# CONSERVATION BIOLOGY
## Evolution in Action

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# 6

# The Importance of Conserving Evolutionary Processes

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Preservation of biodiversity is the primary goal of conservation programs. However, biodiversity is a complex, multifaceted concept that is difficult to define. As a result, developing effective criteria for the measurement of biodiversity has been a challenge and has often been reduced to relying on simple indices. These indices typically include identifying areas for preservation based on levels of endemism, species richness, and degree of threat. Although such a "hotspot" approach is often a valuable first step in ranking regions for preservation, it may fail to capture essential evolutionary processes that promote and sustain diversity. In particular, biodiversity indices may not identify regions where natural and sexual selection have been important in shaping adaptive diversity (Cowling & Pressey, 2001; Crandall et al., 2000; Nicholls, 1998; Smith et al., 1993). In this chapter we illustrate and explore the importance of integrating evolutionary process into conservation decision making. We examine the importance of assessing the roles of natural and sexual selection in promoting adaptive variation and consider how a greater understanding of these evolutionary processes can inform efforts to preserve regional variation in biodiversity.

## HOTSPOT APPROACHES TO PRESERVING BIODIVERSITY

Rank ordering regions for conservation efforts based on species richness, levels of endemism, and degree of threat have figured prominently in efforts to conserve biodiversity (Myers, 2002; Myers et al., 2000a). Using such indices to define hotspots is attractive because obtaining the necessary information is relatively easy, especially for vertebrates with distributions that are relatively well described. Scientists can visit a region, conduct field surveys, tabulate numbers of species, or simply compile existing data sets, and then evaluate levels of threat. For example, Meyer and colleagues (2000a) defined biodiversity hotspots based on levels of endemism and threat with the objective of maximizing the number of species protected per dollar invested, thereby allowing conservation organizations to concentrate efforts in regions of greatest need. In using this approach, they found that 44% of all species of vascular plants and 35% of the vertebrate taxa, including birds, mammals, reptiles, and amphibians, were confined to 25 hotspot areas comprising only 1.4% of the earth's land surface. The hotspot approach, based on levels of endemism

and threat, still determines conservation priorities for some of the major conservation organizations (Mittermeier et al., 1999). Defining hotspots in this way does have advantages; for example, an analysis that rank orders regions can be conducted relatively quickly, with the result that conservation efforts focus on defined geographic regions.

How effective are such indices in capturing biodiversity pattern and process? Do regions defined in terms of endemism also capture regions that are important for species richness? Recent work suggests that the answer to the second question may be no. Orme and colleagues (2005), focusing on birds, examined the congruence of three indices of biodiversity on a worldwide scale. They found that three indices—species richness, richness of threatened species, and endemic species richness—predicted each other poorly. In fact, only 2.5% of hotspot areas were predicted by all three indices, and any single index explained less than 24% of the total variation in the other indices. If taxa other than birds had been included in the analysis (for example, butterflies, trees, and fungi), a scheme that rank orders regions using the aforementioned indices might perform even more poorly (Orme et al., 2005).

Methods to describe and characterize patterns of biodiversity continue to be revised and improved (Ferrier et al., 2000). Priority-setting approaches may now incorporate the concepts of complementarity, which is a measure of the contribution that each area makes to a particular conservation goal (Pressey et al., 1993), and irreplaceability (Pressey et al., 1994), to describe the overall importance of an area to achieving a conservation target. For example, in the succulent Karoo biome of South Africa, irreplaceability has been used to refer to the number of species found only in one particular area and nowhere else (Ferrier et al., 2000; Lombard et al., 1999). Regions with low irreplaceability are less likely to be required for achieving a conservation target, whereas regions of high irreplaceability are likely to be core areas of conservation activity. Although the lexicon of new terms and the analytical approaches for defining patterns of biodiversity expands, there is a growing realization that regions must also be capable of capturing evolutionary processes (Smith et al., 1993).

## THE VALUE OF INTEGRATING EVOLUTIONARY PROCESSES INTO CONSERVATION PRIORITIES

Emphasis on biodiversity pattern does not explicitly consider the processes that preserve adaptive variation and allow populations to evolve with changing environments. Hotspot approaches to species preservation that do not take into account ecological and evolutionary processes are problematic, particularly when applied at small geographic scales. Although it is true that most hotspot approaches are applied across larger geographic scales (Araujo, 2002), preserving populations across uniform habitats such as coniferous forests is analogous to building an investment portfolio made up of a single stock. Conserving populations from diverse habitats may ensure that adaptive variation is maximized. However, a more integrated conservation approach would be to include regions important to the generation and maintenance of biodiversity, regardless of whether these areas harbor endemic species or are particularly rich in species.

With climate change threatening large-scale shifts in species distributions and the habitats on which they depend (Balmford & Bond, 2005), today's hotspots will most certainly shift. Clearly, no approach will be successful unless the effects of multiple stresses from anthropogenic and climatic causes are taken into account. However, by identifying regions in which adaptive variation is maximized, it may be possible to preserve the evolutionary response to changing climate and environmental conditions. Populations are being lost at a much higher rate than species. When populations across diverse habitats go extinct, novel adaptations crucial for meeting future environmental challenges may be lost with them.

New approaches are needed for preserving the adaptive diversity represented by the range of populations within a species, thus ensuring the maximum potential of the species to respond to future environmental conditions. One strategy for preserving the maximum amount of adaptive variation is to identify regions that are particularly important for the generation of new diversity and speciation. But where might such *evolutionary hotspots* occur and what might be their role in promoting natural and sexual selection? These and other questions are discussed in this chapter.

