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### SPECIES CONCEPTS IN ORNITHOLOGY<sup>1</sup>

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*Abstract.* The biological species concept (BSC) has been generally accepted by ornithologists in theory and practice for half a century. The concept has been considered useful both from evolutionary and taxonomic viewpoints. Criticisms of the BSC, largely by non-ornithologists, have not led to substantial modification of the concept in ornithology. We discuss the concepts of grouping individuals into taxa and ranking these taxa as biological species, defined as reproductively isolated groups. The dimensionality of species is discussed, and we suggest that the problems in extending the BSC from nondimensional (sympatric) to multidimensional (polytypic species) situations are too serious to ignore. Reproductive isolation has no consistent genotypic or phenotypic correlates that can serve as predictors of reproductive compatibility of allopatric groups. Thus, many biological species are inappropriate groups for comparative biology or analyses of evolutionary history, as they are frequently conglomerates of several independent, not necessarily monophyletic groups. We discuss why hybrid zones do not necessarily contribute to clarification of species limits. The theoretical and practical limitations of the BSC lead us to advocate a phylogenetic species concept (PSC) (*sensu* Cracraft 1983), in which taxa are monophyletic, diagnosable clusters of individuals and species are the smallest diagnosable clusters. Diagnostic characters are considered to flag independent evolutionary histories and are used to delineate species boundaries. Phylogenetic species are therefore basal evolutionary units that should be the units used in phylogeny reconstruction, speciation analysis, and biogeography. We discuss the potential use of subspecies names, and recommend that they not be used. Problems with the PSC are discussed, such as its apparent neglect of important biological information, its use of seemingly trivial characters to delimit species, its apparent typological nature, and resulting unwieldy classifications. Implementation of the PSC is discussed with reference to practical problems in determining the statistical limits of phylogenetic species.

*Key words:* Species concepts; evolutionary unit; monophyly; speciation; subspecies.

#### INTRODUCTION

In 1961, Paul Ehrlich published a paper entitled, "Has the biological species concept outlived its usefulness?" Others have expressed dissatisfaction with the biological species concept (BSC; Mayr 1969) throughout the last three decades (e.g., Ehrlich 1961, Sokal and Crovello 1970, Sokal 1973, Cronquist 1978, Wiley 1978, Donoghue 1985). It has been suggested that many dif-

ferent kinds of species exist, such as sibling, ring, biological (polytypic), morphological, hybrid, and paleospecies, and that each requires the application of a different species concept (Scudder 1974). This suggestion, although not without merit, side-steps the issue because it results in taxa that are not comparable. We believe that a consistent species concept, irrespective of process, should be sought. However, the word "species" is an ancient one, predating any concept of evolution by millennia; with such a long history it is no wonder there is disagreement about its meaning and importance.

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In ornithology the answer to Ehrlich's query was, evidently, "no," because the BSC still prevails (see Vuilleumier 1976, Mayr 1982b, Fjeldså 1985, Haffer 1986). The BSC has stimulated work on geographic variation, clines, hybrid zones, mate choice, and speciation (Selander 1971). Although Mayr (1982b:280) disagreed with the claim of some authors that the BSC applies mainly to birds, Donoghue (1985:173) expressed a different opinion, "... most botanists (and many zoologists) have long since abandoned [the BSC]." Mayr (1982b) suggested that the BSC, although not without some problems, "works"; this sentiment may account for the popularity of the BSC in ornithology. For North American birds, only 46 populations (of 607 species) posed a problem at the species level (Mayr and Short 1970); i.e., 46 well-differentiated subspecies have each been considered distinct species at one time. Because a species concept is perceived to rank most taxa correctly, however, does not mean that the ranks are appropriate nor that the concept should not be scrutinized, amended or, if necessary, replaced.

Cracraft (1983) recently questioned the application of the BSC in avian biology. Cracraft contended that the BSC hinders comparative analysis of speciation and other aspects of avian evolution. In this paper we examine the species concept proposed by Cracraft (1983). We address several issues we feel he underemphasized, such as the distinction between the species taxon and category (Mayr 1982b), implementation of the PSC, the significance of reproductive isolation, monophyly of species, and the subspecies concept.

This paper is not intended as a review; neither do we claim to solve the "species problem" herein. Instead we hope to stimulate further discussion of species concepts in ornithology.

## DEFINITIONS

Mayr (1970:12) defined species as "groups of interbreeding natural populations that are reproductively isolated from other such groups." He recently (1982b:273) added that these reproductive communities also occupy "a specific niche in nature." Mayr (1982b) distinguished between the species category and the species taxon; this distinction is operational only in sympatry (the "non-dimensional" concept; see below). A taxon is a group of individuals, and is ranked categorically as a population, subspecies, or species. That

is, we *group* individuals into *taxa* and *rank* these taxa into *categories*. We do not group individuals into species directly; the process requires two steps. Thus, in the application of the BSC, the category (rank) of species is defined as those taxa that are reproductively isolated from other such groups. The "grouping" criterion can be any trait, usually it is an aspect of external morphology, such as body size, bill shape, or plumage color pattern; the grouping criteria are judged to reflect reproductive isolation or compatibility. Mayr (1982b:254) stated that most debates about species concepts are actually debates about how one groups individuals into a species taxon, instead of debates over the ranking of taxa.

