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CHAPTER 3

VAINLY BEATING THE AIR: SPECIES-CONCEPT DEBATES NEED NOT IMPEDE PROGRESS IN SCIENCE OR CONSERVATION

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Abstract.—Debate over species concepts has been a persistent theme in biology. We briefly summarize competing species concepts and facets of the debate itself. We maintain that the inherent subjectivity within all species concepts is likely to ensure continued disagreement on where to place species limits. Although the debate itself contributes to the understanding of speciation and evolutionary processes, it can take on political overtones through posturing, caricatures, and provocative statements. Empirically, neither basic nor applied science would seem to have been slowed appreciably because the species-concept debate remains unresolved. Similarly, continued disagreement must be placed in its proper context (e.g., be shelved) when considering the preservation of biodiversity. To a considerable extent, this has occurred within the conservation community. The biological species concept (BSC) and its inclusion of diagnosably distinct populations as subspecies remain dominant in ornithology. This may be attributable, in part, to the seemingly infinitely fine divisions possible under phylogenetic species concepts (PSC)—which, among other things, could strain public credulity over what constitutes a species. Nevertheless, the strengths of each of these concepts are being applied to improve our understanding of biodiversity. The longstanding disagreement over species concepts should not become an impediment to responsible conservation and wildlife management. It probably has not occurred broadly yet, but there may be potential for such an effect in the political arena. *Received 30 July 2006, accepted 23 February 2007.*

Resumen.—El concepto de especie es un tema polémico en biología. Resumimos brevemente los distintos conceptos de especie y las facetas del debate. Consideramos que la subjetividad inherente a todos los conceptos de especie garantiza un continuo desacuerdo en como delimitar las especies. Aunque el debate en si mismo contribuye a entender el proceso de especiación y otros procesos evolutivos, muchas veces se desarrolla en términos demasiado caricaturescos, burlescos y provocativos. De hecho, la continuidad del debate no parece haber ralentizado ni la ciencia básica ni la aplicada. De igual modo, el continuo desacuerdo debe contextualizarse cuando consideramos la conservación de la diversidad. El concepto biológico de especie (BSC) y la inclusión de las poblaciones diagnosticables como subespecies, sigue predominando en ornitología. Esto puede deberse en parte a las infinitas divisiones que se pueden realizar bajo el concepto filogenético de especie (PSC), lo que entre otras cosas, puede afectar el entendimiento del público en general sobre qué es una especie. Sin embargo, los puntos fuertes de cada concepto se están aplicando para llegar a un mejor entendimiento de la biodiversidad. Este desacuerdo histórico sobre el concepto de especie no tiene por qué ser un impedimento para una política responsable para la conservación y gestión de la vida salvaje.

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> ...Nor shall I here discuss the various definitions which have been given of the term species. 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)

> ...But to discuss whether they are rightly called species or varieties, before any definition of these terms has been generally accepted, is vainly to beat the air. (Darwin 1859:49)

What defines a species? This question has divided biologists and been a persistent theme in biology for >150 years (e.g., Darwin 1859; Mayr 1942, 1993; Wiley 1978; Cracraft 1983; Paterson 1985; Templeton 1989; Nixon and Wheeler 1990; Mallet 1995; Avise and Wollenberg 1997; de Quieroz 1998; Harrison 1998; Johnson et al. 1999; Wheeler and Meier 2000; Hey 2001; Coyne and Orr 2004). The debate over species concepts can evoke such passion that arguments often focus on the weaknesses of competing concepts and rarely acknowledge the benefits of the debate itself. Given that we are attempting to place broadly definitive lines upon a continuous process, the debate is certain to continue. At present, no species concept can claim convincingly to provide rigorous methods for objectively defining when speciation has occurred—at least not in a manner that can be usefully applied within or across taxa on a broad scale. Nonetheless, the lack of a unifying species concept has not hindered serious progress in the biological sciences or in the development of appropriate units for conservation priorities.

