

The Ecological Genetics of Speciation

Sara Via*

Department of Biology and Department of Entomology, University of Maryland, College Park, Maryland 20742

ABSTRACT: Ecological interactions and the natural selection they cause play a prominent causal role in biological diversification and speciation. As a discipline, ecological genetics integrates the two components of adaptive evolution (natural selection and genetic variability) to study the mechanisms of evolution. Ecological genetics is a fruitful approach to the study of how reproductive isolation can evolve under natural selection. The essence of this way of thinking and the ways in which it can be used to address persistent open questions in speciation are discussed.

Keywords: adaptation, reproductive isolation, evolutionary mechanisms.

The idea that natural selection can cause speciation through the ecological interactions of organisms with their environment dates back to Darwin himself (1859, chap. 4). Given the remarkable changes in science and technology during the past 140 yr, one might think that we would now understand everything about how new species are formed. This is far from true. We remain remarkably ignorant about many fundamental evolutionary questions about the origin of species, such as, What triggers speciation, and what kinds of genetic changes occur during the speciation process?

Recently, there has been a resurgence of interest in the ecological causes of speciation and the ways in which natural selection may play a primary role in the evolution of reproductive isolation (Schluter 1996, 1998, 2001; Schemske 2000). New theoretical and empirical approaches have shown how interspecies interactions and differences among environments (the causes of natural selection) can interact with the genetics of phenotypic traits to produce the evolution of reproductive isolation and the splitting of lineages into separate species (reviews in Schluter 2001; Via 2001).

* E-mail: sv47@umail.umd.edu.

This interplay between natural selection and genetics is the essence of an approach to the study of evolution known as ecological genetics. This volume concerns some of the ways in which this approach may be useful in the study of speciation. The contributors all combine ecology and genetics in their research on speciation, and the articles concern both theoretical issues and empirical work on a number of nonlaboratory systems. It is unfortunate that we can present here only a sampling of the excellent recent work on the ecological and genetic mechanisms of speciation. We hope that this volume of articles, originally presented as talks in the Vice Presidential Symposium of the American Society of Naturalists in June 2000, will both provide a context for the ecological genetics of speciation and stimulate others to apply this point of view when considering how speciation occurs.

What Is Ecological Genetics?

The cornerstone of ecological genetics is the joint theoretical and empirical analysis of the two components of adaptive evolution—natural selection on the phenotype and genetic variability in phenotypic traits. This integration of ecology and genetics provides a window on both the causes of and constraints on evolution in contemporary populations. Like most branches of science, ecological genetics has undergone its own evolution since its founder, E. B. Ford (1964, p. 1), wrote,

It is a surprising fact that evolution, the fundamental concept of biology, has rarely been studied in wild populations by the fundamental techniques of science, those of observation and experiment. Consequently, the process has seldom been detected and analyzed in action. However, I have for many years attempted to remedy that omission by a method which has in fact proved effective: one which combines fieldwork and laboratory genetics. ... The fieldwork needed in these investigations is of several kinds. It involves detailed observation, ... having strict regard to the ecology of the habitats. Also it often requires long-continued estimates of the frequency of genes or of characters controlled on a polygenic or a multifactorial basis.

Despite many changes in techniques, several constants

have emerged in ecological genetics as an approach to the study of evolution. First, the focus is on the genetics of ecologically important phenotypic traits that affect organisms' interactions with their biotic and abiotic environments. These are the traits that become adaptations under natural selection and that may also lead to premating reproductive isolation. Next, ecological genetics is an experimental approach, with a focus on natural populations rather than on model systems. Finally, field studies of both genetic variability and natural selection have always been central to ecological genetics.

