crataegus*). About 150 years ago, *R. pomonella* was first recorded in the northeastern United States as a pest of cultivated apples (*Malus*), and infestation of apples spread from there. Allele frequencies at many loci differ significantly between apple- and hawthorn-derived flies, showing that gene exchange between them is limited

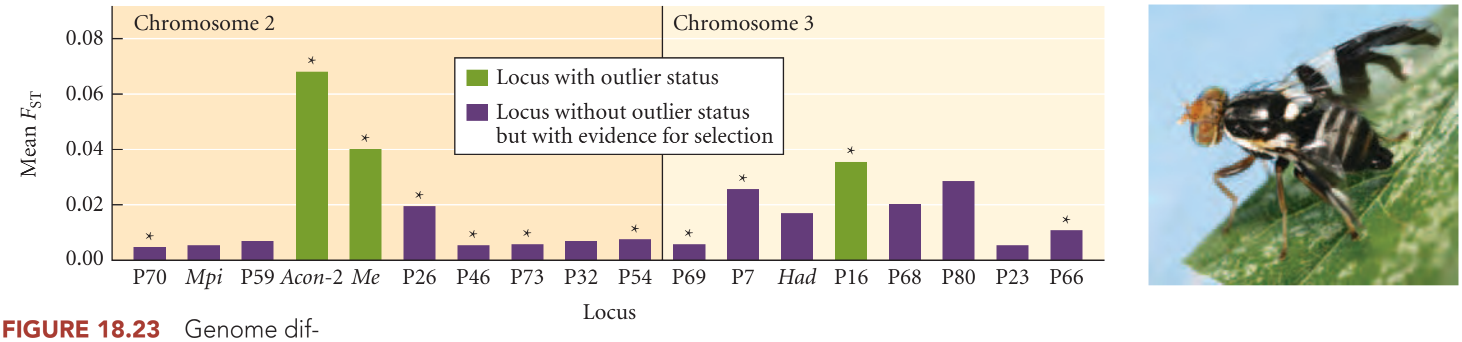


FIGURE 18.23 Genome differences in the apple maggot fly (*Rhagoletis pomonella*), in which populations associated with different host plants have diverged by natural selection. The difference in allele frequency between the populations is measured as F_{ST} for several loci on each of two chromosomes. Similar patterns were found for loci on the other chromosomes. Loci that were statistically distinguishable from neutral differences are shown in green. The purple bars with asterisks below them represent marked regions of the genome that differ less in frequency, but which were shown in two experiments to affect survival in environments corresponding to the different host plants. Bars without asterisks are loci that have significantly different allele frequencies in the two host species. (After Michel et al. 2010.)

(**Figure 18.23**). Gene exchange is reduced (to about 2 percent) by several factors, including a difference in host preference (for apples versus hawthorns) that appears to be based on differences at about four loci (Feder and Forbes 2008), and a difference of about 3 weeks between breeding activity on apple and on hawthorn, corresponding to a difference in the fruiting time of these plants. Because of this timing difference, larvae and pupae in apples experience higher temperatures and a longer pupal period than hawthorn flies. Experiments showed that these differences impose strong divergent selection at several loci (Filchak et al. 2000). Although divergence in host preference presumably occurred in sympatry, the earlier development time evolved in hawthorn-feeding populations in Mexico and was fortuitously advantageous for development on apples (Michel et al. 2007). Thus incipient speciation in this case has had both geographic and sympatric components.

Probably the best-documented examples of sympatric speciation are sister species that inhabit small isolated islands where there has been no opportunity for spatial separation. Several genera of plants conform to this criterion on Lord Howe Island, east of Australia (**Figure 18.24**; Savolainen et al. 2006; Papadopulos et al. 2011). A similar example has been described in two groups of cichlid fishes that are confined to two small crater lakes (Schliewen et al. 1994). Mitochondrial DNA sequence data indicate that the cichlid species in each lake are monophyletic, suggesting that speciation has occurred within the crater lakes. The lakes lie in simple conical basins that lack habitat heterogeneity and opportunity for spatial isolation. It has often been suggested that the enormous diversity of cichlid fishes in the African Great Lakes (see Figure 3.24) arose by sympatric speciation, but there are plentiful opportunities for allopatric speciation within each lake because these sedentary