We find humor in Darwin's statement that defining species is like "vainly beating the air" (Darwin 1859:49), but the ongoing debate has helped to point out areas where further investigation is needed. We propose that taxonomists and systematists put aside arguments for scrapping the current species structure until a more robust and objective alternative can be implemented with broad agreement. To date, we know of no such alternative. Here, we briefly review the species-concept debate and then address several questions: (1) Has the biological species concept (BSC) failed us? (2) Is the phylogenetic species concept (PSC), widely considered the preferred alternative to the BSC in ornithology, an objective and robust concept ready to impose new species boundaries? (3) Is it appropriate to abandon the BSC for promotion of conservation initiatives? And (4) has disagreement about species concepts impeded basic or applied science? Finally, we consider the realities of geographically partitioned variation within species and the scientific and legal (at least in the United States and Canada) bases for continuing to recognize divisions below the species level.

Process-based Species Concepts

Several species concepts focus on reproductive mechanisms or the processes that define species. The concepts receiving most attention in this category include the BSC (Mayr 1942), the recognition species concept (RSC; Paterson 1985), and the reproductive-cohesion species concept (CSC; Templeton 1989). In what is widely referred to as the BSC, Mayr (1963: 19) defined species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." The BSC, and our working model of it, is the most widely accepted definition of species.

Despite its widespread use, the BSC has been criticized for failing to identify species in allopatric populations, for its difficulty in dealing with hybridization, and for its inapplicability to asexually reproducing organisms. Paterson (1985) and Templeton (1989) recognized the usefulness of defining species by isolating mechanisms and attempted to improve the BSC by adding additional criteria for naming species. The RSC emphasizes the evolutionary development of prezygotic isolating mechanisms, defining species as "the most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson 1985:15). The RSC changed the focus in defining species from mechanisms that prevent mating to those that facilitate reproduction. Under the RSC, specific mate-recognition systems serve as signal-and-response interactions between individuals of a species (Paterson 1985) and are the main criteria by which species are defined. Because mate recognition can occur only within a species, hybridization is theoretically impossible under the RSC (King 1993). Although Paterson attempted to improve the BSC by identifying species in hybrid zones, the RSC has received

criticism for difficulty in evaluating specific mate-recognition systems and its inability to deal with asexual or allopatric populations (Templeton 1989, Mayden 1997).

Templeton (1989) introduced the CSC, which focuses on processes that maintain similarity among populations. Under the CSC, species are "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton 1989:12). Rather than focusing on the mechanisms that separate species (i.e., BSC and RSC), the CSC focuses on factors, both genetic and phenotypic, that hold a species together. The CSC merges central ideas from process- and pattern-based concepts into a species concept that is operational for both sexual and asexual organisms. Although the CSC is operational for a wide variety of taxa, it has remained unimplemented, mainly because "phenotypic cohesion" remains largely undefined (Endler 1989). Templeton's effort to incorporate pattern into a species concept was not new; most of the major competing concepts to the BSC are pattern-based.

Pattern-based Species Concepts

Pattern-based species concepts focus on evolutionary history, phylogenetic relationships, and character states. These concepts include the evolutionary species concept (ESC; Wiley 1978), the PSC (Cracraft 1983), the genealogical species concept (GSC; Baum and Shaw 1995), and the genotypic-cluster species definition (Mallet 1995). The ESC, with its roots in paleontology, defines a species as "a single lineage of ancestor—descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978:18). Because the ESC includes ancestral populations, it is difficult to test scientifically and does not seem to be applied much outside the field of paleontology, although others have shown interest in it (e.g., Peterson 1998, Taylor et al. 2005).

The PSC has received the most attention and consideration recently as a potential alternative to the BSC (e.g., Cracraft 1989, 1997; Nixon and Wheeler 1990; Zink and McKitrick 1995), and in ornithology (at least) it is routinely portrayed as the leading opponent to the BSC. There are actually multiple PSCs, but they all share a focus on identification of historically related groups (Coyne and Orr 2004). Here, we focus on the most ornithologically relevant aspects and consider the PSC in the singular. Cracraft (1997:329) defined a species under the PSC as "the smallest population or group of populations within which there is a parental pattern of ancestry and descent and which is diagnosable by unique combinations of character-states." This definition was modified from its original form to address earlier criticisms.

The PSC has been criticized by other proponents of pattern-based concepts for relying too heavily on the principles of cladistics and diagnosing species in terms of apomorphies (characters derived and different from the ancestral condition; Nelson and Platnick 1980, Mallet 1995). A general fear among many of these critics is that perfectly good species that lack such apomorphies will not be diagnosed properly. To avoid the use of apomorphies as the unit of diagnosability, Mallet (1995:296) proposed the genotypic-cluster species definition, which defines species as

> distinguishable groups of individuals that have few or no intermediates when in contact...[C]lusters are recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters).