Early ecological genetic studies emphasized the study of selection on conspicuous visible polymorphisms inherited as single genes or linked "supergenes" (review in Ford 1964). From the 1930s to the 1960s, plant ecologists conducted a number of now-classic reciprocal transplant studies on plant ecotypes, populations that have become locally adapted to different environmental conditions such as grazing or heavy metal in the soil (review in Briggs and Walters 1984). Today, the extent and causes of genetically based divergence among populations due to variation in the environment remain a core focus of ecological genetics. By the 1980s, quantitative genetics, which had been the bailiwick of animal and plant breeders, was increasingly used to study phenotypic evolution of ecologically important traits in natural populations (stimulated in large part by Lande 1979). This period produced a wave of empirical studies describing how patterns of genetic variation (and covariation) among phenotypic traits can either facilitate or constrain the process of adaptive evolution under both natural and sexual selection (reviews in Via 1990; Arnold 1994; Reznick and Travis 1996). Methods were also developed during the 1980s for estimating the forces of natural selection on particular characters in wild populations (Lande and Arnold 1983; Schluter 1988). Most recently, interest has shifted toward efforts to localize, enumerate, and individually study the loci that influence quantitative traits, using techniques known as quantitative trait locus (QTL) mapping (e.g., Lander and Botstein 1989; Tanksley 1993). These techniques hold considerable promise for the study of speciation (Bradshaw et al. 1995; Via and Hawthorne 1998; Schemske and Bradshaw 1999).

Ecological genetics is, however, more than simply a set of techniques. It is a viewpoint on the study of evolution that holds that the process of evolution is ongoing and can be studied in contemporary populations (see Antonovics 1976). In this point of view, speciation is a continuation of the same population genetic processes that cause population divergence (Coyne and Barton 1988). The process of speciation can thus be studied "in action" through the analysis of causes of reproductive isolation in contemporary populations of taxa that are close to the

species boundary (e.g., Butlin 1987; McMillan et al. 1997; Via 1999; Schemske 2000).

For the ecological geneticist, therefore, understanding either adaptive evolution or speciation requires a focus on both ecology and genetics. Ecology is crucial because an organism's interactions with its environment set the stage for natural selection (the differential fitness of individuals with different phenotypes; Lande and Arnold 1983; Endler 1986; Schluter 1988). Genetics is central to the study of speciation because the patterns and type of genetic variation in phenotypic traits determine the rate and direction of the response to selection (Lande 1979) in traits that lead to reproductive isolation. In contrast to population genetics, which often focuses on mechanisms of gene frequency change or changes in DNA sequence with only abstract references to phenotype, ecological genetics emphasizes the genetic analysis of characters directly associated with ecological interactions and adaptation. It is hard to imagine deriving a comprehensive picture of speciation that does not include an explicit focus on the evolution of key phenotypic traits.

An Ecological Genetics View of Speciation

The study of population divergence that leads to reproductive isolation is a natural extension of the ecological genetic tradition. Although debate over species concepts continues (review in Harrison 1998), most students of speciation as a process continue to rely on the biological species concept (Howard 1998; Schemske 2000). Reproductive isolation provides a concrete set of phenotypic characters to study and in most cases is a measurable end point of the speciation process. Indeed, to most ecological geneticists, "The evolution of reproductive isolation is the evolution of speciation" (Coyne 1992, p. 511). If ecological genetics is the study of the evolution of ecologically important characters, then the ecological genetics of speciation is the study of the evolution of characters that cause reproductive isolation or the ways in which natural selection on the phenotype produces postzygotic isolation in geographically separated populations.

From comparisons of experimental and observational studies on a variety of species in different circumstances, we may be able to draw some general conclusions about how natural and sexual selection act on traits that result in reproductive isolation and how the process of speciation is influenced by the genetic architecture of the characters involved. In keeping with the focus on process, it is important to study taxa at various stages of the divergence process, from partially isolated populations, to races, and recently speciated sister taxa (Endler 1977; Jiggins and Mallet 2000). In contrast, studies of anciently diverged taxa are less useful as a window on process because considerable

genetic differentiation and even additional reproductive isolation can evolve after speciation is complete (Templeton 1981).

