Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character

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Summary

A diverse group of theoretical and empirical studies are integrated into a composite model of sympatric speciation via habitat specialization. It is shown that disruptive selection on a continuous distribution of habitat preference can lead to the evolution of prezygotic reproductive isolation as a correlated character. The form of selection eliminates the major theoretical objections to the process of sympatric speciation. The principal difference between this model and the allopatric model of speciation is that the initial barrier to gene flow between subpopulations is produced by the evolution of gaps in the phenotypic distribution of spatial/temporal habitat use, rather than an extrinsic geographical barrier.

Keywords: Disruptive selection, speciation, habitat selection.

Introduction

The idea that speciation can occur in a gradual fashion under sympatric (i.e. non-allopatric) conditions has been contemplated throughout the history of speciation theory (for review see White, 1978; Bush and Howard, 1986). The sympatric speciation concept was severely criticized by Mayr (1942, 1947, 1963), and it was not until the empirical work of Thoday and Gibson (1962) that it was reevaluated by evolutionary biologists. Thoday and Gibson applied disruptive selection to bristle number in *Drosophila melanogaster* and observed a rapid evolution of complete reproductive isolation between high and low selected lines. The experiments of Thoday and Gibson (1962) motivated Maynard Smith (1962, 1966) to model the evolution of sympatric speciation via the following trajectory of events:

(1) Disruptive selection leads to the establishment of a polymorphism (involving 1 or more loci and producing a bimodal phenotypic distribution).

(2) Reduced survival of the offspring from crosses between different modal phenotypes generates selection for assortative mating.

(3) Successful selection for assortative mating requires the buildup of strong linkage disequilibrium between the genes affecting the selected polymorphism and the genes affecting assortative mating (as elaborated by Felsenstein, 1981).

(4) The eventual evolution of complete assortative mating leads to speciation.

Sympatric speciation via this disruptive selection model has been challenged on both empirical and theoretical grounds. Attempts to repeat Thoday and Gibson's experiments with different lines of flies have all failed, as have similar attempts with other species (for review see Thoday and Gibson, 1970). Many theoretical studies followed the original model of Maynard Smith (1966) (for review see Endler, 1977; Templeton, 1981), culminating in the work of Felsenstein (1981). Felsenstein demonstrated that the principal factor interfering with the evolution of reproductive isolation under sympatric conditions is an antagonistic interaction between the processes of selection and recombination (the selection-recombination antagonism). Selection acts to build the requisite disequilibrium between genes affecting assortative mating and those influencing the polymorphism produced by disruptive selection, however recombination acts to destroy this association. Because of the strong mixing effect of recombination when different modal types

mate, selection will rarely, if ever, be sufficiently strong in nature to split a sympatric population into reproductively isolated subunits.

Such empirical and theoretical results would appear to discredit the concept of sympatric speciation via disruptive selection. Yet all of these studies consider only the special form of sympatric speciation outlined by Maynard Smith, i.e. disruptive selection → polymorphism → selection for assortative mating → reproductive isolation. An alternative route to sympatric speciation would occur if disruptive selection were applied to a trait that produces assortative mating as a correlated character (Slatkin, 1982; Rice, 1984). In this instance reproductive isolation is not built directly by natural selection, but evolves indirectly due to pleiotropy. Because the same genetic variability acted upon by disruptive selection also produces assortative mating, no linkage disequilibrium between genes affecting viability and assortative mating need be established, and the selection-recombination antagonism is circumvented. Thus the evolution of reproductive isolation as a correlated character eliminates the principal genetic factor thought to interfere with the evolution of reproductive isolation under sympatric conditions.

What types of traits would be expected to produce strong reproductive isolation as a correlated character? Elsewhere (Rice, 1984, 1985) I have provided theoretical and empirical support for habitat preferences. Here I extend these ideas and examine the evolution of complete and irreversible reproductive isolation between habitat specialists.

Habitat selection as a barrier to gene flow

The idea that habitat specialization can lead to reproductive isolation is not new (for review see Futuyma and Mayer, 1980; Bush and Howard, 1986). Habitat selection was considered in the original mathematical models of sympatric speciation by Maynard Smith (1962, 1966) and has been extensively discussed by both Bush (1969a,b, 1975), for the case of sympatric speciation via host-race formation, and Tauber and Tauber (1977a,b). In a previous paper (Rice, 1984) these oligogenic models are extended to the case of polygenic inheritance and it is described how disruptive selection on habitat preference can bypass the selection-recombination antagonism and produce strong reproductive isolation (under sympatric conditions) as a correlated character.

When individuals mate within their selected habitats, assortative mating is necessarily coupled to habitat choice. Assuming genetic control of habitat preference, this means that the same genes acted upon by natural selection for habitat choice also produce assortative mating. Under these conditions linkage disequilibrium between assortative mating genes and those affecting the disruptively selected trait is no longer a prerequisite for reproductive isolation. Therefore, recombination does not interfere with the evolution of reproductive isolation via habitat specialization.

