

THE MEANING OF SPECIES AND SPECIATION: A Genetic Perspective

Alan R. Templeton

INTRODUCTION

What is a species? This fundamental question must be answered before the process of species formation can be investigated. As any survey of the evolutionary literature will quickly reveal, there are many definitions of species already in existence. These different definitions reflect the diverse types of evolutionary questions and/or organisms with which their authors were primarily concerned. Consequently, a species concept can be evaluated only in terms of a particular goal or purpose. My goal is to understand speciation as an evolutionary genetic process. A fundamental assumption behind this goal is that speciation, regardless of the precise definition of species, is best approached mechanistically by examining the evolutionary forces operating on individuals within populations or subpopulations and tracing their effects upward until they ultimately cause all of the members of that population or subpopulation to acquire phenotypic attributes conferring species status on the group.

This emphasis on the evolutionary genetic mechanisms operating within populations of individuals places speciation fully within the province of population genetics. Accordingly, what is needed is a concept of species that can be directly related to the mechanistic framework of population genetics. To achieve this goal, I will first review three species concepts that have strong supporters in the current literature: the evolutionary species concept, the biological species concept, and the recognition

species concept. All of these species concepts treat species as real biological entities and attempt to define species in terms of some fundamental biological property. In this regard, all of these definitions are biological species concepts, although one of them is often referred to as "the biological species concept." Since "the biological species concept" defines species in terms of isolating mechanisms, it is more accurately known as the isolation concept (Paterson 1985). Paterson's terminology will be used in the remainder of this chapter.

After reviewing the strengths and weaknesses of these three concepts, I will propose a fourth biological species concept, the cohesion concept, which attempts to utilize the strengths of the other three while avoiding their weakness with respect to the goal of defining species in a way that is compatible with a mechanistic population genetic framework. In this manner, a definition of species can be achieved that illuminates, rather than obscures or misleads, the mechanisms of speciation and their genetic consequences.

THREE BIOLOGICAL SPECIES CONCEPTS

The evolutionary species concept

Under this definition, a species consists of a population or group of populations that shares a common evolutionary fate through time. This definition has the advantage of being applicable to both living and extinct groups and to sexual and asexual organisms. Moreover, it emphasizes the fact that a species unit can be held together not only through gene flow but also through developmental, genetic, and ecological constraints. Finally, this concept is useful because it is close to the operational species definition used by most practicing taxonomists and paleontologists. Decisions as to species status are usually made on the basis of patterns of phenotypic cohesion within a group of organisms versus phenotypic discontinuity between groups. However, when a variety of phenotypes are studied, it is often discovered that the patterns of cohesion/discontinuity vary as a function of the phenotype being measured. One fault of the evolutionary species concept is that it provides little or no guidance as to which traits are the more important ones in defining species.

There are two other principal difficulties with this concept. First, there is the problem of judging what constitutes a "common" evolutionary fate. Obviously, polymorphisms can exist even within local populations, and many species are polytypic. Therefore, "common" does not mean "identical" evolutionary fates, so some judgment must be made as to just how much diversity is allowed within a "common" evolutionary fate. Finally, and most importantly with regard to the goal of this chapter, the

evolutionary species concept is not a mechanistic definition. It deals only with the manifestation of cohesion rather than the evolutionary mechanisms responsible for cohesion. Hence it does not provide an adequate framework for integrating population genetic factors into the species concept.

The isolation species concept

The species concept that is dominant in much of the evolutionary literature is popularly known as the biological species concept. Mayr (1963) defined the isolation species concept as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." Similarly, Dobzhansky (1970) states that "Species are systems of populations: the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms." As White (1978) has emphasized, the isolation concept species "is at the same time a reproductive community, a gene pool, and a genetic system." It is these later two attributes that make this concept of species particularly useful for integrating population genetic considerations into the problem of the origin of species. Population genetics is concerned with the evolutionary forces operating on gene pools and with the types of genetic systems that arise from the operation of these forces. The isolation species concept is therefore potentially useful in analyzing speciation from a population genetic perspective, but it unfortunately has some serious difficulties that must be rectified before this potential can be realized.

The difficulties stem from the fact that this species concept is defined in terms of isolating mechanisms. Table 1 presents a brief classification of the types of isolating barriers, and similar tables can be found in any of the books on speciation by Mayr or Dobzhansky. Under the isolation species concept, these isolating barriers define the boundaries of the reproductive community and gene pool and preserve the integrity of the genetic system of the species.

Paterson (1985) has pointed out that a fundamental difficulty with the isolation concept of species is that it is misleading when thinking about the process of speciation. For example, under the classic allopatric model of speciation, speciation occurs when populations are totally separated from each other by geographical barriers. The intrinsic isolating mechanisms given in Table 1 are obviously irrelevant as isolating barriers during speciation because they cannot function as isolating mechanisms in allopatry. Hence, the evolutionary forces responsible for this allopatric speciation process have nothing to do with "isolation." This is true for other speciation mechanisms as well (Templeton 1981). This is not to say that isolation is not

TABLE 1. Classification of isolating mechanisms.

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1. Premating mechanisms that prevent interpopulational crosses
 - a. Ecological or habitat isolation: the populations mate in different habitats in the same general region, or use different pollinators, etc.
 - b. Temporal isolation: the populations mate at different times of the year
 - c. Ethological isolation: potential interpopulational mates meet but do not mate
 2. Postmating but prezygotic isolation
 - a. Mechanical isolation: interpopulational matings occur but no transfer of sperm takes place
 - b. Gametic mortality or incompatibility: sperm transfer occurs but the egg is not fertilized
 3. Postzygotic isolation
 - a. F_1 inviability: hybrid zygotes have a reduced viability
 - b. F_1 sterility: hybrid adults have a reduced fertility
 - c. Hybrid breakdown: the F_2 or backcross hybrids have reduced viability or fertility
 - d. Coevolutionary or cytoplasmic interactions: individuals from a population infected by an endoparasite or with a particular cytoplasmic element are fertile with each other, but fertility and/or viability break down when matings occur between infected and uninfected individuals
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a product of the speciation process in some cases, but the product (i.e., isolation) should not be confused with the process (i.e., speciation). The isolation concept has been detrimental to studies of speciation precisely because it has fostered that confusion (Paterson 1985).

The recognition species concept

Paterson (1985) has argued strongly that this confusion can be avoided by looking at the so-called isolating mechanisms from a different perspective. For example, consider the premating isolation mechanisms listed in Table 1. It is commonplace in the evolutionary literature to find statements that complex courtship rituals, mating signals, etc. function as premating isolating barriers that exist to prevent hybridization with other species. The works of Dobzhansky (1970) indicate how dominant this idea was in the thinking of one of the principal architects and proponents of the biological species concept. Yet, as Tinbergen (1953) has pointed out, such premating mechanisms have several functions in addition to isolation: the suppression of escape or aggressive behavior in a courted animal, the synchronization of mating activities, the persuasion of a potential mate to continue courtship, the coordination in time and space of the pattern of mating, the

orientation of the potential mates for copulation, and, finally, fertilization itself. The importance of these other functions of premating behavior is illustrated by the work of Crews (1983) on pseudomale courtship and copulatory behavior in the all-female parthenogenetic lizard, *Cnemidophorus uniparens*. In these lizards, insemination and premating isolation are totally irrelevant since reproduction is strictly parthenogenetic. Yet females show elaborate courting behaviors that mimic male courtship in closely related species. These behaviors serve as a neuroendocrine primer that coordinates reproductive events. Obviously, mating behavior in these lizards facilitates reproduction, but isolation is irrelevant.

