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Sympatric speciation in animals: new wine in old bottles

Guy L. Bush

Although much has been written and debated on the origin of species, details of the actual processes involved still elude us. Increasing concern for the maintenance of species diversity has stimulated renewed interest in how species arise in nature. The evolution of sympatric sister species (those whose distributions partially or completely overlap) has been a particularly contentious problem. Leading proponents of the neodarwinian orthodoxy^{1,2} still maintain that all sexually reproducing, spatially overlapping, sister species result from secondary contact between species that evolved in geographic isolation. Recent theoretical studies and research on the evolution of natural

populations challenge this widely held view. There is mounting evidence that in some groups of habitat specialists sister species may arise by sympatric speciation³ (Box 1) – a process described by Kondrashov and Mina⁴ in genetic terms as one which ‘in its course the probability of mating between two individuals depends on their genotypes alone’ rather than on physical barriers.

Species are natural populations sufficiently genetically distinct from one another for each to follow independent evolutionary paths (Box 2). To establish the mode and process of speciation in nature, it is necessary to determine how a reduction in gene flow occurs between sister populations sufficient to allow each to become irrevocably committed to different evolutionary paths. Upon reaching this threshold of genetic differentiation, which represents the transitional stage between race and species, gene flow may affect the rate and pattern of divergence, but not the outcome. Unfortunately, we lack specific genetic and biological details about this boundary of irreversible evolutionary commitment for any sexually reproducing animal.

The debate between those who believe sympatric speciation occurs in nature and those who do not boils down to whether or not genetic differences which accumu-

Recent research on natural host races and sympatric sister species, comparative phylogenetic analyses, laboratory experiments and theoretical models has greatly strengthened the case for sympatric speciation. Traits evolving in response to divergent selection experienced by subpopulations adapting to different habitats provide sufficient intrinsic premating isolation for sympatric speciation to occur. The initiation of speciation through a habitat shift in animals which mate within a preferred habitat (such as many phytophagous and parasitic invertebrates and some vertebrates, including birds) requires few genetic changes.

Guy Bush is at the Dept of Zoology, Michigan State University, East Lansing, MI 48824-1115, USA.

late between sympatric sister populations as they adapt to different habitats are sufficient to initiate and eventually complete the speciation process in the absence of physical isolation. Evidence reviewed here indicates that adaptive traits, such as habitat or host preference, selection and fitness, intimately involved in the shift to a new niche are often the same traits that result in habitat specific assortative mating and the evolution of partial or complete reproductive isolation between sympatric populations (Box 3). Once identified, traits responsible for habitat subdivision among habitat specialists which mate only within preferred habitats are amenable to genetic scrutiny, experimentation and

theoretical treatment. The time, place and other circumstances of the origin of such populations are sometimes known or can be deduced.

Several broad and somewhat overlapping approaches are employed to study and test hypotheses of sympatric habitat race formation and speciation in sexually reproducing organisms. These include: (1) characterization of genetic polymorphisms responsible for habitat choice and use; (2) direct ecological, ethological and genetic studies of naturally established sympatric habitat races in the process of divergence; (3) determination of historical factors and traits responsible for the origin and maintenance of sympatric sister species; (4) analysis of cospeciation and habitat or host shifting as revealed by patterns of phylogenetic relationships; (5) laboratory experiments that attempt to simulate aspects of allopatric and sympatric speciation; and (6) development of theoretical models of the speciation process.

Polymorphisms responsible for habitat choice and use

A key element in the initiation of sympatric speciation by habitat shift is the acquisition of genetically based

Box 1. Speciation

The process of cladogenesis (splitting of lineages) whereby gene flow is reduced sufficiently between sister populations to allow each to become irrevocably committed to different evolutionary paths. The following modes of speciation can be distinguished:

Allopatric (with geographic isolation)

Dichopatric (vicariant) speciation: The acquisition of species status by physically isolated subpopulations, each sufficiently large to exclude inbreeding as a factor in the speciation process.

Peripatric (founder effect) speciation: The rapid acquisition of species status as a by-product of inbreeding, selection, drift, genome reorganization and substantial morphological and ecological shifts in a geographically isolated population established by a small number of founding individuals.

Allo-parapatric (reinforcement) speciation: Initial stages of speciation occur in geographically isolated populations and are then completed in sympatry as a result of selection against inter-racial hybrids.

Non-allopatric (without geographic isolation)

Parapatric speciation: Sister species evolve while adapting to contiguous, spatially segregated habitats across a narrow contact zone.

Sympatric speciation: New sister species evolve within the dispersal range of the offspring from a single deme.

