

## THE DEBATE OVER SPECIES CONCEPTS AND ITS IMPLICATIONS FOR ORNITHOLOGY

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**ABSTRACT.**—We review recent developments in the debate over species concepts, exploring differences between the biological species concept (BSC) and the phylogenetic species concept (PSC). Three principal flaws in the BSC are reviewed: (1) the occurrence of paraphyletic or nonhistorical groups; (2) the misrepresentation of the significance of hybridization among differentiated taxa; and (3) the logical difficulty in handling allopatric populations. Simple cline theory shows that likely times to fusion for hybridizing taxa exceed the average duration of most species in the fossil record. We address criticisms of PSCs (of which there are several), including the application of phylogenetic methods to populations, and whether species can be monophyletic. We suggest that the evolutionary species concept and the PSC might be more similar than generally appreciated. Empirical studies of variation in the Brown Towhee (*Pipilo fuscus*) complex and Fox Sparrow (*Passerella iliaca*) reveal that the BSC and PSC can lead to different species limits. Reasons are given for why the PSC is the preferred concept for comparative biology, phylogenetic inference, historical biogeography, estimation of biodiversity, hybrid-zone analysis, conservation biology, and speciation analysis. Despite problems associated with all species concepts, we think that a concept consistent with the PSC should replace “biological” species concepts. Received 12 April 1994, accepted 4 November 1994.

No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species (Darwin 1859:44).

DARWIN'S WORDS ring true even today. We recognize that understanding the nature of species has profound meaning for evolutionary and comparative biologists, whose work depends on species names correctly delimiting evolutionary units and phylogenetic hypotheses depicting hierarchical relationships among species (Felsenstein 1985, Brooks and McLennan 1991, Lynch 1991). Yet, the literature on species concepts continues to feature debates over which concept best serves systematists, evolutionary biologists, ecologists, and ethologists (e.g. Coyne et al. 1988, de Queiroz and Donoghue 1988, 1990a, b, Cracraft 1989, Avise and Ball 1990, Frost and Hillis 1990, Wheeler and Nixon 1990). Although a pessimist might suggest that we have made little progress on the “species question” since Darwin's writing, the historical and ongoing debates reveal that the particular concept of species one adopts influences design and in-

terpretation of many studies. Hence, effort continues to clarify the nature of species.

The biological species concept (BSC) has received considerable support among ornithologists for many years (Haffer 1992), although it is increasingly challenged in both theory (Cracraft 1983, 1989, McKittrick and Zink 1988) and in practice (Atwood 1988, Barrowclough and Gutiérrez 1990, Livezey 1990, Pitocchelli 1990, Prum 1990, Thompson 1991, Zink and Dittmann 1991, Cracraft 1992, Escalante-Pliego and Peterson 1992). Most ornithological challenges to the BSC advocate a phylogenetic species concept (PSC). In this paper, we discuss current issues in the debate about species concepts. We do not review species concepts exhaustively, but attempt to provide sufficient comparison of biological (*sensu* Mayr 1963) and phylogenetic species to emphasize the consequences of their differences. In so doing, we respond to some criticisms that have been expressed about the PSC. We use avian examples to document how these two classes of species concepts lead to the setting of different species limits given the same data. We compare the PSC and ESC because they appear to have more in common than is apparent from much of the literature. We also discuss briefly the role of species concepts in compar-

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ative biology, phylogenetic analysis, historical biogeography, species-diversity studies, research on hybrid zones, conservation biology, and speciation analysis.

#### THE DEBATE ABOUT SPECIES CONCEPTS: GENERAL OVERVIEW

Probably all investigations of organisms refer to those organisms as members of a particular species (Hauser 1987). Therefore, it is surprising that there is so little agreement about the nature of these groupings. Nelson (1989a, b), for example, professed a disbelief in the importance of species as anything other than a taxon at some rank. O'Hara (1993) suggested that systematists should "get over" the species problem. Others have argued that different species concepts are required to accommodate different situations and evolutionary processes (Scudder 1974, Endler 1989, Graybeal 1995). Frost and Hillis (1990) advocated a modification of Wiley's (1981) evolutionary species concept (ESC), and suggested that species are the "largest recovered biparental lineages or uniparental tologenetic arrays". Paterson (1985) coined a "recognition" concept where species are the largest cluster of individuals that share a specific mate recognition system. Templeton (1989) concluded that four "biological" species concepts exist: (1) the evolutionary species concept (Simpson 1951); (2) the biological species concept (Mayr 1963), which he termed the isolation concept; (3) the recognition concept (Paterson 1985; see Lambert and Spencer 1995); and (4) a new concept he termed the cohesion concept. The many species concepts do have areas of agreement, although botanists, paleontologists, and neontologists often emphasize different aspects of the species debate as more important. De Queiroz and Donoghue (1988) reviewed species concepts and noted that two criteria are used most often by neontologists to rank taxa as species—reproductive isolation or monophyly. These two criteria relate to the processes of interbreeding and descent (Graybeal 1995). Emphasis on interbreeding or reproductive isolation typifies the biological species concept (Mayr 1963), whereas phylogenetic species concepts (Rosen 1979, Cracraft 1983) focus on diagnosability, patterns of descent, and monophyly. We maintain that the primary controversy surrounds biological versus phylogenetic species concepts, not which "biological" (sensu Tem-

pleton 1989) concept is best. Thus, we review these two concepts below.

#### BIOLOGICAL SPECIES

The major tenet of the BSC is that the origin of reproductive isolation (the grouping and ranking criterion; see Donoghue 1985) is the crux of speciation (Nei et al. 1983), and a species is the least-inclusive taxon or group of taxa that is reproductively isolated from other such taxa (Mayr and Ashlock 1991). Perceived strengths of this viewpoint are: (1) biological species limits are objective if a test of sympatry is available; and (2) reproductive isolation is the "genetic point of no return" or genetic closure of a lineage. Many criticisms of the BSC have been raised (Cracraft 1983, Donoghue 1985, McKittrick and Zink 1988, Frost and Hillis 1990, de Queiroz and Donoghue 1990a, b). We focus on what continue to be principal objections to the BSC, which we feel have not been adequately addressed by proponents of the BSC (Amadon and Short 1992, Haffer 1992, Mayr 1993). These include the occurrence of nonhistorical groups, significance of hybridization, and status of allopatric populations.

*Nonhistorical groups.*—A serious potential problem of applying the BSC is the occurrence of paraphyletic, or nonhistorical groups (Rosen 1979, Cracraft 1983, McKittrick and Zink 1988). Because reproductive isolation does not necessarily evolve concomitantly with character divergence, uniting differentiated taxa that are reproductively compatible can produce species that are paraphyletic (Rosen 1979). For example, Hillis (1988) provided a phylogeny of recognized species of *Rana* based on molecular evidence. If one mapped hybrid zones on the phylogeny, some occur between nonsister species, whereas other sympatric (and syntopic) sister taxa are reproductively isolated. Species that retain the primitive ability to hybridize (or have reacquired it) need not be sister taxa, and certainly are not "conspecific" in any historical sense. Uniting them leads to paraphyletic or nonhistorical groups (Cracraft 1983, 1987).

An avian example illustrates this point. If Red-shafted and Yellow-shafted flickers (*Colaptes auratus*) are not sister taxa (suggested by mitochondrial DNA [mtDNA] data; Moore et al. 1991), then lumping these taxa creates a paraphyletic taxon (the "Northern Flicker") characterized by the retention of ancestral reproductive compatibility.