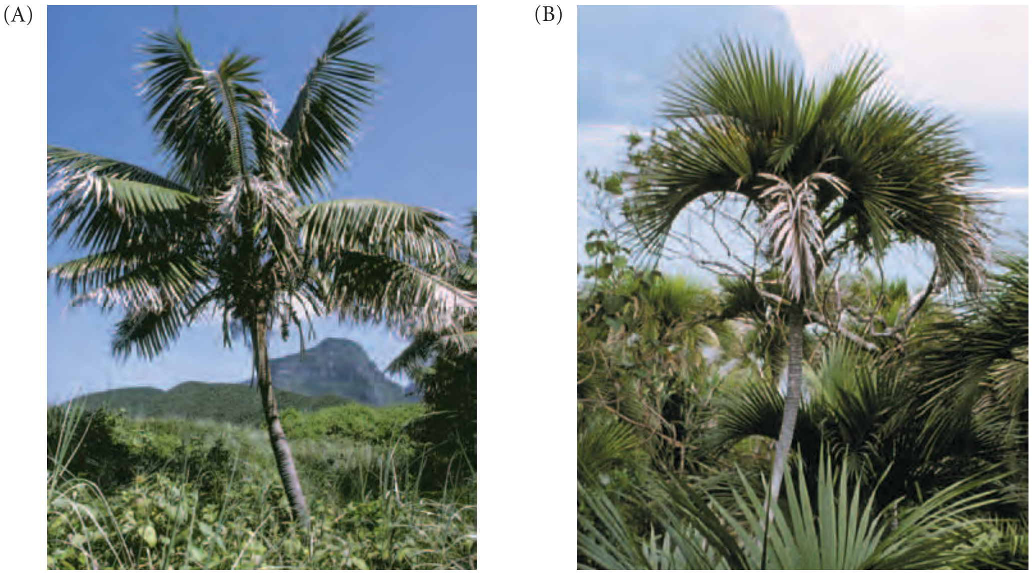


FIGURE 18.24 Sister species of palms on Lord Howe Island, which is less than 12 square kilometers in area. (A) *Howea forsteriana* (kentia palm) has straight leaves with drooping leaflets. (B) *H. belmoreana* (curly palm) has curved leaves with ascending leaflets. (Photos courtesy of W. J. Baker, Royal Botanic Gardens, Kew.)

species are restricted to distinct, discontinuously distributed habitats along the lake periphery. Conspecific populations of these cichlids differ genetically, even over short distances (Rico et al. 2003), suggesting that spatial separation has played a role in their speciation.

Polyploidy and Recombinational Speciation

Polyploidy

A POLYPLOID is an organism with more than two complements of chromosomes (see Chapter 8). A tetraploid, for example, has four chromosome complements in its somatic cells; a hexaploid has six. Polyploid populations are reproductively isolated by postzygotic barriers from their diploid (or other) progenitors, and are therefore distinct biological species. Speciation by polyploidy is the only known mode of instantaneous speciation by a single genetic event.

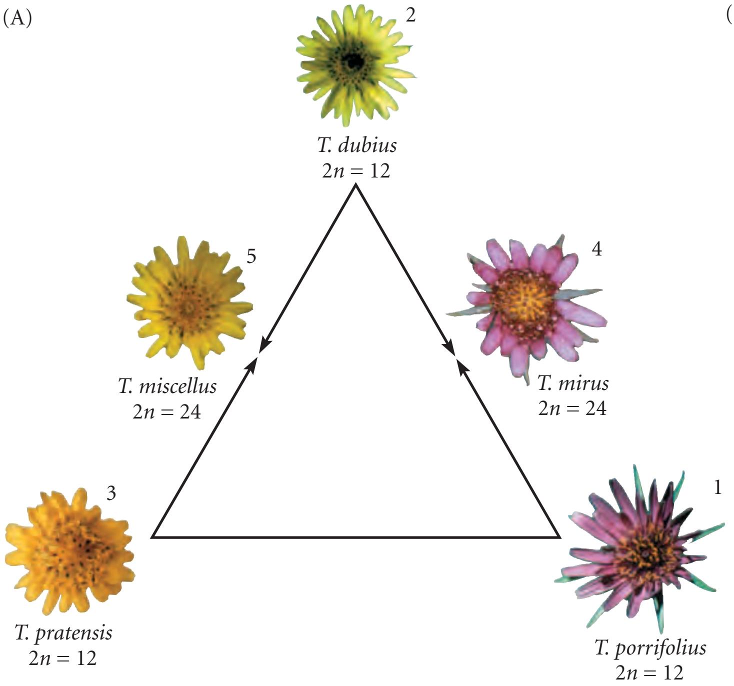
For reasons that are not well understood, polyploid species are rare among sexually reproducing animals, although many parthenogenetic polyploid animals have been described. Polyploidy is very common in plants. Perhaps 30 to 70 percent of plant species are descended from polyploid ancestors (Otto and Whitton 2000), and polyploidy accompanies about 15 percent of speciation events in flowering plants and 31 percent in ferns (Wood et al. 2009). Natural polyploids span a continuum between two extremes, called autopolyploidy and allopolyploidy. An AUTOPOLYPLOID is formed by the union of unreduced gametes from genetically and chromosomally compatible individuals that may be thought of as belonging to the same species. The cultivated potato (*Solanum tuberosum*), for example, is an autotetraploid of a South American diploid species. An ALLOPOLYPLOID is a polyploid derivative of a diploid hybrid between two species.

SPECIATION BY POLYPLOIDY Polyploidy usually occurs because of a failure of the reduction division in meiosis (Ramsey and Schemske 1998). For example, the union of an unreduced ($2n$) gamete with a haploid (n) gamete yields a triploid ($3n$) individual; a tetraploid is then formed if an unreduced $3n$ gamete unites with a reduced (n) gamete. Plants with odd-numbered ploidy (e.g., triploids, $3n$, and pentaploids, $5n$) are generally nearly sterile because most of their gametes are aneuploid. Because the hybrid between a tetraploid and its diploid ancestor would be triploid, the tetraploid is reproductively isolated and is therefore a distinct biological species (and the same is true at higher ploidy levels).

A milestone in the study of speciation was the experimental production of a natural polyploid species by Arne Müntzing in 1930. Müntzing suspected that the mint *Galeopsis tetrahit*, with $2n = 32$ chromosomes, might be an allotetraploid derived from the diploid ($2n = 16$) ancestors *G. pubescens* and *G. speciosa*. By crossing these species and selecting among their hybrid descendants, Müntzing obtained tetraploid offspring that closely resembled *G. tetrahit* in morphology, were highly fertile, and were reproductively isolated from the diploid species, but yielded fertile progeny when crossed with wild *G. tetrahit*.

In this and some other experimental studies of allopolyploids, diploid hybrids between species are mostly sterile and form few bivalents in meiosis, whereas the tetraploid offspring of these hybrids are highly fertile and have normal, bivalent chromosome pairing. In these cases, *the sterility of the diploid hybrid is not due to functional interactions between the genes of the two parent species, but instead to the mechanisms that inhibit chromosome pairing.* The diploid and tetraploid hybrids have the same genes in the same proportions, so genic differences cannot account for the sterility of the one but not the other (Darlington 1939; Stebbins 1950).