Using an ecological genetics approach, we can begin to ask, What types of barriers to gene flow tend to evolve first in a given ecological situation? How does the ecological situation in which speciation occurs affect the type of reproductive isolation that evolves? Does a certain type of ecology or genetic architecture predispose a widespread species to diverge and speciate? What generalizations can be drawn about how the ecology and genetics of diverging taxa influence the process of speciation? To answer these questions, it will be necessary to perform a number of different types of studies, including analyses of the following.

The Natural History of Barriers to Gene Flow

Detailed fieldwork and laboratory work of organisms in their environment is required to determine which characters really influence reproductive isolation (Howard et al. 1998; Via 1999; Via et al. 2000). This first step in the study of speciation is crucial so that investigators focus effort on the traits that are actually involved in speciation. Ideally, one could partition reproductive isolation into separate contributions from different prezygotic and postzygotic factors. By assembling a group of such studies in an array of taxa, we can perhaps begin to make generalizations about which characters most impede gene flow in particular ecological situations.

The Role of Natural Selection in Speciation

In ecological speciation (e.g., Endler 1977; Schluter 1996, 1998), natural selection drives the evolution of barriers to gene flow. For example, populations may experience divergent selection on key traits due to competition, or environmental differentiation may directly affect characters that also influence mating and reproductive isolation. This process may occur in either sympatry or allopatry. In addition, phenotypic evolution by natural selection in isolated populations may lead indirectly to genetic changes that produce incompatibilities if populations come together (so-called by-product speciation; see Schluter 2001). The weight of current evidence clearly suggests that we should not underestimate selection as an engine of speciation. However, understanding the agents of selection involved in speciation in both plants and animals will require a renewed commitment to ecology, as part of the study of speciation, and to experimental measures of selection on traits associated with reproductive isolation in natural populations (Lande and Arnold 1983; Endler 1986; Schluter 1988).

Role of Sexual Selection in Speciation

Sexual selection may also result in divergence of characters associated with mating, leading to rapid premating reproductive isolation (Lande 1981, 1982; Lande and Kirkpatrick 1988; Endler 1989; Higashi et al. 1999). Although we have little hard evidence that any given species pair has evolved reproductive isolation due to sexual selection, it seems likely that sexual selection has often contributed to reproductive isolation, making empirical verification of the role of sexual selection in speciation an important research emphasis (Panhuis et al. 2001). In this volume, Shaw and Parsons (2002) take up this challenge in their article on the evolution of courtship song in Hawaiian crickets.

Genetics of the Traits That Produce Reproductive Isolation

Several approaches exist for the genetic analysis of traits associated with reproductive isolation. These include quantitative genetic analyses of variability, biometrical analyses of genetic architecture, and QTL mapping analyses.

Quantitative Genetic Analyses of Variability. Patterns of genetic variation and covariation among traits causing reproductive isolation can be estimated using the methods of quantitative genetics (e.g., Falconer and MacKay 1996). These methods provide estimates of the average value and genetic variability of the traits that lead to reproductive isolation in different populations and also reveal important genetic correlations among traits. One can use such data to formulate hypotheses about how selection could have acted to produce divergence in these traits between the relevant taxa and even estimate the net selection required for divergence ("retrospective selection"; e.g., Schluter 1984).

Biometrical Analyses of Genetic Architecture. Methods in quantitative genetics can also provide rough estimates of the minimum number of genes influencing a quantitative trait and a picture of composite gene effects on phenotypic traits (i.e., additive, dominance, epistatic effects; reviews in Kearsy and Pooni 1996; Lynch and Walsh 1998, chap. 9). However, these techniques have limited utility because they do not provide a way to study the individual effects of component loci. For this reason, researchers are increasingly turning to linkage-map analyses in the hopes of attaining greater resolution on the genetic changes that lead to adaptation and speciation.