Although the genotypic-cluster definition can diagnose species without apomorphies, it confounds species diagnosis with the requirement that species must be "in contact" (e.g., parapatric or sympatric; Harrison 1998).

Baum and Shaw (1995) also chose to reduce the emphasis placed on character states or apomorphies by the PSC, proposing the GSC (considered by Coyne and Orr [2004] to be a third general version of the PSC). The GSC defines species as "exclusive groups of organisms, where an exclusive group is one whose members are more closely related to each other than any other organisms outside the group" (Baum and Shaw 1995:290). Relatedness under the GSC is determined by the concordance of gene genealogies; however, the amount of concordance necessary between two populations for them to be named genealogical species is not specified (i.e., all gene genealogies or just some; Harrison 1998). The amount of introgression between

species and across a species' genome can vary; consequently, alleles can become fixed at some loci and not at others, resulting in discordant gene genealogies (Harrison 1998). Under these circumstances, the GSC, which requires concordance over a number of loci, may be too stringent in how it defines species limits or boundaries (Harrison 1998).

Finally, with the advent of genetic tools, we are seeing a resurgence in typological species concepts, though proponents are not naming their concepts as such. Typological species concepts based on phenotype have been disfavored since the mid-19th century because of inherent conceptual flaws (Mayr 1963, 1982). Mayr (1963: 5–6) wrote:

> The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology.... Virtually every major controversy in the field of evolution has been between a typologist and a populationist.

Typological species are defined by specifying an arbitrary degree of morphological or genetic difference (Coyne and Orr 2004). Naming groups "species" on the basis of an arbitrary degree of genetic divergence seems to have become widespread (e.g., König et al. 1999, Hebert et al. 2004). Although it is true that genetic divergence generally increases as lineages diverge, there is no genetic measure yet that enables us to determine when speciation has occurred between lineages in the class Aves (e.g., Funk and Omland 2003, Johnson and Cicero 2004, Moritz and Cicero 2004). Genetic diversity is certainly part of biodiversity, but using simplistic genetic distance data to designate species status is decidedly a step backwards in our efforts to understand biodiversity and its generation—in every way a return to the flaws of historical typological species concepts (see Mayr 1963, 1982). Given the stochastic and often selectively neutral processes inherent in DNA mutation and evolution, a lineage showing reciprocal monophyly in a single locus (to some researchers an indication of a phylogenetic species) may represent another of these arbitrary thresholds (see also Avise 2000b, Coyne and Orr 2004). At the least, such approaches do not accurately reflect what we know about the genetics of speciation (Orr 2001; Avise 2000b, 2004; Coyne and Orr 2004).

Should We Abandon the Biological Species Concept?

No—although it has its problems. The BSC does not apply to asexual populations, because it is based on reproductive properties. Mayr (1996: 266) was unapologetic for this flaw, believing that "a species definition that is equally applicable to both sexually reproducing and asexual populations misses the basic characteristics of the biological species definition," and he turned to the specialists to sort out species in these organisms. That no single species concept can be applied equally well to all taxa has been stated repeatedly (e.g., Bock 1992, Mayr 1996).

The BSC's requirement of reproductive isolation creates confusion in naming allopatric species because this requirement is generally not tested. This is commonly viewed as the concept's biggest drawback (e.g., Zink 1996). Mayr's original definition did not include "potentially" with regard to interbreeding natural populations; it was inserted later with the hope that it would diminish the criticism regarding allopatric populations. For some critics, it did not. In areas of allopatry, determinations of reproductive isolating mechanisms are often extrapolated using cues from morphology, behavior, and ecology (Cracraft 1989, Johnson et al. 1999, Helbig et al. 2002) and require a certain degree of subjectivity. In this sense, the BSC is guilty of inferring process from pattern (Harrison 1998). The processes of differentiation create patterns, and making inferences from the latter has been a standard practice in BSC-based taxonomy.