Parapatric and sympatric speciation represent extremes of a continuum in the pattern and extent of habitat-imposed spatial segregation and gene flow reduction that occurs during non-allopatric divergence. Even in cases of sympatric sister populations, intrinsic differences will generate some spatial and/or temporal segregation as they seek out and adapt to different fragmented and patchy habitats.

Box 2. The species problem

Trying to explain speciation within the context of a preconceived species concept places the cart before the horse. It is an understanding of the factors that result in the reduction and eventual elimination of gene flow between sister populations – the very process of speciation itself – that is necessary before a clear species definition is possible. To establish the properties that constitute the boundary between sister species, we must first identify key traits responsible for mate recognition, such as those responsible for habitat choice, non-habitat assortative mating, fitness and genomic incompatibility. Speciation research should focus on the genetics of speciation rather than on the genetics of species differences³⁸.

Species clearly exist in nature, yet it is doubtful whether a single, unequivocal definition of the species category can satisfy all the biological and philosophical criteria deemed essential by authorities of different taxa³. Therefore, I leave it to the reader to select any of the definitions presented in Ereshefsky's³⁹ anthology of species concepts and their attendant philosophical presumptions. The process and outcome of speciation (sympatric or otherwise) does not depend on the *a priori* invocation of any particular species definition.

differences in habitat preference and fitness between the parent and daughter habitat races. When new habitat preference alleles arise in a population they can initiate habitat shifts. When mating is restricted to preferred habitats, these new alleles can lead to the establishment of genetically distinct sympatric habitat races. Over time such races may evolve into distinct species.

Genetic polymorphisms which govern habitat preference and habitat-related fitness appear to be common in sympatric natural populations. Some adaptive feeding polymorphisms are controlled by single genes, and produce rather spectacular phenotypic differences such as handedness of mouth opening in *Perissodus microlepis*, a Lake Tanganyika scale-eating cichlid⁵, and bill size polymorphism in the African finch, *Pyrenestes o. ostrinus*⁶. More subtle, but equally important, habitat- or resource-preference polymorphisms are also well documented^{3,7,8}. Results from studies on insects and other invertebrates suggest that habitat preference may sometimes involve only a few alternative alleles at a single locus, a major locus with modifiers^{5,7,9,10}, or require the action of many loci⁷. Even

when the genetic basis for habitat preference and fitness is polygenic as in recently established habitat races of an estuarine gammarid amphipod, *Eogammarus confervicolus*, divergence can occur rapidly and contribute significantly to sympatric population subdivision¹¹.

The study of naturally established habitat races

The study of sister populations in various stages of geographic and habitat race formation and speciation is the most reliable way to distinguish key genetic changes responsible for speciation from other differences accumulated after reaching the speciation threshold. A habitat or host race is a population of a species that is partially reproductively isolated from other conspecific sympatric sister populations as a direct consequence of adaptation to a specific host or habitat^{12,13}. Postmating hybrid incompatibility between habitat races is absent, and the races show habitat-associated trade-offs in fitness. Although sympatric habitat races offer the best opportunity to study species *in statu nascendi*, evidence for their existence was initially regarded as unconvincing and the possibility of their sympatric origin questioned on theoretical grounds^{1,14}. Contributing to this view is the fact that conditions that promote the formation of habitat races, such as the availability of a new habitat or resource, occur infrequently. Furthermore, once established, new habitat and host races appear to rapidly acquire the attributes of species.

Criteria for the recognition and characterization of such races are now available^{3,13}. It is not surprising that most examples of habitat races involve insects that have shifted onto introduced hosts and have become major pests. For this reason, their origin and subsequent history are fairly well documented.

Of the several well-documented examples of sympatric habitat races, the most thoroughly studied is the native hawthorn (*Crataegus* spp.) infesting haw fly (*Rhagoletis pomonella*). This species established a new host race on introduced Old World apples (*Malus pumila*) well within the range of *Crataegus* along the Hudson River, USA, in about 1860¹³. The apple population diverged in several key traits from the native haw flies and now represents a distinct race¹⁵ or incipient species. Not only do the two sympatric races differ genetically in host preference, eclosion time and host-associated fitness trade-offs, but they also consistently maintain distinct frequency differences at several allozyme loci. A considerable degree of allochronic and spatial isolation occurs between these host races because they mate only on their host plants which fruit at different times. Also, a genetically based difference between the races in their response to chemical cues emitted by the host fruit plays a key role in host choice¹³. This restriction of movement between host species by genetic differences alone is sufficient to allow strong habitat-directed selection to overcome the effects of gene flow, and thus maintain the distinct racial difference from year to year. Similar cases of habitat race formation by recent habitat shifts are documented in several invertebrates^{11,12,16-18}.