Molecular studies have cast additional light on the origin of polyploid species. For example, three diploid European species of goatsbeards (Asteraceae), *Tragopogon dubius*, *T. porrifolius*, and *T. pratensis*, have become broadly distributed in North America. F_1 hybrids between them have low fertility. In 1950, Marion Ownbey described two fertile tetraploid species, *T. mirus* and *T. miscellus*, and postulated that *T. mirus* was a recent tetraploid hybrid of *T. dubius* and *T. porrifolius*, and that *T. miscellus* was likewise derived from *T. dubius* × *T.*



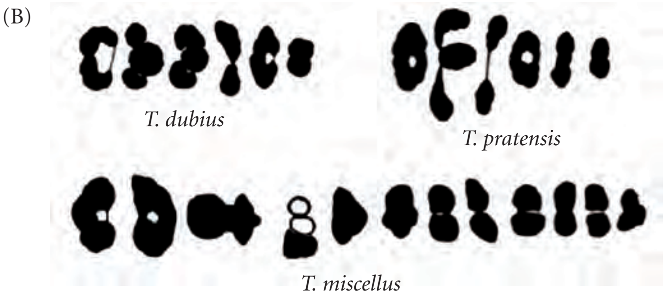
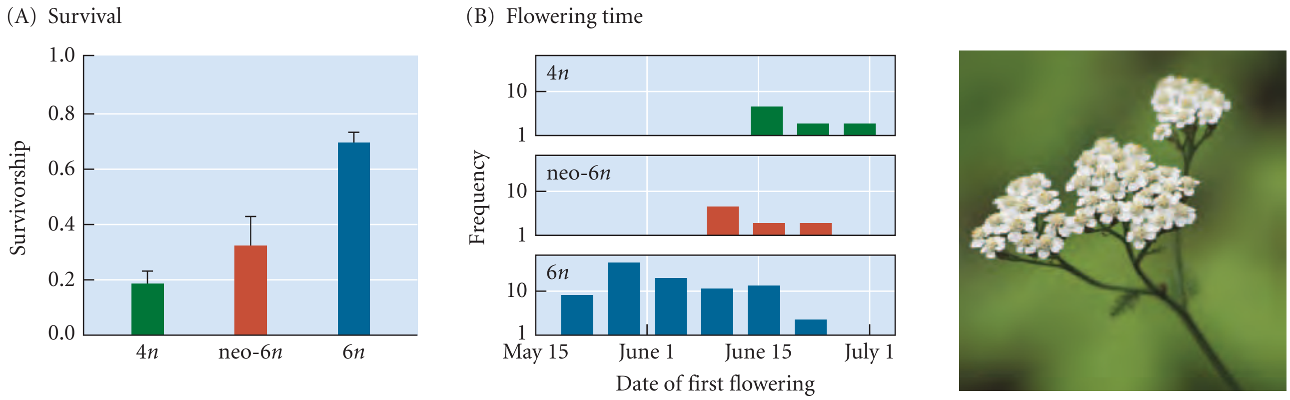


FIGURE 18.25 Allotetraploid species of goatsbeards (*Tragopogon*). (A) The flower heads of the diploid species *T. porrifolius* (1), *T. dubius* (2), and *T. pratensis* (3) and of the fertile tetraploid species *T. mirus* (4, from 1 × 2) and *T. miscellus* (5, from 2 × 3). (B) Drawings of the chromosomes of the diploids *T. dubius* and *T. pratensis* and of their tetraploid hybrid derivative, *T. miscellus*. The tetrapoid has twice as many chromosomes as the diploid species. (A from Pires et al. 2004; B from Ownbey 1950.)

FIGURE 18.26 Differences between a newly formed polyploid and its ancestor may confer ecological differences that could reduce the opportunity for crossing between them. Survival (A) and flowering time (B) of a newly originated hexaploid (neo-6*n*) yarrow (*Achillea*), planted in a dry dune, were intermediate between its tetraploid parent (4*n*) and an existing hexaploid (6*n*) species. (After Ramsey 2011.)



pratensis (**Figure 18.25**). Decades later, Douglas Soltis, Pamela Soltis, and their collaborators (2004) found that the tetraploid species have exactly the combinations of DNA markers from the diploid species that are predicted by Ownbey's hypothesis. In *Tragopogon* and other plants, allopolyploid species have typically arisen independently several times by hybridization between their diploid parents (Pires et al. 2004).

ESTABLISHMENT AND FATE OF POLYPLOID POPULATIONS How polyploid species become established is not fully understood. If a newly arisen tetraploid within a diploid population crosses at random, its reproductive success is expected to be lower than that of the diploids because many of its offspring will be inviable or sterile triploids, formed by backcrossing with the surrounding diploids. A study of mixed experimental populations of diploid and tetraploid fireweeds (*Chamerion angustifolium*) showed that the lower the frequency of tetraploids in the population, the lower their seed production, as a result of increased pollination from the diploids (Husband 2000).