Disruptive selection on habitat preference is expected to produce a bimodal phenotypic distribution for habitat preference when the combination of selection and habitat-based assortative mating is sufficiently strong (see below). If suitable habitats are separated in space and/or time, disruptive selection can be quite intense in nature. The bimodality in habitat preference generated by disruptive selection can consequently produce a strong barrier to gene flow and permit the semi-independent evolution of habitat specialists. As discussed later, the strong assortative mating produced by habitat preference can greatly enhance the capacity of a single population to 'discover' and colonize multiple adaptive modes within a mosaic of contiguous habitat patches.

Once disruptive selection on habitat preference produces an incomplete barrier to gene flow, two forces will act on the semi-isolated gene pools: migration will act as a homogenizing force, and differing selection between the two selected habitats will act as a differentiating force. If selection in the two selected habitats is similar, then small amounts of gene flow would tend to swamp genetic differentiation (Crow and Kimura, 1970 p. 469; Endler, 1977) and both progres-

sive and stochastic evolution within the two gene pools would be unlikely to differ substantially. If selection in the two habitats were different, however, additional reproductive isolation could evolve via pleiotropy. This idea has been discussed by Slatkin (1982) for the case of parapatric speciation and also can be applied to habitat-based sympatric speciation once an initial barrier to gene flow has evolved. The evolution of pre-zygotic reproductive isolation as a correlated character that evolves as an indirect response to habitat specialization is discussed below. Thus reproductive isolation is assumed to evolve not in direct response to selection for assortative mating, but indirectly due to selection on other characters.

The evolution of reproductive isolation under allopatry

Much of the criticism directed at models of sympatric speciation via disruptive selection centers on differences in the process by which reproductive isolation can evolve under sympatry and allopatry. Here I briefly outline the mechanisms by which reproductive isolation is thought to evolve under allopatry. Later, I suggest that these are essentially the same mechanisms by which reproductive isolation would be expected to evolve under sympatric conditions.

When populations are allopatric there can be no direct selection for reproductive isolation. As a consequence, any reproductive isolation that evolves in allopatry must be a result of the pleiotropy of genetic differences that evolve due to sampling drift, differential selection, or a combination of these two evolutionary forces (Muller, 1942). It is important to note that both sampling drift and differential selection can produce a high degree of gene pool differentiation without complete isolation (see for example Haldane, 1930; Antonovics, 1968; Nagylaki, 1977). Slatkin (1982) has shown that local adaptation, through pleiotropy, can lead to the evolution of both pre- and post-reproductive isolation despite gene flow between subpopulations.

In the case of strict allopatric speciation, in which the completion of the evolution of reproductive isolation is not brought about by reinforcement during secondary contact, independent evolution, and its associated pleiotropy, are the sole agents responsible for speciation. Slatkin's (1982) theoretical work, demonstrating that genes that pleiotropically produce reproductive isolation can accumulate in semi-isolated populations, lays the theoretical foundation for sympatric speciation to evolve in exactly the same fashion as allopatric speciation.

A synthetic speciation model

The model developed here is a composite of the ideas developed by many authors. The major contributors include Thorpe, 1945; Thoday and Gibson, 1962; Maynard Smith, 1962, 1966; Antonovics, 1968; Paterniani, 1969; Crosby, 1970; Bush, 1969, 1975; Dickson and Antonovics, 1973; Balkau and Feldman, 1973; Soans *et al.*, 1974; Endler, 1977; Caisse and Antonovics, 1978; Tauber and Tauber, 1977a,b; Rosenzweig, 1978; Moore, 1979, 1981; Pimm, 1979; Udovic, 1980; Felsenstein, 1981; Halliburton and Gall, 1981; Slatkin, 1982; Howard and Harrison, 1984; Rice, 1984, 1985; Colwell, 1986; Wilson and Turelli, 1986. The model developed here is not just a summary, however, but represents a synthesis, especially with respect to extending former oligogenic models to a polygenic domain.

To describe the speciation model it is assumed that species X initially persists only within habitat A which is included within a matrix of habitat types. Environmental change generates a new habitat (type B, separated in space and/or time from habitat A) that is suitable for colonization by species X. Will species X divide into two reproductively isolated populations exploiting the two spatially and/or temporally separated habitats?

Because the relevant ecological factors differ between plants and animals this question will be

addressed by considering first a hypothetical plant species, second a hypothetical animal species, and finally generalize from these examples to a model for habitat-based sympatric speciation. The two examples are extensively described in order to point out that the natural history conditions permissible for speciation via habitat specialization may occur in a wide variety of contexts, and should not be considered to be idiosyncratic to phytophagous insects or other species with similar life history characteristics.