Cracraft (1983:170) espoused a phylogenetic species concept (PSC) as an alternative to the BSC: "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." This resembles the definition of Nelson and Platnick (1981:12). Cracraft (1983:170) noted that whereas "most species will be defined by uniquely derived characters," this uniqueness cannot be part of the definition of species because ancestral forms will have no unique characters and therefore could not be part of a species. The clause "parental pattern of ancestry and descent" requires that the organisms included in any given species actually constitute a lineage, such that juveniles, adults, males, and females are not placed in separate species. It also implies that species-specific traits are inherited, and not maintained solely by the environment. Donoghue (1985) offered a definition similar to that of Cracraft, but he stressed the distinction between grouping and ranking criteria.

To make the above definitions consistent, we suggest that the grouping criteria of the PSC are diagnosability and monophyly, which are assessed by cladistic analysis of character variation. The smallest diagnosable cluster is given the rank of species. The concept is "multidimensional" (see below) because of (1) the temporal dimension that monophyly implies and (2) its applicability to allopatric populations. In these definitions, reproductive compatibility is not grounds for conspecificity because it is analogous to grouping individuals by an ancestral trait (the ability to interbreed).

We agree with Donoghue (1985) that the distinction between the species category and taxon is ambiguous in the BSC. The BSC uses repro-

ductive isolation (indirectly) for both grouping and ranking of allopatric populations. Also the BSC focuses more on ranking than on grouping, whereas we believe (like Donoghue) that this emphasis should be reversed. Because reproductive isolation is difficult to measure and is inconsistently related to phenotypic and genotypic differentiation, a "better species concept . . . might best be tied to a more general and less controversial theory, namely that evolution occurs and produces a hierarchy of monophyletic groups" (Donoghue 1985:175).

The PSC emphasizes discernible patterns and permits a more objective analysis of speciation. Cracraft (1983:160) viewed speciation as "the phylogenetic deployment of differentiated taxonomic units through space and time." Donoghue (1985) considered speciation to be the "process of origination of a separate lineage characterized by a new trait" (p. 179). Such units and lineages should be called species. By focusing on discernible patterns of variation, the delimitation of phylogenetic species and analysis of their origin becomes increasingly objective: it does not depend on predictions of reproductive isolation where no information is available, such as in allopatric populations.

#### ALLOPATRIC POPULATIONS

An often-cited problem in the application of the BSC is the subjective judgment of the status of allopatric forms (Futuyma and Mayer 1980). Mayr and Short (1970:2) stated this difficulty clearly: "The biological species concept has a meaning only for populations that coexist or are contiguous in space and time. Here it is self-operationally defined and it is only here that its application is truly important." Mayr and Short (1970) did not consider this to be a critical problem, and they used biological species, containing allopatric components, as units of comparison.

It is the concept of dimensionality that renders tests of sympatry unimportant. Mayr (1982b) distinguished between the nondimensional biological species concept (at the level of rank or category) and the multidimensional species taxon (determined by some grouping criterion). In the former, only sympatric populations are important because it is only here that the criterion of reproductive isolation (compatibility) is meaningful and applicable. In this situation, as in studies of community ecology, there is no necessary reference to geography or time; hence, the

concept is said to be nondimensional. The multidimensional species taxon, an example of which is the polytypic species, is extended from the nondimensional species concept only by inference (Mayr 1982b:273). Therefore, lack of tests of sympatry among allopatric populations is considered essentially unimportant to the concept of the biological species category, rather it is a problem in grouping individuals into a taxon. In fact, for biologists, excluding "... taxonomists, paleontologists, and evolutionists . . . . Whether or not two populations that are not in contact with each other either in space or time are conspecific is in most cases biologically uninteresting, if not altogether irrelevant" (Mayr 1982b:286). In other words, the category "biological species" is not compromised by the inability to test for reproductive isolation among allopatric units. We appreciate the position taken by Mayr but do not agree that polytypic species are a desirable consequence of the extension from the nondimensional to the multidimensional situation. The theoretical inapplicability of the BSC to allopatric units is an underemphasized problem because there are thousands of allopatric avian populations. The phylogenetic species concept is operational for both sympatric and allopatric forms. For this and other reasons, we cannot agree with Mayr (1982b:296) that the biological species is the basic unit of evolutionary biology. Phylogenetic species are appropriate units for use by all biologists, including those interested in geographic variation, speciation, phylogeny, and biogeography, in addition to those who study nondimensional situations. The logical basis for systematic and many other comparative studies is the evolutionary unit, which biological species often are not.

Despite the proclaimed irrelevance of the concept to allopatric populations (Mayr 1982b:286), ornithologists do rank such populations. Species limits are based on whether morphological or behavioral attributes of allopatric populations are of the same quality as those apparently serving as reproductive barriers between sympatric, non-interbreeding populations (i.e., the grouping and ranking criteria are the same). Mayr (1948:210) noted that "Most of the morphological characters studied by the taxonomist are neutral in regard to the maintenance of isolating mechanisms," but he later (1969:28-29) acknowledged that morphological and ecological criteria could be used to infer reproductive isolation. No ob-

jective framework exists for this procedure. Considerable among-population divergence in morphology and behavior may precede the origin of reproductive isolation (Mayr 1982b, Donoghue 1985, Zink and Remsen 1986). It is this divergence, rather than the retention of reproductive compatibility, that permits systematists to document the evolutionary history of populations or species. Although genetic and morphological divergence and reproductive isolation are related, the relationship is imprecise. Reproductive isolating mechanisms will arise *eventually*, given sufficient time for divergence in allopatry. Nevertheless, it is very difficult to predict the presence of reproductive isolation from assessment of the differences between allopatric populations (Amadon 1950).