This problem has been stated clearly by many biologists, but perhaps nowhere better than Frost and Hillis (1990): "If reproductive compatibility among populations is seen for what it is, a shared primitive feature, discordance between overall similarity and evolutionary (=phylogenetic) relatedness should not be surprising." In other words, uniting taxa because they hybridize can lead to nonhistorical groups, which are of no value in comparative biology, speciation analysis, phylogeny reconstruction, or historical biogeography (Hennig 1966, Brooks and McLennan 1991) because they misrepresent patterns of evolutionary history. Proponents of the BSC (e.g. Mayr 1982, 1992, 1993, Bock 1986, Amadon and Short 1992, Haffer 1992) simply have not responded to this criticism, which is viewed by many as the principal theoretical flaw in the BSC: "Therefore, as a working concept, the biological species concept is worse than merely unhelpful and non-operational—it can be misleading" (Frost and Hillis 1990).

*Significance of hybridization and reproductive compatibility in species concepts.*—A second area of concern for the BSC is the interpretation of hybridization. Some investigators (e.g. Barton and Hewitt 1983) assert that reproductive isolation must be complete, whereas others (e.g. Mayr 1982) do not. Mayr (1982) noted that the existence of a stable hybrid zone, within which random mating of parentals and backcrosses occurs, requires the parental taxa to be recognized as distinct species because of the unlikelihood of complete introgression. Hybrid zones, however, can take thousands of generations to stabilize (Barton and Hewitt 1983). This point has been misinterpreted. For example, Sibley and Monroe (1990:57) implied that the hybridizing flicker taxa (*C. a. auratus* and *C. a. cafer*) are the same species because the hybrid zone is stable. "Hybridization" implies the interaction of taxa with once-independent evolutionary histories. To recognize two hybridizing taxa as a single species anticipates introgression and fusion (Barton and Hewitt 1983) and discounts their historical status. Two hybridizing taxa rarely could be considered a single historical unit (especially if nonhistorical, such as the Northern Flicker), which we believe evolutionary and ontological theories require of species' names. The following example illustrates another reason why current gene exchange might be an unsuitable reason for uniting two hybridizing taxa.

The Yellow-rumped Warbler (*Dendroica coronata*) breeds across northern and western North

America. The two principal forms, the eastern Myrtle Warbler (*D. c. coronata*) and western Audubon's Warbler (*D. c. auduboni*), meet and hybridize in at least two restricted passes through the Rocky Mountains (Barrowclough 1980), and it is unclear whether the two forms are sister taxa. The governing nomenclatural body of the American Ornithologists' Union, the Committee on Classification and Nomenclature, treated the two forms as conspecific because of the existence (although limited) of hybridization between these wood-warblers (AOU 1983). This suggests that the two forms might fuse, which is one logical implication of giving them the same name. Because future fusion is considered a reason for uniting hybridizing taxa as single biological species, we investigated this issue using cline theory.

Barrowclough (1980) used cline theory to model hybridization in Yellow-rumped Warblers. One can predict the width ( $w$ ) of a cline in selectively neutral characters as

$$w = 1.68lT^{0.5}, \quad (1)$$

where  $l$  is the root-mean-square dispersal distance,  $T$  is the number of generations since secondary contact, and 1.68 is a constant related to how  $l$  is measured (Endler 1977). Using estimates of 7,500 years for  $T$  and 1.0 km/generation for  $l$ , Barrowclough (1980) predicted that the cline width should be 145.5 km. The measured width was 147.3, suggesting that the estimated parameters were of the correct order of magnitude.

Of importance for discussion of biological species is that we can solve for  $T$  and predict the time-to-fusion of these two wood-warbler taxa (i.e. time required for erasure of evidence of their independent evolutionary histories and final step in reticulate evolution of the wood-warbler taxon resulting from complete fusion of *coronata* and *auduboni*). It requires 3,200,000 generations (likely over 6,000,000 years) for the fusion of these two taxa to include 3,000 km (only a part of the total range). This time to fusion estimate is an underestimate because the formula is for a stepping-stone (linear) model rather than the more likely but more time-consuming island (or two-dimensional) model, and because density troughs can trap a cline (Hewitt 1988) and prevent introgression. The time-to-fusion greatly exceeds the estimated time for the duration of a passerine species in the fossil record (0.5 to 1.0 million years; Brodtkorb 1971). It appears unreasonable to consider the two taxa

as one species because they hybridize and might fuse at some future time. Advocates of the PSC prefer to recognize the status quo (there are two basal historical entities) and not to speculate about events in the very distant future (i.e. possible fusion).

The confusing application of the BSC is apparent in ornithology. For example, the widely hybridizing Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers are considered distinct biological species (AOU 1983), yet the former is replacing the latter because of hybridization. In contrast, the trickle of hybridization between *D. c. coronata* and *D. c. auduboni* is seen as evidence of conspecificity.

The significance of hybridization has been considered by other biologists, particularly botanists. Mayr (1992) concluded that the BSC was easily applied to plants, even though hybridization is seen as a problem for implementation of this species concept, and hybridization is frequent in plants. Mayr did not emphasize that botanists routinely describe hybrid swarms between species of plants without questioning the species status of the parental species themselves (e.g. Ellstrand et al. 1987, Nason et al. 1992). For instance, Rieseberg et al. (1993) noted that rare endemic plant species are often pushed to extinction by hybridization with more common species. Application of the BSC in most vertebrate systems would require rampant hybridization to be evidence of conspecificity (except, perhaps in the case of the wood-warblers discussed above). Rieseberg et al. (1993) did not consider hybridization between two species, even if it resulted in elimination of one species, to be reason enough to consider the two forms the same species; that is, species can and do hybridize. Practicing systematists working with many if not most major classes of organisms (e.g. plants and insects) do not regard hybridization as proof of conspecificity (Donoghue 1985). It is probably fair to state that most organisms in the world are delimited by a non-BSC paradigm.

Emphasis on the significance of hybridization stems from the central role that reproductive isolation is thought to play in speciation. Because of its emphasis on reproductive isolation as the ranking (and grouping) criterion, the BSC confounds information about the past with speculations about the future (Cracraft 1983). If one were interested in whether an allele could pass from one taxonomic group to another, re-

productive compatibility would be of interest. More important than the potential avenues of gene flow is the past history of diversification; the latter provides the framework for comparative biology (Brooks and McLennan 1991).

The evolution of reproductive isolation is an important evolutionary event (McKittrick and Zink 1988). Nei et al. (1983) suggested that mutations in relatively few genes might underlie reproductive isolation between most closely related species. Templeton (1981) indicated that there might be some common genetic aspects of the evolution of reproductive isolation, although tests of this idea are methodologically complicated. Coyne and Orr (1989a, b) reviewed "Haldane's Rule" and concluded that reproductive isolation might often involve changes on the unique member of the pair of sex chromosomes. Coyne and Orr (1989b) also documented a relationship between allozymic distance and prezygotic reproductive isolation in drosophilids. Therefore, study of reproductive isolating mechanisms is valuable, although not, in our opinion, a part of the process of delimiting species.

*Status of allopatric populations.*—A long-recognized drawback of the BSC is its difficulty in ranking allopatric populations (Mayr and Short 1970, Cracraft 1983, McKittrick and Zink 1988), and BSC proponents have done little to amend this drawback. The way one applies the BSC to allopatric populations results in subjective species limits. For example, Banks (1964) studied geographic variation in White-crowned Sparrows (*Zonotrichia leucophrys*), and concluded that:

Since the coastal birds do not meet other white-crowned sparrows in the breeding season, the question of their specific status as determined by natural reproductive isolation is *unanswerable*. The birds are, however, quite similar in ecologic, behavioral, and physiologic characters, and on this basis one could postulate that the two types would interbreed. In the present state of knowledge I follow Grinnell's opinion (1928) that the forms are best considered to be subspecies [pp. 113-114, italics added].