## THE ROLE OF NATURAL SELECTION IN PROMOTING ADAPTIVE DIVERSITY

### By-product Speciation

Given the central role that natural selection plays in producing adaptive variation and biodiversity, it is surprising that conservation efforts have not focused more on conserving features of the environment that promote selection. Recent reviews of the processes that promote speciation suggest a dominant role for natural selection in leading to divergence and the evolution of reproductive isolation (Coyne & Orr, 2004; Schneider, 2000). Natural selection may promote speciation in various ways. One dominant way can be summarized by the term *by-product speciation*, where ecological differences between populations result in divergent selection on morphological, behavioral, or physiological traits. Reproductive isolation is achieved as the by-product of natural selection acting on traits that are associated with pre- or postzygotic isolation (Rice & Hostert, 1993). For example, populations occurring in distinctly different habitats would be expected to experience divergent selection regimes. As populations adapt to their respective habitats, traits important in reproductive divergence are expected to accumulate genetic changes (Coyne & Orr, 2004; Rice & Hostert, 1993). This may happen either via pleiotropy or hitchhiking, where traits important in reproductive isolation are correlated with those on which divergent selection is acting (Rice & Hostert, 1993). Thus, populations from different environments are expected to be more reproductively divergent from one another than populations from similar habitats, regardless of their recent evolutionary histories. This may happen singly, when a population invades a new habitat, or repeatedly, as in the case of parallel speciation, when an ancestral population invades two distinct habitats (Fig. 6.1). Speciation will occur most rapidly with a complete cessation of gene flow, although divergence and speciation is predicted to occur even under moderate levels of gene flow (Gavrilets et al., 2000).

An excellent example of ecologically driven divergence and incipient speciation can be found in the walking-stick insect *Timema* (Nosil et al., 2002). These insects occur in chaparral habitats of the western United States and Mexico where
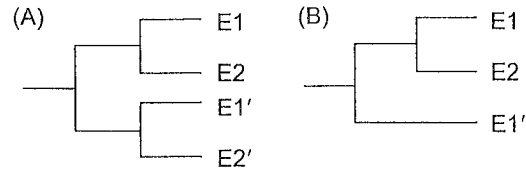


**FIGURE 6.1** (A) Parallel speciation (Schluter, 2000). E1 and E2 represent populations adapted to different ecological environments. The phylogeny shows that different populations adapted to the same ecological environment (for example, E1 and E1′) are more distantly related than populations adapted to different environments (for example, E1 and E2). A role of ecological divergence in the evolution of reproductive isolation is supported by the inequalities RI (E1 × E2) > RI (E1 × E1′) and RI (E1 × E2) > RI (E2 × E2′), where RI is a measure of the reproductive incompatibility (for example, assortative mating and hybrid inviability) between populations. The reverse inequalities would support the role of some mechanism unrelated to the environmental difference under study. Tests can be repeated by comparing RI (E1′ × E2′) with RI (E1 × E1′) and RI (E2 × E2′). (B) In this case, E1′ is ancestral and only a single population (E2) has invaded a new habitat. RI (E1 × E2) > RI (E1 × E1′) would support a role of ecologically driven reproductive isolation. The advantage of the model in (B) is that it does not require repeated colonization events within a taxon and might therefore apply to a greater number of study organisms. The disadvantage of this model is that only one independent comparison of reproductive isolation can be made. Additional independent comparisons could be achieved by repeating the test in (B) across numerous taxa (for example, fish, insects, birds). Combined results would address the general role of ecology versus drift in speciation across taxa. (Modified from Orr and Smith [1998].)

they show a genetically determined color–pattern polymorphism in which different morphs are associated with different host plants. Predation by birds and lizards is intense and has resulted in divergent selection for crypsis on respective host plants. In *T. cristinae*, striped morphs are more common on the chamise, *Adenostoma fasciculatum*; whereas unstriped morphs are more common on the greenbark ceanothus, *Ceanothus spinosus*. Local adaptation to host plants has also resulted in divergence in other morphological traits such as body size and shape, host preference, and resting behavior. Furthermore, phylogenetic analyses indicate
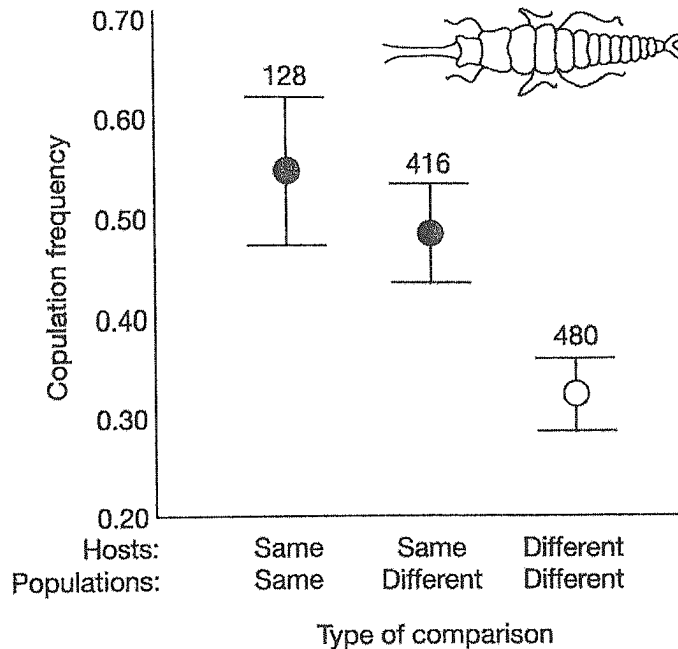
FIGURE 6.2 Copulation frequencies for ecologically similar and different populations of the walking insect *Timema cristinae* on similar and different host plants. Numbers of mating trials for each pairing is shown above each bar. (Modified from Nosil and colleagues [2002].)

that populations using the same host plants do not form monophyletic groups, thus suggesting differentiation and reproductive divergence has occurred repeatedly across the range, revealing a pattern of parallel evolution. Moreover, copulation frequencies are higher for individuals using the same host plants than for individuals using different hosts (Fig. 6.2). Thus, reproductive divergence in *Timema* has apparently evolved as a by-product of adaptation to different hosts (Nosil et al., 2002).

