Evolutionary Behavior Genetics

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It has often been said that behavior is one of the most labile traits in animal evolution. Whether this is so remains to be demonstrated, but it is clear that rather minor genetic changes can sometimes have profound effects on behavior without affecting morphology (Ehrman and Parsons 1981). It is also common for closely related species to be reproductively isolated by premating isolating mechanisms alone, indicating that genes affecting behavior often may be the first and most important components of the genome to undergo divergence in speciation. Although I recognize that in some taxa sterility barriers and other postcopulatory factors are important in some modes of speciation, I would like to focus my attention today on the contribution that behavior genetics can make to our understanding of the evolution of reproductive isolation and speciation, and explore where this approach is likely to take us.

Invertebrates are exceptionally well suited for evolutionary, behavior genetic studies. Their behavioral repertoire includes species specific, hierarchically organized, fixed action patterns. The modification of behavior within an individual's lifetime, as a result of habituation or associative and exploratory learning, appears to be strongly restricted by sensory and neurological constraints that limit response only to a narrow range of stimuli (Matthews and Matthews 1978). Certain tasks can be mastered while others cannot. Invertebrate behavior is highly stereotyped and predictable, thus facilitating the study of the genetic basis of specific behavioral traits.

Much of the research on the behavioral genetics of invertebrates has dealt with intraspecific variation found in various general maintenance activities such as taxis, feeding and learning, and the response of this variation to selection. Although the results of these investigations have demonstrated that many aspects of behavior are under genetic control and can respond rapidly to selection, they provide little insight into how behavioral differences among species evolve, or what role the evolution of these differences plays in speciation. Comparative genetic studies directed toward unraveling the genetic bases for behavioral differences between and within species or biologically distinct races are more useful in this regard. Especially important are studies of habitat selection and various types of communicatory activity usually associated with mating success. This comparative evolutionary approach to the study of the genetics of precopulatory reproductive isolating mechanisms is now beginning to reveal the role such traits play in the speciation process, and as a result we should eventually be able to develop more precise and realistic models of speciation.
Quantitative genetic studies of mating behavior have been carried out on only a few organisms such as *Drosophila* and crickets. By studying the pattern of inheritance of several components of the calling song in F1 hybrids produced by crossing related crickets, Hoy and his colleagues (Hoy 1974) were able to demonstrate that pulse rates, intervals, and progressions are controlled by a complex, polygenic, multichromosomal system. Polygenic control of mating was also inferred in a quantitative genetic study of hybrids and backcrosses made between closely related "semispecies" in the *Drosophila paulistorum* complex (Ehrman 1965). The details of these polygenic control systems have yet to be worked out.

Thus, although differences in mating behavior are recognized as a major cause of reproductive isolation, we know little about their genetic bases, control, or even which genes are important in the evolution of sexual behavior in most organisms. Furthermore, sexual behavior may not be the only behavioral factor responsible for reproductive isolation, and in some cases may play no direct role. There is no *a priori* reason to assume that differences that may now exist in sexual activity between two closely related species played a key role in the development of reproductive isolation during speciation. Such traits could have evolved long after the speciation event that was initiated by, and dependent upon, some other cause of reproductive isolation. The response to ecological cues, for instance, may be much more important in initiating and maintaining reproductive isolation than mating behavior. Monophagous parasitic species living on different hosts may be more strongly isolated from one another by host selection behavior than by sexual behavior (Diehl and Bush 1984); sometimes, the genes controlling such behavior may be few in number (Huettel and Bush 1972, Gould 1983).

The lack of appreciation by population geneticists of the role and great diversity of precopulatory reproductive isolating mechanisms in speciation has resulted in the development of biologically untenable and untestable genetic models of speciation. In the absence of hard data on the genetic basis for these traits, model builders and theorists have been free to pick and choose the genetic criteria for speciation that best suited their needs and computational limitations without reflecting on how their models relate to specific natural speciation events. The value of these theoretical scenarios as evidence for or against one mode of speciation or another is, therefore, questionable (Bush and Diehl 1982).

A more direct approach to the problem of speciation is to establish the genetic basis of specific behaviors identified as key traits in reproductive isolation. Since many closely related species pairs are isolated strictly by differences in behavior, particularly sympatric sibling species in the early stages of divergence (Diehl and Bush 1984), an understanding of the genetic basis for precopulatory reproductive isolation can provide unique insight into the speciation process. I do not advocate this strictly reductionist view as an answer to all our problems, but only as a necessary and rewarding tactic designed to advance our understanding of the genetics of speciation and provide a basis for the development of more biologically meaningful speciation models.

It is, therefore, encouraging that some of the contributions to this volume deal with the genetic basis of reproductive isolation. But how do we identify key behavioral traits important in reproductive isolation and speciation? Although most questions concerning the origin and evolution of reproductive isolation arise as a result of a systematic or phylogenetic investigation, such studies provide little more than a few indirect clues, inferred from morphological characters, as to which behavioral traits might be important. The only way to pinpoint key behavioral traits is to conduct a thorough analysis of the ecology and mating behavior of the species in question. Anyone who undertakes such a task is immediately struck by the apparent complexity of the behavioral repertoire and by how intrinsically these behaviors are tied to ecological factors. The immediate reaction is to conclude that differences that exist between
even very closely related species must represent the accumulation of a great many gene changes during the course of speciation. On closer examination, this necessarily may not be the case.