Because reproductive isolation is an epiphenomenon (or emergent property) of divergence, it is not easily related to descriptions of how characters vary geographically (which is what Banks actually studied). With enough experience, one might be able to judge on average whether two populations could interbreed. However, allowing such judgements to super-

sede or overrule evolutionary patterns will still lead, inappropriately, to nonhistorical taxa (see below).

Rensen et al. (1991) attempted to rank allopatric populations under a BSC framework. They implied that diagnosable geographic units that were presumably able to interbreed constitute valid subspecies rather than phylogenetic species. Rensen et al. (1991) determined whether a particular population was distinct by asking four persons to judge independently whether it was diagnosable. However, there was no statement outlining the data (characters) used by these individuals, their methods of analysis, their experience with the characters and taxa under study, levels of statistical significance, or whether derived or ancestral traits were used to delineate taxa. This does not appear to be a promising solution to the problem of judging the status of allopatric populations.

Mayr (1993:133) dismissed the problem in applying the BSC to allopatric populations:

For instance, for someone who studies the song sparrows of the San Francisco Bay region from the point of view of ecology, adaptation, or behavior, it is quite irrelevant whether one calls the song sparrows of the Aleutian Islands conspecific or a full species. However one ranks the Aleutian song sparrow will have no effect whatsoever on the study of the song sparrows of the San Francisco Bay region.

This statement is extremely misleading. If species limits are set according to patterns of reproductive compatibility and not evolutionary history, it is necessary to know to which species the Aleutian form belongs, and how the forms are related.

One cannot assume that features of Song Sparrows living in the Bay Area are direct responses to that current environment without reference to a phylogenetic hypothesis. Brooks and McLennan (1991) noted that one must consider several aspects of an "adaptation," namely its origin, maintenance, and modification. In Figure 1 we show a hypothetical phylogeny of Song Sparrow taxa. The origin of the adaptation of interest (adaptation a) predates the origin of the Bay Area taxon, and one would need to consider all relevant populations to study this adaptation. Only if adaptation a arose in the Bay Area taxon after it split from the most recent common ancestor with A and B could one search for causal factors involved in the origin of the trait in the Bay Area; otherwise, one would be

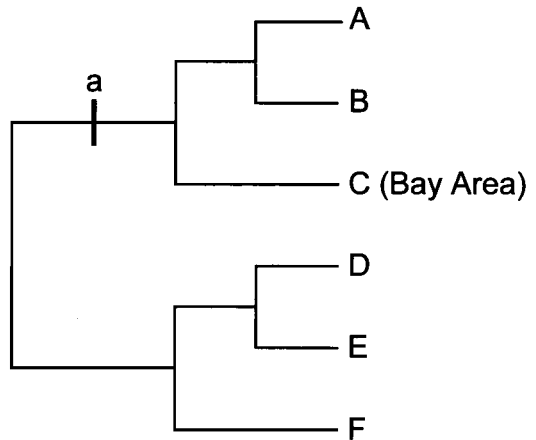


Fig. 1. Hypothetical phylogenetic pattern among populations of Song Sparrow. Thick bar indicates origin of adaptation a.

studying the maintenance or modification of the trait. Furthermore, assume that the two sister lineages of song sparrow taxa included some taxa that were reproductively incompatible and hence biological species, and that the Bay Area population retained the primitive ability to hybridize with a geographically adjacent taxon (D). We would then have a paraphyletic biological species, CD, in which the trait of interest occurred in one member (C) and not the other, and two (A, B) members of the other biological species (A, B, E, F). Therefore, one might postulate, incorrectly, the parallel acquisition of the trait in parts of each of the two species, or the loss of the trait in taxa D, E, or F. Thus, we think that Mayr (1993) is wrong to suggest that one's taxonomy is irrelevant to interpreting an adaptation. If species limits are inconsistent with phylogenetic patterns, interpreting adaptations will be difficult (Brooks and McLennan 1991). It seems inappropriate to have a system of naming species in which species names would misinform comparative analyses.

Mayr (1992) claimed that the BSC "worked" in a local population of plants for 93.5% of the species, meaning that the species can be identified because of lack of hybridization. However, forms that do not interbreed in sympatry are considered species by all species concepts; this then is not a unique advantage of the BSC. What Mayr's (1992) defense of the BSC does not account for is the difficulty in determining the status of allopatric populations; the 93.5% must certainly be adjusted downwards. Most species

include allopatric components, which means that the species concept used should be applicable to them in theory and practice.

In summary, the perceived strengths of the BSC (objectivity in sympatry, and reproductive isolation being a point of "no return") are arguable. Furthermore, the oft-noted weaknesses of the BSC (occurrence of nonhistorical groups, judgement of allopatric populations, and arbitrariness of degree of hybridization required for conspecificity) have caused many authors to call for the abandonment of the BSC.

#### PHYLOGENETIC SPECIES

Several PSCs have been published. Nelson and Platnick (1981:12) defined species as "simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters." Cracraft (1983:170) wrote that "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Nixon and Wheeler (1990:211) indicated that "We define species as the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)." Advocates of PSCs (Cracraft 1983, Donoghue 1985, Mishler and Brandon 1987, Wheeler and Nixon 1990) use character analyses to delimit taxa, and basal, or least diagnosable groups, are equated with species. The character conferring diagnosability could be any feature or set of features, ranging from single fixed nucleotide substitutions to major phenotypic (but genetically based) features. If characters conflict in circumscribing taxa, parsimony can be used to arbitrate taxon limits. The trait(s) must show a pattern of ancestry and descent; that is, single individuals, males and females of sexually dimorphic species, and individuals or groups of individuals with distinct mtDNA clones do not qualify as phylogenetic species (de Queiroz and Donoghue 1988). Phylogenetic species exhibit reproductive cohesion, but are described independently of known or hypothesized patterns of reproductive compatibility. Reproductive compatibility does not indicate conspecific status.

PSCs have been criticized (Avisé and Ball 1990, Amadon and Short 1992, Baum 1992, Mayr 1992, Mallet 1995). There is, for example, the practical problem of what constitutes a diagnosable group

(i.e. 95 or 99% of all individuals possessing the diagnostic condition; McKittrick and Zink 1988, Cracraft 1992). In addition, proponents of phylogenetic species concepts disagree about the proper procedures for establishing phylogenetic species limits, and whether species are monophyletic (de Queiroz and Donoghue 1990a, b, Wheeler and Nixon 1990, Graybeal 1995), as we discuss below.

*Delimiting phylogenetic species and the role of population analysis.*—Avisé and Ball (1990) noted that, with modern molecular methods, each individual of most biparental species can be shown to be genetically "diagnosable" and, therefore, these authors wondered if individual organisms could qualify as phylogenetic species. Furthermore, they argued that numerous overlapping "diagnosable" groups of individuals within populations could be based on comparisons of independent gene genealogies (e.g. Avisé et al. 1987). That is, analysis of different genes, such as mitochondrial DNA (cytoplasmic inheritance) and allozymes (nuclear inheritance) reveals groups of individuals, but these groups could be overlapping (i.e. not mutually exclusive), which would confuse delimiting species boundaries. Avisé and Ball (1990) described species as groups of individuals that share a significant number of concordant nuclear-gene genealogies; however, they left "significant" undefined. Avisé and Ball (1990) potentially confounded phylogenetic with phenetic species concepts when they defined species as groups of individuals with a given level of congruence among gene genealogies. Their definition might be acceptable to proponents of the PSC if parsimony analysis was used to delimit groups; however, Avisé and Ball (1990) considered groups that hybridize to be conspecific, which can lead to nonhistorical groupings.