A plant example

Consider a hypothetical herb species that is found within a large contiguous stand of deciduous, north-temperate forest. The entire life cycle (flowering cycle) of the herb is carried out during the interval of high solar input occurring after snow melt (or the last hard frost) but prior to the time that the canopy of deciduous trees produces foliage and shades the understory. Many herb species possess such a life cycle (e.g. Schemske *et al.*, 1978). Next suppose climatic change causes a drying of the forest and, as a consequence, a mosaic of discrete dry meadows are formed along south facing aspects within the forest. Because these meadows are isolated from other grasslands, assume that they will have a depauperate flora and that interspecific competition initially will be low. Will a new meadow-adapted herb species evolve?

If the demands of the environment were identical in woodland and meadow there is no reason to expect the formation of forest- and meadow-adapted gene complexes. However the optimal phenotype for these two habitats may differ substantially. One important difference could be the optimal timing of germination and/or flowering. In the woodland, the life cycle of the herb must take place during the early spring prior to shading by the deciduous canopy. This same time period in the meadows may be suboptimal. For example, radiation frosting and wind shear, which would be ameliorated in the forest, may interfere with early growth and flowering in the meadow. These and other factors may favour delayed germination and flowering in the meadow subpopulations.

Will early and late flowering subpopulations evolve? This question can be addressed with a standard 'Continent-island' model (Hedrick, 1983 p. 278), or more generally with a 'disruptive selection on habitat preference' model as described in Rice (1984). The results of my simulation work on disruptive selection on spatial/temporal habitat preference are summarized in Fig. 1. A unimodal habitat preference distribution can be converted to a non-overlapping bimodal distribution by extreme disruptive selection alone (i.e. when intermediate phenotypes are inviable; note that in this case no reproductive isolation between modal types occurs), by very strong assortative mating alone (i.e. when each phenotypic class mates virtually exclusively among themselves), or by moderate levels of disruptive selection when applied to a trait that also produces positive assortative mating. Moderate, strong etc. are defined in Rice (1984). What these simulations demonstrate is that biologically feasible levels of disruptive selection, when applied to a continuous habitat preference trait (such as flowering time) that produces positive assortative mating, can be expected to split a unimodal population into two widely separated modal types. As the modes of the population diverge, an increasing level of reproductive isolation is achieved.

In the case of disruptive selection on flowering time in the hypothetical herb, two factors promote positive assortative mating between individuals with similar flowering time phenotypes. First, if pollen and seed movement is low relative to the size of the meadows, then differential selection in the woodland and meadow will spatially cluster similar phenotypes and promote positive assortative mating. Second, early and late flowering phenotypes will necessarily mate assortatively due to the temporal difference in their flowering periods. Thus disruptive selection (produced by the simultaneous occurrence of woodland and meadow habitats) on flowering time can readily produce a bimodal phenotypic distribution for flowering time and indirectly lead to
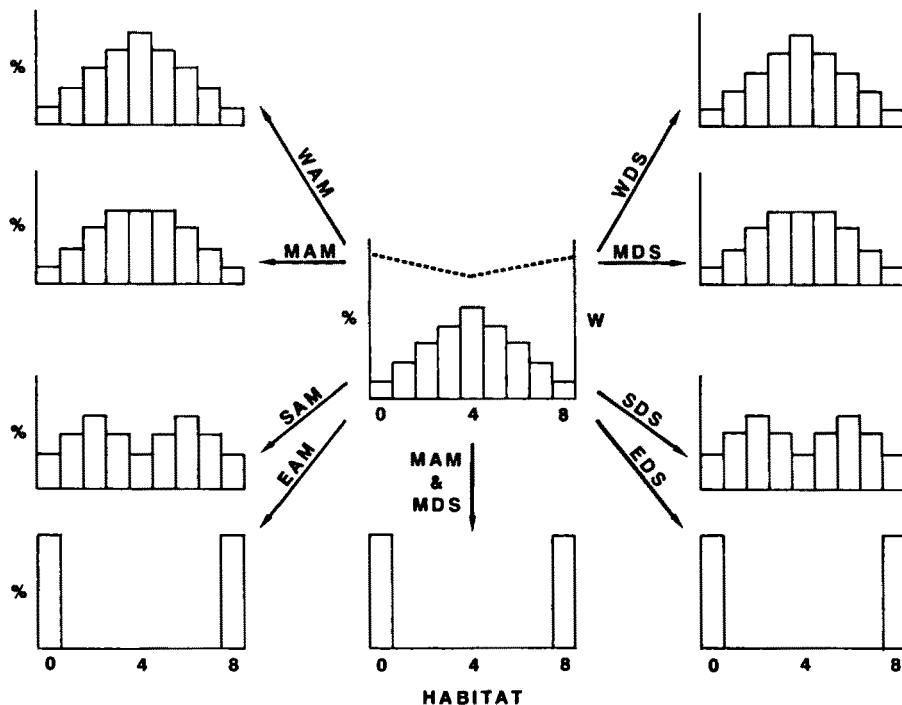
Figure 1. Summary of the simulation analysis of Rice (1984). The horizontal axes are habitat preference phenotype (0 and 8 representing opposite ends in a cline of habitat patch types), the right [left] vertical axis is relative fitness [frequency]. The V-shaped curve (dotted) depicts the relative fitness of habitat preference phenotypes. The steeper the slope of the two arms of the V, the greater the level of disruptive selection. Figures to the right [left] correspond to weak (W), moderate (M), strong (S), and extreme (E) disruptive selection (DS) [assortative mating (AM)]. A non-overlapping biomodal phenotypic distribution is achieved with extreme positive assortative mating, extreme disruptive selection on habitat preference, or with a combination of only moderate levels of both disruptive selection (on habitat preference) and habitat based assortative mating. See Rice (1984) for details.