The difficulty in applying the BSC to allopatric forms is exemplified in the analysis of species limits in the brown towhee (genus *Pipilo*) complex. This complex includes four taxa: Abert's Towhee (*P. aberti*), White-throated Towhee (*P. albicollis*), and eastern ("*fuscus*") and western ("*crissalis*") components of the Brown Towhee (*P. fuscus*) (Davis 1951). Analyses of the phenotypic and taxonomic relationships (Davis 1951), behavior (Marshall 1964), and zoogeography (Hubbard 1973) of the complex have revealed differences between the eastern and western forms of the Brown Towhee. The American Ornithologists' Union Committee on Classification and Nomenclature (AOU 1983) concluded without documentation that the two forms were conspecific. Zink (1988) studied patterns of genetic and phenotypic variation among the four taxa (including *crissalis* from Baja California, Mexico) using protein electrophoresis. *Pipilo albicollis* and *P. f. fuscus* were genetically more similar to one another than either was to the western form of the complex (*P. f. crissalis*); because the distances passed the relative rate test we infer that genetic distances track phylogeny and therefore the two taxa are sister species. In the brown towhee example the BSC has probably been misapplied in the absence of information on interbreeding (i.e., in a case of allopatry), because the grouping characters were judged in relation to their potential value as reproductive isolating mechanisms (the BSC ranking criterion). The genetic data corroborated phenotypic patterns and clarified that the "Brown Towhee" is a paraphyletic taxon as presently described and

actually comprises two species. We recognize that the brown towhees might be considered distinct under the BSC (AOU 1983:685). However, interpretation of the patterns of variation would differ under the two species concepts if hybridization occurred. If the two brown towhees met and hybridized, they would constitute one species under the BSC; this would not affect the interpretation under the PSC. More studies are needed to determine if such situations are widespread.

In other cases one wonders why inferences of species status have not been made. For example, the Florida and California Scrub Jays (*Aphelocoma coerulescens*) exhibit different breeding systems; the former is a group breeder and the latter is not (Woolfenden 1975). The eastern and western Scrub Jays are morphologically distinct, and do not overlap geographically. Pitelka (1951: 375) suggested they be considered conspecific "until further evidence indicates that some of the races are better regarded as species . . ." He further noted (p. 375) that "the onus of proof lies in the view which assumes specific distinction rather than that which assumes conspecificity." We view this as a matter of opinion. At any rate, the Scrub Jays are a good candidate for consideration from the perspective of alternative species concepts (or for reconsideration using the BSC). J. W. Fitzpatrick (pers. comm.) noted that 300 to 500 allopatric populations of Scrub Jay occur in Florida, and suggests that each constitutes a phylogenetic species. However, allopatry alone is insufficient for species status (although it is probably necessary)—unless there is *evidence* of speciation (diagnostic traits), we will be unable to detect it.

The western populations of Marsh Wren (*Cistothorus palustris*) have larger song repertoires and a larger archistriatum (one of the telencephalic nuclei of the brain) than eastern populations. These differences have a genetic basis (Kroodsma and Canady 1985). Such behavioral and anatomical features may indicate that reproductive incompatibility exists. In the Scrub Jay and wren cases, these populational differences are clearly perceptible. There may be other cases, however, where differences are more subtle, and reproductive isolation does not exist. Do such differences warrant species status by PSC criteria? We believe they do, provided they are heritable and widespread throughout a population (i.e., not aberrations; see "Criticisms of the

phylogenetic species concept," below). That biological species include distinct but allopatric evolutionary units, some of which are not monophyletic (e.g., brown towhees) is sufficient reason for an extensive modification of the biological species concept.

### REPRODUCTIVE ISOLATION

The evolution of reproductive isolation is considered to be the crux of speciation (Nei et al. 1983). We think, however, that the role of reproductive isolation has been misinterpreted: it does not cause evolutionary diversity, it maintains it (whereas geographic isolation probably precedes divergence, divergence precedes reproductive isolation and not the converse). We suggest, as do others (Rosen 1979, Nelson and Platnick 1981, Cracraft 1983), that reproductive isolation should not be a part of species concepts.

Whereas the phylogenetic species concept does not necessarily consider all interbreeding groups conspecific, it will not permit reproductively isolated groups to constitute a single species. This is not a contradiction to the foregoing discussion. If males and females do not recognize each other for mating purposes then they are not members of the same species because monophyly requires reproductive continuity (de facto). Reproductive isolation (pre- or postmating) results from usually unknown genetic changes. These changes are in effect apomorphies, and the resultant reproductive isolation can constitute a diagnostic, species-specific trait. As Cracraft (1987) noted, all species concepts (even purely typological ones) include reproductive cohesion within species.