The critical question then becomes, which of these many functions (or which combination) is important in the process of speciation? Paterson (1985) has argued that isolation is an irrelevant function in the process of speciation. Consequently, to examine the reason why a premating "isolating" barrier arose, it is necessary to focus attention on the other functions of these premating mechanisms and to examine the evolutionary forces operating on these functions (Paterson 1985). In this regard, all the other functions of these premating behaviors can be thought of as facilitating reproduction, not hindering it as in the isolation function. The isolation function can indeed arise as a by-product of the evolution of the other functions, but in general it is not an active part of the process of speciation.

Consequently, isolating mechanisms are a misleading way of thinking about the process of speciation. Although all of the mechanisms listed in Table 1 are defined in terms of preventing reproduction between populations, they can also be thought of in an intraspecific fashion as facilitating reproduction within populations. In general, it is this positive inverse of the functions given in Table 1 that plays the major role in speciation. Paterson (1985) has focused upon the positive function of these mechanisms in facilitating reproduction among members of a certain population. Accordingly, Paterson accepts the premise, shared by the isolation concept, that a species is a field for gene recombination. Unlike the isolation concept, which defines the limits of this field in a negative sense through isolating mechanisms, Paterson defines the limits of this field in a positive sense through fertilization mechanisms, that is, adaptations that assist the processes of meiosis and fertilization. Species are defined as the most inclusive population of individual biparental organisms which share a common fertilization system.

In a sense, the isolation and recognition concepts of species are two sides of the same coin. Flipping the coin is worthwhile because the recognition concept yields a clearer vision of evolutionary process versus pattern, whereas the isolation concept is actively misleading. Hence, given

the goal of defining species in such a manner that it facilitates the study of speciation as an evolutionary process, the recognition concept is clearly superior to the isolation concept.

Paterson (1985) has burdened the recognition concept with several restrictions that do not necessarily follow from his primary definition. The most serious of these is his exclusive use of fertilization mechanisms to define a species. Obviously, a field of genetic recombination requires more than fertilization; it requires a complete life cycle in which the products of fertilization are viable and fertile. Moreover, the so called "fertilization" mechanisms of Paterson have other evolutionary functions that he ignores, as is well illustrated by the courtship behavior of the parthenogenetic lizards previously discussed. Hence, just as Paterson criticized isolation mechanisms because they may evolve for reasons other than isolation, his "fertilization" mechanisms may likewise evolve for reasons other than fertilization.

Other minor criticisms of Paterson's concept can be made (Templeton 1987), but I want to concentrate on two serious and fundamental difficulties that are shared by both the isolation and recognition concepts. As with many other problems in the biological world, these problems are caused by sex—either too little or too much.

SEXUAL HANGUPS OF THE ISOLATION AND RECOGNITION CONCEPTS

Too little sex

Both the isolation and recognition concepts of species are applicable only to sexually reproducing organisms (Vrba 1985). Accordingly, large portions of the organic world are outside the logical domain of these species definitions. This is a serious difficulty to people who work with parthenogenetic or asexual organisms.

One particular troublesome aspect of excluding nonsexual species is that most parthenogenetic "species" display the same patterns of phenotypic cohesion within and discontinuity between as do sexual species. For example, Holman (1987) examined the recognizability of sexual and asexual species of rotifers. Contrary to the predictions made by the isolation concept, he discovered that species in the asexual taxa are actually more consistently recognized than those from the sexual taxa. Thus, he concluded that for asexual rotifers "species are real and can be maintained by nonreproductive factors." As this example illustrates, the asexual world is for the most part just as well (or even better) subdivided into easily defined biological taxa as is the sexual world. This biological reality should not be ignored.

Ignoring nonsexual taxa is a major failure of the isolation and recognition concepts, but this failure is actually more extensive than many people realize. For example, the evolutionary genetics of self-mating populations is simply a special case of automictic parthenogenetic populations (e.g., Templeton 1974a). Hence, self-mating sexual species are also outside the logical domain of the isolation and recognition concepts. But the problem does not stop with self-mating sexual species. For example, many species of wasps have mandatory sib mating (Karlin and Lessard 1986). Such a system of mating, as well as any other closed system of mating, will display evolutionary dynamics that can be regarded as a special case of automixis, just as self-mating can. Hence, all sexual taxa with a closed system of mating are outside the logical domain of the isolation and recognition concepts.

The problem does not stop here, however. Models for analyzing multilocus selection in automictic and self-mating populations were very successfully applied to a barley population that was 99.43% self-mating (Templeton 1974b). The reason for this success is straightforward: with this much selfing, the evolutionary dynamics of the population closely approximate that of a 100% selfing population. When outbreeding is at such a low level, its primary role is to introduce genetic variability into the population. Once introduced, the evolutionary fate of that variation is more like that of a selfing population than that of an outcrossing population. Moreover, the genetic impact of the occasional outbreeding is further reduced by isolation by distance, which causes most outbreeding to be between nearly genetically identical individuals. Consequently, from a population genetic perspective, this barley population could not be regarded in any meaningful way as a "field for genetic recombination," and accordingly it lies outside the logical domain of both the isolation and recognition concepts.

The problem of isolation by distance previously mentioned creates a further restriction on the logical domain of the isolation and recognition concepts. An outcrossing population characterized by very limited gene flow and small local effective sizes has much the same genetic consequences and evolutionary dynamics as a predominantly selfing population. Ehrlich and Raven (1969) were among the first to point out in strong terms that many animal and plant species cannot be regarded as fields of genetic recombination in any meaningful sense with respect to basic evolutionary mechanisms, and therefore are also outside the logical domain of the isolation and recognition concepts.

The barley example leads to an interesting question. If a 99.47% selfing population is outside the logical domain of the isolation and recognition concepts, what about a 99% selfing population or a 95% selfing population? Ehrlich and Raven's (1969) work leads to a similar set of questions. At what point is isolation by distance and population subdivision sufficiently weak to bring a taxa into the logical domain of the isolation and recognition con-

cepts? Although this is not an easy question to answer, the problem of genetically closed taxa is usually dismissed in a sentence or two, with sexual and genetically closed taxa being treated as distinct categorical types (e.g., Mayr 1970; Vrba 1985). However, from the viewpoint of evolutionary mechanisms (and, hence, from the viewpoint of speciation as an evolutionary process), there is a continuum from panmictic evolutionary dynamics to genetically closed evolutionary dynamics. Consequently, the logical domain of the isolation and recognition concepts is not at all clear or well defined. The only thing that is certain is that this domain is much more restrictive and limited than is generally perceived.