QTL Mapping Analyses. Recent advances in linkage mapping (e.g., Lander and Botstein 1989; Tanksley 1993; Zeng

1994) and the enhanced availability of molecular markers outside of model systems is revolutionizing ecological genetics. The techniques known as QTL mapping are an advance over composite studies of genetic architecture because they permit the genetic determination of ecologically important phenotypic traits to be localized to small segments of chromosomes (e.g., Bradshaw et al. 1995). Though it is still a long way from the chromosome block to the gene(s) (e.g., Falconer and MacKay 1996; Paterson 1997; Doebley 2000; Frary et al. 2000), many important issues in speciation can be addressed with even a coarse QTL analysis (review in Via and Hawthorne 1998). In this volume, Howard et al. (2002), Rieseberg and Buerkle (2002), Hodges et al. (2002), Shaw and Parsons (2002), and Via and Hawthorne (2002) all use these methods to approach different issues in speciation.

Genetic Analysis of Hybrid Zones. Hybrid zones have long been a focus of study for researchers in speciation (e.g., Harrison 1990; Barton and Gale 1993). Studies of the introgression of marked chromosome blocks (and presumptive QTL) across hybrid zones extend this tradition by revealing traits that may isolate the hybridizing taxa (Rieseberg et al. 1999). Chromosomal blocks that influence traits associated with reproductive isolation are slow to move across hybrid zones due to divergent selection. In contrast, genes affecting other traits, particularly genes with advantageous effects in both taxa, are expected to move across hybrid zones rapidly. Loren Rieseberg's contribution to the volume includes several elegant examples of this approach to the study of reproductive isolation.

Further Considerations

From Model Systems to Natural Populations

There is no question that the study of model systems is crucial for understanding basic genetic mechanisms. However, any complete understanding of the mechanisms of speciation will require comparing and contrasting the genetics of reproductive isolation in many different kinds of taxa that are thought to have diverged in different ways. This cannot be accomplished unless we study the evolution of reproductive isolation in natural populations as well as in those model systems with sufficient ecological substance. Moreover, because ecology and natural selection may play pivotal roles in speciation, it is important to ensure that organisms are studied within a realistic ecological context, or important causes of reproductive isolation may be missed. Although natural populations may lack the full array of genetic tools available for species like *Drosophila*, nonmodel species are becoming more accessible for genetic analyses than ever before.

Fieldwork and Laboratory Work Are Both Important in Ecological Genetics

Testing the performance of individual genotypes under field conditions has always been part of ecological genetics. Some of the most elegant recent studies of the mechanisms of adaptation and speciation employ a combination of field and laboratory experimentation (Schluter 1996, 1998; Schemske and Bradshaw 1999; Hodges 2002).

Phylogeny and Phylogeography Provide Crucial Information for Studies of Speciation

Increasingly, ecological geneticists are employing phylogenetic analyses in conjunction with their studies of speciation. For example, placing the focal taxa within an accurate phylogenetic context could reveal pairs of sister species that might be of interest to study. Phylogenetic analyses can also reveal the occurrence of parallel speciation, which can guide experimenters in formulating hypotheses about mechanisms of speciation (Rundle et al. 2000). Finally, phylogeographic analysis may permit investigators to test hypotheses about sympatric or allopatric origins of divergent populations (Berlocher 1998; Barraclough and Vogler 2000).

Ideally, Theory Guides Empirical Work (and Is Guided by It)

Advances in ecological genetics can come from advances in theory that spur new possibilities for empirical work in several ways. First, theory can suggest how a new type of data can be used to study evolution, as Lande (1979) stimulated estimates of quantitative genetic parameters in natural populations and Lande and Arnold (1983) stimulated estimates of natural selection. Theory can also guide empiricists by revealing important assumptions to test or parameters to measure (e.g., for sympatric speciation, see review in Via 2001). In turn, empirical estimates of the nature of selection or genetic architecture in different situations will be a crucial aid in formulating realistic models of speciation. In this volume, Kirkpatrick and Ravigné (2002) summarize theoretical contributions on the roles of natural and sexual selection in speciation.

Conclusions

This is an exciting time to study speciation. Recent theoretical and experimental work in the spirit of ecological genetics has produced results that call into question some time-honored beliefs about species formation, suggesting the following.