reproductive isolation between woodland and meadow populations. This process is shown diagrammatically in Fig. 2.

The degree of reproductive isolation produced by a difference in the optimum flowering time in woodland and meadow depends on a variety of factors, the most obvious of which is the magnitude of the difference. If the optimal flowering time for the woodland and meadow were widely separated (e.g. spring vs fall respectively, assuming such disparate flowering times could evolve; see below) then this difference alone could lead to complete reproductive isolation between the two modes of the flowering time distribution. Complete reproductive isolation would require the elimination of intermediate flowering-time phenotypes. This would occur, for example, when intermediate flowering phenotypes were competitively inferior (on an inter- and/ or intraspecific basis) in both habitats, and the phenotypic variance in flowering time was sufficiently small to prevent overlap between early and late flowering modes of the phenotypic distribution.

When the optima in flowering times are very widely separated it is easy to see how reproductive isolation could evolve indirectly as a correlated response to disruptive selection on flowering time. However, it must commonly occur that the optima in flowering time are not sufficiently

a

%   W

b

%   W

c

%   W

d

%   W

●arly   late
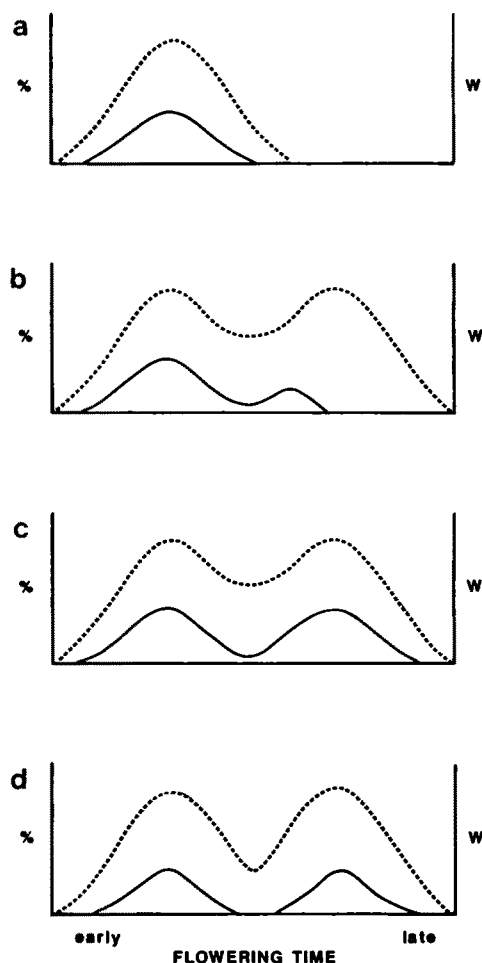FLOWERING TIME

Figure 2. A schematic diagram illustrating how disruptive selection on flowering time can lead to the evolution of reproductive isolation. The smooth [dotted] curves depict relative number of individuals [relative fitness]. In frame a the new habitat is absent. In frame b the new habitat is introduced and colonization begins. Because late flowering is favored in the new habitat, it produces disruptive selection for flowering time. The assortative mating between late flowering genotypes promotes the development of a later flowering mode (see text). In frame c the two modes of flowering time are fully established but gene flow between modes occurs via intermediate flowering sub-populations. In frame d the intermediate flowering sub-popuations are eliminated via competition, further change in the environment, etc. as explained in the text.

different to produce complete reproductive isolation. A second mechanism that could enhance reproductive isolation when it became stalled due to insufficiently separated differences in optimal flowering time, is disruptive selection on flower structure. For example, suppose the ancestral woodland species had small, insect pollinated flowers. If a different suite of pollinators were available in meadows compared to the woodland (e.g. bird pollinators more available in the meadow) selection on flower morphology might differ between the habitats. The partial reproductive isolation, due to differences in the timing and place of flowering, would facilitate local adaptation of flower morphology to the meadow habitat. To the extent that flower morphology

changed in the meadow populations (e.g. red coloration, long corolla, etc.), this could further reduce gene flow between the two modes of the flowering time distribution.