Several conditions—self-fertilization, vegetative propagation, higher fitness than the diploid, or ecological and habitat segregation from the diploid—might enable a new polyploid to increase and form a viable population (Fowler and Levin 1984; Rodríguez 1996). Indeed, many polyploid taxa reproduce by selfing or vegetative propagation, and most differ from their diploid progenitors in habitat and distribution, and so would be segregated from them. Increases in ploidy alter cell size, water content, rate of development, and many other physiological properties (Levin 1983; Otto and Whitton

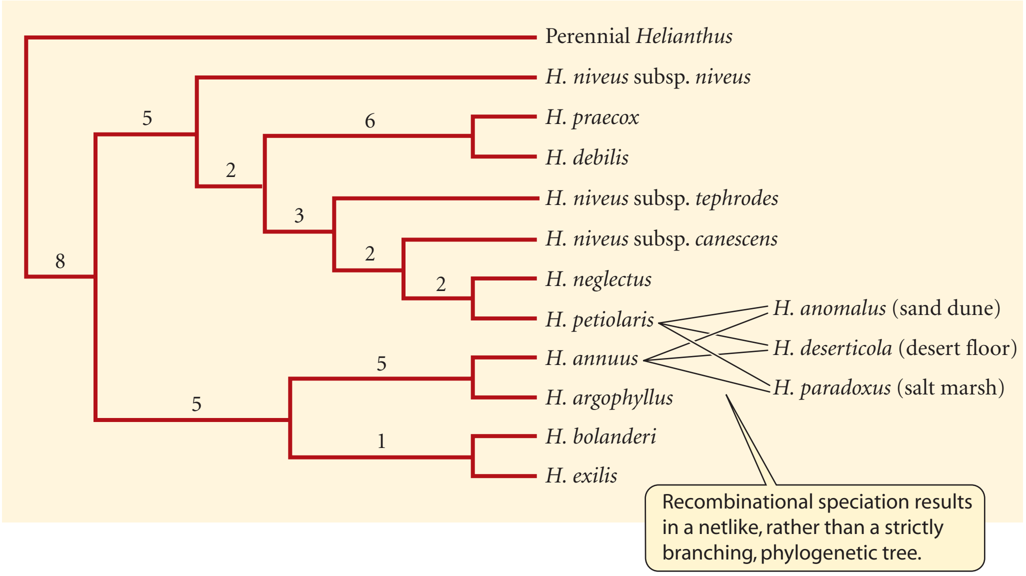
2000). But do polyploids display such differences from diploids when they are first formed? If the yarrow *Achillea borealis* is representative, the answer is yes. In California, tetraploids and hexaploids grow in wetter and drier habitats, respectively. Justin Ramsey (2011) planted seedlings of both forms, as well as "neohexaploids" that had originated de novo from tetraploid parents, in dry dunes. The neohexaploids survived better and flowered earlier than the tetraploids (**Figure 18.26**), showing that they would be partly isolated from the tetraploids, by habitat and flowering time, immediately upon their origin.

Because it apparently confers new physiological and ecological capabilities, polyploidy may play an important role in plant evolution; moreover, the increased number of genes in polyploids may enhance their adaptability (Otto and Whitton 2000). However, polyploidy does not confer major new morphological characteristics, such as differences in the structure of flowers or fruits, and it seems unlikely to cause the evolution of new genera or other higher taxa (Stebbins 1950).

Recombinational speciation

Hybridization sometimes gives rise not only to polyploid species, but also to distinct species with the same ploidy as their parents. Among the great variety of recombinant offspring produced by F_1 hybrids between two species, certain genotypes may be fertile but reproductively isolated from the parent species. These genotypes may then increase in frequency, forming a distinct population (Rieseberg 1997; Gross and Rieseberg 2005). This process has been called **recombinational speciation** or HYBRID SPECIATION (Grant 1981).

Hybrid speciation seems to be more common in plants than in animals (Rieseberg 1997; Mallet 2007). In a molecular phylogenetic analysis of part of the sunflower genus, *Helianthus*, Loren Rieseberg and coworkers found that hybridization between *Helianthus annuus* and *H. petiolaris* has given rise to three other distinct species (*H. anomalus*, *H. paradoxus*, and *H. deserticola*; **Figure 18.27**). Although F_1 hybrids between the parent species have low fertility, the derivative species are fully fertile and are genetically isolated from the parent species by postzygotic incompatibility. The recombinant species grow in very different (drier or saltier) habitats than either parent species, flower later, and have unique morphological and chemical features. *H. anomalus*, for example, has thicker, more succulent leaves and smaller flower heads than either parent species. Such "extreme" traits transgress the range of variation between the two parent species. Rieseberg and coworkers (2003) crossed *H. annuus* and *H. petiolaris*, the parent species, and grew the backcross progeny in a greenhouse for several generations. Using genetic markers on all the chromosomes, they found



Recombinational speciation results in a netlike, rather than a strictly branching, phylogenetic tree.

FIGURE 18.27 The hybrid origin of some diploid species of sunflowers. The phylogeny, based on sequences of chloroplast DNA and nuclear ribosomal DNA, shows that *Helianthus anomalus*, *H. paradoxus*, and *H. deserticola* have arisen from hybrids between *H. annuus* and *H. petiolaris*. The numbers of synapomorphic base pair substitutions are shown along the branches of the phylogenetic tree. (After Gross and Rieseberg 2005.)

that the experimental hybrids had combinations of *annuus* and *petiolaris* chromosome segments that matched those found in the three hybrid species—confirming that those species indeed arose from hybridization. Almost all the extreme, "transgressive" traits of *H. anomalus* and the other two hybrid species, such as small flower heads, occurred among the experimentally produced hybrids. To a considerable degree, then, the hybridization experiment replayed the origin of these species.

How Fast Is Speciation?

The phrase "rate of speciation" has several meanings (Coyne and Orr 2004). One is the duration of the process, or **time for speciation** (**TFS**)—the time required for (nearly) complete reproductive isolation to evolve once the process has started. Another is the BIOLOGICAL SPECIATION INTERVAL (BSI), the average time between the origin of a new species and when that species branches (speciates) again. The BSI includes not only the TFS, but also the "waiting time" before the process of speciation begins again. For example, in a clade that speciates by polyploidy, a new polyploid species may originate rarely (i.e., the waiting time, and therefore the BSI, is long), but when it does, reproductive isolation is achieved within one or two generations (the TFS is very short).