The study of sympatric sister species

The mate recognition systems, life history traits and lack of convincing evidence of prior geographic isolation of several sympatric sister species suggests that they evolved sympatrically rather than as a result of geographic isolation (consult Ref. 3 for specific citations). They are habitat specialists which use their habitat or host as a rendezvous for courtship and mating and generally show little evidence of postmating incompatibilities. Represented are Diptera

(*Rhagoletis* and *Drosophila*³), Neuroptera (lacewings³), Homoptera (treehoppers and aphids³), Hymenoptera (socially parasitic ants and parasitic wasps^{3,19}), Lepidoptera (*Spodoptera* moths and *Heliconius* butterflies³), Acarina (hummingbird flower mites³), Crustacea (parasitic copepods³), Mollusca (pulmonate snails³), Teleostei (rainbow smelt²⁰ and sticklebacks²¹) and Aves (crossbills²²). Although each example combines a unique set of biological conditions, they share one important characteristic: mate choice occurs only on or within a preferred habitat or host. Once it appears in such habitat specialists, genetic variation for habitat preference promotes habitat assortative mating resulting in population subdivision, adaptation and divergence³. Subdivision and the reduction in gene flow under these conditions result from genetic rather than geographic barriers.

Comparative phylogenetics of sister species

Phylogenetic reconstruction offers an indirect approach for establishing the mode of speciation within a taxon by testing for concordance between patterns of relationships and distribution among sister species²³. Lynch²⁴, using phylogenetic trees, compared species ranges of representative vertebrate groups (freshwater fish, frogs and birds) with ancestral ranges estimated from the sum of all descendants' ranges. He found that classical dichopatric (Box 1) events explain the origin of most species (71%). However, post-speciation dispersal could not account for the origin of some sister species (6%) which appear to have speciated sympatrically. Although there was evidence of peripatric speciation (Box 1) (15%), Lynch suggests that, in vertebrates, this mode of speciation may be even rarer than sympatric speciation. Microdichopatric or parapatric divergence is a more parsimonious argument for their evolution because dispersal does not explain the distribution of species in the groups studied. A general weakness of this approach is its inability to distinguish between microdichopatric, allo-parapatric, peripatric and parapatric divergence (Box 1). Without ecological data, it is difficult to evaluate the incidence of non-allopatric speciation by an ecotone or habitat shift.

The contribution of habitat shifts to the speciation process becomes more apparent when it is possible to factor ecological information into a phylogenetic analysis. For example, there is a tight correlation between color patterns used in interspecific and intraspecific communication by warblers of the genus *Phylloscopus* and light intensity of the habitat²⁵. Species with the brightest colors inhabit dark, forest habitats while those with duller plumage live in open habitats. Sister species with contrasting plumage patterns occupy adjacent habitats. This parapatric pattern of association between sister species, coupled with the fact that conspicuousness is habitat related and mating occurs within preferred habitats, suggests that these species have diverged parapatrically through a combination of habitat shifts and sexual selection acting on courtship and territorial displays.

Phylogenetic methods are useful in evaluating the incidence of cospeciation (speciating with the host) versus host shifts in the evolution of insect groups. Mitter *et al.*²⁶ found that clades of phytophagous insects are consistently more species rich than their primitively non-phytophagous sister groups. This suggests that herbivory promotes diversity. In a survey of examples from 14 phytophagous insect families and genera²⁶, 10 showed little or no phylogenetic concordance between the insect and host plant phylogenies, three showed partial concordance, and one

Box 3. Sympatric speciation and reinforcement

An obstacle to reaching a consensus on the likelihood of sympatric speciation is the widely held perception that it requires some form of reinforcement⁴⁰. However, in animals that mate within a preferred habitat after dispersal, the reduction of gene flow and isolation between subpopulations evolves while they adapt to different habitats, not as an outcome of selection to reduce the production of inferior hybrids³². Directed selection within each habitat promotes a runaway process²⁸. This combination accelerates incorporation of variants that improve fitness and habitat choice, thus reducing errors in mate choice. It also results in the reduction of competition for mates and resources, and reduces or eliminates selection to restrict hybridization between subpopulations.

showed extensive concordance and thus evidence of cospeciation where speciation of parasite and host apparently occurred simultaneously. The majority of speciation events in these phytophagous insect specialists are accompanied by shifts to new hosts, and cospeciation events are much less frequent. If this pattern holds for the majority of other host or habitat specialists, such as insect parasitoids, nematodes and mites with similar parasitic life histories, then sympatric divergence via host shifting may be very common. Although it is argued that allopatric speciation in parasites occurs via host shifts in peripheral isolates followed by the extinction of the original hosts^{23,27}, evidence from contemporary host and habitat shifts, such as *Rhagoletis* and other examples cited above, does not support this view. These shifts occurred well within the normal dispersal range of the parent population and were followed by rapid genetic and phenotypic divergence.