In addition to changes in flower structure, the optimum diurnal pattern of flower opening may differ between habitats. Suppose the spatial and/or temporal isolation of the woodland and meadow subpopulations permitted the evolution of different diurnal patterns of flowering (e.g. morning vs evening, see Raven, 1961; Moore, 1979); in this case the pool of pollinators serving the subpopulations could change, further enhancing reproductive isolation.

A fourth factor (i.e. in addition to flowering place, period and structure) that could promote reproductive isolation is pre-flowering survival. As described below, the optima for many factors besides flowering time may differ between woodland and meadow. As the meadow sub-population becomes increasingly adapted to this environment, the competitive ability of woodland migrants to the meadow should progressively decline. A parallel decline in the competitive ability of migrants from the meadow to the woodland should also take place. Thus, competitive elimination of migrants (prior to flowering) from the woodland and meadow habitats can further enhance the degree of positive assortative mating.

In addition to prezygotic reproductive isolation, postzygotic isolation is expected to evolve when the optimal phenotype is sufficiently different between the two habitats (see Antonovics, 1968; Slatkin, 1982). Meadow and woodland are expected to differ in their optima for phenotypic characters such as life-history attributes, biotic and abiotic interactions. For example, the suite of pests and pathogens will frequently differ between habitats as will the abiotic attributes such as light intensity, desiccation stress, and nutrient availability. To the extent that these differences require different adaptations, semi-independent evolution in the two habitats can potentially produce differing coadapted gene complexes and thus interfere with the adaptedness of hybrids from matings between the two habitats.

In summary, disruptive selection on spatial/temporal habitat preference can lead to substantial reproductive isolation (as a correlated character) between different habitat preference types. This isolation can then lead to the evolution of different mating structures which further enhances reproductive isolation and the potential for increasingly independent evolution. Semi-independent evolution in the two habitats, promoted by substantial but incomplete reproductive isolation and differing selective regimes, can further enhance assortative mating by eliminating competitively inferior migrants prior to reproduction. And lastly, differential adaptations promoted by partial reproductive isolation and differing selective regimes may gradually build postzygotic reproductive isolation. All of the reproductive isolation evolves as a correlated response and not in direct response to selection for assortative mating.

An animal example

Because habitat preference in carabid beetles has been extensively studied (for review see Thiele, 1977), a hypothetical predatory carabid beetle will be used in this example. Consider the same environmental change described in the plant example. Will a subpopulation of a woodland species of carabid beetle colonize the meadows and subsequently speciate into a meadow specialist? A sequence of events potentially leading to this result is given below.

Habitat preference in extant species of carabid beetles can be quite extreme, often with different species occupying forest and meadow habitats that are separated by only a few meters (Thiele, 1977). Laboratory experiments support the conclusion that this habitat preference is innate and not simply the result of competitive exclusion (Thiele, 1977). If preadapted meadow-species did not colonize from outside areas, and if sufficient prey were available in the new meadow habitats, then an 'empty niche' would become available for colonization by the woodland population of beetles. Assuming sufficient genetic variation in habitat preference, a small

proportion of the woodlot population would utilize meadow habitat. Since mating occurs locally in most carabid beetles (as well as many other animal species), those selecting meadow instead of woodlot habitat would tend to mate amongst themselves. The presence of the new meadow habitat produces disruptive selection on habitat preference, assuming that suitable combinations of photo-preference, hygro-preference, thermo-preference, etc. are sufficiently different in woodland and meadow.

Breeding seasons frequently differ between closely related carabid species, with woodlot species typically mating in the spring and field species in the fall (Thiele, 1977). This pattern observed in extant species indicates that selection on breeding time may differ between woodlot and meadow habitats. Changes in the modality of breeding time could act to enhance further the spatial reproductive isolation between woodlot and meadow subpopulations. There is also a difference in diurnal activity pattern between extant woodlot and meadow species with most woodlot species restricting their activity primarily to night hours while meadow species are either less temporally specialized or daylight specialized (Thiele, 1977). If differential selection in the two habitats produced temporal difference in diurnal activity, then this factor also could enhance reproductive isolation between woodland and meadow subpopulations.