### Divergence with Gene Flow

Another way to assess the role of natural selection in promoting divergence and speciation is to examine divergence in adaptive traits as a function of gene flow. If natural selection is a potent force leading to adaptive divergence and, potentially, to speciation, one would predict that between-habitat differences in adaptive traits would show greater divergence than within-habitat comparisons per unit level of gene flow or genetic distance (Fig. 6.3). A pattern of greater divergence in between-habitat versus within-habitat comparisons is a central prediction

of the divergence-with-gene-flow model of speciation (Rice & Hostert, 1993), a form of by-product speciation in which the likelihood of speciation depends on the magnitude of selection and the level of gene flow. The more intense the selection and the weaker the gene flow, the greater the likelihood of speciation. This model of speciation, which centers on the balance between selection and gene flow, contrasts with the simple dichotomy presented by sympatric and allopatric speciation.

What features of the environment favor speciation? A growing number of studies suggest that ecological gradients play a particularly important role. Ecological gradients, resulting in divergence and incipient speciation, have been implicated in a diverse array of wild populations, including birds (Smith et al., 2005a), fish (Hendry et al., 2002; Lu & Bernatchez, 1999; Maan et al., 2006), and lizards (Calsbeek & Smith, 2003; Jordan et al., 2005; Ogden & Thorpe, 2002; Schneider et al., 1999). In addition, recent theoretical studies (Doebeli & Dieckmann, 2003; Gavrilets, 2000b) indicate that natural selection may be particularly important in leading to divergence along gradients. In the case
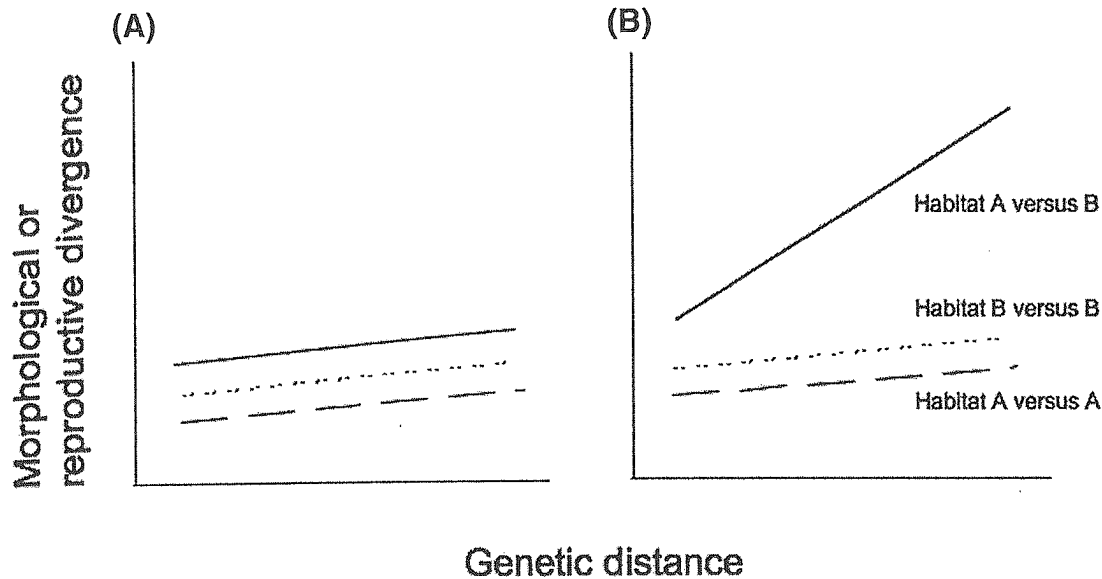
**FIGURE 6.3** The divergence-with-gene-flow model (Rice & Hostert, 1993) predicts that as the intensity of divergent selection increases and gene flow decreases, the likelihood of speciation increases. One way to document the influence of habitat using this model is to contrast traits between populations that differ ecologically. The figure compares values of trait divergence (y-axis) and genetic distance, a measure of gene flow (x-axis) between populations from different habitats (habitat A vs. habitat B, unbroken line), and between populations from the same habitat (habitat A vs. habitat A, dashed line; habitat B vs. habitat B, dotted line). (A) This view shows the pattern when ecological differences between habitats are unimportant. Comparisons within and between habitats show a similar slope, which is predicted if ecological differences between habitats do not result in divergence. (B) When ecological differences between habitats lead to differential selection and divergence, the slope of between-habitat comparisons (habitat A vs. habitat B) should be positive and larger than within-habitat comparisons (habitat A vs. habitat A or habitat B vs. habitat B). In both (A) and (B), within-habitat comparisons (and between-habitat ones in the case of [A]) show a slightly positive slope because of the interaction of drift and genetic distance. Because measuring morphological divergence between populations is generally easier than measuring divergent selection, the approach has wide application. This same approach could be used to assess the strength of reproductive divergence. Indices of reproductive divergence could be obtained from mate choice experiments or vocal differences (if they are important in mate choice). In all instances, it is important to ascertain a genetic basis for the trait(s) under study. (Modified from Orr and Smith [1998].)

studies presented later in this chapter we examine how gradients may be studied and integrated into conservation planning.

## THE ROLE OF SEXUAL SELECTION IN PROMOTING ADAPTIVE DIVERSITY

Sexual selection arises from competition for mates and operates in three basic modes: mate choice, intrasexual competition, and intersexual conflict (for a comprehensive review, see Andersson, 1994a). As a biodiversity-generating process, sexual selection is potentially more important than most other forms of natural selection. The traits affected by sexual selection can contribute directly to prezygotic isolation, which is thought usually to be the first step toward speciation. Sexual selection may also contribute to postzygotic isolation by reducing the mating success of hybrids. Thus, human activities that interfere with sexual selection can stop or even reverse the speciation process.

The traditional view is that the influence of sexual selection on biological diversity in general, and speciation in particular, is largely decoupled from

ecology. The modern roots of this view can be traced to a mathematical model showing that a process of sexual selection originally described by Fisher (1930) could lead to rapid speciation (Lande, 1981). In the "Fisherian" process, linkage disequilibrium (a genetic association) develops between a female mate preference and a male secondary sexual character, leading to a positive feedback loop in which the female preference and male character coevolve unpredictably. Reproductive isolation could arise between populations merely as a by-product of this process. Evolutionary conflicts of interest between the sexes (in other words, intersexual conflict) can also cause sexual traits to evolve in ecologically arbitrary directions and promote speciation (Arnqvist et al., 2000; Gavrilets, 2000a).