Expounding on classic methods regarding relative differentiation between forms, Mayr (1969:196–97) suggested that the status of reproductive isolation in allopatric populations be inferred by using phenotypic divergence as a yardstick, employing three types of divergence data in closely allied taxa "to calibrate such a scale": differences between sympatric species, between intergrading subspecies within species, and between hybridizing populations. Such methods are hardly foolproof (Mayr 1969), but this approach remains important today (see Remsen 2005). Experimental approaches to determining whether reproductive isolation exists between allopatric populations are possible (e.g., through playback, captive breeding, or mate-choice experiments), but interpretation of results is confounded by many factors (Mayr

1969), not the least of which is the difficulty of determining the fitness of hybrid individuals in relation to pure individuals of the parent lineages.

Known hybridization of distinct BSC species has been proposed as another major limitation of this concept (Cracraft 1997). Although ~10% of bird species can hybridize (Grant and Grant 1992), the extent of this problem is limited because much hybridization does not result in production of fertile offspring or in individuals with increased fitness likely to drive evolutionary change. Also, effective gene flow and its effects are considered important by the working model of the BSC; the extent and nature of hybridization can be studied and incorporated within this concept (e.g., Johnson et al. 1999). Basically, the failure of prezygotic isolating mechanisms to prevent hybridization still leaves the opportunity for postzygotic isolating mechanisms such as reduced fertility or fitness to operate to prevent the likelihood of lineage reticulation. Additionally, such lineage crossings are likely a challenge to any species concept when they make it difficult to recover evolutionary history (Grant and Grant 1992).

Mace and Collar (2002) did not consider a movement to a phylogenetic species concept useful from the conservation perspective, but they recognized that a needed "unlumping" of biological species of birds was given impetus by PSC advocates in their criticisms of the BSC. They, like Avise (2000a), considered that the best way forward was through accommodation (Mace and Collar 2002). This accommodation is probably coming to pass, at least in part (see below). Despite many criticisms, the BSC remains the preferred species concept in well-studied groups such as birds (Avise and Wollenberg 1997, Johnson et al. 1999, Avise 2004). Although its many strengths have been widely recognized, perhaps the most important of these is its inherent inclusion of population thinking (see, e.g., Avise 2000a, Coyne and Orr 2004).

Should We Implement the Phylogenetic Species Concept to Define New Species Boundaries?

The ability to name asexual organisms is an advantage of the PSC, but by emphasizing pattern the PSC has the potential to ignore processes important to speciation in sexually reproducing organisms. Proponents of the PSC may recognize the importance of process (interbreeding, reproductive isolation, and barriers to genetic exchange), but process is not among the criteria used to define phylogenetic species (Harrison 1998). We know, however, that gene flow is of profound importance in the speciation process.

Another criticism of the PSC concerns its emphasis on cladistics and the identification of apomorphies. Advocates of the PSC acknowledge this concern but remark that all species are hypotheses and that designations may change with the advent of new information (Cracraft 1997). In this approach, PSC proponents assume that phenotypic diagnostic characters are genetically based. By relying on these identification techniques, the PSC confines the speciation process to a simple presence–absence condition.

This is apparent in the manner in which the PSC deals with reticulation (the evolutionary reuniting of differentiated lineages) and hybridization. The PSC has been accused of ignoring reticulation and the existence of paraphyly (a species derived from a common ancestor but which does not include all the descendants of that ancestor), and the single-locus approach of mitochondrial DNA (mtDNA) phylogenetic studies and determination of species limits can clearly run afoul of polyphyly (a species derived from two or more ancestors) and paraphyly (Patton and Smith 1989, Avise and Wollenberg 1997, Johnson et al. 1999, Funk and Omland 2003). The BSC is able to group nonhistorical taxa as species when those taxa come into contact and freely interbreed (e.g., Northern Flicker, *Colaptes auratus*; Moore et al. 1991). The PSC, by focusing on historical pattern, could diagnose freely hybridizing non-sister taxa as separate species; the PSC simply ignores gene flow between them. Advocates of the PSC maintain that hybridization is a useless criterion in delineating species (Cracraft 1997). But in attacking the BSC on hybridization, PSC advocates tend to view the ability to interbreed as a single "character" rather than as the complex, variable process for genetic interchange that it is. In ornithology, the working model of the BSC does not treat hybridization as a presence–absence "character state," but rather assesses its likely importance by its degree and probable evolutionary consequences. This working model of the BSC ignores hybridization between lineages

that is an evolutionary dead end (e.g., compare Gray 1958 and American Ornithologists' Union [AOU] 1998; see also Johnson et al. 1999).