Avisé and Ball's (1990) criticism of the PSC is based on two misinterpretations: (1) that traits (and not groups of individuals) are monophyletic; and (2) that only single characters delimit phylogenetic species. Although mtDNA lineages and some nuclear-gene lineages (those without recombination) can be monophyletic, the PSC refers to monophyly of the organismal phylogeny, not single-gene genealogies. If one observes overlapping gene genealogies, the limits of a phylogenetic species are probably more inclusive than those indicated by the gene under examination. Therefore, it is critical to emphasize that the PSC does not base species

limits *only* on single characters, although a single character could be used if it happened to be congruent with the principal phylogenetic pattern in other characters, or if it were the only varying character. Our earlier paper (McKittrick and Zink 1988) did not make this point clear.

The problem of overlapping characters is a general issue in systematics. Different characters often suggest different overlapping groupings of taxa at all taxonomic levels (i.e. if homoplasy occurs), which is analogous to overlapping gene genealogies. Of course, a real difference between overlapping gene genealogies and homoplasy is that the latter results from mistakes by systematists in encoding characters (Mickevich and Weller 1990), whereas the former is an actual property of independent gene lineages (Neigel and Avise 1986, Pamilo and Nei 1988). Whatever the cause, systematists usually use maximum-parsimony analysis of multiple characters to discover clades, despite the occurrence of homoplasy. The same procedure can be used to resolve groups of individuals into irreducible basal clusters (phylogenetic species), despite different gene genealogies. In many cases, geographic barriers will set the limits of such clades, although such barriers are not required as part of the PSC.

Discordance of mtDNA and nuclear-gene trees is exemplified in Patton and Smith's (1994) study of pocket gophers (genus *Thomomys*). MtDNA data circumscribe a group of gopher populations, whereas allozyme (nuclear) data suggest a different, overlapping set of relationships. In birds, Degnan (1993) showed that a mtDNA and a nuclear-gene tree resolved different but overlapping groups of individuals. In these two studies, mtDNA data (effectively a "single gene tree"; Avise 1989) apparently do not reflect the organismal phylogeny and, as a result, species limits based solely on mtDNA would be incorrect. In sexually reproducing organisms, unique mutations can be traced through a population pedigree (termed tokogenetic relationships), but they will not necessarily delimit mutually exclusive nested sets of individuals in the same way that characters delimit monophyletic groups at higher taxonomic levels (Hennig 1966, Nixon and Wheeler 1990, DeSalle et al. 1994, Graybeal 1995). Phylogenetic analysis of individuals in populations, or populations that are in reproductive contact can be flawed because the units are not independent parts of a hierarchy, which is what cladistic analysis requires

(Hennig 1966). That is, one would expect different characters to suggest different groupings of individuals because of the nature of inheritance in bisexual species (Davis and Nixon 1992). This underscores the need to examine multiple characters and determine if the populations are independent evolutionary units, and whether they are taxa that should be ranked as phylogenetic species.

Given the concern over applying phylogenetic methods to populations that might be in reproductive contact (i.e. genealogical relationships are reticulating), Davis and Nixon (1992) proposed a method for analyzing populations for phylogenetic-species limits. Their method, population-aggregation analysis, works by first tabulating characters for individuals within population samples. For each character, a population is scored as either fixed or polymorphic. Davis and Nixon (1992) used "trait" to describe variable characters that are not fixed among populations. Populations are then compared pairwise, and those that exhibit no fixed differences are aggregated. As an example, consider data set A in Table 1. Only character 9 functions to separate the two species, all others being "not fixed" among the two populations (i.e. a "1" versus a "±" is considered not fixed).

This method of delimiting phylogenetic species differs from others. Davis and Nixon (1992) used population-aggregation analysis to discover the limits of phylogenetic species, whereas others use phylogenetic analysis of population samples. To illustrate the differences, we applied maximum-parsimony analysis to data set A (Table 1), which yielded six minimum-length trees (length = 6,  $CI = 100$ ,  $RI = 100$ ); the strict-consensus tree supports two groups of populations or phylogenetic species. In both population aggregation analysis and parsimony analysis, species 1 includes populations 1, 3, 4, and 5, and species 2 the other three populations. Thus, in this example, the two methods give the same results.

We next applied these methods to an expanded set of data (data set B in Table 1). Characters 11 and 12 introduce homoplasy, which allows us to investigate the problem of overlapping character phylogenies identified by Avise and Ball (1990). Applying population-aggregation analysis, we found five phylogenetic species (Table 1). Using phylogenetic analysis, seven equally-parsimonious trees (not shown) were found (length = 10,  $CI = 0.80$ ,  $RI = 0.75$ ),

TABLE 1. Summary of hypothetical character variation in populations: (0) absent; (1) present; ( $\pm$ ) polymorphic in population sample. Character data for 1 to 10 from Davis and Nixon (1992:table 2); characters 11 and 12 added for this analysis. Data matrix below is result of applying population-aggregation analysis to characters 1-10, and 1-12.

Population (P) and species (S)	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
P1	1	$\pm$	1	$\pm$	$\pm$	0	0	1	0	$\pm$	1	1
P2	1	0	1	1	$\pm$	$\pm$	$\pm$	1	1	1	0	1
P3	$\pm$	$\pm$	1	0	$\pm$	0	$\pm$	1	0	0	0	0
P4	$\pm$	1	1	0	$\pm$	0	$\pm$	1	0	0	0	0
P5	0	$\pm$	1	0	$\pm$	0	0	$\pm$	0	0	0	0
P6	1	0	1	1	0	1	$\pm$	$\pm$	1	1	1	0
P7	1	$\pm$	1	1	$\pm$	1	$\pm$	$\pm$	1	$\pm$	0	0
<b>Data set A (characters 1-10)</b>												
S1 (P1, 3, 4, 5)	$\pm$	$\pm$	1	$\pm$	$\pm$	0	$\pm$	$\pm$	0	$\pm$		
S2 (P2, 6, 7)	1	0	1	1	$\pm$	$\pm$	$\pm$	$\pm$	1	$\pm$		
<b>Data set B (characters 1-12)</b>												
S1 (P1)	1	$\pm$	1	$\pm$	$\pm$	0	0	1	0	$\pm$	1	1
S2 (P2)	1	0	1	1	$\pm$	$\pm$	$\pm$	1	1	1	0	1
S3 (P 3, 4, 5)	$\pm$	$\pm$	1	0	$\pm$	0	$\pm$	$\pm$	0	0	0	0
S4 (P6)	1	0	1	1	0	1	$\pm$	$\pm$	1	1	1	0
S5 (P7)	1	$\pm$	1	1	$\pm$	1	$\pm$	$\pm$	1	$\pm$	0	0

and the consensus tree was completely unresolved, suggesting a single species. However, inspection of the seven trees shows that populations 3, 4, and 5 lack autapomorphies, which would be evidence that they are conspecific, whereas populations 1, 2, 6, and 7 have autapomorphies, which would support their status as phylogenetic species. The status of populations 3, 4, and 5 as a fifth species could be controversial as they do not share a single diagnostic character (see below). Thus, phylogenetic analysis might not correctly delimit phylogenetic species unless one carefully examines character support for trees of populations.