Endler (1992) was among the first to emphasize the multitude of ways in which the strength and direction of sexual selection could be influenced by the environment. He coined the term *sensory drive* to refer to the idea that sensory systems and sensory conditions in the environment "drive" evolution in particular directions. The evolution of male courtship displays, for example, could be influenced by biases in the visual system of females, ambient light conditions at the times and locations where courtship occurs, and the visual systems and activity patterns of predators. Sensory drive was offered not as an alternative to the ecologically arbitrary processes of sexual selection, but instead as a context within which these and other processes are likely to occur in natural systems.

From a conservation standpoint, the relative importance of ecologically driven versus ecologically arbitrary processes is critical. If speciation is largely a product of ecologically arbitrary processes, then conservation efforts should be directed toward preserving the most phylogenetically divergent populations of a species, regardless of whether such populations are the most divergent ecologically. In contrast, if speciation is largely a product of ecologically driven processes, then conservation efforts should be directed toward preserving the most ecologically divergent populations. Given that both types of processes appear to be operating in nature, phylogenetic and ecological divergence should both be taken into account when setting conservation priorities. Determining how much weight should be placed on these two factors is an important topic for future research (the answer will probably vary by taxonomic group). It should also be noted that

the traditional hotspot approach to conservation, which focuses on standing levels of biodiversity, takes neither ecological nor phylogenetic divergence into account.

Resolving the extent to which ecologically arbitrary versus ecologically driven processes are responsible for variation in sexual traits and mate preferences is an open area of study. Our primary focus here is to show how environmental gradients can promote prezygotic isolation by accelerating divergence between populations in sexual traits and mate preferences. Another way that environmental gradients could cause prezygotic isolation is by causing divergence between populations in the timing or location of mating activity.

Processes that can cause divergence in sexual traits or mate preferences along environmental gradients fall into three broad categories: (1) selection arising from changes in the local optima of secondary sexual traits or mate preferences, (2) indirect selection on secondary sexual traits or mate preferences caused by changes in the local optima of genetically correlated traits, and (3) plastic changes in the development or expression of environmentally sensitive secondary sexual traits or mate preferences. These categories are not mutually exclusive because changes in the environment can have multiple effects. Here we describe each group of processes in general terms and provide supporting examples.

## Selection Arising from Changes in the Local Optima of Secondary Sexual Traits or Mate Preferences

Much of the diversity in secondary sexual characters can be explained as a product of direct selection on these traits in response to changes in the physical or biotic environment (reviewed in Andersson, 1994). Although much less well studied, environmental factors can also affect the selective optima of mate preferences (Boughman, 2002). Mate choice frequently involves time and energy costs, and may also increase vulnerability to predators (see, for example, Gibson & Bachman, 1992). Environmental gradients that influence the costs of mate preferences could cause populations to diverge in mate choice criteria. Environmental variation may also affect the benefits of mate preferences by altering the relationship between sexual traits and mate quality (Grether, 2000). In theory, this could cause losses,

gains, or shifts in the magnitude of mate preferences and, in turn, alter the evolutionary trajectory of sexual traits.

Prospects for ecological speciation are enhanced when mate preferences and sexual traits evolve in parallel with niche divergence. One illuminating example is in the lakes of British Columbia, Canada, where the threespine stickleback occurs as two ecologically and morphologically distinct species pairs, or *ecotypes*. One ecotype is benthic and forages in the littoral zone whereas the other ecotype is limnetic and forages primarily on zooplankton in open water. After the last retreat of the glaciers some 10,000 to 12,000 years ago, species pairs in each of several lakes evolved independently from their marine ancestor, *Gasterosteus aculeatus*. Limnetic and benthic ecotypes within a lake are more closely related to each other genetically than they are to fish of the same ecotype in different lakes (Rundle et al., 2000). Benthics and limnetics within a lake are reproductively isolated in the wild. In laboratory mating trials, benthics and limnetics from different lakes show a degree of prezygotic isolation similar to that of benthics and limnetics from within the same lake. Within an ecotype, however, fish from different lakes mate and hybridize readily in the laboratory, a result suggesting that the same prezygotic isolating barriers evolved independently in different lakes.

In a study of three different lakes in British Columbia, Boughman and colleagues (2005) confirmed that male coloration and body size have diverged between limnetics and benthics in the same direction in all three species pairs. Furthermore, in all three species pairs, prezygotic isolation was caused by the same two factors: size-assortative mating and asymmetrical female choice based on male color. Color divergence between benthics and limnetics can be explained, at least in part, by differences in the color of the water in their respective nesting habitats. Compared with limnetics, benthics tend to nest in deeper parts of the lake with more vegetative cover and where the light transmission spectrum of the water is "red-shifted" to longer wavelengths. Boughman (2001) found a strong negative relationship between the total area of red coloration on males and the degree to which the water was red-shifted. Boughman (2001) also reports that across each of six stickleback populations there have been parallel changes in sensitivity of females to red light, and in the strength of female preference for red coloration. Moreover, population-level differences

in male coloration and strength of female preference correlated positively with degree of prezygotic isolation between populations. These results are consistent with the sensory drive hypothesis and, in any case, argue strongly against the hypothesis that prezygotic isolation arose through ecologically arbitrary processes. What makes this example more compelling than most is that sexual traits and mate preferences have evolved in parallel with morphological changes associated with divergence in foraging niches.

## Indirect Selection on Secondary Sexual Traits or Mate Preferences Caused by Changes in the Local Optima of Genetically Correlated Traits

Genetic correlations between phenotypic traits can arise from linkage disequilibrium or pleiotropy. Pleiotropy refers to the fact that genes often have multiple phenotypic effects. Examples in this section illustrate how populations could diverge in sexual traits or mate preferences as a by-product of divergent selection on genetically correlated traits.