It has been argued that the PSC is not applicable in its current form because of difficulties in implementing species diagnoses (Avise and Wollenberg 1997; see also Avise 2000b). Critics suggest that using detailed morphological analyses and modern molecular evolutionary techniques will lead to a proliferation of the number of species (Mayr 1993) and ultimately to the ability to diagnose individuals (Avise and Ball 1990; Avise 2000b, 2004; Mallet 1995). The PSC provides no definition of "diagnosable character states," leading to subjectivity in recognizing species. This subjectivity has the potential to create an imbalance between taxa (King 1993), creating new species in well-studied organisms while cryptic species in less-studied organisms may go undetected. Thus, as Collar (1997) pointed out, the PSC may produce species that are not the smallest diagnosable clusters, but rather those diagnosable to the point at which the search was abandoned. Johnson et al. (1999) presented evidence that this has been done already. Indeed, molecular techniques are so robust in diagnosing lineages to the individual level that Avise (2004:361) stated that "most individuals and family units within sexually reproducing species can be distinguished from one another with high-resolution molecular assays." Clearly, diagnosability under such modern methods requires some subjectively placed thresholds to associate diagnosed units with species limits.

Several species concepts have been proposed under process- and pattern-based ideologies, and their introduction has contributed to the understanding of speciation and the evolutionary process. Insofar as species concepts have been forged and reforged to aid progress in understanding biodiversity and evolutionary processes, the absence of agreement on a species concept has probably not been a major impediment to scientific progress. It even seems likely that some principles of competing concepts have been helpfully incorporated into taxonomy in cases that are difficult to resolve under any concept. But a fervent debate continues, especially between proponents of the BSC and the PSC, with each side extolling the virtues of one concept and emphasizing the flaws of the other. The PSC, in particular, has generated heated discussions of species limits, but it has little likelihood of being adopted wholly (see, e.g., Avise 2000b). We believe that phylogenetic research can help us to define species boundaries, develop taxonomic hierarchies, infer evolutionary relationships, and help prioritize conservation. However, we find that the PSC is no less subjective in defining species limits than the BSC; it simply moves the subjectivity to another dimension of the problem (see also Avise and Wollenberg 1997, Johnson et al. 1999, Remsen 2005). Single-locus reconstructions of the evolutionary history of populations or species can be illuminating or deceiving regarding species units (e.g., Cronin 1993, Talbot and Shields 1996, Funk and Omland 2003, Avise 2004). In this regard, the simplistic totting up of largely neutral genetic changes between lineages (e.g., König et al. 1999, Hebert et al. 2004) should be shunned as another potential metric by which to determine species status; this setting of arbitrary thresholds, as noted above, is a throwback to typological thinking and its associated overly simplistic species concept.

The Reality of Subspecies

Within zoology, ornithology has been perhaps the most stalwart bastion of the recognition of subspecies as formally named intraspecific taxonomic units (Cutright and Brodhead 1981), despite a nihilistic attitude toward this taxonomic entity by some PSC advocates (e.g., McKitrick and Zink 1988, Zink 2004). Subspecies—interbreeding (or likely capable of interbreeding) but phenotypically diagnosable populations—have long been considered by many to be a useful, albeit messy, taxonomic unit. Although subspecies have been neglected by the American Ornithologists' Union since the 5th edition of the *Check-list of North American Birds* (AOU 1957), they nevertheless remain an important aspect of described avian biodiversity (e.g., Peters et al. 1934–1986, del Hoyo et al. 1992–2005, Dickinson 2003).

Mitochondrial DNA sequence data indicate that conspecific populations can be structured at a wide variety of evolutionary depths (Avise 2000a). Although subspecies have fallen into disfavor with some because they comprise a mixed bag of units representing variable and often unknown levels of evolutionary differentiation, the PSC would elevate these units

to full species status when diagnosable. This would, in effect, decrease the average level of differentiation among species while increasing the variation of among-species differentiation encompassed within a genus. Furthermore, it would ignore geographically partitioned variation below the species level if not fully diagnosable (e.g., through reciprocal monophyly of molecular markers). Although many subspecies under the BSC will prove to be perfectly good species with further study, changing species concepts to make it so seems rather extreme. In addition, to sweep remaining intraspecific variation under the proverbial rug by denying any formal taxonomic status for those subspecies not making species status (under whatever sort of revision or criteria) is, in our view, a disservice to historic studies and to modern understanding of avian diversity.