Too much sex

As discussed, genetically closed reproductive systems cause serious difficulties for the isolation and recognition concepts, but so do genetically open systems. For example, Grant (1957), one of the stronger proponents among botanists of the isolation concept, concluded that less than 50% of the outcrossing species in 11 genera of Californian plants were well delimited by isolation from other species. Again and again in plants, taxonomists have defined species that exist in larger units known as syngameons that are characterized by natural hybridization and limited gene exchange. Grant (1981) defines the syngameon as "the most inclusive unit of interbreeding in a hybridizing species group." The frequent occurrence of syngameons in plants creates serious difficulties for both the isolation and recognition concepts because the field of genetic recombination is obviously broader than the taxonomic species and the groups that are behaving as evolutionarily independent entities. One solution is simply to deny the species status of the members of the syngameon. For example, Grant (1981) refers to the members of a syngameon as "semispecies." Under the recognition concept, the syngameon itself would be the species, since Grant's definition of syngameon is virtually identical to Paterson's (1985) definition of species. However, botanists have not made these taxonomic decisions arbitrarily. The species within a syngameon are often real units in terms of morphology, ecology, genetics, and evolution. For example, the fossil record indicates that balsam poplars and cottonwoods (both from the genus *Populus*) have been distinct for at least 12 million years and have generated hybrids throughout this period (Eckenwalder 1984). Even though the hybrids are widespread, fertile, and ancient, these tree species have and are maintaining genetic, phenotypic, and ecological cohesion within and distinction between and have maintained themselves as distinct evolutionary lineages for at least 12 million years (Eckenwalder 1984). Hence, cottonwoods and poplars are real biological units that should not be ignored.

It is commonplace for zoologists to acknowledge that the isolation concept runs into serious difficulties when it is applied to outbreeding, higher plants, but then to argue that the isolation concept works reasonably well for sexually reproducing, multicellular animals. However, this view is no longer tenable with the increased resolution that recombinant DNA techniques provide. For example, in mammals, studies are being carried out in my laboratory on baboons, wild cattle, canids, and gophers and cotton rats, examples, respectively, of primates, ungulates, carnivores, and rodents—the four major mammalian groups. In every case, there is evidence for naturally occurring interspecific hybridization (Baker et al. 1989; Davis et al. 1988; unpublished data). In spite of hybridization, many of the taxonomic units within these groups represent real biological units in a morphological, ecological, genetic, and evolutionary sense. For example, wolves and coyotes can and do hybridize. Yet, they are morphologically quite distinct from each other, have extremely different behaviors in terms of social structure and hunting, and represent distinct evolutionary lineages with diagnostic genetic differences (Figure 1). Moreover, the fossil record indicates that they have evolved as distinct and continuous lineages for at least 0.5 million years (Hall 1978) and perhaps for as much as 2 million years (Nowak 1978). Although these taxa do not satisfy the criterion of the isolation species concept, Hall (1978) argues that these are biologically real groups and that species status is clearly appropriate.

Animal syngameons are by no means limited to mammals. *Drosophila heteroneura* and *D. silvestris* are two Hawaiian *Drosophila* species on which we have worked. Although they are phylogenetically very close and broadly sympatric on the Island of Hawaii (Carson 1978), they are morphologically extremely distinct, with the most dramatic difference

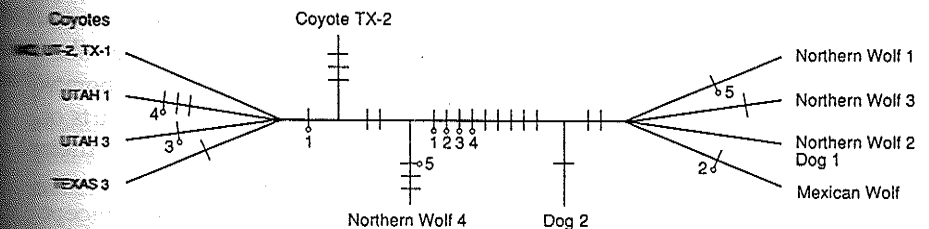


FIGURE 1. Unrooted cladogram of North American coyotes, wolves, and dogs as constructed by maximum parsimony. The cladogram is based upon restriction endonuclease site mapping of mitochondrial DNA. Each line that crosses a segment of the cladogram indicates a single evolutionary change in the map within that evolutionary segment. Five sites were inferred to have changed twice, and their two inferred positions within the cladogram are indicated by the numbered cross-lines.

being that *silvestris* has a round head and *heteroneura* a hammer-shaped head (Val 1977). They can be hybridized in the laboratory, and the hybrids and subsequent F_2 and backcrosses are completely fertile and viable (Val 1977; Templeton 1977; Ahearn and Templeton 1989). Because the morphology of hybrids is known from these laboratory studies, Kaneshiro and Val (1977) were able to discover that interspecific hybridization occurs in nature. Our molecular studies (DeSalle and Templeton 1987) confirm that hybrids are indeed formed in nature, and, moreover, that these hybrids can and do backcross to such an extent that a *heteroneura* mitochondrial haplotype can occasionally be overlaid on a normal-looking *silvestris* morphology. In spite of this natural hybridization, the species can and do maintain their very distinct, genetically based morphologies (Templeton 1977; Val 1977) and have distinct nuclear DNA phylogenies (Hunt and Carson 1983; Hunt et al. 1984) in spite of the limited introgression observed with mitochondrial DNA (DeSalle et al. 1986). Hence, both morphology and molecules define these taxa as real, evolutionarily distinct lineages.

As these and other studies illustrate, animal taxa frequently display natural hybridization that yields fertile and viable hybrids. These taxa have often been recognized as species because of their distinct morphologies and ecologies and because modern molecular studies have revealed that they are behaving as independent evolutionary lineages, at least with respect to their nuclear genomes. In other words, many animal species are members of syngameons, just as plants are. Hence, the problem of syngameons is a widespread one for the isolation and recognition concepts.

THE COHESION SPECIES CONCEPT

Another biological definition of species is now possible, which I call the cohesion concept of species. The cohesion concept species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Table 2). I will now elaborate on the meaning of this species concept, showing how it borrows parts of the evolutionary, isolation, and recognition concepts, while it avoids their serious defects.

As with the evolutionary species concept, the cohesion species concept defines species in terms of genetic and phenotypic cohesion. As a consequence, the cohesion concept shares with the evolutionary concept the strengths of being applicable to taxa reproducing asexually (or by some other closed or nearly closed breeding system) and to taxa belonging in syngameons. Unlike the evolutionary species concept, the cohesion concept defines species in terms of the mechanisms yielding cohesion rather than the manifestation of cohesion over evolutionary time. This is a

TABLE 2. Classification of cohesion mechanisms.