The diversification rate, R, or increase in species number per unit time, equals the difference between the rates of speciation (S) and extinction (E). R can be estimated for a monophyletic group if the age of the group (t) can be estimated and if we assume that the number of species (N) has increased exponentially according to the equation

$$N_t = e^{Rt}$$

(We encountered this approach in Chapter 7 when we considered long-term rates of diversification in the fossil record.) The average time between branching events on the phylogeny is $1/R$, the reciprocal of the diversification rate. This number estimates the BSI, the average time between speciation events, if we assume there has been no extinction ($E = 0$). According to estimates made using this approach, BSI in animals ranges from less than 0.3 My (in the phenomenal adaptive radiation of cichlid fishes in the African Great Lakes) to more than 10 My in various groups of molluscs. When estimates of E from the fossil record are taken into account, BSI is about 3 My for horses and is still very long (6–11 My) for bivalve molluscs.

An upper bound on TFS can be estimated if geological evidence or calibrated DNA sequence divergence enables us to judge when young pairs of sister species were formed. For example, endemic species of *Drosophila* have evolved on the "big island" of Hawaii, which is less than 800,000 years old. Two research groups that used the sequence divergence of mitochondrial DNA to measure TFS disagreed on the average time since sister species of North American birds diverged, but agreed that some originated since the Pleistocene epoch began (**Figure 18.28**). By correlating the degree of prezygotic or postzygotic reproductive isolation with estimated divergence time (see Figures 17.9 and 17.10), Coyne and Orr (1997) estimated that complete reproductive isolation takes 1.1 to 2.7 My for allopatric species of

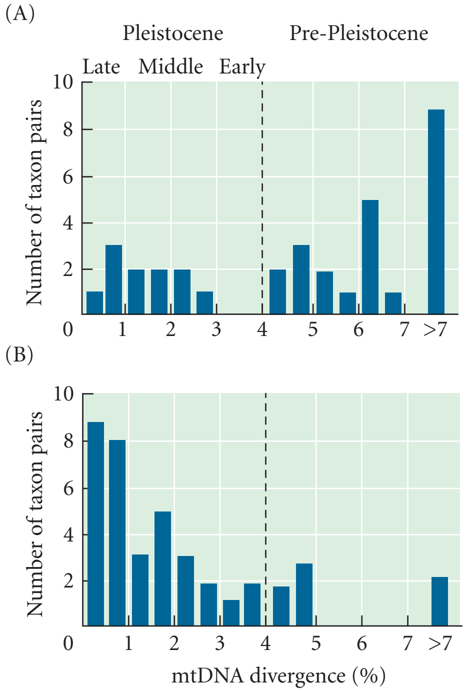


FIGURE 18.28 Two estimates of mitochondrial DNA divergence between pairs of closely related North American songbirds. Assuming that the sequence divergence rate of mtDNA is 2 percent per My, less than 4 percent sequence divergence suggests that speciation occurred during the Pleistocene, and that TFS is less than 2 My. (Since the time of these studies, the beginning date of the Pleistocene has been revised from 1.8 Mya to 2.6 Mya.) (A) Data from a study by Klicka and Zink (1997), who concluded that most speciation occurred before the Pleistocene. (B) Data from a study by Johnson and Cicero (2004), who came to the opposite conclusion. Johnson and Cicero argued that their data are based only on sister species and that some of Klicka and Zink's species pairs were not sister taxa. Johnson and Cicero also classified some forms as species that were classified as subspecies by other authors. (After Lovette 2005.)

Drosophila, but only 0.08 to 0.20 My for sympatric species. (They attributed this difference to reinforcement of prezygotic isolation between sympatric forms.) A similar approach suggested that frogs take 1.5 My, on average, to complete speciation (Sasa et al. 1998).

Clearly, time for speciation varies greatly—as we would expect from theories of speciation. We expect the process of speciation to be excruciatingly slow if it proceeds by mutation and drift of neutral alleles; we expect it to be faster if it is driven by ecological or sexual selection, and to be accelerated if reinforcement plays a role. Allopatric speciation could be slow or very rapid, depending on the strength of divergent selection and on genetic variation in relevant traits. Some possible modes of speciation, such as polyploidy, recombinational speciation, and sympatric speciation, should be very rapid when they occur—although they may occur rarely, resulting in long intervals (BSI) between speciation events. As we have already seen, ecological speciation can be rapid (Hendry et al. 2007): substantial reproductive isolation apparently evolved within about a century in the apple maggot fly and the hybrid sunflower species *Helianthus anomalus*. On the other hand, some sister taxa of snapping shrimp (*Alpheus*) on opposite sides of the Isthmus of Panama have not achieved full reproductive incompatibility in the 3.5 My since the isthmus arose (Knowlton et al. 1993).

What characteristics favor high rates of speciation (low BSI)? The best way to approach this question is to compare the species diversity of replicated sister groups that differ in the characteristics of interest (see Figure 18.12), although it is often hard to tell whether those characteristics enhance the speciation rate or diminish the extinction rate. Among the characteristics studied so far, those that seem most likely to have increased the speciation rate as such seem to be animal (rather than wind) pollination in plants and features that indicate intense sexual selection in animals (Coyne and Orr 2004). These observations suggest that diversification in some groups of animals owes more to the simple evolution of reproductive isolation (due to sexual selection) than to ecological diversification. This conclusion may call into question the hypothesis that ecological divergence is the main engine of evolutionary radiation (Schluter 2000).