Radiation of Darwin's finches into different ecological niches of the Galapagos Islands involved divergence in beak morphology associated with naturally occurring variation in food sources (for example, large seeds, small seeds, insects, and so forth). Beak morphology places biomechanical and acoustic constraints on song production, and thus song has diverged in parallel with morphology (Podos, 2001). Reproductive isolation between sympatric species is largely the result of female choice based on male song (Grant & Grant, 1996), but whether the specific song features affected by beak morphology contribute to reproductive isolation is not yet known. Cultural divergence in song may also contribute to reproductive isolation in this group (Grant & Grant, 1996).

Seddon (2005) contrasted predictions based on pleiotropy and local adaptation and found evidence for both mechanisms in the songs of Neotropical antbirds. As predicted from the biomechanics of song production, pitch and temporal patterning of songs correlated with body mass and bill size, respectively. After controlling for the effects of body mass, however, song pitch correlated with acoustic transmission properties of the forest strata in which antbirds typically sing—specifically, higher pitch songs in the midstory compared with the understory

and canopy. Thus, both biomechanical constraints (pleiotropy) and sensory drive (a direct selection hypothesis) appear to have shaped the evolution of Neotropical antbird song.

When two traits compete for limited resources during development, a change in the environment that favors increased investment in one trait may cause a reduction in the other as a correlated response. This may explain some of the spectacular diversity in the horns that male *Onthophagus* dung beetles use to compete for females in underground tunnels. *Onthophagus* spp. vary in horn size and shape as well as in the position of the horns on the exoskeleton. Much of horn diversity appears to be unrelated to ecology and may be a product of ecologically arbitrary processes such as random genetic drift or selection favoring novelty per se (novel horns may confer a tactical advantage), but some evolutionary changes in horns are associated with changes in ecology (Emlen et al., 2005). Developing dung beetle larvae are constrained by the finite amount of food provided by their parents in the form of a dung ball. Horns are expensive structures that negatively affect development of nearby structures. Thus, species with large thorax horns tend to have small wings, and species with large head horns tend to have small eyes or antennae. Using a molecular phylogeny, Emlen and colleagues (2005) tested for statistical association between changes in ecology and evolutionary gains and losses of horns at specific morphological positions. They found that gains of horns on the thorax usually occurred in lineages characterized by very high population densities, whereas loss of horns from the head was associated with shifts from diurnal to nocturnal flight. These trends can be explained in terms of the relative strength of selection on thorax horns versus wings and head horns versus eyes, respectively. Because beetle horns are used in fights between males rather than in courtship, horn divergence is unlikely to contribute directly to prezygotic isolation. Nevertheless, horn divergence could result in unidirectional gene flow (for example, if males with one horn type outcompeted males with a different horn type) and could favor reinforcement of any existing prezygotic barriers by reducing the fitness of male hybrids.

Some mate preferences appear to be derived from sensory biases that evolved in an ecological context. In some cases, these preferences still appear to serve their original sensory functions. For example, in the water mite *Neumania papillator*, females

assume a particular posture (*net stance*) to detect vibrations produced by copepod prey. When a male *N. papillator* detects a female via chemical cues, he vibrates his legs at a frequency that mimics copepod vibrations. Females orient to and clutch trembling males as though they were prey, which puts the males in a good position for presenting spermatophore packets. The response of females to the male leg-trembling display appears to be nothing more than an unmodified adaptation for ambushing prey (Proctor, 1991). Phylogenetic analysis indicates that the leg trembling evolved concomitantly with (or after) the evolution of the female net-stance posture (Proctor, 1992). Presumably, if a change in the environment led to further changes in female predatory behavior, this would select for further changes in male courtship.

## Plastic Changes in the Development, or Expression of Environmentally Sensitive Secondary Sexual Traits or Mate Preferences

Secondary sexual characters typically are not expressed fully until sexual maturity and tend to be unusually sensitive to environmental perturbations of development (Andersson, 1994; but see Cotton et al., 2004). We know less about the environmental sensitivity of mate preferences, but behavioral traits in general tend to be phenotypically plastic. Depending on the nature of phenotypic effects, changes in the environment that alter expression of sexual traits or mate preferences may reduce or increase gene flow between populations.

When changes in the environment weaken expression of mate preferences, this can lead to hybridization between closely related species and, in extreme cases, a complete breakdown of species boundaries and a loss of biodiversity. This appears to have happened in Lake Victoria, the largest of the African Great Lakes. Hundreds of species of cichlids are endemic to the lake, and some species are genetically isolated from each other only by female preferences based on male coloration. In recent times, human activities have caused eutrophication in parts of the lake. Several lines of evidence indicate that species (and color) diversity has decreased through hybridization in the turbid parts of the lake because the transmission spectrum of the water is too narrow for females to express color preferences (Seehausen et al., 1997). This represents partial reversal of the processes responsible for

the extraordinarily high rate of speciation in this taxon.

When a parasitic species colonizes a new species of host, the abrupt change in host environment can trigger immediate changes in sexual characters and mate preferences. Under the right conditions, such host shifts may even cause sympatric speciation. The classic, albeit controversial, example is that of phytophagous insects colonizing new species of host plants (reviewed in Berlocher & Feder, 2002). Brood-parasitic indigobirds (*Vidua* spp.) provide another interesting case. Female indigobirds lay their eggs in the nests of particular host species where indigobird nestlings later imprint on the songs of their host. As adults, male indigobirds mimic host songs and females use these songs to choose mates and to pick which nests to parasitize (Payne et al., 2000). Thus, when novel hosts are parasitized, new host-specific species of indigobirds may arise suddenly. Conversely, when a female parasitizes a host normally used by a different indigobird species, hybridization is the expected result. Molecular genetics and behavioral observations provide support for this model of sympatric speciation with occasional introgression (Sorenson et al., 2003).