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- I Genetic exchangeability: the factors that define the limits of spread of new genetic variants through *gene flow*
 - A. Mechanisms promoting genetic identity through *gene flow*
 - 1. Fertilization system: the organisms are capable of exchanging gametes leading to successful fertilization
 - 2. Developmental system: the products of fertilization are capable of giving rise to viable and fertile adults
 - B. Isolating mechanisms: genetic identity is preserved by the lack of *gene flow* with other groups
 - II Demographic exchangeability: the factors that define the fundamental niche and the limits of spread of new genetic variants through *genetic drift* and *natural selection*
 - A. Replaceability: *genetic drift* (descent from a common ancestor) promotes genetic identity
 - B. Displaceability
 - 1. Selective fixation: *natural selection* promotes genetic identity by favoring the fixation of a genetic variant
 - 2. Adaptive transitions: *natural selection* favors adaptations that directly alter demographic exchangeability. The transition is constrained by:
 - a. Mutational constraints on the origin of heritable phenotypic variation
 - b. Constraints on the fate of heritable variation
 - i. Ecological constraints
 - ii. Developmental constraints
 - iii. Historical constraints
 - iv. Population genetic constraints
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mechanistic focus similar to that taken by the isolation concept, although in this case the focus is on cohesion mechanisms rather than isolation mechanisms. By defining a species in terms of cohesion mechanisms, the cohesion concept can easily be related to a mechanistic population genetic framework and can provide guidance in understanding speciation as an evolutionary process. In particular, speciation is now regarded as the evolution of cohesion mechanisms (as opposed to isolation mechanisms). This also means that the cohesion concept focuses primarily on living taxa rather than fossil taxa.

As pointed out by Paterson (1985), it is useful to define the mechanisms underlying species status in such a way that the definitions reflect the most likely evolutionary function of the mechanisms during the process of speciation. Accordingly, cohesion mechanisms will be defined to reflect their most likely evolutionary function. The basic task is to identify those cohesion mechanisms that help maintain a group as an evolutionary lineage. The very essence of an evolutionary lineage from a population genetic perspective is that new genetic variants can arise in it, spread, and

replace old variants. These events occur through standard microevolutionary forces such as gene flow, genetic drift, and/or natural selection. The fact that the genetic variants present in an evolutionary lineage can be traced back to a common ancestor also means that the individuals that comprise this lineage must show a high degree of genetic relatedness. The cohesion mechanisms that define species status are therefore those that promote genetic relatedness and that determine the populational boundaries for the actions of microevolutionary forces.

The isolation and recognition concepts are exclusively concerned with genetic relatedness promoted through the exchange of genes via sexual reproduction. These definitions have elevated a single microevolutionary force—gene flow—into the conclusive and exclusive criterion for species status. There is no doubt that gene flow is a major microevolutionary force, and hence the factors that define the limits of spread of new genetic variants through gene flow are valid criteria for species status. Accordingly, genetic exchangeability is included in Table 2 as a major class of cohesion mechanisms. Genetic exchangeability simply refers to the ability to exchange genes via sexual reproduction. This implies a shared fertilization system in the sense of Paterson (1985). Effective exchange of genes also demands that the products of fertilization be both potentially viable and fertile (Templeton 1987). As shown in Table 2, the role of gene flow in determining species status can be defined in either a positive (I.A in Table 2) or a negative (I.B in Table 2) sense. As stated earlier, the positive sense generally provides a more accurate view of the evolutionary processes involved in speciation.

Gene flow is not the only microevolutionary force that defines the boundaries of an evolutionary lineage. Indeed, genetic drift and natural selection play a far more potent and universal role because these two classes of microevolutionary forces are applicable to all organisms, not just outcrossing sexual species. An important question is, therefore, what factors define the limits of spread of new genetic variants through genetic drift and natural selection? Since these forces can operate in asexual populations, it is obvious that the factors that limit the field of action of drift and selection are not necessarily the same as those limiting the actions of gene flow. As seen, gene flow requires genetic exchangeability, that is, the ability to exchange genes during sexual reproduction. For genetic drift and natural selection to operate, another type of exchangeability is required: demographic exchangeability (Table 2).

From an ecological perspective, members of a demographically exchangeable population share the same fundamental niche (Hutchinson 1965), although they need not be identical in their abilities to exploit that niche. The fundamental niche is defined by the intrinsic (i.e., genetic) tolerances of the individuals to various environmental factors that deter-

mine the range of environments in which the individuals are potentially capable of surviving and reproducing. The realized niche (Hutchinson, 1965) refers to that subset of the fundamental niche that is actually occupied by a species. The realized niche is usually a proper subset of the fundamental niche because of the lack of opportunity to occupy certain portions of the fundamental niche (e.g., the environmental ranges might be within the tolerance limits in some locality, but geographical barriers prevent the colonization of that locality) or because of interactions with other species that prevent the exploitation of the entire range of ecological tolerance. Hence, the realized niche is influenced by many extrinsic factors, but demographic exchangeability depends only on the intrinsic ecological tolerances.

To the extent that individuals share the same fundamental niche, they are interchangeable with one another with respect to the factors that control and regulate population growth and other demographic attributes. It is demographic exchangeability that is used to define populations in most models of population and community ecology. Indeed, most models from these ecological disciplines do not even specify the mode of reproduction, so genetic exchangeability is not used to define a population.

From a genetic perspective, the chances of a neutral or selectively favorable mutation going to fixation in a demographically exchangeable population are nonzero regardless of the particular individual in which the mutation occurred. In other words, every individual in a demographically exchangeable population is a potential common ancestor to the entire population at some point in the future. Ancestor-descendant relationships can be defined just as readily in asexual populations as in sexual populations. Hence, demographic exchangeability does not require genetic exchangeability and is a distinct biological attribute at the population level.

Just as genetic exchangeability can vary in strength, so can demographic exchangeability. From an ecological perspective, complete demographic exchangeability occurs when all individuals in a population display exactly the same ranges and abilities of tolerance to all relevant ecological variables. Demographic exchangeability is weakened as individuals begin to differ in their tolerance ranges or abilities. From a genetic perspective, a population is completely demographically exchangeable if the probability of a neutral or selectively favorable mutation going to fixation is exactly the same regardless of the individual in which it occurs. A weakly demographically exchangeable population would consist of members who display very different (but still nonzero) fixation probabilities.

Demographic exchangeability allows us to readily incorporate microevolutionary forces other than gene flow as being important in defining an

evolutionary lineage. One such microevolutionary force is genetic drift, which promotes genetic cohesion through ancestor-descendant relationships (i.e., the concept of identity-by-descent in population genetics). For the special case of neutral alleles (alleles that have no selective importance), the rate at which genetic drift promotes identity-by-descent depends only on the neutral mutation rate and is therefore equally important in both large and small populations. Interestingly, this prediction about the neutral rate of evolution and the other basic predictions of the standard neutral theory do not depend upon the assumption of sexual reproduction—these predictions are equally applicable to asexual organisms. Although the neutral theory does not require genetic exchangeability, demographic exchangeability is a critical and necessary assumption (e.g., Rothman and Templeton 1980). Making *only* the assumption of demographic exchangeability, it is inevitable that at some point in the future all the alleles will be descended from one allele that presently exists. It makes no difference for the operation of genetic drift whether alleles or the individuals carrying the alleles are exchangeable. Hence, demographic exchangeability must be regarded as a major cohesion mechanism because it defines the populational limits for the action of genetic drift. This aspect of demographic exchangeability is called “replaceability” in Table 2.