Speciation Does Not Always Take a Long Time

Recent discussions of ecological speciation emphasize that reproductive isolation may evolve extremely rapidly when driven by selection (e.g., Schluter 1996, 1998). This is in direct contrast to the relatively slow accumulation of postzygotic genetic incompatibility that occurs as a by-product of independent evolution in allopatric populations (Orr and Orr 1996).

Sympatric Speciation Is Likely in Some Situations

After decades of controversy (e.g., Futuyma and Mayer 1980), it now appears probable that reproductive isolation in sympatric populations can evolve rapidly under selection (Via 2001). Sympatric speciation may occur through adaptation to different environments (e.g., Bush 1994; Schluter 1998) or through other mechanisms (Kawecki 1997; Kondrashov et al. 1998; Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999).

Reinforcement Can Occur

Recent genetic models suggest that reinforcement is more likely in a variety of circumstances than previously thought (Liou and Price 1994; Servedio and Kirkpatrick 1997; Servedio 2000).

Hybridization Is Not Always Disadvantageous

Although allopatric speciation may result from the accumulation of postzygotic incompatibility that results in depressed hybrid fitness, recent empirical studies suggest that hybrid progeny in other cases may be highly fit (reviewed in Arnold 1997). Moreover, hybridization serves as an important source of genetic variability (Grant and Grant 1996) and can even lead to the formation of hybrid species (Rieseberg 1997). Even when selection does act against hybrids, the disadvantage may be ecological rather than genetic (Arnold 1997; Hatfield and Schluter 1999).

Selection Impacts Speciation in Ways Other than Depressed Hybrid Fitness

Although hybrid unfitness due to genetic incompatibilities is undoubtedly an important cause of speciation, selection may play a variety of other roles in speciation. For example, divergent natural selection may drive species formation directly through adaptations as taxa adapt to different environments or resources (Schluter 1998, 2001; Schemske 2000), and sexual selection may also lead to speciation through alterations in mate-recognition characters (Lande 1981, 1982; review in Panhuis et al. 2001).

Speciation is a complex process that undoubtedly occurs in a variety of ways. As we search for generalities, it is time to adopt a pluralistic attitude, recognizing that both the ecological situation and the genetic constitution of diverging taxa will determine the mode of speciation. Moreover, we must remember that adaptive phenotypic evolution may often be at the root of speciation (Schemske 2000). It is our job as ecological geneticists and evolutionary biologists to draw generalizations without limiting the possible array of mechanisms that could be involved. Integrated studies of the ecological genetics of reproductive isolation in diverging or recently diverged taxa of all sorts will play an important part in deriving these generalizations. It is our hope that the articles in this volume will stimulate additional work in this spirit.

Acknowledgments

I am grateful to the members of the American Society of Naturalists for the opportunity to organize this symposium. M. Caillaud, J. Endler, D. Hawthorne, D. Howard, and R. Hufbauer provided useful comments on the manuscript. I first learned the Ecological Geneticist's Creed under the tutelage of Janis Antonovics, as part of a lucky generation of susceptible evolutionary biologists at Duke University. My work on speciation has been supported by the National Science Foundation (DEB9207573 and DEB9629081).

Literature Cited

- Antonovics, J. 1976. The input from population genetics: the new ecological genetics. *Systematic Botany* 1: 233–245.
- Arnold, M. L. 1997. *Natural hybridization and evolution*. Oxford University Press, New York.
- Arnold, S. J. 1994. Constraints on phenotypic evolution. Pages 258–278 *in* L. A. Real, ed. *Behavioral mechanisms in evolutionary ecology*. University of Chicago Press, Chicago.
- Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155:419–434.
- Barton, N. H., and K. S. Gale. 1993. Genetic analysis of hybrid zones. Pages 13–45 *in* R. G. Harrison, ed. *Hybrid zones and the evolutionary process*. Oxford University Press, New York.
- Berlocher, S. H. 1998. Can sympatric speciation via host or habitat shift be proven from phylogenetic and biogeographic evidence? Pages 99–113 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Bradshaw, H. D., S. M. Wilbert, K. G. Otto, and D. W. Schemske. 1995. Genetic mapping of floral traits asso-