Body size of extant woodlot and meadow species differs; larger numbers of smaller species are found in meadow habitat. To the extent that body size affects mating preference (see Halliburton and Gall, 1981; Snead and Alcock, 1985), the evolution of smaller body size in meadows may also enhance reproductive isolation between the two subpopulations. The efficiency of mate-attracting stimuli (pheromones, sound, vibration, coloration, etc.) may also differ between the relatively dark, moist woodlot and the drier, lighter meadow (see Stratton, 1986 for a discussion of this pattern in spiders). These differences could lead to the evolution of differing mating signals in the two habitats, further enhancing reproductive isolation. For example Markow (personal communication) has selected for positive phototaxis in a strain of *Drosophila melanogaster* for 320 generations. Analysis of the mating behaviour of this selected strain showed that the males have evolved an increased use of visual signals in their courtship display, and that females have evolved increased preference for these visual signals. This strain is strongly ethologically isolated from another strain which orginated from the same founder stock but was simultaneously selected for negative phototaxis. Thus there is at least preliminary empirical support for the idea that selection on habitat preference (or sensory modality) may produce a correlated response in sexual signalling that can lead to substantial reproductive isolation.

Lastly, differing environmental conditions between woodlot and meadow (e.g. prey spectrum, background coloration, competitors, pathogens, predators, etc.) may favour quite different phenotypes in the two habitats. As local adaptation happened, promoted by partial spatial and temporal reproductive isolation, it would be expected to reduce the competitive abilities of migrants and further enhance both pre- and post-zygotic reproductive isolation as described in the plant example.

The idea that adaptation to different environmental conditions can rapidly lead to strong reproductive isolation as a correlated character has been demonstrated experimentally by Kilias *et al.* (1980). These researchers reared replicate *Drosophila melanogaster* populations under identical (or different) environmental conditions for five years. Populations reared under identical (different) environmental conditions evolved little or no (strong) reproductive isolation.

In summary, a change in climate produces a new 'niche' spatially separated from (but contiguous with) that used by the extant beetle species. This produces disruptive selection on habitat preference. The spatial separation of differing habitat preference phenotypes (genotypes) produces positive assortative mating and hence partial reproductive isolation between the woodland and the meadow subpopulations. This partial reproductive isolation permits semi-

independent evolution that can lead to differences in such characters as breeding period, diurnal activity period, and mating structures which would act to further increase reproductive isolation. These factors, in combination with the reduced competitive ability of migrants owing to the local adaptations to the meadow, may ultimately lead to complete reproductive isolation between the two habitat morphs.

The general model

From the two hypothetical examples it can be seen that prezygotic reproductive isolation can evolve as a correlated character in a variety of ways. These include differences in mating-place, -time, -structures, and -competitive ability. I will refer to each of these general sets of characters as axes upon which disruptive selection can act to produce reproductive isolation as a correlated character. Simultaneous and/or sequential selection on different axes can act to increase substantially the level of reproductive isolation that could potentially evolve via any single axis. This is shown diagrammatically in Fig. 3. The first axis shown is mating place. This axis applies to plants and animals differently.

In the case of animals, active genetically-controlled habitat choice can be a powerful sorting mechanism that produces assortative mating between similar habitat preference phenotypes (genotypes). Large difference in habitat preference between many extant sibling species and the high precision of habitat preference within many of these same species (see Thiele, 1977), provides empirical support for the idea that spatial habitat preference can be genetically controlled and can respond to natural selection. My modelling and empirical work on disruptive selection for habitat preference suggests that this type of selection can lead to substantial reproductive isolation (Rice, 1984, 1985). It is the active sorting of individuals into habitats that can make disruptive selection on spatial habitat preference such a powerful isolating mechanism in animals.

In the case of plants, active spatial habitat preference is unlikely to be as important. While there are clear cases of active habitat preference in plants (for example Salzman, 1985), these occur on a very local scale and are unlikely to produce substantial reproductive isolation between individuals genetically predisposed to choose different habitat types. Passive habitat preference may be accomplished by changing the design of the seed coat (or fruit, etc.) which changes the identity and/or the affinity of the dispersal agent, and hence where the seeds are dispersed. A second form of passive habitat preference is simply the elimination or reduction of dispersal, causing offspring to remain in the habitat of the parents (Balkau and Feldman, 1973).
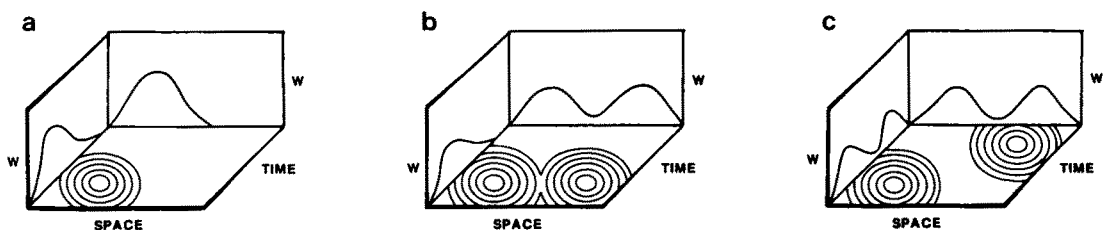

Figure 3. A multi-dimensional diagram showing how disruptive selection on different axes (mating-place and mating-time) can combine to increase reproductive isolation. The curve on the back [left] panel depicts relative fitness of different spatial [temporal] habitat preference phenotypes. The contour lines within the central square depict relative numbers of individuals with different combinations of spatial and temporal habitat preference. In frame a the new habitat is absent. In frame b it is introduced (producing disruptive selection on spatial habitat preference) and colonization begins. In frame c successful colonization of the new habitat produces disruptive selection on mating time.