### EXPERIMENTAL TESTS

In criticizing the subjective ranking of allopatric populations, we realize that experiments can be used to "test," at least indirectly, for characteristics of reproductive isolation (Ratcliffe and Grant 1985). The importance of vocalizations for mate recognition has been demonstrated conclusively for some passerine birds (e.g., Dilger 1956; Stein 1958, 1963; Lanyon 1963; Emlen 1972). In Darwin's finches, both song and morphology are necessary for mate discrimination (Grant 1986). In other species the advertising song is more important in eliciting response from territorial males than is the physical appearance of a model or stuffed specimen presented in conjunction with sound recordings. For example,

Great Crested Flycatchers (*Myiarchus crinitus*) were equally vigorous in attacking mounts of conspecifics and of Eastern Kingbird (*Tyrannus tyrannus*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Yellow-browed Tyrant (*Satrapa icterophrys*), Baltimore Oriole (*Icterus galbula*), and Red-eyed Vireo (*Vireo olivaceus*) when these were accompanied by recordings of *crinitus* vocalizations, but not when they were accompanied by vocalizations of other species of *Myiarchus* (Lanyon 1963). Lanyon (1978, 1982, pers. comm.) used playbacks to determine that the South American *Myiarchus s. swainsoni* and *M. s. ferocior* do not respond to each other's vocalizations in allopatry. In a zone of contact, however, the two forms are morphologically intermediate and will respond to recordings from *allopatric* populations of both *swainsoni* and *ferocior*. Because of the importance of vocalizations for species recognition in the *Myiarchus* flycatchers (Lanyon 1963, 1967, 1978), Lanyon advocated conspecificity for *swainsoni* and *ferocior*. However, *swainsoni* and *ferocior* would probably be separate phylogenetic species because of the distinctness of the parental (allopatric) forms.

The results of playback experiments have different implications for the biological and phylogenetic species concepts. Both concepts require reproductive continuity within species, and consequently reproductive gaps reflect species boundaries for both concepts. Lack of response to playbacks, with proper controls and under appropriate circumstances, may aid in determining limits of either biological or phylogenetic species. A positive (conspecific) response to a recorded vocalization, however, is analogous to the expression of an ancestral trait, as is the occurrence of interbreeding; it does not necessarily reflect conspecificity under the phylogenetic species concept (furthermore it might not always reflect conspecificity under the BSC, if controls are improper and circumstances inappropriate). It should also be noted that some species are interspecifically territorial (Johnson 1980:116).

### THE EVOLUTIONARY SIGNIFICANCE OF REPRODUCTIVE ISOLATING MECHANISMS

In advocating a phylogenetic species concept we do not imply that reproductive isolation and the origin of mechanisms that maintain it are not of evolutionary importance (see Nei et al. 1983).

Because many species are (eventually) sympatric, sometimes with their close relatives, reproductive isolation maintains evolutionary independence and diversity (Futuyma 1987). The "closure" or sealing of a gene pool is therefore an important evolutionary event. In effect, reproductive isolation permits species diversity to increase. We believe that other proponents of the PSC (Cracraft 1983, Donoghue 1985) have not sufficiently emphasized the importance of reproductive isolation as an evolutionary factor. However, we believe that the criterion of reproductive isolation confounds the understanding of the origin of species, both because it can obscure phylogenetic relationships and because speciation can occur without it. Nor do we feel that the "mate recognition concept" of Paterson (1985; see also Butlin 1987) justifies interbreeding as the primary criterion of conspecificity. Biological species are initially recognized by systematists by the phenotypic markers that usually accompany reproductive isolation (i.e., there are no avian species recognized solely because they are reproductively isolated) (Cracraft 1983). Because the ability to interbreed is a primitive state, members of different phylogenetic species that hybridize are not "making a mistake," "defying" our attempts to rank them in taxonomic categories, nor "telling" us they are the same species. Under the PSC, such hybridization tells us that reproductive isolation is incomplete.

#### HYBRIDIZATION AS AN INDEX TO PHYLOGENETIC RELATEDNESS

Prager and Wilson (1975) showed that the ability to hybridize was not correlated with level of differentiation in many bird species, and therefore hybridization (i.e., lack of reproductive isolation) is not an adequate index of phylogenetic relatedness. We recognize the distinction between hybrid swarms (or zones) and occasional intra- or intergeneric hybridization (Short 1965:417, 1969). However, to our knowledge no one has demonstrated conclusively that the former occurs, in birds, only between sister species, or that the propensity for hybridization somehow tracks phylogenetic patterns (at least among congeners). In general the phylogenetic analyses required to establish such sister-species relationships are lacking (a situation that makes application of any species concept more difficult). The occurrence of interspecific hybrids suggests only that the parental forms are part of a clade of unknown size

and species composition, not that the two forms are necessarily sister species (or conspecific).

#### GENE FLOW, HYBRID ZONES, AND BIOLOGICAL SPECIES

Many authors consider hybrid zones the proving grounds of biological species. Several reasons can be advanced for emphasizing the importance of hybridization (gene flow), and for understanding why many authors consider differentiated populations that hybridize to be conspecific. Differentiated forms that hybridize in sympatry might maintain a genetic "cohesion" and be prevented from evolving independently. As long as reproductive isolating mechanisms are absent, these forms might coalesce because of gene flow or converge because of similar selective pressures (and transmission across a hybrid zone of the genetic response to natural selection). However, consideration of the nature and genetics of hybrid zones reveals the complexity of assessing the taxonomic status of hybridizing forms (Barton and Hewitt 1983, 1985). If two differentiated forms meet, mate nonassortatively, and form a *stable* hybrid zone, one must conclude that the forms are different biological species. Mayr (1982b:285) implied that such forms should be accorded species status because they will not "fuse into a single population." Unfortunately, judging the stability of a hybrid zone is complicated, and might require hundreds or thousands of years of observation (Barton and Hewitt 1983). In ornithology, the "null hypothesis" seems to be that hybrid zones are fluid or dynamic, because many hybridizing forms, in the Great Plains for example, are considered conspecific. In a study of the flicker (*Colaptes*) hybrid zone in the Great Plains, Moore and Buchanan (1985) noted that the hybrid zone is stable and not becoming broader (fusion) or narrower (origin of premating isolating mechanisms).