- ciated with reproductive isolation in monkeyflowers (*Mimulus*). *Nature* 376:762–765.
- Briggs, D., and S. M. Walters. 1984. *Plant variation and evolution*. 2d ed. Cambridge University Press, Cambridge.
- Bush, G. L. 1994. Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology & Evolution* 9: 285–288.
- Butlin, R. K. 1987. A new approach to sympatric speciation. *Trends in Ecology & Evolution* 2:310–311.
- Coyne, J. A. 1992. Genetics and speciation. *Nature* 355: 511–515.
- Coyne, J. A., and N. H. Barton. 1988. What do we know about speciation? *Nature* 331:485–486.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. 1st ed. J. Murray, London.
- Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–357.
- Doebley, J. 2000. A tomato gene weighs in. *Science* (Washington, D.C.) 289:71–72.
- Endler, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton University Press, Princeton, N.J.
- . 1986. *Natural selection in the wild*. Princeton University Press, Princeton, N.J.
- . 1989. Conceptual and other problems in speciation. Pages 625–648 *in* D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, Mass.
- Falconer, D. S., and T. F. C. MacKay. 1996. *Introduction to quantitative genetics*. 4th ed. Chapman & Hall, New York.
- Ford, E. B. 1964. *Ecological genetics*. Chapman & Hall, London.
- Frery, A., T. C. Nesbitt, A. Frery, S. Grandillo, E. van der Knaap, B. Cong, J. Liu, et al. 2000. *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. *Science* (Washington, D.C.) 289:85–88.
- Futuyma, D. J., and G. C. Mayer. 1980. Non-allopatric speciation in animals. *Systematic Zoology* 29:254–271.
- Grant, B. R., and P. R. Grant. 1996. High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology* 77:500–509.
- Harrison, R. G. 1990. Hybrid zones: windows on evolutionary process. *Oxford Surveys in Evolutionary Biology* 7:69–128.
- . 1998. Linking evolutionary pattern and process: the relevance of species concepts for the study of speciation. Pages 19–31 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment-dependent hybrid fitness. *Evolution* 53:866–873.
- Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. *Nature* 402: 523–526.
- Hodges, S. A., J. B. Whittall, M. Fulton, and J. Y. Yang. 2002. Genetics of floral traits influencing reproductive isolation between *Aquilegia formosa* and *Aquilegia pubescens*. *American Naturalist* 159(suppl.):S51–S60.
- Howard, D. J. 1998. Unanswered questions and future directions in the study of speciation. Pages 439–448 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Howard, D. J., M. Reece, P. G. Gregory, J. Chu, and M. L. Cain. 1998. The evolution of barrier to fertilization between closely related organisms. Pages 279–290 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Howard, D. J., J. L. Marshall, D. D. Hampton, S. C. Britch, M. L. Draney, J. Chu, and R. G. Cantrell. 2002. The genetics of reproductive isolation: a retrospective and prospective look with comments on ground crickets. *American Naturalist* 159(suppl.):S8–S21.
- Jiggins, C. S., and J. Mallet. 2000. Bimodal hybrid zones and speciation. *Trends in Ecology & Evolution* 15: 250–255.
- Kawecki, T. J. 1997. Sympatric speciation via habitat specialization driven by deleterious mutations. *Evolution* 51:1751–1763.
- Kearsey, M. J., and H. S. Pooni. 1996. *The genetical analysis of quantitative traits*. Chapman & Hall, London.
- Kirkpatrick, M., and V. Ravigné. 2002. Speciation by natural and sexual selection: models and experiments. *American Naturalist* 159(suppl.):S22–S35.
- Kondrashov, A. S., and F. A. Kondrashov. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400:351–354.
- Kondrashov, A. S., L. Y. Yampolsky, and S. A. Shabalina. 1998. On the sympatric origin of species by means of natural selection. Pages 90–98 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. *Evolution* 33:402–416.
- . 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the USA* 78:3721–3725.
- . 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* 38:213–223.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- Lande, R., and M. Kirkpatrick. 1988. Ecological speciation