When changes in the environment perturb the development of sexual characters away from local optima, selection may favor genetic changes that restore the ancestral phenotype in the new environment. This process, known as *genetic compensation*, could reduce gene flow between populations because hybrids are likely to develop suboptimal phenotypes in both environments (Grether, 2005).

A clear example of the consequences of genetic compensation is provided by the Pacific salmon, which occurs as either the anadromous sockeye or the nonanadromous kokanee. Sockeye "residuals" (in other words, individuals that remain in freshwater lakes or streams throughout their lives instead of migrating to the ocean), develop green coloration at sexual maturity whereas sockeye that mature in the ocean develop red coloration (Craig et al., 2005, and references therein). Red color is produced by carotenoid pigments, compounds that animals in general cannot synthesize. Thus, residuals are green because carotenoid availability is lower in lakes and rivers than in the ocean. Kokanee, which may have evolved from sockeye residuals multiple times in different drainages, are red despite developing in freshwater lakes because they have evolved higher carotenoid assimilation rates than sockeye.

Hybrids between kokanee and sockeye have been found in lakes where the two ecotypes spawn sympatrically, but mate choice tests show that green color is a disadvantage and thus hybrids, which are green at maturity, are expected to have low mating success (Craig et al., 2005). If kokanee had not reevolved red coloration, then presumably they would not discriminate against residuals or hybrids on the spawning grounds. The counterintuitive conclusion is that reevolution of the ancestral (sockeye) phenotype in kokanee has reduced gene flow between sockeye and kokanee.

This is just a sample of the ways in which environmentally induced changes in sexual characters and mate preferences could foster (or hinder) adaptive divergence and speciation.

## CASE STUDY

Important information on the pattern and process of natural and sexual selection across gradients and in different regions can be incorporated into conservation planning successfully. Here we describe a case study in which evolutionary studies have helped to inform conservation planning and reserve design.

Sub-Saharan Africa has a rich fauna and flora, and harbors many endemic species, especially in mountainous regions. Efforts to conserve this region's biota for the past several decades have largely been driven by hotspot approaches based on theories of refugial isolation and speciation. For example, the Pleistocene Forest Refugia Hypothesis (Mayr & O'Hara, 1986) has been an important conceptual tool for establishing protected spaces, and has led specifically to the identification of three large refugial areas thought to be isolated during the Pleistocene glacial periods. Essentially a vicariant or allopatric model of speciation, the Pleistocene Forest Refugia Hypothesis stresses the role that large forest refugia isolated during glacial periods have played in isolating populations and ultimately in generating new taxa and high species diversity. Numerous reserves and national parks have been established to capture this diversity, and current strategies for conserving biodiversity have targeted these areas as hotspots and priorities for conservation (Myers et al., 2000a).

In contrast, little attention has focused on the conservation importance of ecological gradients formed between regions of rainforest and savanna. Evaluating the role of gradients in generating

biodiversity is especially important in sub-Saharan Africa, where deforestation rates are higher than for any other tropical region (Achard et al., 2002). This transition zone, or ecotone, formed by the border of forest and savanna, can be more than 1,000 km wide and in total comprises more than 8,000,000 sq. km of sub-Saharan Africa (Millington et al., 1992). The ecotone is a mosaic of habitats and is characterized by forest fragments embedded in savanna, with fragment size decreasing as one moves away from the central rainforest. Forest fragments found in the ecotone differ ecologically from contiguous rainforest in many ways. Annual rainfall is typically two to three times more variable in fragments than in the rainforest, and the vegetation structure is different, with forest fragments in ecotones having lower forest canopies. Moreover, species assemblages and available foods differ (Chapin, 1954), as does the prevalence and diversity of some pathogens (Sehgal et al., 2001).

Chapin (1954) was one of the first to recognize that ecotones are ecologically dynamic. He identified many species and subspecies of birds that appeared to have their contact zones in these regions and noted many morphological differences in species across this savanna–forest gradient. Furthermore, in an evolutionary context, Endler (1982) showed that 52% of the avian contact zones between species occurred in the ecotone, with 39% within, and only 9% existing between, purported refugial areas. If refugial isolation was the engine driving speciation, one would have expected the majority of contact zones to be concentrated between refugia. Instead, the majority are concentrated in the gradient between savanna and forest. In support of Ender's work, Arctander and Fjeldså (1994), using phylogenic data, found recently diverged taxa were concentrated in transitional zones, such as ecotones, and in mountainous regions. Collectively, these studies suggest that the ecotone formed by the transition between forest and savanna may form a selection gradient that fosters divergence and speciation.

To examine the importance of ecotones in divergence and speciation, we have been examining patterns of morphological, genetic, and behavioral variation in the little greenbul *Andropadus virens*, a small passerine bird common to both the rainforest and the ecotone (Slabbekoorn & Smith, 2002; Smith et al., 1997, 2005a). Examining morphological divergence with genetic differentiation, we tested a central component of

the divergence-with-gene-flow model (Fig. 6.3). We contrasted divergence in morphological traits known to be important in fitness (including wing, tarsus, and tail length, and bill length and depth) with genetic distance estimated with 10 microsatellite markers (Smith et al., 2005a). We examined relative divergence across four different habitats in Lower Guinea, including forest, ecotone, mountain, and island. Bivariate plots of genetic divergence (estimated from either $F_{ST}/(1 - F_{ST})$ and Nei's genetic distance) against normalized Euclidean distance of morphological characters revealed that ecotone–forest and forest–mountain comparisons were more divergent than comparisons within habitat, including forest–forest, ecotone–ecotone, and mountain–mountain (Fig. 6.4). Morphological divergence per unit genetic distance was greatest between forest and ecotone populations. The only between-habitat comparison to show little morphological divergence was between mountain and ecotone. However, subsequent habitat analyses using remote sensing data have revealed that the vegetative structure of mountain and ecotone habitat, as measured by canopy cover, does not differ, which appears to explain the lack of morphological divergence between mountain and ecotone (T. Smith, unpublished data). Genetic divergence between mountains tended to be higher, whereas morphological divergence was lower. In fact, the two mountains separated by only 91 km were more genetically divergent from each other than forest populations more than 800 km apart. Nevertheless, morphological divergence between mountains was very low (0.94). As with sticklebacks, genetic isolation of little greenbul populations within similar habitats contributed little to morphological divergence.