Barton and Hewitt (1983) noted that parental forms are often genetically rather divergent, a phenomenon inconsistent with the idea of genetic fusion. Thus, the premise of genetic cohesion predicted by attributing conspecific status to forms that hybridize may not be valid; forms on either side of a hybrid zone may evolve independently. In other words, two taxa that form a hybrid zone may not be genetically the "same species." If traits that are used to distinguish parental forms are selectively neutral, fusion may take a long time (Barton and Hewitt 1983).

Therefore, calling distinct but hybridizing forms (e.g., flickers, orioles, yellow-rumped warblers) separate phylogenetic species recognizes the status quo, instead of an unpredictable future outcome (viz., fusion) of current hybridization; we advocate the former.

## SPECIES AS MONOPHYLETIC GROUPS

### HISTORICAL BACKGROUND

Until the publication of *On the Origin of Species* (Darwin 1859), classification had as its vague goal the grouping of organisms according to the essentialistic concept of "naturalness" (see discussion in Popper 1950). Darwin's work infused the already active field of taxonomy with a new theoretical foundation, namely that organisms are related to others by "propinquity of descent" (1859:413) and that classifications should reflect this. Considering that the essentialism of the ancient philosophers had prevailed for 2,000 years, this Darwinian view gained a relatively rapid foothold in taxonomy and permitted the birth of a new discipline called systematics, a primary goal of which is the study of phylogenetic patterns and the processes that produce them.

One of the admitted goals of classification in our time is to group organisms in a manner that reflects genealogy: "evolutionary classification demands the delimitation of taxa consisting of closest relatives" (Mayr 1969:83). Yet Mayr criticized classifications that do just that, using as an example two dissimilar taxa, the crocodylians and birds. These are considered by some authors to be sister taxa among living groups (Martin 1983; for review see Gauthier and Padian 1985). Mayr stated (1969:75): "If a descendant group, such as the birds among the archosaurian reptiles, evolves more rapidly than the other collateral lines, it not only can but it must be ranked in a higher category than its sister groups." This is because, according to Mayr (1969:78), classifications should "combine maximal information content with maximal ease of retrieval of this information"; i.e., they should reflect both branching and "different rates of evolutionary change in different phyletic lines" (1969:71). Mayr (1969) also noted that the resulting taxa, Aves, Crocodylia, and Reptilia are nevertheless monophyletic. This characterization of monophyly is not the one currently accepted by many evolutionary biologists, namely that monophyletic groups are those containing all the known descendants of a single common ancestor (Farris

1974); rather it is the definition of Simpson (1961), that "Monophyly is the derivation of a taxon through one or more lineages, from one immediately ancestral taxon of the same or lower rank" (see discussion of this dichotomy of definitions in Wiley [1981:255 ff.]).

Mayr (1969:76) stated that "the concept of monophyly is important only at the level of the higher categories. Taxa that are still crossable, like subspecies, may produce hybrids which by definition would not be monophyletic. Yet the zoologist is not concerned with monophyly at the species level."

We believe that the zoologist's concern with monophyly should begin at the level of the species, which should be both the evolutionary unit and the fundamental unit of classification. We agree with Mayr that classifications should maximize the ease of information retrieval, but this goal can conflict with the stated aim that they should include information on both branching and degree of divergence. In such a classification some taxa will be constructed with both kinds of information; in other cases sister taxa may have diverged at equal rates and hence the two sets of information give the same taxonomic answer. From the end product there is no way to tell which kinds of information were used and, of course, no way to determine the author's phylogenetic hypothesis. This has been discussed extensively elsewhere (e.g., Cracraft 1981, Wiley 1981, Raikow 1985; see also Donoghue 1985 for an excellent discussion of monophyly and the biological species concept). The conflict between the goals of phylogenetic and evolutionary or eclectic systematics is directly analogous to the conflict between the phylogenetic and the biological species concepts. The latter produces inconsistencies in classification (both clades and grades) whereas the former yields classifications that are isomorphic with phylogenetic hypotheses.

### CAN SPECIES BE MONOPHYLETIC?

We believe that species not only can but must be monophyletic. Wiley (1981:198) stated that "the species is considered monophyletic by virtue of its individual nature. (Individuals are neither monophyletic, paraphyletic, or polyphyletic)." This presumably depends on the unit adopted for the definition of monophyly. If a monophyletic group is the descendant *species* of a single common ancestral species, then the def-

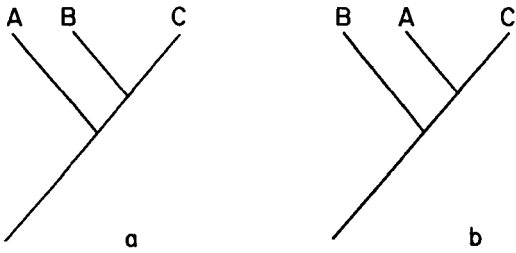


FIGURE 1. a. True phylogeny of taxa A, B, and C. b. Phylogeny inferred from BSC criterion of interbreeding between taxa A and C, and not B and C.

initiation would appear not to apply, logically, to species. If no units are assumed then there is no problem in applying the definition to species or any other group. A monophyletic group is a complete lineage and species are terminal components of such lineages. Regardless of the semantics of definitions and whether or not species should be considered individuals or classes (Ghiselin 1974; Hull 1976, 1980), Wiley's statement evades a critical issue: the biological species concept permits the misapprehension of patterns of phylogenetic change.