- by sexual selection. *Journal of Theoretical Biology* 133: 85–98.
- Lander, E. S., and D. Botstein. 1989. Mapping Mendelian factory underlying quantitative traits using RFLP linkage maps. *Genetics* 121:185–199 (correction 136:705).
- Liou, L. W., and T. D. Price. 1994. Speciation by reinforcement of premating isolation. *Evolution* 48: 1451–1459.
- Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer, Sunderland, Mass.
- McMillan, W. O., C. D. Jiggins, and J. Mallet. 1997. What initiates speciation in passion-vine butterflies? *Proceedings of the National Academy of Sciences of the USA* 94:8628–8633.
- Orr, H. A., and L. H. Orr. 1996. Waiting for speciation: the effect of population subdivision on the time to speciation. *Evolution* 50:1742–1749.
- Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. *Trends in Ecology & Evolution* 16:364–371.
- Paterson, A. H. 1997. Prospects for cloning the genetic determinants of QTLs. Pages 289–294 *in* A. H. Paterson, ed. *Molecular dissection of complex traits*. CRC, Cleveland.
- Reznick, D., and J. Travis. 1996. The empirical study of adaptation in natural populations. Pages 243–290 *in* M. R. Rose and G. V. Lauder, eds. *Adaptation*. Academic Press, San Diego, Calif.
- Rieseberg, L. 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics* 28:359–389.
- Rieseberg, L., J. Whitton, and K. Gardner. 1999. Hybrid zones and the genetic architecture of a barrier to gene flow between two sunflower species. *Genetics* 152: 713–727.
- Rieseberg, L. H., and C. A. Buerkle. 2002. Genetic mapping in hybrid zones. *American Naturalist* 159(suppl.): S36–S50.
- Rundle, H. D., L. Nagel, J. W. Boughman, and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. *Science (Washington, D.C.)* 287: 306–308.
- Schemske, D. W. 2000. Understanding the origin of species. *Evolution* 54:1069–1073.
- Schemske, D. W., and H. D. Bradshaw, Jr. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences of the USA* 96:11910–11915.
- Schluter, D. 1984. Morphological and phylogenetic relationships among the Darwin's finches. *Evolution* 38: 921–930.
- . 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* 42:849–861.
- . 1996. Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 351:807–814.
- . 1998. Ecological causes of speciation. Pages 114–129 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- . 2001. Ecology and the origin of species. *Trends in Ecology & Evolution* 16:372–380.
- Servedio, M. R. 2000. Reinforcement and the genetics of non-random mating. *Evolution* 54:21–29.
- Servedio, M. R., and M. Kirkpatrick. 1997. The effects of gene flow on reinforcement. *Evolution* 51:1764–1772.
- Shaw, K. L., and Y. M. Parsons. 2002. Divergence of mate recognition behavior and its consequences for genetic architectures of speciation. *American Naturalist* 159(suppl.):S61–S75.
- Tanksley, S. D. 1993. Mapping polygenes. *Annual Review of Genetics* 27:205–233.
- Templeton, A. R. 1981. Mechanisms of speciation—a population genetic approach. *Annual Review of Ecology and Systematics* 12:23–48.
- Via, S. 1990. Ecological genetics in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Annual Review of Entomology* 35: 421–446.
- . 1999. Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* 53:1446–1457.
- . 2001. Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology & Evolution* 16: 381–390.
- Via, S., and D. J. Hawthorne. 1998. The genetics of speciation: promises and prospects of quantitative trait locus mapping. Pages 352–364 *in* D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- . 2002. The genetic architecture of ecological specialization: correlated gene effects on host use and habitat choice in pea aphids. *American Naturalist* 159(suppl.):S76–S88.
- Via, S., A. C. Bouck, and S. Skillman. 2000. Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. *Evolution* 54:1626–1637.
- Zeng, Z.-B. 1994. Precision mapping of quantitative trait loci. *Genetics* 136:1457–1468.