Natural selection is another powerful force that can help define an evolutionary lineage. The concept of natural selection does not require genetic exchangeability because selection models are as easily formulated for genetically closed populations as for genetically open ones (e.g., Templeton, 1974a, 1974b). As pointed out by Darwin, natural selection requires two demographic conditions: (1) that organisms can produce more offspring than are needed for strict replacement, and (2) that unlimited population growth cannot be sustained indefinitely. When these demographic conditions are coupled with heritable variation in traits influencing survival and reproduction, the logical consequence is that the offspring of some individuals will displace those of others within the population. This aspect of demographic exchangeability is called “displaceability” in Table 2.

Natural selection promotes cohesion both through favoring genetic relatedness and through affecting the limits of demographic exchangeability itself. Whenever natural selection causes a new, favorable mutation to go to fixation, genetic relatedness at that locus is obviously a direct consequence. Moreover, as this mutation goes to fixation, that subset of the species' genetic variation that remains linked to the new mutation likewise goes to fixation. This is known as the hitchhiking effect, and it is important to note that as genetic exchangeability declines in importance, hitchhiking effects increase in importance, for the simple reason that

genetic recombination is less effective in breaking down the initial linkage states that were created at the moment of mutation. Hence, selective fixation of one allele by another is an extremely powerful cohesion mechanism in populations with genetically closed systems of reproduction (Levin 1981). As an example, Figure 2 shows the results of selection in a parthenogenetic strain of *D. mercatorum* (Annest and Templeton 1978). As can be seen from that figure, the population rapidly converged to a single genotype for all the marker loci being examined. The dynamics of this convergence indicated that very strong selective forces were operating (Annest and Templeton 1978). Other replicates of this same population, all subject to genetic recombination during the first parthenogenetic generation, selectively converged to other genotypic states at the marker loci, thereby indicating that the marker loci were not being selected directly. Thus, selection at perhaps a few loci promoted genetic identity at all loci in these parthenogenetic populations.

The extent of demographic exchangeability is intimately intertwined with the ecological niche requirements of the organisms and the habitats that are available for satisfying those requirements. It is these very same

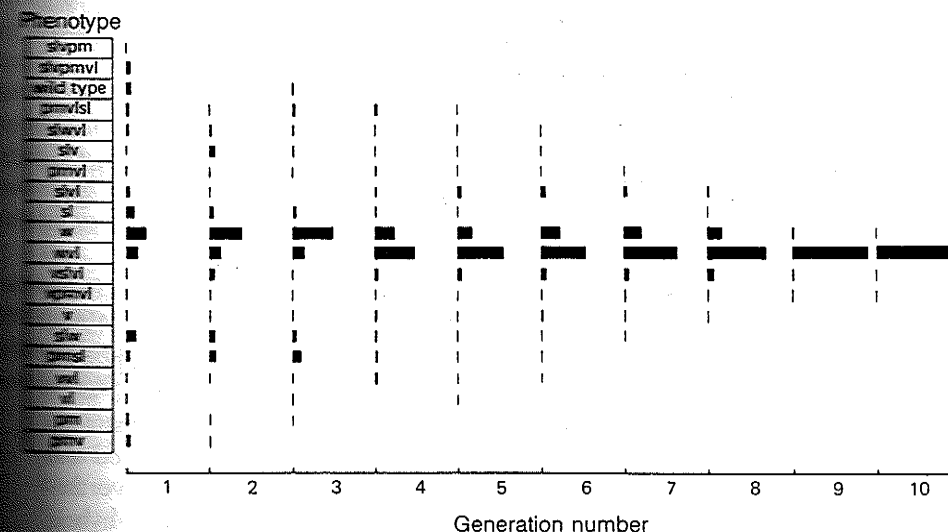


FIGURE 2. Clonal selection in a parthenogenetic population of *Drosophila mercatorum*. The initial generation was heterozygous for several visible markers on all the major chromosomes (sl, w, v, pm, and vl). Parthenogenetic reproduction during the initial generation creates a large number of genotypes since meiotic recombination and assortment occur in these autotictic strains. After the first generation genetic recombination is irrelevant since virtually all flies are totally homozygous. From Annest and Templeton (1978).

ecological requirements and available habitats that provide many of the selective forces that drive the process of adaptation. Hence, the process of adaptation by natural selection can directly alter the traits that determine the extent of demographic exchangeability. Adaptive transitions therefore play a direct role in defining demographically exchangeable groups of organisms.

The importance of adaptive transitions in defining demographic exchangeability opens up a whole new set of cohesion mechanisms that constrain the possible courses of adaptive transitions, as shown in Table 2 (II.B.2). The first is mutational constraints that limit the types of phenotypic variants that are likely to be produced. Such constraints make it difficult to alter some aspects of the existing genetic/developmental system, but facilitate evolutionary change along other lines. For example, the genus *Drosophila* consists of some flies that have pigmented spots, clouds, or patterns on their wings, such as the Hawaiian "picture-wings," and others that have clear wings, such as *D. melanogaster*. Yet, as Basden (1984) points out, no picture-winged *Drosophila* has ever produced a clear-winged mutant, nor has a clear-winged species produced a picture-winged mutant. This negative result is of biological significance for *D. melanogaster*, for probably no other higher eukaryote has been examined more thoroughly for visible mutations. Thus, Basden concluded that at the species level there is a block to certain types of mutations. This is simply another way of stating that constraints exist that make certain types of mutations impossible or highly improbable.

Given that phenotypic variation has been produced by the mutational process, there are constraints that influence the selective fate of that variation (Table 2, II.B.2.b). First, there are ecological constraints that select against certain phenotypes and that restrict the range of environmental variability experienced by the species. Moreover, for an adaptive transition to persist, a niche must be available for the organisms with the new adaptation. Ecological constraints are undoubtedly one of the more important cohesion mechanisms maintaining species within syngameons, as is demonstrated by what happens within syngameons when the constraints are altered. For example, under most environmental conditions, red and black oaks live together in the same woods and cross-pollinate. Nevertheless, they remain two distinct, cohesive populations because the F_1 hybrid acorns do not germinate well under the dark, cool conditions of a mature forest. When a forest is partially cleared and thinned (mostly by humans), the black oak and red oak acorns germinate poorly, whereas the hybrid acorns do very well. As a result, many current woods consist of a continuous intergradation between black and red oaks. Hence, the normal cohesion of red and black oak populations is lost when the ecological constraints are altered.

Ecological constraints are also important in asexual taxa because these constraints often determine the populational limits of selective fixation, which, as previously mentioned, is a major cohesion mechanism in taxa with closed systems of reproduction. Moreover, the work of Roughgarden (1972) predicts that asexual populations can evolve more sharply delimited niche widths than can otherwise equivalent sexual populations. This property may help explain the greater recognizability of asexual species over sexual species (Holman 1987).

Developmental constraints constitute the second class of cohesion mechanisms related to the fate of heritable variation in adaptive transitions. When there is strong selection on one trait, pleiotropy (a form of developmental constraint) ensures that other traits will evolve as well. Hence, pleiotropy can facilitate evolutionary changes that would otherwise not occur. Although many people have emphasized the nonadaptive, even maladaptive nature of these pleiotropic-induced changes, Wagner (1988) has shown that pleiotropy is essential for the evolution of complex adaptive traits. He examined a model in which fitness depends on the simultaneous states of several traits and then contrasted models of adaptive evolution in which all traits are genetically independent (no pleiotropy or developmental constraints) with a model in which developmental constraints were imposed. He found that, when there are no developmental constraints, the rate of adaptive evolution decreases dramatically as the number of characters involved in functional integration increases. Hence, developmental constraints and pleiotropy seem to be necessary for the evolution of functionally integrated phenotypes.