Consequences of Speciation

The most important consequence of speciation is diversity. For sexually reproducing organisms, every branch in the great phylogenetic tree of life represents a speciation event, in which populations became reproductively isolated and therefore capable of independent, divergent evolution, including, eventually, the acquisition of those differences that mark genera, families, and still higher taxa. Speciation, then, stands at the border between MICROEVOLUTION—the genetic changes within and among populations—and MACROEVOLUTION—the evolution of the higher taxa in all their glorious diversity.

In their hypothesis of punctuated equilibrium, Eldredge and Gould (1972; see also Stanley 1979; Gould and Eldredge 1993) proposed that speciation may be required for morphological evolution to occur at all (see Figure 4.19). They suggested, based on Mayr's (1954) proposal that founder events trigger rapid evolution from one genetic equilibrium to another, that most evolutionary changes in morphology are triggered by and associated with peripatric speciation. However, population geneticists argued (Charlesworth et al. 1982), and Gould (2002) himself conceded, that there is no compelling reason to think that speciation (acquisition of reproductive isolation) triggers morphological evolution. Morphological characters vary among populations of a species, just as they do among reproductively isolated species, and there is little evidence that founder-flush effects account for most speciation.

Nevertheless, evolutionary change often appears to be correlated with speciation. Speciation seems to be associated with morphological evolution in the great majority of lineages of unicellular foraminiferans (see Figure 4.3), which have a detailed enough fossil record to distinguish cladogenesis from anagenesis (Strotz and Allen 2013). Moreover, the rate of evolution of a lineage, and therefore the amount of evolutionary change from the root of a phylogenetic tree to any extant species (PATH LENGTH), is expected to increase

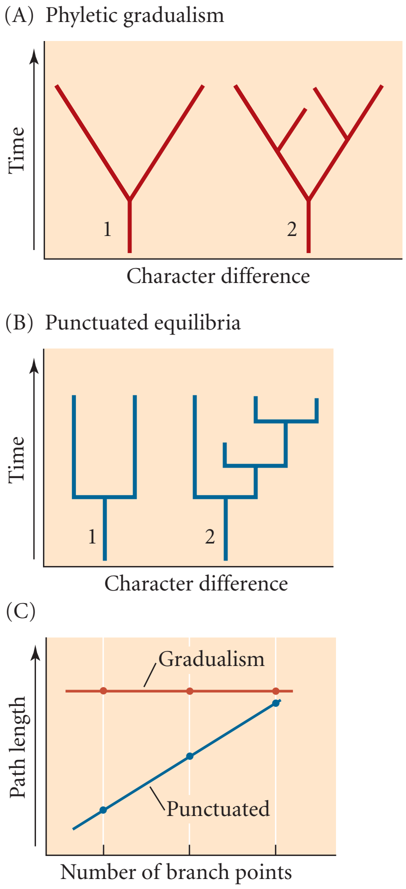


FIGURE 18.29 Models of (A) phyletic gradualism and (B) punctuated equilibria suggest how phylogenetic data might be used to determine whether speciation is associated with enhanced evolution of molecular or morphological characters. In both models, lineages 1 and 2 differ in the number of speciation events (branch points). With phyletic gradualism, the variation among living species (character difference) and the amount of evolutionary change from the root to any living species (path length) are not affected by the number of speciation events. The correlation between path length and number of branch points in the phylogeny is expected to be zero, as indicated by the horizontal line in (C). In the punctuated equilibria model, character evolution occurs only at speciation, so the variation among living species, and thus the path length, is expected to be correlated with the number of branch points. Note that if some species have become extinct, as illustrated, the number of branch points in the phylogeny of extant species will underestimate the number of speciation events. (C after Pagel et al. 2006.)

with the number of speciation events in the punctuated equilibrium model, but not in the phyletic gradualism model (**Figure 18.29**). Mark Pagel and colleagues (2006) found that in 27 percent of the phylogenies of animals, fungi, and plants, path lengths, as measured by numbers of nucleotide substitutions, were significantly correlated with the number of species, as predicted if speciation accelerates evolution. In a related approach, Tiina Mattila and Folmer Bokma (2008) concluded that speciation explains more than two-thirds of the variance in body mass among species of mammals, and that gradual evolution accounts for little variation. Perhaps as a consequence, the body sizes of terrestrial vertebrates show almost no accumulated change in less than a million years, even though size is genetically variable and can evolve rapidly over very short intervals (**Figure 18.30**; Uyeda et al. 2011). Evidently, most such short-term changes are impermanent fluctuations.

What might cause these patterns? Morphological change might be associated with speciation because reproductive isolation enables morphological differences between populations to persist in the long term (Futuyma 1987; Eldredge et al. 2005). Although different local populations may diverge rapidly as a result of selection, local populations are ephemeral: as climate and other ecological circumstances change, divergent populations move about and come into contact sooner or later. Much of the divergence that has occurred may then be lost by interbreeding—unless reproductive isolation has