To what extent are differences in habitat that yield differences in morphology also producing differences in secondary sexual traits important in reproductive isolation? To answer this question, we analyzed song variation of male little greenbuls from ecotone and forest habitats (Slabbekoorn & Smith, 2002), where song may play a powerful role in reproductive isolation. We recorded greenbul songs from six ecotone habitats and six rainforest habitats. Little greenbul song is complex, with four alternative song types. Moreover, we found statistically significant differences in frequency measures and song-note delivery rates from the two habitats (Slabbekoorn & Smith, 2002). Further investigations of song transmission rates showed that these
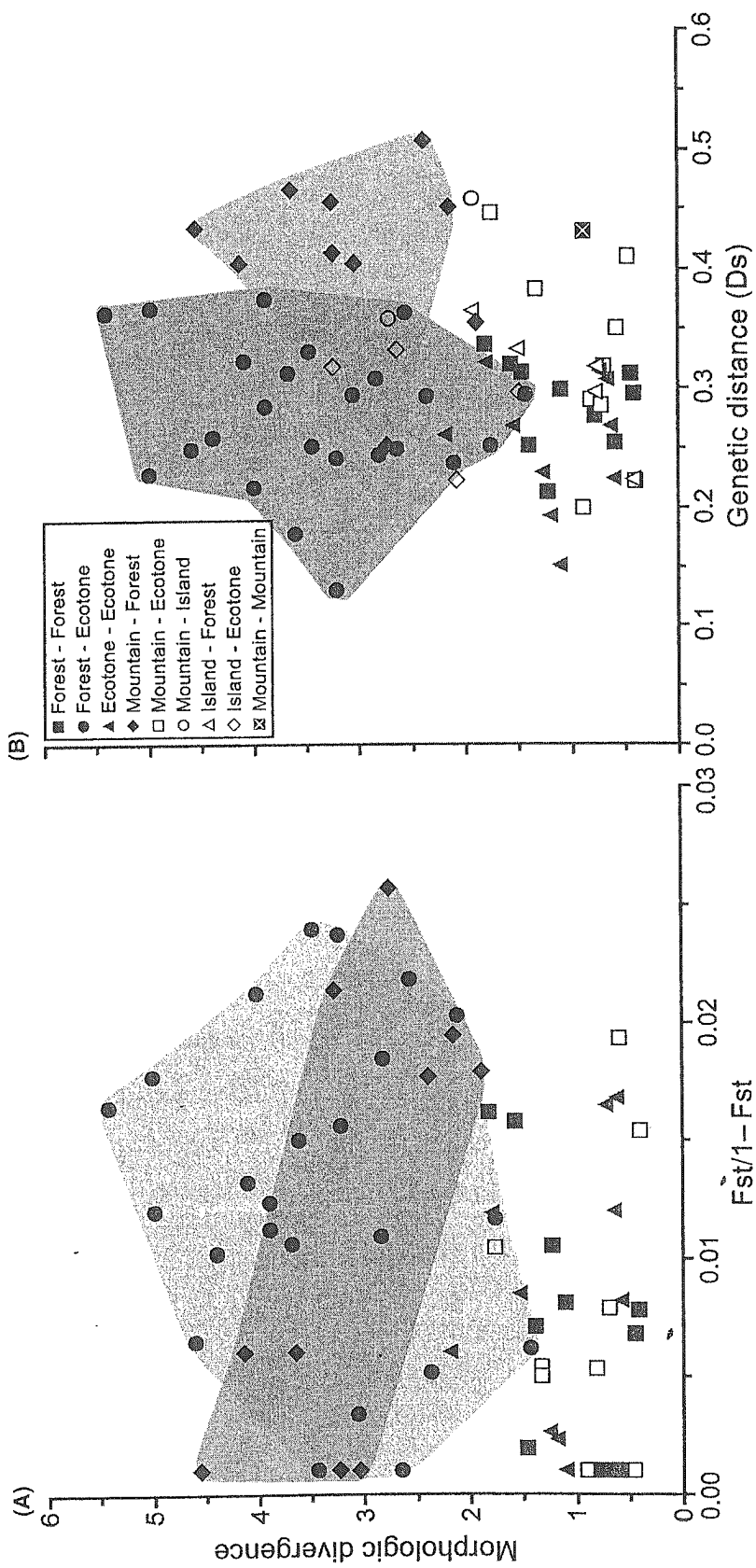
**FIGURE 6.4** (A, B) Plot of normalized euclidean distance of morphological character divergence against $F_{ST}/1 - F_{ST}$ (A) and Nei's genetic distance (B) for habitats in Lower Guinea. Shaded areas highlight the two habitats that exhibit the highest divergence (for example, ecotone–forest and mountain–forest). Island habitats are similar to forest habitats on the mainland and show little divergence between them. (Modified from Smith and colleagues [2005].)

parameters were not differentially influenced by the physical structure of the habitat. However, ambient noise levels were found to differ significantly between forest and ecotone—a difference that may explain variation in song.

Do males and females from different habitats respond differently with respect to song? Preliminary results from song playbacks directed at male little greenbuls in Cameroon rainforests show that these birds responded more aggressively to both Cameroon forest and Uganda forest song than to Cameroon ecotone song (Alexander Kirschel, personal communication, October 2005). These preliminary results are particularly salient because they showed males were responding to songs from the same habitat more strongly than they were to songs from different habitats, even if those similar habitats were thousands of kilometers away, as in the case of Uganda.