In Davis and Nixon's (1992) view of phylogenetic species, "phylogenetic" refers to the process whereby terminal taxa are delimited for phylogenetic analysis. Davis and Nixon (1992: 428) stated that "phylogenetic species are the least inclusive populations or sets of populations among which there is character-based evidence, in the form of fixed differences, that gene exchange does not occur", and that "the lowermost point at which hierarchic descent relationships are discoverable by cladistic analysis is the point at which hierarchically related units exist and are marked by characters." What is not clear from the Davis and Nixon (1992) approach is how to deal with populations that are demonstrably hybrid in origin. It might be that hybridizing taxa that are not sisters, such

as the flickers discussed above, would be considered conspecific under the population-aggregation-analysis approach, which would be inconsistent with the PSC as we envision it.

Investigators should be aware of different methods of delimiting phylogenetic species. The two methods of analysis used here could yield different species limits when applied to population data. Character evidence should exist before assigning a group of individuals to a unique phylogenetic species. The analyses also reveal why multiple characters are needed to resolve species limits; characters 11 and 12 conflict, and species limits based on either character alone would be incorrect because they would not represent the species tree.

*Monophyly and phylogenetic species.*—Debate has involved the application of the concept of monophyly to phylogenetic species. De Queiroz and Donoghue (1990a) noted that there are two considerations of monophyly at the species level: (1) that of single characters, such as gene genealogies; and (2) that of lineages, which we consider now. In Figure 2, ancestral species B does not become extinct at the speciation event leading to taxon C. In this situation, extant species B is not monophyletic (as in populations 3, 4, and 5 in the above example), although it is still diagnosable because its individuals express synapomorphy b (note that fixed differences separate populations). Speciation in peripheral



or isolated populations must occur often in this manner (Patton and Smith 1994). Thus, monophyly in the strict cladistic sense will not apply (contrary to our earlier statement to this effect; McKittrick and Zink 1988). Donoghue (1985) termed a taxon such as B a metaspecies, a proposal that generated considerable debate (Kluge 1989, Wheeler and Nixon 1990, Graybeal 1995). Metaspecies, such as those "taxa" without apomorphies (character evidence) identified above in our phylogenetic analysis, meet requirements for basal evolutionary taxa and, if a new mutation became diagnostic for the taxon, it would be a phylogenetic species. We favor, as a null hypothesis, species status for diagnosable "plesiomorphic" basal taxa—there is no evidence that suggests they are not a cohesive basal evolutionary unit. Nelson (1989a) suggested that ancestral taxa (e.g. B) are by definition paraphyletic and, therefore, artificial taxa. Of course, any terminal taxon with an autapomorphy cannot be an ancestor of another extant taxon at the same rank.

Graybeal (1995) recently suggested a system of naming taxa that are at the interface of reticulation (i.e. the process of interbreeding) and diversification (i.e. the divergence of populations). Her naming system is designed to accommodate groups at different stages of evolutionary divergence. She suggested that her method—which deserves study—will alleviate the tension between those who favor primary emphasis on either interbreeding or monophyly.

Davis and Nixon (1992) stated that "Because less inclusive units than a phylogenetic species cannot be the subject of phylogenetic analysis, subunits within a phylogenetic species cannot be demonstrated to be related to each other hierarchically in a manner that would justify use of the term 'monophyletic' for the species itself." Phylogenetic species *sensu* Davis and Nixon (1992) are least-divisible units that are characterized by the possession by all individuals of a fixed character state, and they are "terminals" in a phylogenetic analysis. Monophyly of species will probably remain controversial.

#### PHYLOGENETIC SPECIES AND EVOLUTIONARY SPECIES

The goal of a PSC is to recognize basal evolutionary taxa as species (Cracraft 1983). That is, groups of individuals on independent evo-

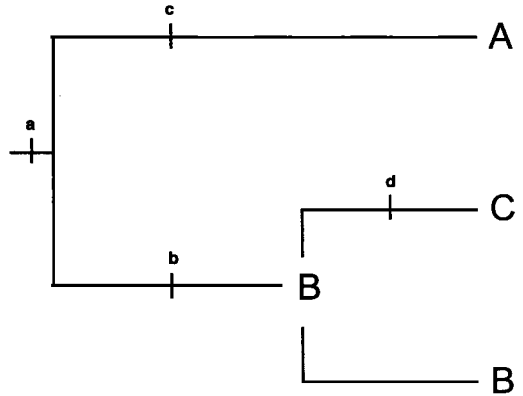


Fig. 2. Hypothetical pattern of evolution for three taxa in which ancestral species B is extant (and possesses no autapomorphies).

lutionary trajectories should be called species. This characterization resembles the ESC (e.g. Frost and Hillis 1990). Wiley and Mayden (in press) recharacterized the ESC as follows: "An evolutionary species is an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies." Wiley and Mayden (in press) suggested that the existence of an entity, such as a species, should be considered independently of the procedure used to discover it. Thus, they criticize PSCs for including the criterion of diagnosability, and consider most PSCs to be in conflict with the ESC. Furthermore, they criticize the PSC of Cracraft (1983) because it is "burdened with a necessary search for the smallest evolutionary unit."

Species limits in the Spotted Owl (*Strix occidentalis*) might exemplify differences between the ESC and PSC. Barrowclough and Gutiérrez (1990) found a significant allelic frequency difference between allopatric populations of the Spotted Owl. They argued that this frequency difference (i.e. not a fixed difference) was evidence of historical isolation, and they suggested that the two groups of owls were separate evolutionary species. Wiley and Mayden's (in press) concern about discovering species limits is apparent here because the PSC would not support the two groups of owls as separate species because all individuals in each group do not share the same diagnostic character. The two species concepts might lead to different species limits because, operationally, the PSC could limit one's ability to discover evolutionary species of these

owls (note, we only speculate whether Wiley and Mayden would agree that the two groups of owls are evolutionary species). We are not convinced that specifying the procedure for recognizing a phylogenetic species compromises the PSC. Although an evolutionary (or phylogenetic) species could exist without character evidence to diagnose it, many groups of organisms that are not evolutionary species might show frequency differences, such as the owls, owing to differing selection regimes. One might never know whether a group was a species and, if species have only frequency differences among them, their use in phylogenetic analysis will be challenging. Requiring fixed-character evidence before a hypothesis of lineage independence is advanced seems a reasonable alternative to naming taxa that are not independently evolving, both in theory and practice.

Wiley and Mayden (in press) indicated that requiring or searching for least-diagnosable units leads to the recognition of individual organisms as species, a perception we considered invalid above. These authors also are concerned that proponents of the PSC equate character evolution with speciation. However, one does not "define" species by the traits their constituents possess, because subsequent evolution might change the characters and our diagnoses, but not the status of the group as a phylogenetic species. Therefore, each newly evolved autapomorphic character does not mean that a new species evolved, although our diagnosis would be amended to reflect the new evidence. Lineages, not characters diagnosing them, are equated with species.

We view phylogenetic species as basal evolutionary entities that cannot be further subdivided, and they are recognized by examining the distribution of character variation within and among individuals and populations. To Wiley and Mayden (in press), species are equated with the largest tokogenetic unit (i.e. groups of reproductively cohesive individuals in a population pedigree that maintain their own historical fate and tendency, and that are consistent with recovered phylogenetic patterns; Frost and Hillis 1990). The notion of the largest tokogenetic unit can be difficult to conceptualize—does it mean actually or potentially "largest"? The notion of historical tendencies and fates seems to cloud further the ESC, because as Frost and Hillis (1990) stated, "one can only

tell where lineages (or their parts) have been, not where they are going." Nonetheless, it is possible that the largest tokogenetic unit with its own historical fate and tendency is basically what PSC proponents mean by basal evolutionary units.