Laboratory experiments of allopatric and sympatric speciation

Rice and Hostert²⁸ review many of the experiments of the past half century that attempted to duplicate all or part of the processes of allopatric and non-allopatric speciation. Their survey found little experimental evidence that sampling drift, genetic bottlenecks and reinforcement are directly responsible for the development of pre- or post-mating reproductive isolation, although these factors may contribute to divergence which in turn may pleiotropically cause isolation. This view is supported by a recent detailed study involving replicated large-scale experimental tests. Galiana *et al.*²⁹ found that a change in assortative mating leading to speciation is not likely to occur under conditions of the founder-flush-crash model of speciation. Mounting experimental²⁸ and theoretical³⁰ evidence indicates that peripatric speciation (Box 1) by founder effects, viewed as the major source of new species^{1,2}, occurs infrequently in nature. In contrast, there is substantial experimental documentation for the evolution of reproductive isolation as a result of strong selection, pleiotropy and/or hitchhiking effects²⁸, with or without physical isolation.

Theoretical models and computer simulations

The maintenance of habitat-specific polymorphisms occurs most easily when individuals of different genotypes are able to select the habitat in which they are most fit. Jaenike and Holt⁷ modeled a life cycle in which there is habitat selection and global random mating as follows: '(start generation t) zygote formation \Rightarrow dispersal and habitat choice \Rightarrow habitat residence and selection (differential mortality) \Rightarrow random mating across entire population (start of generation $t + 1$)'. They confirmed previous studies that habitat selection coupled with some frequency and/or density dependent selection (soft selection) broadens conditions for the maintenance of niche polymorphisms.

However, as long as habitat preference is random with respect to mate choice, as in the above life cycle, habitat race formation and speciation will not occur. Gene flow prevents the formation of strong linkage disequilibrium between habitat related preference and fitness alleles, a process required for the evolution of different mate-recognition systems between races and species. This reduction in gene flow occurs when mating takes place at random within a habitat following dispersal to a preferred habitat, such as in the following life cycle: (start generation t) zygote formation \Rightarrow habitat residence and selection (differential mortality) \Rightarrow dispersal and habitat choice \Rightarrow random mating among individuals within a preferred habitat (start of generation $t + 1$). Computer simulations of single- or multiple-variation models examine the properties of this life cycle based on a correlated response between habitat selection and mate choice and their effects on sympatric speciation^{8,31,32}. Assuming independent regulation of population size, such habitat-specific assortative mating promotes the fixation of mutations that increase habitat fidelity and survivorship. These models show that sympatric race formation and speciation may occur when individuals with strong habitat-dependent positive assortative mating experience superior fitness over genotypes of intermediate fitness. Conditions for sympatric speciation are further relaxed if habitat preference is epistatic to fitness⁸.

This contrasts with the results of Felsenstein³³, who explored a model with variation in non-habitat-associated positive assortative mating and habitat fitness genes based on the following life cycle: (start generation t) zygote formation \Rightarrow habitat-independent assortative mating \Rightarrow random dispersal across habitats \Rightarrow habitat residence and selection (start of generation $t + 1$). In this model, habitat choice is random and adults mate assortatively independent of the habitat. When there is no correlated response between habitat choice and mate choice, conditions of selection, gene flow, linkage and gene penetrance necessary to surmount the antagonism between recombination and selection are so restrictive that non-allopatric speciation is unlikely to occur.

Obviously, life-cycle and mating-system components significantly influence the speciation process. To broaden our understanding of sympatric speciation, it is essential to explore models incorporating other factors that promote divergence, such as, runaway sexual selection³⁴, population size⁴, temporal isolation³⁵, resource availability³, environmental complexity and variability³, small body size and short generation time³⁶, and non-genetic environmental effects³⁷. These models should also examine the effects of combining both non-habitat- and habitat-based assortative mating genes.

Conclusions

It is no longer possible to dismiss sympatric divergence as a mode of speciation in animals, particularly in those taxa in which mate choice is directly dependent upon habitat or resource choice. Sympatric speciation is likely to be far more common than has been assumed in some sexually reproducing animal groups such as insects, mites and nematodes which represent the majority of animal species. We need in-depth biological and evolutionary research on allopatric and sympatric habitat races and sister species of known age and place of origin in these groups. Only then can we gain a true perspective on the frequency of allopatric and non-allopatric modes of speciation.

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