In addition to these studies, we have also found strikingly similar patterns of divergence in other bird and lizard species, suggesting that patterns of divergence across the forest–ecotone boundary may be ubiquitous across taxa, as Chapin (1954) and others have suggested. If we are interested in preserving not only patterns of diversity, but also the processes that generate and maintain them, then clearly preserving the ecotonal region of Central Africa should be a priority. Although current hotspot approaches still focus largely on regions of high endemism and species richness in regions under the greatest threat, the direction and scope of conservation efforts are nevertheless beginning to change.

In 1997, after publishing the results of one our first papers on the role of ecotones in generating rainforest biodiversity (Smith et al., 1997), we were contacted by environmental planners for the World Bank. Our publication generated media attention and had been circulated among members of the conservation community. The World Bank had recently joined a consortium of oil companies and governments in Central Africa to develop an oil pipeline connecting oil fields in southern Chad with the coast of Cameroon where oil could be loaded onto tankers and shipped to world markets. A prerequisite for World Bank participation in the project included development of mitigation projects focused on biodiversity and impacts on indigenous communities. As part of mitigation efforts related to biodiversity, the consortium was interested in establishing new national parks in Cameroon. Previously, much

of the emphasis on park development focused on establishment of either rainforest or savanna parks. Little or no conservation efforts had been directed toward establishing ecotone parks. Through many meetings and discussions, we helped convince planners from the World Bank of the importance of preserving a portion of Cameroon's ecotone and, in 2000, the government of Cameroon, in collaboration with the World Bank, established one of the first ecotone parks in Central Africa (Nadis, 2005). The recently gazetted 42,000-ha Mbam-Djerem National Park spans both rainforest regions to the south and savannah to the north, and is the largest national park in Cameroon. Interest in establishing other ecotone parks is increasing. Conservation International is developing new reserves in Brazil that incorporate portions of Brazilian ecotone or Cerrado (Nadis, 2005), and efforts are also focused on the protection of elevation gradients in the Andes and elsewhere.

## FUTURE DIRECTIONS

How can evolutionary processes be taken into account when choosing regions for conservation? To preserve both the pattern of biodiversity and the processes that produce and maintain it, conservation decision makers must take a more integrated approach. It will not be sufficient to identify biodiversity hotspots based solely on species richness and levels of threat. Dynamic regions where evolutionary processes are occurring at high rates will also need to be given high priority. Moreover, given climate change and the likelihood of a 3- to 5-degree increase in global mean temperature, the hotspots of today will likely not be the hotspots of tomorrow, as habitats and populations shift to adjust.

Although biodiversity hotspots are fairly easy to identify (based on survey data), intensive research is needed to identify *evolutionary hotspots*. When decisions are made about which populations of a species to protect, genetic divergence and ecological divergence should both be taken into account. Genetic distance is usually measured at "neutral" loci, which means that it may not provide an accurate representation of the degree of adaptive divergence between populations. Even with moderate rates of gene flow, populations in different environments can diverge in ecologically significant ways. As discussed earlier, prezygotic isolation, and thus speciation, can arise merely as a by-product of

ecological divergence. As a general rule of thumb, the most phenotypically divergent populations (for example, with respect to coloration, morphology, behavior, or physiology) are likely to be the furthest along in the speciation process. For any given taxonomic group, however, some phenotypic traits are likely to be more important than others as barriers to interpopulation gene flow. As the Pacific salmon example illustrates, adaptive divergence between populations may be masked by genetic compensation. Individuals from populations that appear phenotypically identical may not be able to develop normally in the other population's environment. Common-garden or cross-fostering experiments may be required to detect cases of genetic compensation and to determine whether phenotypic differences between populations are genetic or environmentally induced.

Further research is needed to evaluate the relative importance of geographic isolation versus environmental gradients as agents of speciation. As a first step, regions might be ranked in terms of genetic and ecological uniqueness. Populations that are high on both scales should be given the highest conservation priority and, conversely, populations that are lowest on both scales should be given the lowest priority. Research efforts could then be directed at the subset of populations that score high in either genetic or ecological uniqueness. New approaches that allow genetic and adaptive phenotypic data to be mapped onto a landscape (Manel et al., 2003) permit different regions to be compared with regard to their genetic and adaptive features. Integrating these data with levels of species richness and endemism, coupled with environmental layers gained from remote sensing, would be one way to integrate pattern and process into conservation planning. After adaptive and genetic features are mapped, several modeling techniques are now available (see, for example, Phillips et al., 2006), making it possible to correlate them with various types of environmental data. This in turn allows one to make predictions regarding how the distribution of adaptive and genetic traits may change with climate warming. This would allow for the creation of parks and reserves that maximize preservation of biodiversity pattern and process under both current and future climates. Specific steps involved in establishing new protected areas might include: (1) examining and quantifying regional biodiversity, ideally at all levels in the biological hierarchy (from genes to ecosystems) in a reserve network; (2) integrating across all levels of biological organization to quantify as many ecological and evolutionary processes as possible, including phenotypic and genetic divergence among populations as well as the geographic context of diversification; (3) quantifying the correspondence among regions identified as centers of species diversity with regions important to adaptive and genetic diversity; and (4) quantifying current and historical socioeconomic factors that might affect the priority and feasibility of establishing parks or reserves (Smith et al., 2005b).

As illustrated in this chapter, greater emphasis on preserving environmental gradients is paramount for two reasons. First, natural and sexual selection along ecological gradients are powerful drivers of adaptive variation and, under the right conditions, speciation. Second, given the reality of climate change, preserving gradients (and their associated adaptive variation) may offer a bet-hedging approach—the hope that at least some portion of the population will be adapted to new climate conditions.

## SUGGESTIONS FOR FURTHER READING

Smith and colleagues (2005) provide an overview of how one might integrate pattern and process into conservation planning, and Crandall and colleagues (2000) provide an excellent review of the steps important in rank ordering regions according to adaptive variation. For an excellent summary primer on ecological speciation, see Albert and Schluter (2005), and for greater in-depth treatment see Schluter (2000). Endler (1992) provides an excellent starting point for delving deeper into the literature on sensory drive and related processes. For more examples of genetic compensation, and its potential importance for conservation, see Grether (2005).

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