At intraspecific levels we expect the largely neutral genetic variation that dominates current genetic-sequence-based data sets to be decoupled from differentiation attributable to selection. Thus, mtDNA sequence data have little bearing on the validity of named subspecies, which are based on among-population differences in phenotype that are more likely than mtDNA differences to be the result of selection (e.g., Mumme et al. 2006). However, subspecific variation provides a suggestion of underlying genetic differentiation, and genetic data can help us understand some of the evolutionary history of intraspecific variation. Genotypic data also can be valuable for genetic diagnoses of populations and regions that warrant special management or conservation importance—as long as we understand the nature of concordance and discordance between phenotypic and genotypic data sets.

An excellent example of subspecific variation that exhibits both morphological and genetic concordance among described subspecies (i.e., partitioned geographic variation correlated in both phenotype and genotype) occurs among Song Sparrow (*Melospiza melodia*) populations in northwestern North America. Genetic study of populations in this region showed a strong concordance between population-level microsatellite data and previously described, morphologically based subspecies (Fig. 1; Pruett and Winker 2005). These subspecific units do not meet anyone's definition of species, with gene flow occurring among most populations and a lack of reciprocal monophyly exhibited among traditionally used characters (Gibson and Kessel 1997, Pruett 2002, Pruett and Winker 2005). However, we believe that they clearly indicate the value to basic and applied science of formal taxonomic recognition of geographically partitioned variation. The BSC's inclusion of such subspecific units can be viewed as a decided advantage, but this does not validate the reality of all described subspecies. For example, the only other Song Sparrow subspecies (*M. m. amaka*) in this region that did not fit this pattern was found to be an undiagnosable and, thus, an invalid taxon after additional genetic and morphological study (Pruett et al. 2004; similar treatment without presentation of relevant data was provided by Gibson and Kessel [1997] and Arcese et al. [2002]).

Although some subspecies do not reflect biological reality (often having been based on insufficient evidence) and thus are virtually useless or even deceiving, others appear to be good indicators of how variation is distributed across a species' geographic range. Continued recognition of subspecies has several advantages. As Mayr (1969) pointed out, the trinomial informs us about the closest relationship and the allopatric condition of breeding populations. Subspecies are also taxonomic bookmarks, informing scientists and wildlife managers that a species is not homogeneous throughout its range. Finally, the trinomial can serve as a form of conservation triage, in that it relegates minor geographic variants to a lower rank (and thus a lower conservation priority) than the more distinct units that practically everyone would agree are species (J. V. Remsen, Jr. pers. comm.).

As Hey (2001) pointed out, evolutionary processes that created the patterns recognized today occurred largely in the past, and the place where these groups exist now is at the "wave front" of the evolutionary processes of the present. Too great a focus on events of the distant past risks a disregard for diversity generated in response to recent selection (see also Crandall et al. 2000); subspecific morphology may reflect more of the latter than the former. Debates about the meaning of such partitioned variation with regard to adaptation, natural selection, and environmental influences on development (phenotypic plasticity) are another issue that we will not consider here; the causes of subspecific variation represent a suite of questions