There might be, in principle, little difference between the ESC and our view of phylogenetic species. If one requires that at least a single character be present to recognize phylogenetic species, then the phylogenetic and evolutionary species concepts are different in theory. Whether the two concepts will differ frequently in practice is unclear. For now, we suggest that a phylogenetic concept is a better choice than the ESC, without ruling out a merging of the basic parts of each. Such a merging would result in a concept inconsistent with the BSC.

#### SPECIES CONCEPTS AND ONTOLOGY

O'Hara (1993) suggested that systematists need to "get over" the species problem. O'Hara argued that all three classes of species concepts (evolutionary, biological, and phylogenetic) carry with them certain assumptions about the past or expectations about the future. This may be considered a weakness in all concepts. The evolutionary concepts make reference to historical fate, biological concepts in effect predict genetic cohesion of interbreeding forms, and phylogenetic concepts flag patterns of "ancestry and descent." The thrust of O'Hara's thesis is that, when organismal history is considered in terms of an individual organism's ancestor-descendant (tokogenetic) relationships, which include many complex reticulation events, any concept is limited in its ability to represent those relationships in a classification system. In O'Hara's (1993) view, we should recognize those limits and stop worrying about them. This view sidesteps the issue that these concepts have different goals, and the primary goal of the BSC does not include representation of history. Thus, in one sense, proponents of the BSC have already gotten over the species problem.

When one views organismal lineages as systems of tokogenetic relationships, it is easy to see them as historical individuals with complicated interactions. As with other individuals, these lineages can acquire and lose parts with no effect on their ontological status (McKittrick 1994). O'Hara discussed the example of acqui-

sition by the English language of words from Algonquian and other languages, and stated that "English shares derived states with both German and Algonquian, and the concept of clade is imperfectly defined here . . . because the underlying chronicle is partially reticulate." We argue that in this case the chronicle is not reticulate, but rather that one language has simply acquired words from another. This is quite different from saying that two languages have mixed to form a new language. One linguistic lineage has simply acquired parts from another. Similarly the acquisition by an organismal lineage of parts of other lineages affects the delineation of the lineage, but not its status as a lineage. The more extensive the reproductive interactions among lineages the more difficult it is to recover historical pattern at the level available to the researcher; to follow O'Hara's analogy, for instance, we may have a map with a 1:20,000,000 scale rather than the 1:1,000 scale that we need.

If a lineage experiences a reticulation, such that part of it joins with part of another to form a new lineage rather than just a stable hybrid zone, then naming the new lineage would be a proper representation of history. It would be incorrect, however, to group the remaining parental lineages with the descendant lineage as one named species because such an action would misrepresent what actually happened, namely the joining of parts of two independent lineages that had (by definition) two separate histories. The joining of parts forms an entity with its own historical tendencies, but the histories of the remaining parental lines should not be obscured with a new name. Rather than getting over the species problem, we need to get over the inclination to obliterate history by changing the names of historical entities whenever reticulation or, as is more often the case, limited exchange or donation of parts has been detected or inferred. We need to make a commitment to represent history accurately and precisely at all levels of classification. There is more than one species concept that involves this commitment, but the BSC is not one of them. In short, the BSC and PSC yield logically different outcomes in many situations, and these outcomes have important implications for biology. The task is to determine which concept creates the fewest problems resulting from emphasis on interbreeding or history (see Graybeal 1995). Given the uses to which species are put, we believe it

is clear that representing history correctly is of most value.

#### EXAMPLES OF DIFFERENCES BETWEEN THE PSC AND BSC

In theory, the consequences of the PSC and BSC differ. In practice, the situation is unclear. Some biological species might be equivalent to: (1) a single phylogenetic species; (2) a monophyletic group of two or more phylogenetic species; or (3) a paraphyletic assemblage of phylogenetic species. Amadon and Short (1992) were concerned that McKittrick and Zink (1988) advocated the PSC, but failed to give a practical example. Determining species limits in the Brown Towhee (*Pipilo fuscus*) complex and the Fox Sparrow (*Passerella iliaca*) reveal clear differences between the two species concepts.

*Brown Towhee.*—The Brown Towhee complex includes the following four primary taxa: Abert's Towhee (*P. aberti*); White-throated Towhee (*P. albicollis*); Canyon Towhee (*P. fuscus*); and California Towhee (*P. crissalis*). The latter two allopatric taxa previously were considered distinct only at the level of subspecies (AOU 1983). It was presumed that the morphological, ecological, and call-note differences between the two taxa were insufficient to result in assortative mating in the event that the two forms were to come into contact. Thus, these allopatric groups were judged conspecific under the BSC. Zink (1988) and Zink and Dittmann (1991) showed that *fuscus* and *crissalis* are not sister taxa. Therefore, the "Brown Towhee" as constituted under the BSC was a nonhistorical taxon. The Committee on Classification and Nomenclature (which follows the BSC) declared (AOU 1989) the two forms distinct species based on Zink's (1988) genetic (allozyme) evidence. Hence, even practitioners of the BSC now recognize the two towhee taxa as species. If the two forms came into contact and hybridized, however, the Committee would reverse its decision and recognize a demonstrably nonhistorical taxon (*fuscus* plus *crissalis*) as a single species (*fuscus* because of nomenclatural priority) if the Committee continues to follow the BSC (AOU 1983). Under the PSC one would recognize each form as a distinct species (McKittrick and Zink 1988). The BSC and PSC lead to different species limits given the same data.

*Fox Sparrow.*—Early writers (e.g. Coues 1894, Bailey 1902) recognized four major phenotypic

TABLE 2. Nature of hybridization between phylogenetic species of the Fox Sparrow. Pairs of species not listed are not in contact during breeding season.

Comparison	Extent of hybridization
<i>iliaca</i> and <i>unalaschcensis</i>	Very limited
<i>iliaca</i> and <i>schistacea</i>	Very limited
<i>unalaschcensis</i> and <i>schistacea</i>	Very limited
<i>schistacea</i> and <i>megarhyncha</i>	Narrow hybrid zone

groups of the Fox Sparrow: (1) the reddish group that inhabits the taiga from Newfoundland to western Alaska (*iliaca*); (2) the sooty-plumaged group that inhabits coastal regions from the Aleutian islands to Vancouver Island (*unalaschcensis*); (3) the thick-billed grayish group from southern California (*megarhyncha*); and (4) the grayish small-billed group that inhabits mountain riparian thickets in western Canada and United States (*schistacea*). Bailey (1902) considered the groups to be species, whereas Coues (1894) was equivocal. The AOU (1983) considered all of the forms a single species.

Zink (1994) found that each of the four major phenotypic groups had a distinct set of mtDNA haplotypes. Studies of mtDNA variation revealed that hybridization was limited to a narrow zone between *megarhyncha* and *schistacea* at the interface of the Great Basin and Sierra Nevada/Cascades, and sporadically among the three forms in British Columbia and Alaska (*iliaca*, *unalaschcensis*, and *schistacea*). Zink (1994) suggested that the four forms are phylogenetic species owing to the congruent patterns of mtDNA and plumage variation (not solely mtDNA variation). Interpretation of the species limits under the BSC is complicated because of hybridization among the four forms (Table 2). If one were to apply the BSC strictly, only a single species exists because all four forms are linked by at least some hybridization. However, a less strict application might recognize two species—(1) *iliaca*, and (2) *megarhyncha* + *schistacea* + *unalaschcensis*—because *iliaca* apparently hybridizes with other forms very infrequently (there is no hybrid swarm), whereas there is greater hybridization among the other three groups. A moderate view might result in species status for *iliaca* and *unalaschcensis* because of the limited hybridization between them (again, no hybrid swarm is evident), and conspecific status for *schistacea* and *megarhyncha* because of the hybrid zone between them. This example re-

veals the arbitrariness of the BSC when it is used to make decisions about the limits of hybridization tolerated between biological species, and it challenges the opinion of those (e.g. Amadon and Short 1992) who claim that species are "real" and not constructs of systematists (see also Nelson 1989a).