Consider a simple three-taxon pattern (Fig. 1a). This depicts a situation in which B and C are sister species, i.e., they share a more recent common ancestor than either does with A; B and C are a monophyletic group. Assume that Figure 1a represents the best phylogenetic hypothesis for A, B, and C, as determined by cladistic analysis of morphological and/or biochemical data. Suppose, however, that whereas B and C are sympatric and do not interbreed, A and C are observed to interbreed extensively (i.e., mating is nonassortative). According to the BSC, A and C will be considered a single species, AC (Fig. 1b). From the classification constructed on this basis, one could not retrieve the information that B and C are sister taxa; in other words we would misrepresent the evolutionary history of this group. An example of this type of situation occurs in the quail-thrushes (*Cinclosoma*) of Australia (Cracraft 1986). We consider the potential for paraphyly to be a serious flaw with the biological species concept. Here, paraphyletic taxa result from observations of interbreeding, whereas in the brown towhee example (above), a paraphyletic taxon resulted when interbreeding was only inferred. We should add that many if not most biological species probably are monophy-

letic, but probably most polytypic biological species contain more than one evolutionary unit. Because biological species each contain an unknown number of evolutionary units, they are not comparable. Phylogenetic species, however, are comparable because they are evolutionary units (although this does not imply that the diagnostic traits themselves are comparable).

We believe the use of the BSC in ornithology has not encouraged detection of examples of phylogenetic relationships that are inconsistent with the (reproductive) limits of biological species. Even the classic monographs in ornithology lack explicit hypotheses of relationships among component forms of biological species.

#### PREDICTIVENESS IN CLASSIFICATIONS

Mayr (1969:79–80) suggested that classifications should be predictive, such that once one has identified an organism as a member of a given taxon, one can "make precise statements concerning its skeleton, heart, physiology, and reproduction without ever testing it." By this view, stating that two individuals are members of the biological species AC (from the previous example and Fig. 1b) should let us predict that individuals of AC share certain traits, but these will all be primitive traits at the level of taxon ABC. We would be unable to retrieve the information that B and C are sister taxa, and indeed, the discovery of the same derived traits in B and C would have to be viewed as homoplasies rather than synapomorphies! Predictiveness is desirable in scientific hypotheses, but we see no merit in the ability to predict the sharing of primitive traits.

#### THE SUBSPECIES CATEGORY

The phylogenetic species concept has implications for the taxonomic category of subspecies. In a recent forum on subspecies (1982, *Auk* 99: 593–615), eleven authors almost unanimously disapproved of the way in which geographic variation has been represented nomenclatorially. A common thread through most of these authors' essays is that the formal names reflect discontinuity where frequently none exists, as in the naming of populations that are parts of smooth clines (see also Wilson and Brown 1953). There is currently no particular biological definition of subspecies (Storer 1982, Zusi 1982). Whereas most authors contributing to the forum on subspecies advocated modifications of the category,



Cracraft (1983) advocated abandoning the subspecies category entirely.

Current subspecies names can indicate appropriate groups for study of geographic variation (Johnson 1982). If a trinomial represents a population that is distinct from other populations in one or more characters, it would be called a species by our criteria. It seems likely, however, that many named subspecies are valid neither as subspecies nor as phylogenetic species. Some subspecies might be distinguishable only with the application of multivariate statistical procedures, such as a discriminant function analysis. Gene flow among such populations might be low or nonexistent, permitting independent evolution, and yet no *single* character may exist by which the populations may be distinguished. Although an individual's discriminant score might be a diagnostic "character," whether it is heritable and indicates a monophyletic group is unclear. A name for such populations may be defensible on the grounds that it signals phenotypic divergence and a reduction of gene flow; in other words, the populations might be potential incipient phylogenetic species (PIPS?). However, until a procedure is agreed upon, we advocate not naming subspecies. We add that lack of a subspecies category under the PSC does not mean that phylogenetic species lack geographic variation, nor that study of processes and patterns of geographic variation are uninteresting (Zink and Remsen 1986).

#### CRITICISMS OF THE PHYLOGENETIC SPECIES CONCEPT

*The PSC leads to too many species.* Mayr (1982a) noted that the concept of subspecies underwent a phase of maturation between the 1880s and 1920s, when 315 North American geographic isolates first described as species were reduced to subspecies status—"an extraordinary simplification of taxonomy at the species level" (Mayr 1982a:594). Implicit in the latter statement is the view that simple classifications, or ones with fewer species, are better than complex ones. Simple classifications are easier to comprehend but are misleading when phylogeny is complex. The standardized use of phylogenetic classification of evolutionary units will make classifications more comparable among vertebrate groups; this would enhance efforts to account for differing patterns of diversity and rates of evolution (e.g., Sibley

and Ahlquist 1982, Wyles et al. 1983, Hafner et al. 1984, Raikow 1986).