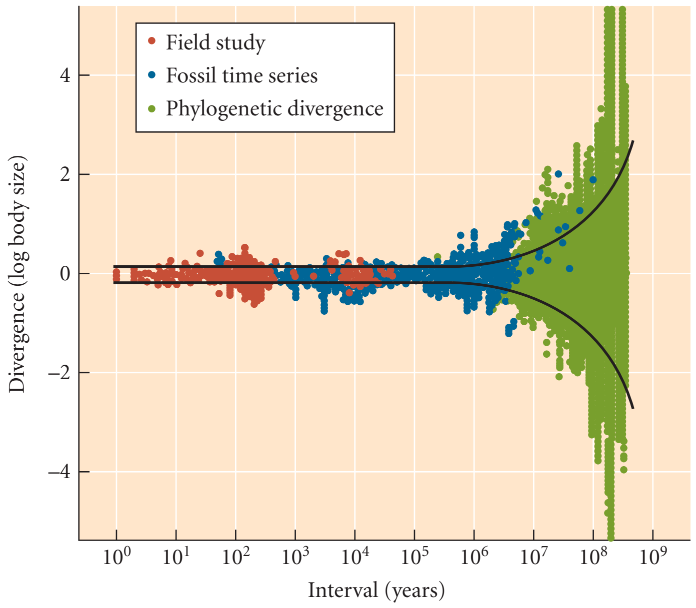
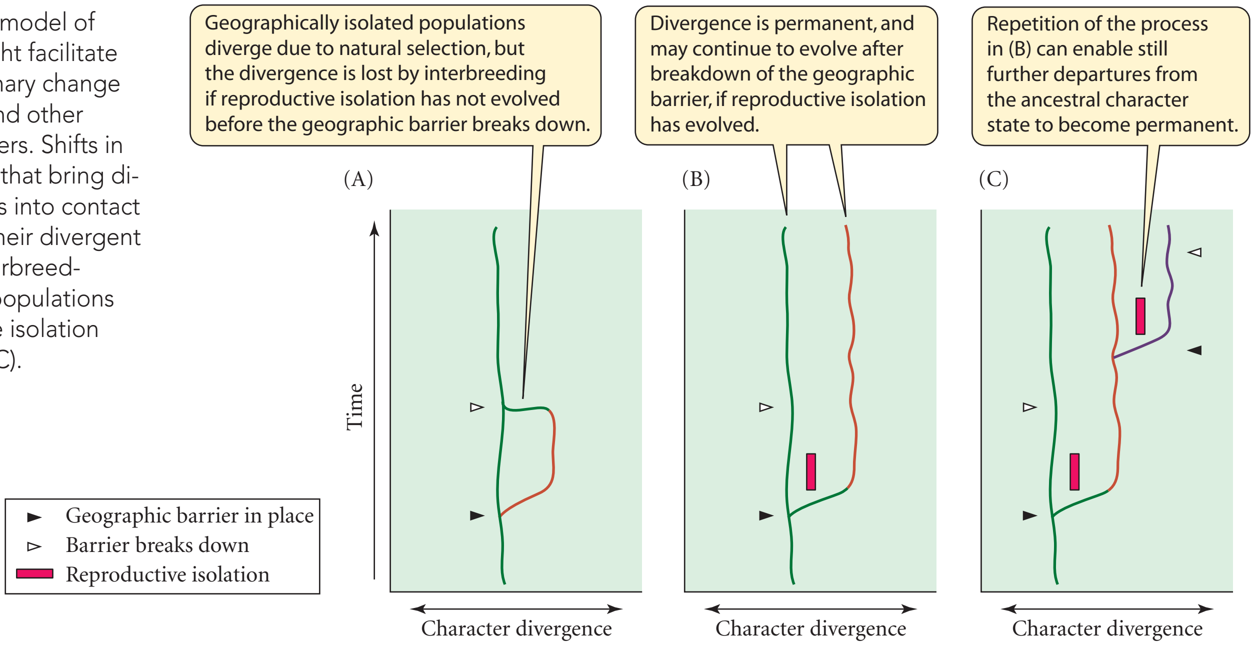


FIGURE 18.30 The amount of evolutionary change in body size in various terrestrial vertebrates, in relation to the elapsed time between samples. Using the change in the logarithm of size standardizes for absolute size (enabling comparison of evolutionary changes in mice with those in elephants). The key shows the kind of data used (field study of recent and contemporary changes; the fossil record; and divergence inferred from time-calibrated phylogenies of living species). Even though rates of change are high on short time scales (see Figure 4.23), little change accumulates before about a million years. (From Uyeda et al. 2011.)

FIGURE 18.31 A model of how speciation might facilitate long-term evolutionary change in morphological and other phenotypic characters. Shifts in geographic ranges that bring divergent populations into contact may cause loss of their divergent features due to interbreeding (A), unless the populations evolve reproductive isolation while allopatric (B, C).


Geographically isolated populations diverge due to natural selection, but the divergence is lost by interbreeding if reproductive isolation has not evolved before the geographic barrier breaks down.

Divergence is permanent, and may continue to evolve after breakdown of the geographic barrier, if reproductive isolation has evolved.

Repetition of the process in (B) can enable still further departures from the ancestral character state to become permanent.

evolved (**Figure 18.31**). A succession of speciation events, each "capturing" further change in a character, may result in a long-term trend. Perhaps, as Ernst Mayr (1963, p. 621) wrote, "Speciation…is the method by which evolution advances. Without speciation, there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution."