A further complication in Fox Sparrows is that the two phylogenetic species that form a narrow hybrid zone, *schistacea* and *megarhyncha*, apparently are not sister taxa (Zink 1994). Lumping them into one biological species because they hybridize would create a nonhistorical group. Other examples of hybrid zones between apparently nonsister taxa include the flickers (*Colaptes auratus* and *C. cafer*; Moore et al. 1991) and the orioles (*Icterus bullocki* and *I. galbula*; Freeman and Zink 1995). Thus, there is growing evidence that hybridization is not limited to sister taxa.

The Fox Sparrow mtDNA study (Zink 1994) provides an example of the concern Avise and Ball (1990) and Davis and Nixon (1992) expressed about single-character diagnoses of species limits. In particular, Zink (1994) found multiple mtDNA haplotypes within each of the four major clades of the Fox Sparrow. Phylogenetic analysis resolved these haplotypes into their probable evolutionary relationships. Therefore, one could use the haplotype phylogeny to subdivide further the four species. These haplotype phylogenies do not suggest geographically coherent patterns, however, and no other characters suggest similar groupings. Thus, although there is mtDNA variation and morphologically defined subspecies within each group, species limits are "attracted" to the congruence afforded by mtDNA and morphology (and geographic distribution). Because mtDNA is inherited as a single genetic unit, it should not be used alone to describe species limits.

#### IMPLICATIONS OF SPECIES CONCEPTS

*Comparative biology.*—The Brown Towhee example illustrates that pooling differentiated interbreeding taxa could result in paraphyletic groups, a practice that can have profound implications for comparative biology. For example, consider the evolution of the character "pale or white throat" in *P. fuscus* and *P. albicollis*. If *fuscus* and *crissalis* were considered conspecific because of interbreeding (if it were detected), one might postulate independent acquisition of

TABLE 3. Character-state matrix for five hypothetical taxa. D1 and D2 are considered a single biological species because they hybridize.

Taxon	Character							
	1	2	3	4	5	6	7	8
A	0	0	0	0	0	0	0	0
B	1	0	1	0	0	0	0	1
C	1	1	0	1	0	0	1	0
D1	1	1	0	0	1	1	1	0
D2	1	0	1	0	1	1	1	1

pale/white throat in *albicollis* and the paraphyletic taxon *fuscus* (actually *fuscus* plus *crissalis*), rather than its unique origin in the common ancestor of *albicollis* and *fuscus*. Because species limits under the PSC are consistent with recovered evolutionary patterns, one does not need to wonder if species include nonsister taxa that would result in incorrect mapping of traits onto phylogenetic trees.

*Species concepts and phylogenetic analysis.*—Systematists often use species as the basic unit in a phylogenetic analysis. If two differentiated (but interbreeding) units were considered conspecific, serious errors could occur. In Table 3, we show a data set in which two differentiated taxa (D1, D2) are considered a single biological species, D, because they hybridize. If the systematist chose D1 to represent species D, the single most-parsimonious tree (not shown) suggests that "D" and C are sister taxa. If D2 were chosen, then "D" and B are sister taxa. If both D1 and D2 were included in the study, two equally-parsimonious trees result (Fig. 3), and the sister-group relationships are ambiguous. Another possibility is to code the taxon as polymorphic. Nonetheless, this example shows that, if two differentiated taxa were pooled because they could interbreed, an error could result by assuming they were equally representative of a "species." Recognizing them each as phylogenetic species would not cause this problem. Actual examples of this problem can be found in Livezey (1986).

*Species concepts and historical biogeography.*—The vicariance school of biogeography (Nelson and Platnick 1981, Wiley 1987) argues that fragmentation of ancestral biotas creates congruent patterns of variation among taxa in codistributed lineages. At the finest level of geographic resolution, searches for congruence also reveal common events that separate gene pools among populations in a coincident fashion (Berming-

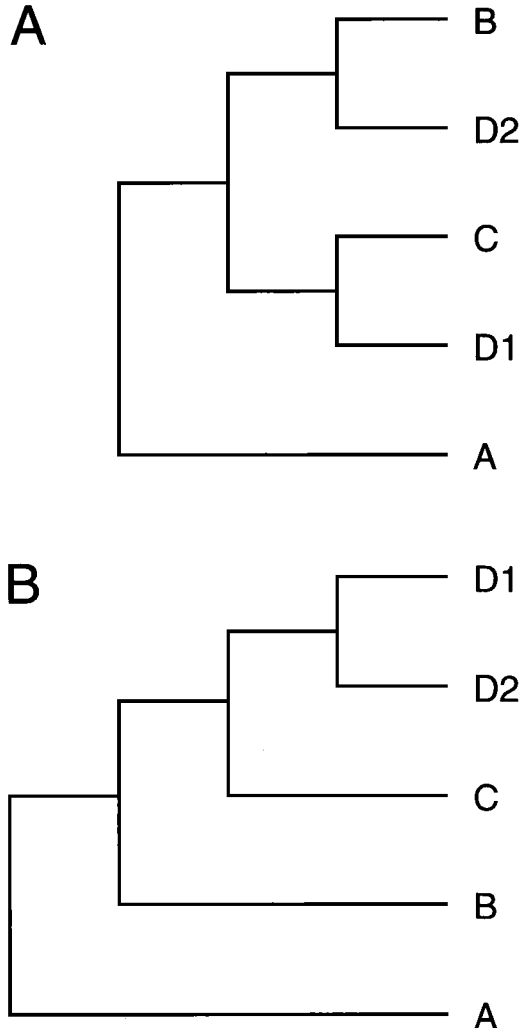


Fig. 3. Two equally-parsimonious trees resulting from analysis of data in Table 3. Tree length is 11, consistency index is 0.73, and rescaled consistency index is 0.36.

ham and Avise 1986, Avise 1992). If phylogeographic patterns are concealed by biological-species limits, investigators not familiar with the taxon could overlook evidence bearing on biogeographic reconstructions. In the Brown Towhees, for example, if *fuscus* and *crissalis* were merged (as they would be if interbreeding was detected), the phylogenetic pattern would not be apparent from species limits in classifications (as in Fox Sparrows and Yellow-rumped Warblers) and biogeographic analysis would be hampered.

Many avian biological species likely include

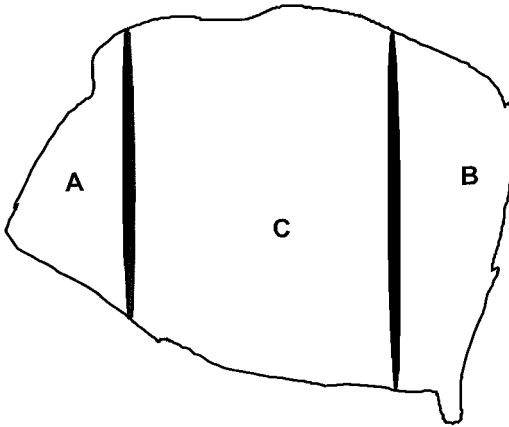


Fig. 4. Geographic relationships among three taxa (A, B, C) with hybrid zones shown as shaded areas.

more than one phylogenetic species (Mayr 1993). Zink and Hackett (1988) discussed several species, such as flickers and orioles mentioned above, in which there are eastern, western, and southwestern elements that currently are considered subspecifically distinct. If the subspecies prove to be phylogenetic species, the BSC would obscure this potential test of area relationships by pooling hybridizing taxa. These examples underscore the problem of allowing diagnosable basal evolutionary groups to be either species or subspecies.