Cracraft (1983) implied that the actual number of diagnosable evolutionary units (species) might not exceed the number of subspecific taxa in the 1957 AOU Checklist (a good place to begin searching for phylogenetic species), and it could be lower (see our discussion of subspecies, above). However, scrutiny of morphological, behavioral, or biochemical characters on the "microgeographic" level will reveal the existence of many more phylogenetic species. The notion that there should be an upper limit to the number of species described does not appear to have any value, heuristic or otherwise. Detection and analysis of phylogenetic species is a goal that can only improve our understanding of avian evolutionary biology.

*Species concepts should include biological criteria.* The biological, polytypic species concept is said to yield taxa that are "much more distinct, real entities of nature" than those based on morphological criteria (Mayr 1982a:594). We have discussed (above) some reasons why criteria of reproductive compatibility, although significant, perhaps weaken species concepts. Despite historical emphasis on the theoretical importance of interbreeding for species-level taxonomy, relatively few species are actually delimited on the basis of reproductive compatibility. The North American flickers (*Colaptes*; Short 1965), juncos (*Junco*, AOU 1983, but see Miller 1941), and orioles (*Icterus*; Sibley and Short 1964) provide well known recent examples. Yet even these studies, which are among the most thorough of any taxa, lack complete information on reproductive compatibility of all constituent forms. Furthermore, interbreeding was frequently only inferred, not tested—especially between populations at opposite ends of their distributions. Thus, the "biological" component of allopatric forms of biological species is phenotypic similarity; in practice the BSC is no more biological than the PSC.

*Evolutionary units can be diagnosed on the basis of trivial characters.* Suppose we discovered that a group of Trumpeter Swans (*Cygnus buccinator*) from a well-circumscribed geographic region possessed one extra hooklet on a barb of the seventh primary. We suspect that many ornithologists would argue that such a character is too trivial to serve as a descriptor of species. Probably implicit in this view is the notion that

such a character must be “biologically significant,” or that it is too likely to vary individually, making phylogenetic hypotheses based upon it suspect (McKittrick 1985a, 1985b, 1986). To be sure, the latter possibility should be tested and ruled out before the character can be used to diagnose evolutionary units, necessitating examination of large samples. Chernoff (1982) documents how environmental influences on phenotypic expression lead to inaccurate reconstruction of historical patterns. Such studies are only beginning for birds (James 1983).

What is the significance of such cryptic (“trivial”) traits? If members of a given population(s) consistently possess the trait, and it has a genetic basis (which is testable through heritability studies), then its presence suggests that the population’s recent evolutionary history is independent of that of its ancestral and sister taxon/taxa. There is no theory to suggest that a trait must be of a certain quality or magnitude to provide historical information or to delimit species. The concept that taxonomic characters must have a high probability of unique occurrence (Bock 1967) or be related to reproductive isolation has introduced, we think, a bias against subtle characters or characters of unknown adaptive significance. Whether or not these characters function as isolating mechanisms is not relevant to our use of patterns of character variation to infer evolutionary history. Thus, no character is potentially more or less useful as a tool to reconstruct patterns of speciation (*sensu* the PSC). Cryptic characters may render field identification difficult in some cases. This is a practical (not a theoretical) problem for any species concept. The challenge to field biologists that such a problem would present will no doubt lead, not to chaos, but to an increased understanding of avian natural history and evolution.

*The PSC is typological.* The typological species concept was damned for its emphasis on specimens rather than populations: “A purely morphological species definition is employed. Many species are known only from single or at best a very few specimens” (Mayr 1942:6). The use of morphological (or biochemical or physiological) criteria to delineate species does not imply typology, however, when one also employs a criterion of ancestry and descent (monophyly). The units of the PSC are not specimens, they are lineages. These lineages (clades) are *hypothesized* to be such on the basis of morphological, genetic,

or other features, and the population is still of importance to the practicing systematist. The discovery of evolutionary novelties in one or a few organisms does not lead to the description of a new species (see discussion of Practical Applications below); such would result in arbitrary dismembering of lineages. We are concerned here with cladogenesis. The PSC is therefore concerned with species as individuals (Ghiselin 1974; Hull 1976, 1980), whereas the typological (morphological) species concept of the “old systematics” (Mayr 1942:6) regarded species as classes.

*Why not simply retain biological species but only describe subspecies that possess characteristics of evolutionary units (phylogenetic species)?* A frequent comment is that the distinction between the PSC and the BSC is a semantic one—the advantages of the PSC could be realized within the structure of the BSC if the latter is more rigorously applied. We disagree, but consider the option: If diagnostic characters of subspecies are genetic rather than environmental in origin, subspecies (even if they interbreed) could be denoted as evolutionary units. We would thereby formally recognize differentiated monophyletic groups while retaining the information that the groups interbreed or are thought to be able to do so. This would often be an improvement over current conditions, especially if we really did have information on interbreeding and monophyly. Thus, it could be argued that reproductive isolation need not be abandoned as a ranking criterion as long as only monophyletic groups were permissible. In this case “species” could include many evolutionary units, whereas other species might be single evolutionary units; hence, species would not be comparable. Although such species might still be clades (as many current biological species might be), we nevertheless find this objectionable. Of what use would such species be? Comparative biologists would use evolutionary units (subspecies) in their analyses, and few would wish to use the new biological species as units of analysis. Species should consistently be single evolutionary units. We are again left with the problem of inferring reproductive compatibility of the component allopatric units of these “biological species.” As noted above, patterns of reproductive compatibility need not correspond to patterns of evolutionary history. Felsenstein (1985) illustrated the importance of knowing the underlying phylogeny when comparing attributes of related organisms.