For example, in the fruit fly genus *Rhagoletis*, the group with which I am most familiar, mating follows a sequence of steps, each encompassing a set of fixed action patterns, that are undoubtedly under the control of many genes. As mating occurs on the host fruit, both sexes must first locate and identify the right host plant before courtship can be initiated. This orientation phase requires the recognition of several long- and short-range visual and olfactory cues emanating from the plant and fruit. Once on the fruit, the adults, which are brightly marked with distinct wing patterns, use highly stereotyped wing and body displays as well as short-range contact pheromones to complete the mating sequences. This is the general pattern of mating behavior displayed by all *Rhagoletis* and many other Tephritidae as well (Boller and Prokopy 1976, Zwolfer 1983).

Each step leading to a successful mating in these flies is essential and requires a complicated set of genetically controlled behavioral traits. However, only a few genetic changes, such as in loci affecting host selection, actually play a critical role in reproductive isolation (Huettel and Bush 1972, Bush and Diehl 1982). Although courtship includes a series of stereotyped wing waves, posturing, and contact pheromones, we have found no evidence that any of the four *pomonella* group sibling species can discriminate between one another either in the laboratory or once they are on a fruit. Apparently, the courtship behavior of the four is so similar that they are unable to tell each other apart. Because their host plant serves as a rendezvous for courtship and mating, host selection is the key behavior separating species. In these insects, and many other parasites as well, a change in genes controlling chemosensory or other responses involved in host selection can have a profound and evolutionarily significant effect on mate choice.

As for host selection, we have found that although visual, tactile, and chemical cues are important components of searching behavior in these flies, it is the chemical cues emanating from the fruit that are used primarily to discriminate between potential host plants (Prokopy et al. 1973). Recently, Fein et al. (1982) and Reissig et al. (1983) have reported that the apple maggot, *Rhagoletis pomonella* (Walsh), is attracted to five volatile compounds found in apple fruits. A different, but related, set of attractants has recently been identified in blueberry fruit which attracts *R. mendax* (Curran), a closely related sibling species to *R. pomonella* (Silk, personal communication).

We know from past experience that these two species can be hybridized easily and backcrossed in the laboratory and are interfertile in all combinations. Thus, it is now possible to carry out a detailed genetic analysis of interspecific host preference differences and establish the number and type of genes directly involved in the expression and control of this important behavioral trait. A genetic model of speciation that focuses on the relationship between host and mate selection should be far more meaningful, as we have pointed out elsewhere (Bush and Diehl 1983), than one based exclusively on mechanisms of assortative mating without host or habitat selection, such as the model of sympatric speciation recently proposed by Felsenstein (1981). Previous sympatric speciation models have generally failed to incorporate specific biological attributes and unique genetic systems characteristic of a particular group of organisms and, thus, usually bear little resemblance to the natural process of speciation.

Because genetic studies often indicate polygenic control of mating and other behavioral patterns, it is usually assumed that the evolution of species differences in such traits proceeds by mutations that have small effects (Mayr 1963). Furthermore, these genes are thought to be
part of highly coadapted gene complexes resistant to selection and change. This view has led evolutionists to reject relatively simple speciation models based on two or three polymorphic genes. They accept instead the concept that speciation results from differences that accumulate in many genes during long periods of geographic separation, or by a genetic revolution resulting from inbreeding and drift in small founder populations. An examination of the evidence that adaptation always occurs by microevolution indicates that much of it is circumstantial at best (Bush 1982), and the widely held theory of broad coadaptation of the genome has been seriously challenged (Hedrich et al. 1978).

We actually know very little about the genetic control of behavior or what kind of mutations are necessary for altering key adaptive traits such as those involved in reproductive isolation. To assume that changes at many loci are necessary for such alterations seems premature. In fact, a significant difference in mating behavior or habitat choice could result from a change in one or two genes active at different periods during development that alter the hard-wired neuronal pattern in the central nervous system by simply shifting the timing of a specific developmental cue. Such a mutation, possibly involving a regulatory locus, could, in this way, simultaneously affect the expression of many genes associated with a particular pattern of behavior.

If the control of genes is hierarchial, as now seems likely (Hunkapiller et al. 1982), and certain controlling elements have multigenic effects on the expression of a trait, the role and importance of single major gene mutations for speciation and the evolution of behavior can no longer be ignored. The recent discoveries in molecular genetics are revolutionizing our view of how the eukaryotic genome is organized and functions. The genetic complement of an organism is far more mobile and flexible than we previously suspected and there appears to be a continuous repatterning of gene arrangements within the genome. This reorganization is likely to have far reaching evolutionary implications.

Many of the topics to be covered in this symposium focus directly on the questions raised here concerning the genetics of mate and habitat selection, and all are pertinent to our understanding of the genetics of speciation. We have come a long way since the early selection experiments on the genetics of photo- and geotaxis in *Drosophila*. Obviously, behavior genetics has come of age. It should be interesting to see what sort of fruit this maturity bears.

**Literature Cited**