Disruptive selection on spatial habitat preference alone will probably rarely be sufficient to produce complete reproductive isolation. Disruptive selection on additional axes can alleviate this problem (Fig. 3). When selecting on mating time differs between habitats and when at least some of the genetic variability for mating time is orthogonal to that for spatial habitat preference, then selection on this axis can enhance that produced by spatial habitat preference alone. In a similar manner, disruptive selection on mating structures and habitat-specific competitive ability can further enhance the degree of reproductive isolation.

The graphical model shown in Fig. 3 illustrates how genetic variability for a wide variety of characters can be used to gradually build prezygotic reproductive isolation in a manner that bypasses the selection-recombination antagonism. This eliminates the major genetical obstacle to sympatric speciation via disruptive selection since it does not evolve via the classically assumed trajectory of events (i.e. disruptive selection → polymorphism → selection for assortative mating → eventual complete assortative mating and speciation) but instead reproductive isolation evolves indirectly as a correlated character. Once subtantial reproductive isolation evolves in this manner, postzygotic isolating mechanisms can evolve as described by Slatkin (1982), and irreversible reproductive isolation will result. It is important to point out that spatially/temporally separated habitats are likely to provide independent carrying capacities which facilitate the persistence of the two modal phenotypic classes.

A factor that can stall the proposed speciation process is the establishment of 'bridging populations', i.e. populations adapted to the intermediate habitats that separate major habitat types. For example, in the case of flowering time, gene flow between spring and fall flowering subpopulations could be maintained if a gradient of summer flowering subpopulations persisted. Such a gradient of intervening populations could certainly stop the speciation process, but there are many factors that may interfere with their establishment and persistence.

Intra- and interspecific competition are obvious candidates to interfere with bridging populations. Early in the speciation process both types of competition may be low due to the lowered levels of adaptation (of all colonizing species) to the new habitat. Thus intermediate flowering populations may have been competitively viable early, but not later, due to the ever increasing level of competition that accompanies local adaptation and/or the eventual invasion of pre-adapted species from distant areas. A second mechanism is the gradual development of a new habitat. Gradual development provides a continuous but transient environmental bridge between habitats that is eliminated as differentiation of the new habitat continues. And lastly, 'genetic swamping' may eliminate bridging populations. Single locus models predict local adaptation only when differences in selection are large relative to gene flow (see for example Hedrick, 1983 p. 296). Thus when bridging populations are small (and/or unidimensionally arranged) and/or when environmental demands of ecotonal areas are not sufficiently different from those of the two major habitats, gene flow may swamp adaptation to ecotonal areas and subpopulations adapted to intermediate habitat conditions may not persist (or initially develop).

Discussion

The first major point to be made by the model presented here is that no new theory is needed to predict, with feasible assumptions, the evolution of reproductive isolation under sympatric conditions. The array of models previously developed can be integrated to demonstrate that sympatric speciation is feasible and can proceed by essentially the same genetic mechanisms that have been postulated to promote speciation in allopatry. The principal constraint is that organisms mate locally within relatively discrete spatially and/or temporally separated habitats, and

that the environmental demands (concerning mating-place, -time, -structures, and competitive ability) be sufficiently different between habitats. Most of the criticism directed at the concept of sympatric speciation has centered on the evolution of assortative mating via the classical trajectory of events as described earlier. What frequently has been ignored is that there are other reasonable trajectories.

Some might argue that the model presented here does not represent genuine sympatric speciation since it is based on the spatial and/or temporal separation of individuals. This objection seems trivial, since it is assumed that both habitats are simultaneously utilized by the same ancestral population that gives rise to the two new species. The criterion that individuals be within the 'cruising range' (Mayr, 1963) of each other is realized in the model. What differs between this model and the classical allopatric model of speciation is the absence of a physical barrier to movement between subpopulations. There is no insurmountable mountain range, river, ocean, etc. separating subpopulations. Instead, subpopulations are gradually separated by gaps in the distribution of phenotypes, gaps that are produced by disruptive selection and act to reduce gene flow. Thus, it is the phenotypes of the organisms themselves that produce isolation rather than an external environmental obstacle.