Further adaptive evolution can be facilitated even when the primary adaptation induces pleiotropic effects that are maladaptive. This phenomenon can be illustrated by malarial adaptations in humans (Templeton 1982). The primary malarial adaptations (such as sickle cell) often induce highly deleterious pleiotropic effects (such as anemia), which, in turn, generate secondary adaptive processes on modifiers to diminish or eliminate the deleterious effects (such as persistence of fetal hemoglobin to suppress anemia). In this manner a single adaptive transition can trigger a cascade of secondary transitions, which cumulatively can have a large impact on demographic exchangeability.

Another cohesion mechanism that constrains the selective fate of phenotypic variability is historical constraint. Evolution is an historical process and, consequently, the evolutionary potential of a lineage is shaped by its past adaptive transitions. For example, a prerequisite for the evolution of aposematic coloration in insects with gregarious larvae is the evolution of unpalatability. Without the prior existence of distastefulness, there is no selective force for warning coloration within the broods (Templeton 1979). Hence, the adaptation of distastefulness is an historical constraint

on the evolution of aposematic coloration and gregarious larvae. This prediction was recently tested by Sillen-Tullberg (1988), who showed through a phylogenetic analysis that in every case in which resolution was possible, distastefulness evolved prior to the evolution of gregarious, aposematic larvae. As shown by this example, one adaptation can make a second one more likely, thus reinforcing the cohesion of the lineage that shares these adaptive transitions.

Population genetic constraints also limit the selective fate of new phenotypic variability. These constraints arise from the interaction of population structure (system of mating, population size, population subdivision) with the genetic architecture underlying selected traits (the genotype-phenotype relationship, number of loci, linkage relationships, etc.). For example, in 1924 Haldane showed that selectively favorable dominant genes are much more likely to be fixed than selectively favorable recessive genes in randomly mating populations. However, this constraint disappears if the system of mating is changed from random mating to inbreeding (Templeton 1982). Thus, an alteration of system of mating can alter the phenotypic and genetic cohesion of a population by making whole new classes of genetic variability responsive to natural selection.

ADVANTAGES OF THE COHESION CONCEPT OF SPECIES

The cohesion concept of species defines a species as an evolutionary lineage through the mechanisms that limit the populational boundaries for the action of such basic microevolutionary forces as gene flow, natural selection, and genetic drift. The genetic essence of an evolutionary lineage is that a new mutation can go to fixation within it; and genetic drift and natural selection as well as gene flow are powerful forces that can cause such fixations. Hence, there is no good rationale for why gene flow should be the only microevolutionary mechanism that is used to define an evolutionary lineage; yet this is precisely what the isolation and recognition concepts do.

Under the cohesion concept, many genetically based cohesion mechanisms (Table 2) can play a role in defining a species. Not all species will be maintained by the same cohesion mechanism or mixture of cohesion mechanisms, just as proponents of the isolation concept acknowledge that not all isolating mechanisms are equally important in every case. By adjusting the mixture of cohesion mechanisms, it is possible to take into account under a single species concept asexual taxa, the taxa that fall within the domain of the isolation and recognition concepts, and the members of syngameons.

Figure 3 gives a simplified graphic portrayal of the relative importance of genetic versus demographic exchangeability in defining species over

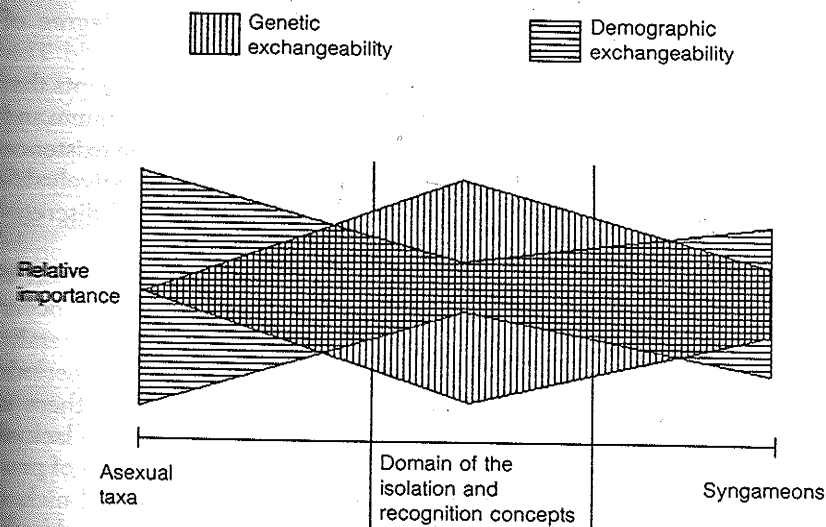


FIGURE 3. The relative importance of demographic and genetic exchangeability over the reproductive continuum. The areas marked by vertical lines indicate the importance of genetic exchangeability, with the width of that area at any particular point in the reproductive continuum indicating its importance in defining species. Similarly, the areas marked by horizontal lines are used to indicate the importance of demographic exchangeability. The diagram gives only the general trend in relative importance. Because the strength of both genetic and demographic exchangeability can vary continuously, the relative importance can be altered from that shown in the diagram at virtually any point in the reproductive continuum, except for asexual taxa.

the entire reproductive continuum. For asexual taxa, genetic exchangeability has no relevance, and species status is determined exclusively by demographic exchangeability. As the reproductive system becomes more open, not only does genetic exchangeability become a factor, but demographic exchangeability is diminished in importance because selective replacement becomes increasingly less effective in promoting genetic relatedness. In the middle range, genetic exchangeability dominates because the factors determining the limits of gene flow also limit the actions of drift and selection in outbreeding Mendelian populations. In this domain, the recognition and isolation concepts are valid, and hence, both are special cases of the more general cohesion concept of species. Finally, in moving toward the syngameon end of the continuum, genetic exchangeability decreases in importance relative to the ecological constraints that define demographic exchangeability.

This continuity of applicability of the cohesion concept is consistent

with the biological reality that there is a continuum in the degree of genetic openness of reproductive systems found in the organic world. This is a tremendous advantage over the recognition or isolation concepts that are applicable only to the middle range of this reproductive continuum and that deal with the remainder of the range either by denying the existence of species outside this range (e.g., Vrba 1985) or by using qualitatively different species concepts (e.g., Mayr 1970) to impose an artificial discreteness on the reproductive continuum.