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Summary

1. Probably the most common mode of speciation is allopatric speciation, in which gene flow between populations is reduced by geographic or habitat barriers, allowing genetic divergence by natural selection and/or genetic drift.
2. In vicariant allopatric speciation, a widespread species becomes sundered by a geographic barrier, and one or both populations diverge from the ancestral state.
3. In a simple model of the evolution of reproductive isolation, complementary allele substitutions that do not reduce the fitness of heterozygotes occur at two or more loci in one or both populations. Epistatic interactions between alleles fixed in the two populations may reduce the fitness of hybrids formed when the populations meet. Likewise, genetic divergence may result in prezygotic isolation.
4. Reproductive isolation between allopatric populations appears to evolve as a side effect of divergent ecological or sexual selection. Both processes require further study before their relative importance can be assessed. There is no evidence that reproductive isolation evolves by random genetic drift.
5. Prezygotic isolation evolves mostly while populations are allopatric, but may be reinforced when the populations become parapatric or sympatric.
6. Peripatric speciation, or founder effect speciation, is a hypothetical form of allopatric speciation in which genetic drift in a small peripheral population initiates rapid evolution, and reproductive isolation is a by-product of that evolutionary change. It may be especially likely if colonization is followed by rapid population growth, during which genetic drift is reduced and new adaptive gene combinations may be fixed. The likelihood of this form of speciation differs depending on the mathematical model used, and although some possible examples have been described, there is little evidence that this form of speciation is common.
7. Speciation with gene flow, i.e. parapatric or sympatric speciation, may occur if divergent selection is stronger than gene flow. Sympatric speciation—the origin of reproductive isolation within an initially randomly mating population—is controversial. The sympatric evolution of sexual isolation is opposed by recombination among loci affecting mating and loci affecting the disruptively selected character. Sympatric speciation may occur, however, if recombination does not oppose selection. For example, if disruptive selection favors preference for different habitats and if mating occurs within those habitats, prezygotic isolation may result. How often this occurs is debated.
8. Instantaneous speciation by polyploidy is common in plants. Allopolyploid species arise from hybrids between genetically divergent populations. Establishment of a polyploid population probably requires ecological or spatial segregation from the diploid ancestors because backcross offspring have low reproductive success. Polyploid species can have multiple origins.

9. In recombinational (hybrid) speciation, some genotypes of diploid hybrids are fertile and are reproductively isolated from the parent species, and so give rise to new species. This process has been documented more often in plants than in animals.
10. Genomic comparisons of diverging populations and species can be used to locate some of the genetic differences that have been caused by natural selection, including those that underlie reproductive isolation. The number and extent of divergent genomic regions are affected by several factors and vary among species.
11. The time required for speciation to proceed to completion is highly variable. It is shorter for some modes of speciation (polyploidy, recombinational speciation) than others (especially speciation by mutation and drift of neutral alleles that confer incompatibility). The process of speciation may require 2 to 3 My, on average, for some groups of organisms; it is much longer in some cases and very much shorter in others.
12. Speciation is the source of the diversity of sexually reproducing organisms, and it is the event responsible for every branch in their phylogeny. It probably does not stimulate evolutionary change in morphological characters, as suggested by the hypothesis of punctuated equilibria. Rates of evolutionary change may nevertheless be correlated with speciation, perhaps because speciation prevents interbreeding between populations from undoing the changes wrought by natural selection or genetic drift.

Terms and Concepts

allopatric speciation
assortative mating
ecological speciation
founder-flush speciation
parapatric speciation
peripatric speciation
recombinational speciation
reinforcement
reproductive character displacement
sympatric speciation
time for speciation (TFS)
vicariance

Suggestions for Further Reading

As noted in Chapter 17, *Speciation*, by J. A. Coyne and H. A. Orr (Sinauer Associates, Sunderland, MA, 2004), is the most comprehensive recent work on the subject. Those with a mathematical bent will enjoy the wide-ranging treatment of models of speciation by S. Gavrilets in *Fitness Landscapes and the Origin of Species* (Princeton University Press, Princeton, NJ, 2004). An essay by the Marie Curie Speciation Network, "What do we need to know about speciation?" [Butlin et al., *Trends in Ecology and Evolution* 27: 27–39 (2012)], succinctly reviews present knowledge and directions of future research in speciation.

Problems and Discussion Topics

1. Why is it difficult to demonstrate that speciation has occurred parapatrically or sympatrically?
2. Coyne and Orr (1997) found that sexual isolation is more pronounced between sympatric populations than between allopatric populations of the same apparent age, and took this finding as evidence for reinforcement of sexual isolation. It might be argued, though, that any pairs of sympatric populations that were not strongly sexually isolated would have merged, and so would have been unavailable for study. Thus the degree of sexual isolation in sympatric compared with allopatric populations might be biased. How might one rule out this possible bias? (Read Coyne and Orr after suggesting an answer.)
3. Can postzygotic isolation (low hybrid fertility or viability) be reinforced (i.e., accentuated) by natural selection in hybrid zones? Is this a way in which natural selection can reduce mixing between gene pools? See Grant (1966) or Coyne (1974).
4. Suppose that full reproductive isolation between two populations has evolved. Can speciation in this case be reversed, so that the two forms merge into a single species? Under what conditions is this probable or improbable?
5. Referring to the discussion of parallel speciation in sticklebacks, can a single biological species arise more than once (i.e., polyphyletically)? How might this possibility depend on the nature of the reproductive barrier between such a species and its closest relative?
6. The heritability of an animal's preference for different habitats or host plants might be high or low. How might heritability affect the likelihood of sympatric speciation by divergence in habitat or host preference?
7. Biological species of sexually reproducing organisms usually differ in morphological or other phenotypic traits. The same is often true of taxonomic species of asexual organisms such as bacteria and apomictic plants. What factors might cause discrete phenotypic "clusters" of organisms in each case?
8. In many groups of plants, low levels of hybridization between related species are not uncommon, yet only a few cases of the origin of "hybrid species" by recombinational speciation have been documented. What factors make recombinational speciation likely versus unlikely?
9. If speciation occurs by divergent pathways of sexual selection in different populations, what might cause the nature of sexual selection to differ?
10. Genetic drift and natural selection give rise to geographic variation among populations of a species. How do we account, then, for the features that are uniform among all populations of a species? (See Morjan and Rieseberg 2004.)
11. Choose a topic from this chapter and discuss how its treatment would be altered if one adopted a phylogenetic species concept rather than the biological species concept.