An important objection to this revised biological species concept is that reproductive compatibility does not necessarily yield taxa that are monophyletic. Given three evolutionary units that interbreed nonassortatively in parts of their range, we could classify them as three subspecies of a biological species. There is a fourth evolutionary unit that is a sympatric sister group of one of these three subspecies, but it does not interbreed with any of the three. By the criteria of the revised biological species concept, however, this fourth unit would be excluded from the three-subspecies taxon, and our classification omits an important piece of information about the history of this four-unit clade. Thus we do not believe such a modified BSC would be preferable to the PSC. The differences between the PSC and the BSC clearly transcend the semantic.

#### THE PHYLOGENETIC SPECIES CONCEPT IN PRACTICE

The criteria to be used in implementation of the PSC have not been clearly specified, and there is concern that small groups within populations might qualify as phylogenetic species. However, small groups within populations are unlikely to satisfy *both* the grouping criteria of monophyly and diagnosability. Furthermore, if a focal group consists of more individuals than one can logistically study, the grouping criterion of diagnosability is obviously a probabilistic one. Whether the population should be 95% or 99% diagnosable before species status is warranted is unresolved, and depends on the nature and pattern of character variation.

As a first attempt at outlining practical applications, we offer the following. Zink and Remsen (1986) outlined a program of sampling and analysis for studies of geographic variation, including the search for diagnosable groups of individuals; as we suggest herein, these should be called species. However, not evident is what to do in the event of incomplete diagnosability (see above discussion of subspecies). Several possible outcomes require comment, and to anticipate the following, the key will be a consideration of the nature of character variation. Suppose that a phylogenetic species is observed, in which 5% of the individuals have a unique derived variant of the character that distinguishes this species from all others. Although the species is 100% diagnosable from other species its members do not all possess the same state of the diagnostic trait.

We would still conclude that the species is monophyletic but that possibly we were observing the origin of a new diagnostic trait (or an atavism; Hall 1984)—that is, we might have observed a transformation in progress (Hanken 1982, 1984; McKittrick 1986).

Suppose that two groups are nearly diagnosable, but each contains breeding individuals with the diagnostic trait of the other group. A possible interpretation is that these individuals dispersed into the other's range and that each is a separate species. For example, three well-differentiated groups of Fox Sparrow (*Passerella iliaca*) exist, and each may be a phylogenetic species (Zink 1986:105). If a few individuals from species A were observed in the breeding population of B, the B individuals nevertheless form a monophyletic group and must still be considered a phylogenetic species (i.e., hybridization does not imply conspecificity). Monophyly of the parental types is not compromised by gene flow between them, and hybrid individuals do not belong to either species. The individuals that contribute to nondiagnosability are identifiable as belonging to a different species. It is well to note that we diagnose groups by characters, not by geography. A second interpretation is that the two diagnostic traits once existed as a polymorphism in a widespread population; the occurrence of the alternative character state could represent a "relict" situation. It is difficult to distinguish among the possible causes of lack of diagnosability (dispersal and hybridization, plesiomorphy) when it is due to character states shared between two or more groups. Perhaps the groups can be tentatively considered two phylogenetic species even if they are less than 100% diagnosable; only if we have evidence that neither group is monophyletic must the two groups be considered conspecific. Similarly, differentiated groups connected by smooth clines would also be conspecific (e.g., character analysis might reveal that the biological species *Colinus virginianus* is also a single phylogenetic species).

It is important to note that no one knows the probability of observing a lineage at a point when it is 100% diagnosable—whether because of anomalies or atavisms as discussed above, or because subsequent anagenesis leads to changes in the diagnosing characters. This will complicate, but not necessarily compromise, our attempts to reconstruct history. For example, we have no difficulty in recognizing snakes to be

members of the Tetrapoda, although they lack feet. Monophyly is determined by compatibility of characters, but there will undoubtedly be instances when historical patterns cannot be recovered. This cannot be construed as a sign that our philosophy or our methods are flawed. Rather, these methods enable us to pinpoint where the gaps in our knowledge lie.

## CONCLUSIONS

The biological species concept is relevant only in the nondimensional sense, as it does not apply to allopatric populations. By using reproductive isolation as both a grouping and a ranking criterion, the BSC permits the recognition of species that are not monophyletic and do not accurately represent the results of evolution. The phylogenetic species concept requires that species be monophyletic groups, and suggests that they will be distinguishable from other such groups in one or more characters. However, not every individual will always possess each of the characters by which the unit is recognized. Individuals may be "aberrant" due to abnormal development, atavisms, hybridization, external environmental modification, or anagenesis; these are some of the factors that contribute to variance within evolutionary units. We believe that the PSC constitutes a step forward, because it demands a thorough and rigorous search for and analysis of patterns of variation (Zink and Remsen 1986), as well as bringing consistency in the hierarchical ordering of organisms down to the fundamental level, namely the level of species. It focuses attention on the results of evolution, i.e., units of diversification, and facilitates the reconstruction of historical patterns. Furthermore, it is appropriate in the multidimensional sense. We do not expect the PSC to have an immediate impact on the status quo, particularly with regard to the filing and housing procedures in existing museum collections. We do hope, however, that consideration of the PSC will encourage ornithologists to reevaluate species concepts and stimulate further research at the level of populations and species.

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