Another strength of the cohesion concept is that it clarifies what is meant by a "good species" and the nature of the difficulties that can occur with the isolation and recognition concepts. "Good species" are generally regarded as geographically cohesive taxa that can coexist for long periods of time without any breakdown in genetic integrity. The fact that there is no breakdown in genetic integrity in spite of sympatry implies the lack of genetic exchangeability between the taxa. However, the condition of prolonged coexistence also implies that they have distinct ecological niches (Mayr 1970). Hence, "good species" are those that are well defined both by genetic and demographic exchangeability. (Similarly, members of a "good" higher taxa lack both genetic and demographic exchangeability.) Given this definition of a "good species," there are two principal ways to deviate from this ideal. One occurs when the population boundaries defined by genetic exchangeability are more narrow than those defined by demographic exchangeability. This is precisely the problem of asexual taxa previously discussed. The other mode of deviation occurs when the boundaries defined by genetic exchangeability are broader than those defined by demographic exchangeability—in other words, the problem posed by the syngameon. Hence, these two seemingly very disparate problems with the isolation and recognition concepts actually have a common underlying cause: the boundaries defined by demographic exchangeability are different than those defined by genetic exchangeability.

Speciation is generally a process, not an event (Templeton 1981). While the process is still occurring, the tendency is to have "bad" species. Although the taxa associated with these incomplete speciation processes are the bane of the taxonomist, they provide the most insight into speciation. By providing a precise definition of "bad species" (the conflict between genetic and demographic exchangeability), the cohesion concept is a useful tool for gaining insight into the process of speciation. "Bad species" need no longer be regarded as a diverse set of special cases; rather, the cohesion concept provides the means for seeing the patterns found in these troublesome taxa. For example, Levene (1953) long ago postulated a model in which different genotypes display different fitnesses in niches that are demographically independent. However, in this model there is complete genetic exchangeability and there is still sufficient

demographic exchangeability among all the genotypes within the various realized niches (through within-niche selective displacement) that this is clearly a model of intraspecific polymorphism. The situation modeled by Levene (1953) bears some resemblance to the syngameon examples discussed earlier in that a conflict arises between genetic and demographic exchangeability (through adaptation to different realized ecological niches that alter the intrinsic tolerances that define the fundamental niche). Hence, there can be a continuum in relative strength between these conflicting species boundary criteria. Interestingly, there has been an implicit acknowledgment of this tension in the speciation literature. Most models of sympatric speciation start with a Levene-type model, with the model of Wilson (this volume) being an example (also see Maynard Smith 1966). Although these models differ greatly in detail, the cohesion concept clarifies the evolutionary significance of this entire class of speciation models: it is the evolution of demographic *non*exchangeability that triggers the speciation process in these cases, and speciation proceeds through shifts in the relative importance of demographic and genetic exchangeability within and between populations adapting to different realized niches. Thus, a seemingly diverse set of speciation models all have a common theme, and the cohesion concept allows that theme to be clearly discerned.

Note also that natural selection is the driving force of speciation in all of these sympatric speciation models, with the effects on gene flow being secondary. Because the cohesion concept explicitly incorporates a broad set of microevolutionary forces as being important in speciation, we can deal directly with natural selection as being the primary trigger of speciation in these models rather than having to constantly rephrase the evolutionary significance of natural selection in terms of its secondary effects on gene flow. The cohesion concept therefore facilitates the study of speciation as an evolutionary process by making explicit the role played by a broad array of evolutionary forces that includes, but is not limited to, gene flow.

As illustrated by the Levene-type speciation models, one of the evolutionary forces important in speciation is natural selection. Natural selection is important in defining a species under the cohesion concept in part because of the impact of adaptive transitions on demographic exchangeability. Interestingly, Mayr (1970) argues that most species have distinct ecological niches (that is, they are not demographically exchangeable), and that this ecological distinctiveness is the "keystone of evolution" because it serves as the basis of diversification of the organic world, adaptive radiation, and evolutionary progress. Although Mayr therefore concludes that the "evolutionary significance of species" lies in their ecological distinctiveness, he still argues that adaptive transitions and natural

selection generally play no direct role in speciation and contribute to defining a species only through the "incidental by-product" of isolating mechanisms. Mayr does allow for selective pressures to reinforce isolating mechanisms and to accentuate ecological exclusion if sympatry has been established, but he emphasizes that this occurs only after the process of speciation has been basically completed. Hence, under the isolation concept, the factors responsible for the "evolutionary significance of species" play no direct role in defining species. Under the cohesion concept, the evolutionary significance of a species can arise directly out of its defining attributes.

SPECIATION

Now that species has been defined, what is speciation? Speciation is the process by which new genetic systems of cohesion mechanisms evolve within a population. This process can be thought of as being analogous to the process of genetic assimilation of individual phenotypes. Genetic assimilation is a process discussed by Waddington (1957) in light of his work with the fruit fly, *Drosophila melanogaster*. For example, he discovered that by subjecting strains of this fly to a heat shock, many of the flies would express the phenotype of lacking a certain vein on their wings. Initially, this "crossveinless" phenotype appeared to be purely environmental. By artificially selecting those flies expressing the phenotype, Waddington discovered he was selecting for the genetic predisposition to express this phenotype as well. Therefore, over several generations this "environmental" phenotype acquired a genetic basis to such an extent that the phenotype eventually came to be expressed even in the absence of the heat shock. Similarly, a purely environmental alteration in the manifestation of cohesion can lead to evolutionary conditions that favor the assimilation of the new pattern of cohesion into the gene pool. For example, consider the case of allopatric speciation in which an ancestral taxa that was continuously distributed in a region is now, by the erection of some geographical barrier, split in two totally isolated subpopulations. The erection of the geographical barrier potentially alters the manifestation of several cohesion mechanisms. For sexual taxa, genetic relatedness through gene flow has been altered, and for both sexual and asexual taxa, the potential for genetic relatedness through genetic drift and natural selection is altered as soon as the populations become demographically independent due to geographical separation. Moreover, if the geographical barrier is associated with altered environments and/or altered breeding systems, alterations in the constraints on adaptive transitions could be directly induced and a new realized niche may be occupied. However, none of this constitutes speciation until these alterations in the manifestation of genetic

and demographic exchangeability are genetically assimilated into the gene pool as new cohesion mechanisms. Thus, speciation is the genetic assimilation of altered patterns of genetic and demographic exchangeability into intrinsic cohesion mechanisms.

This is a simple definition of speciation, but because of the breadth of the cohesion species concept, this definition can be used to study a wide variety of evolutionary processes that contribute to the formation of a new species within a single mechanistic framework. This is an exciting prospect, and one that I hope will result in a deeper application of evolutionary genetics to the problem of the origin of species.

SUMMARY

The "biological species concept" defines species as reproductive communities that are separated from other similar communities by intrinsic isolating barriers. However, there are other "biological" concepts of species, so the classic biological species concept is more accurately described as the "isolation" species concept. The purpose of this chapter was to provide a biological definition of species that follows directly from the evolutionary mechanisms responsible for speciation and their genetic consequences.

The strengths and weaknesses of the evolutionary, isolation, and recognition concepts were reviewed and all three were judged to be inadequate for this purpose. As an alternative, I proposed the cohesion concept that defines a species as the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability. This concept borrows from all three biological species concepts. Unlike the isolation and recognition concepts, it is applicable to the entire continuum of reproductive systems observed in the organic world. Unlike the evolutionary concept, it identifies specific mechanisms that drive the evolutionary process of speciation. The cohesion concept both facilitates the study of speciation as an evolutionary process and is compatible with the genetic consequence of that process.