*Species concepts and biological diversity.*—Several authors have estimated global species diversity (e.g. May 1992), without specifying explicitly the species concept employed. Moritz (1994) proposed a genetic criterion for an evolutionarily significant unit for conservation that is consistent with phylogenetic species limits. We contend that biological species are inappropriate units for biodiversity analysis because they can contain variable numbers of evolutionary units. For example, to compute continental species diversity, it would be incorrect to equate the Whooping Crane (*Grus americana*) and the Yellow-rumped Warbler because they represent different numbers of evolutionary units. Phylogenetic species are appropriate units for describing biological diversity. The PSC would lead to greater consistency, both within ornithology and in comparisons of birds with most other groups of organisms. As noted above, botanists routinely refer to "species" that nonetheless hybridize with other "species."

Thus, species concepts are indeed important for assessing biodiversity. If, for example, each biological species contains two phylogenetic taxa on average (Mayr 1993), estimates of global avian species diversity would double from that estimated by Sibley and Monroe (1990). Although Mayr (1993) suggested that 20,000 species of birds in the world are far too many, we believe his view is indefensible. Botanists and entomologists routinely deal with much larger numbers of species. Use of the PSC would make species of birds more comparable with species in other major groups.

*Species concepts and hybrid zones.*—Cracraft (1989) discussed how the PSC facilitates study of hybrid zones. In the scenario depicted in Figure 4, three parapatric diagnosable units hybridize. Under the BSC, these would be considered one species because of interbreeding, and one might attempt to distinguish primary from secondary zones by estimating the steepness of clines (Endler 1977). However, phylogenetic analysis reveals that taxa A and C are sister groups. Therefore, the hybrid zone between B and C is likely to be a secondary one (Cracraft 1989), whereas that between A and C is unclear. In the Fox Sparrow, a hybrid zone exists between two nonsister taxa (Zink 1994); similar evidence exists for flickers (Moore et al. 1991) and orioles (Freeman and Zink 1995). Such studies suggest secondary contact.

An important question is how interpretation of hybrid zones would be altered by adopting the PSC. Study of hybrid zones involves a phylogenetic component in which the investigator attempts to determine whether interacting taxa are sister taxa (Cracraft 1989). For example, Parsons et al. (1993) documented introgression between two species of manakins (*Manacus*). They discovered a unidirectional spread of secondary sexual plumage traits through the hybrid zone. The analysis might have been enriched by a phylogenetic perspective, because one could ask if the traits spreading were ancestral or derived. Furthermore, if the taxa were not sisters, one could evaluate whether the directionality was due to mating asymmetry in which the relatively more derived taxon recognized males of both species as mates, whereas females of the more basal taxon did not recognize the more derived males.

Hybrid zones would remain important for evaluating gene flow, and the effects of mixing

genomes that have evolved measurable differences (either in allopatry or across an ecotone). One also could detect relationships between parental and hybrid genotypes and their ecological settings. However, studies of hybrid zones would not be viewed as "testing" grounds for species status (Mayr 1963), as reproductive compatibility is not part of the PSC.

*Species concepts and conservation biology.*—Several authors have discussed species concepts in relation to conservation (Dowling et al. 1992a, b, Rojas 1992, Wayne 1992). Effective conservation strategy depends on systematists consistently delimiting basic units for consideration. Because the BSC pools differentiated yet interbreeding units, a single species name may represent several evolutionarily distinct units worthy of conservation efforts. For example, if the eastern form of the biological species "Yellow-rumped Warbler" were on the verge of extinction, would this be acceptable because the trickle of genes from its western form (perhaps not its sister taxon) means they are the same species? Although the Endangered Species Act can apply to subspecies, the PSC is preferable for conservation biology because it consistently equates basal taxa with species (Cracraft 1992). Hence, one would not be forced to argue that sometimes subspecies, and other times species, require management.

If conservation biology is moving away from a species focus to a community focus (Avisé 1992, Moritz 1994), it will be important to describe accurately and precisely geographic patterns of biological diversity across taxonomic groups. Perhaps a narrowly distributed phylogenetic species, which might have been previously subsumed within a larger biological species, would be an unlikely candidate for individual preservation efforts, given limited resources and conflicting land-use demands. Distributions of phylogenetic species, however, provide more accurate and precise descriptions of patterns of biodiversity than biological species. Such descriptions are likely to become the basic requirement for community or ecosystem-level conservation and management practices. The PSC, therefore, would provide an appropriate species definition for conservation purposes.

*Species concepts and the study of speciation.*—The particular concept of species adopted by an investigator influences study of speciation (Cra-

craft 1989). Under some uses of the BSC, speciation is the origin of reproductive isolation, and a study of speciation would focus on traits that influence mate choice. Bush (1995:38), however, stated that "Speciation (the splitting of lineages), may occur long before *complete* reproductive isolation evolves." Bush (1995) therefore views speciation as diversification, and that "Reproductive isolation is only the end product of the speciation process, not its cause . . ." It is unclear to us how this view of biological species would be implemented to delimit species boundaries. Under the PSC, the origin of distinct evolutionary units characterizes speciation.

When studying speciation in the Fox Sparrow, for example, one would be interested in learning how the four species came into existence—what are their historical relationships, when did they evolve, where did they evolve, and why did the diagnostic characters that characterize them evolve (Zink 1994)? One would attempt to determine if the diagnostic characteristics were a result of natural selection, sexual selection, or genetic drift.

Under the PSC, there is no special "speciation mechanism" because isolation leads groups to different evolutionary trajectories and, hence, phylogenetic species status, and many processes affect characters that reveal these different evolutionary paths. Mallet (1995) feared this would trivialize speciation analysis. We think that adopting the PSC would clarify the relationship between the analysis of geographic variation and the analysis of speciation, because the data used for each—character differences within and among taxa—are the same. One would not endeavor to guess what phenotypic features might influence mate choice among allopatric populations. By contrast, under the BSC, one cannot effectively measure the most critical component, reproductive isolation, in allopatric situations (Donoghue 1985).

## CONCLUSIONS

Because reproductive isolation does not evolve concomitantly with other characters that record history, using these two aspects to rank taxa leads to different species limits. These different limits are not simply degrees of inclusion of taxa, but have different phylogenetic conse-

quences, specifically that biological species can be nonhistorical. Species limits should be consistent with patterns of character evolution and not determined by the presumed or actual occurrence of reproductive compatibility. Reproductive isolation is important in its own right as the mechanism that maintains diversity, but it does not generate diversity. Hence, we continue to advocate that ornithology should adopt a species concept consistent with the PSC.

#### ACKNOWLEDGMENTS

We are grateful to numerous colleagues who have argued these issues with us for years: J. C. Avise, G. F. Barrowclough, J. M. Bates, J. Cracraft, D. C. Cavanaugh, H. P. Gelter, S. J. Hackett, M. S. Hafner, T. W. Reeder, J. V. Remsen, and D. P. Pashley. They, of course, do not necessarily endorse the ideas expressed herein. We apologize to J. W. Fitzpatrick for misrepresenting his views on the number of scrub-jay species in our earlier paper. We thank E. Wiley for providing his in press manuscript. For helpful comments on versions of the manuscript we thank R. O. Prum, D. M. Green, D. A. Good, S. Degnan, S. Altizer, S. J. Weller, M. S. Hafner, J. Cracraft, D. P. Pashley, P. D. Sudman, and two anonymous reviewers.

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