The second major point to be made is that the proposed model has important limitations. The availability of new habitats in no way guarantees that speciation will take place. It frequently will not. There are important prerequisites that must be met. First, there must be sufficient variation in habitat preference for the new habitat (or an intermediate leading to the new habitat) to be 'discovered' by neighboring extant species. This variation must be accessible to natural selection, i.e. linkage and antagonistic pleiotropy must not preclude a response to disruptive selection on habitat preference. Second, habitat preference must be sufficiently precise, genetically controlled, and heritable to act as a barrier to gene flow. Species that lack strong spatial/temporal habitat preference will be unlikely to speciate via the model presented here. Third, habitat boundaries must be relatively sharp. If an extensive ecotone exists between habitat types then 'bridging populations' may persist and act to facilitate gene flow between habitats as described earlier. Fourth, the immigration of preadapted species must not competitively exclude the successful colonization by non-preadapted species, i.e. an 'empty niche' must be available. And lastly, differential selection between the new and old habitats must be sufficient to produce subpopulation divergence in traits affecting pre- and post-zygotic reproductive isolation.

This set of prerequisites will frequently not be met, especially in environments that already possess a large and diverse fauna and flora. In this case the immigration of preadapted species may preclude radiation by extant species. In new environments, however, the prerequisites may frequently be met. For example: (1) in the wake of the extinction of ecologically equivalent taxa (Colwell, 1986), (2) on large, ecologically diverse islands that are distantly separated from a pool of preadapted migrants, (3) in the wake of retreating continental glaciers, (4) within isolated, nascent deserts, and (5) on isolated mountain ranges, especially those in tropical areas where high altitude produces temperate and arctic conditions embedded within a large buffer of tropical vegetation. Even in 'saturated communities', however, habitat-based speciation may be important when a taxonomic group evolves a novel adaptation that permits it to invade new habitat types from which it was previously excluded.

The principal genetic factor making disruptive selection on habitat preference such a powerful speciation mechanism is the coupling of disruptive selection with the consequence of assortative mating. This coupling has two important effects. First it eliminates the selection-recombination antagonism identified by Felsenstein (1981) as discussed above. Simulation work by Crosby (1970) and Rice (1984) in combination with the empirical work of Paterniani (1969) and Rice (1985) demonstrate that the splitting of a unimodal population into reproductively isolated

subunits is readily accomplished when the disruptively selected trait also produces assortative mating, but is virtually impossible otherwise (with the unrepeated exception of Thoday and Gibson, 1962). Second, the coupling of disruptive selection with assortative mating facilities the splitting of a unimodal phenotypic distribution into a bimodal population exploiting different adaptive modes within an adaptive landscape (see Fig. 2). When extreme habitat preference phenotypes mate assortatively, the reduced levels of matings between different habitat preference phenotypes (genotypes) increases the realized heritability of habitat preference (Crow and Felsenstein, 1966), and also permits the tails of the phenotypic distribution to evolve in a semi-independent fashion (Rice, 1984).

When a tail of the phenotypic distribution extends across an adaptive trough (Figure 2b) it will evolve toward the new adaptive peak whenever the combination of selection and assortative mating is sufficiently strong. Thus assortative mating between extreme habitat preference phenotypes facilitates the capacity of a population to 'discover' new adaptive peaks and to adapt simultaneously to two or more peaks within an adaptive habitat preference landscape (Fig. 2). Because new recombinant genotypes will continually enter the tails of a phenotypic distribution, a continual stream of new genetic variability can move into the subpopulation of the newly developing phenotypic mode. Thus the two modes of the phenotypic distribution may rapidly diverge, producing even greater reproductive isolation as they do. Empirical studies of directional selection on quantitative traits (Falconer, 1981 p. 195) indicate that sufficient extant variability is present to move the mode of many phenotypic traits 10–30 standard deviations. The empirical work of Paterniani (1969) and Rice (1985) supports the conclusion that similar levels of variability are accessible for habitat-preference traits that are subject to disruptive selection.

In conclusion, the availability of new habitat types can create disruptive selection on habitat preference phenotypes (genotypes) whenever the immigration of preadapted species is limited. When sufficient heritable variation is present within extant neighboring species to 'discover' this new habitat type, substantial though incomplete reproductive isolation may be rapidly produced. This permits semi-independent evolution to proceed when selective demands are sufficiently different relative to the level of gene flow between habitats. Subpopulation differentiation for traits such as mating-period, mating-structures, and competitive ability prior to reproduction can lead to virtually complete reproductive isolation between subpopulations in the two habitats. Differential selection for traits affecting viability, and sampling drift, will gradually erode the potential for cross mating due to pleiotropy (Slatkin, 1982), and irreversible reproductive isolation will result. Because reproductive isolation between subpopulations may rapidly develop, and because the differences in environmental demands between environments may be large, the rapid evolution of phenotypic differences between habitat specialists is expected. The genetic mechanism by which reproductive isolation evolves in this sympatric model is identical to those postulated to occur in the process of allopatric speciation. The only difference between the proposed speciation model and the classical model of allopatric speciation is that the initial barrier to gene flow is the development of gaps in the distribution of spatial/temporal habitat preference instead of an extrinsic physical environmental barrier.

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