ACKNOWLEDGMENTS

The ideas in this chapter were greatly influenced by my discussion with the other participants at the symposium and with the people working in my laboratory, and I thank them all for the challenging intellectual stimulation that they have provided. Special thanks go to Allan Larson and John Endler for their helpful comments on an earlier version of this manuscript. This work was supported by NIH Grant R01 GM31571.

LITERATURE CITED

- Ahearn, J. N., and A. R. Templeton. 1989. Interspecific hybrids of *Drosophila heteroneura* and *D. silvestris*. I. Courtship success. *Evolution* 43:347-361.
- Annest, L., and A. R. Templeton. 1978. Genetic recombination and clonal selection in *Drosophila mercatorum*. *Genetics* 89:193-210.
- Baker, R. J., S. K. Davis, R. D. Bradley, M. J. Hamilton, and R. A. Van Den Bussche. 1989. Ribosomal DNA, mitochondrial DNA, chromosomal and electrophoretic studies on a contact zone in the pocket gopher, *Geomys*. *Evolution*, in press.
- Basden, E. B. 1984. The species as a block to mutations. *Drosophila Inform. Serv.* 60:57.
- Carson, H. L. 1978. Speciation and sexual selection in Hawaiian *Drosophila*. Pp. 93-107 in: P. F. Brussard (ed.), *Ecological Genetics: The Interface*. Springer-Verlag, New York.
- Crews, D. 1983. Alternative reproductive tactics in reptiles. *BioScience* 33:562-566.
- Davis, S. K., B. Read, and J. Balke. 1988. Protein electrophoresis as a management tool: Detection of hybridization between Banteng (*Bos javanicus* d'Alton) and domestic cattle. *Zoo Biol.* 7:155-164.
- DeSalle, R., L. V. Giddings, and A. R. Templeton. 1986. Mitochondrial DNA variability in natural populations of Hawaiian *Drosophila*. I. Methods and levels of variability in *D. silvestris* and *D. heteroneura* populations. *Heredity* 56:75-85.
- DeSalle, R., and A. R. Templeton. 1987. Comments on "The Significance of Asymmetrical Sexual Isolation." *Evolution*. *Biol.* 21:21-27.
- Dobzhansky, Th. 1970. *Genetics of the Evolutionary Process*. Columbia University Press, New York.
- Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. III. Paleobotany and evolution. *Can. J. Bot.* 62:336-342.
- Ehrlich, P., and P. Raven. 1969. Differentiation of populations. *Science* 165:1228-1232.
- Grant, V. 1957. The plant species in theory and practice. Pp. 39-80 in: E. Mayr (ed.), *The Species Problem*. American Association for the Advancement of Science, Publication No. 50, Washington, D. C.
- Grant, V. 1981. *Plant Speciation*, 2nd ed. Columbia University Press, New York.
- Haldane, J. B. S. 1924. A mathematical theory of natural and artificial selection. Part 1. *Trans. Cambridge Philos. Soc.* 23:19-41.
- Hall, R. L. 1978. Variability and speciation in canids and hominids. Pp. 153-177 in: R. L. Hall and H. S. Sharp (eds.), *Wolf and Man: Evolution in Parallel*. Academic Press, New York.
- Holman, E. W. 1987. Recognizability of sexual and asexual species of rotifers. *System. Zool.* 36:381-386.
- Hunt, J. A., J. G. Bishop III, and H. L. Carson. 1984. Chromosomal mapping of a middle-repetitive DNA sequence in a cluster of five species of Hawaiian *Drosophila*. *Proc. Natl. Acad. Sci. U.S.A.* 81:7146-7150.
- Hunt, J. A., and H. L. Carson. 1983. Evolutionary relationships of four species of Hawaiian *Drosophila* as measured by DNA reassociation. *Genetics* 104:353-364.
- Hutchinson, G. E. 1965. The niche: An abstractly inhabited hypervolume. Pp. 26-78 in: *The Ecological Theatre and the Evolutionary Play*. Yale University Press, New Haven.
- Kaneshiro, K., and F. C. Val. 1977. Natural hybridization between a sympatric pair of Hawaiian *Drosophila*. *Am. Natur.* 111:897-902.
- Karlin, S., and S. Lessard. 1986. *Theoretical Studies on Sex Ratio Evolution*. Princeton University Press, Princeton, N.J.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. *Am. Natur.* 87:311-313.
- Levin, B. R. 1981. Periodic selection, infectious gene exchange and the genetic structure of *E. coli* populations. *Genetics* 99:1-23.
- Maynard Smith, J. 1966. Sympatric speciation. *Am. Natur.* 100:637-650.
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- Mayr, E. 1970. *Populations, Species, and Evolution*. Belknap Press, Cambridge, MA.
- Nowak, R. M. 1978. Evolution and taxonomy of coyotes and related *Canis*. Pp. 3-16 in: M. Bekoff (ed.), *Coyotes: Biology, Behavior, and Management*. Academic Press, New York.
- Paterson, H. E. H. 1985. The recognition concept of species. Pp. 21-29 in: E. S. Vrba (ed.), *Species and Speciation*. Transvaal Museum Monograph No. 4, Pretoria.
- Bothman, E. D., and A. R. Templeton. 1980. A class of models of selectively neutral alleles. *Theor. Pop. Biol.* 18:135-150.
- Roughgarden, J. 1972. Evolution of niche width. *Am. Natur.* 106:683-718.
- Sillen-Tullberg, B. 1988. Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. *Evolution* 42:293-305.
- Templeton, A. R. 1974a. Density dependent selection in parthenogenetic and self-mating populations. *Theor. Pop. Biol.* 5:229-250.
- Templeton, A. R. 1974b. Analysis of selection in populations observed over a sequence of consecutive generations. I. Some one locus models with a single, constant fitness component per genotype. *Theor. Appl. Genet.* 45:179-191.
- Templeton, A. R. 1977. Analysis of head shape differences between two interfertile species of Hawaiian *Drosophila*. *Evolution* 31:630-642.
- Templeton, A. R. 1979. A frequency-dependent model of brood selection. *Am. Natur.* 114:515-524.
- Templeton, A. R. 1981. Mechanisms of speciation—a population genetic approach. *Annu. Rev. Ecol. System.* 12:23-48.
- Templeton, A. R. 1982. Adaptation and the integration of evolutionary forces. Pp. 15-31 in: R. Milkman (ed.), *Perspectives on Evolution*. Sinauer, Sunderland, MA.
- Templeton, A. R. 1987. Species and speciation. *Evolution* 41:233-235.
- Imbergen, N. 1953. *Social Behaviour in Animals*. Methuen, London.
- Val, F. C. 1977. Genetic analysis of the morphological differences between two interfertile species of Hawaiian *Drosophila*. *Evolution* 31:611-629.
- Vrba, E. S. 1985. Introductory comments on species and speciation. Pp. ix-xviii in: E. S. Vrba (ed.), *Species and Speciation*. Transvaal Museum Monograph No. 4, Pretoria.
- Waddington, C. H. 1957. *The Strategy of the Genes*. Allen & Unwin, London.
- Wagner, G. 1988. The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. *J. Evol. Biol.* 1:45-66.
- White, M. J. D. 1978. *Modes of Speciation*. Freeman, San Francisco.