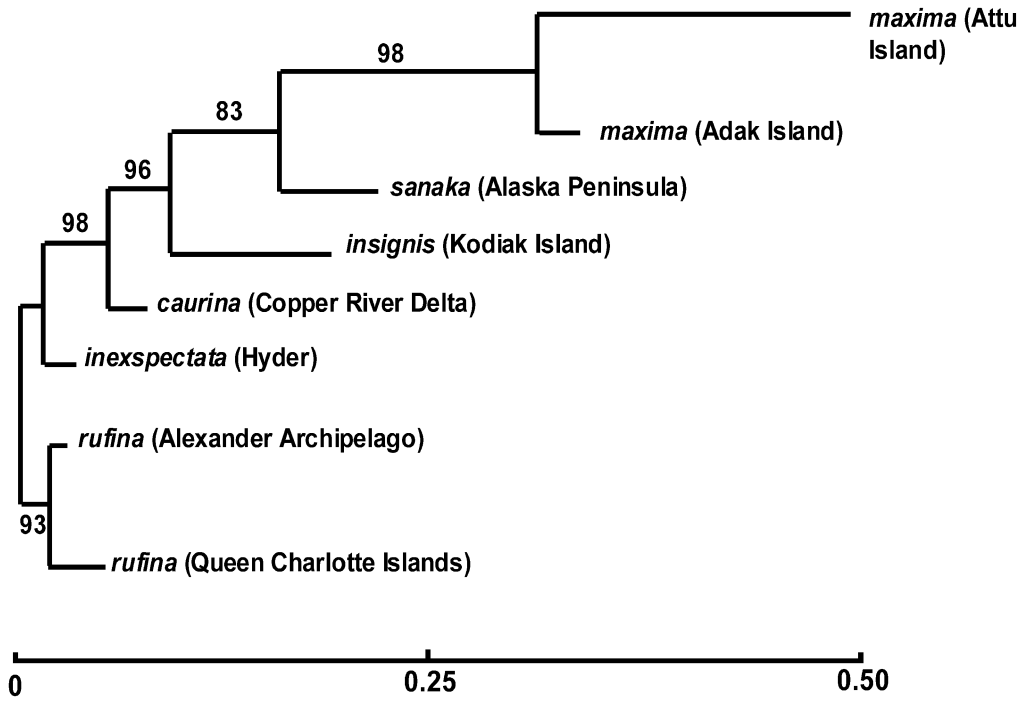

FIG. 1. Bootstrapped distance tree of Song Sparrow (*Melospiza melodia*) populations and subspecies across northwestern North America based on Nei's (1978) genetic distance using eight microsatellite loci. Genetic distance values are shown below the tree and bootstrap support for each branch is listed above that branch (adapted from Pruett and Winker 2005).

stimulated in large part because we recognize that such variation exists. Finally, as long as adaptation remains a possible reason for partitioned phenotypic variation, management and conservation of such evolutionary potential remains a legitimate goal.

CONSERVATION

Conservation biology has the potential to be more affected by a change in species concept than any other discipline. How can we conserve what we cannot define? Realizing the effects that a species concept can have on preserving biodiversity, both sides of the BSC–PSC debate have looked to conservation biology to support their positions. For example, proponents of the PSC have claimed that "lumping" genetically diverse, evolutionarily distinct, and geographically separate populations into single species is detrimental to conservation efforts and have therefore recommended a change in concept (Zink and McKitrick 1995, Cracraft 1997). As conservation efforts move from a species- to a community-level focus, PSC advocates believe that an understanding of patterns of diversity and evolutionary history is essential (Zink and McKitrick 1995). Cracraft (1997) claimed that lower species limits under the PSC would give international governing agencies more legal incentive to protect these units. How such perennially resource-limited agencies would find the support to widen conservation efforts under a simple definition change, however, is unclear. Some conservation biologists believe that implementing the PSC would increase the total number of threatened species and devalue their status (e.g., Collar 1997). Conversely, BSC supporters charge that a change in species concepts is not only logistically impossible, but unnecessary because the Endangered Species Act (ESA) in the United States specifically includes protection of subspecies of vertebrates and plants and distinct population segments of vertebrates (ESA 1973). Setting conservation priorities for these subspecific units is not at all unusual (e.g., O'Brien and Mayr 1991), and Canada has recently adopted similar subspecific protections

(e.g., Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2005).

Appropriate units for conservation attention can be and have been developed without assigning formal taxonomic status. The taxonomic "trick" of lowering species boundaries will not magically increase funding or concern for biological diversity in various national or international governing agencies. Although conservation biology can be considered a crisis discipline, taxonomy probably should not be (but see Godfray 2002, Mace 2004). We believe that lowering the bar for species recognition by changing the definition of what constitutes a species is a bit of professional legerdemain that will cause a portion of the nonprofessional public to lose faith in the biological sciences, especially in how we treat such widely visible groups as birds and other vertebrates. Applying the term "species" to vertebrate groups that are not discernible to the untrained observer (or even to professionals without genetic analyses, for example) is something to be strenuously avoided. More than 100 years ago, Teddy Roosevelt (before he was President of the United States) eloquently expressed this same barrier to acceptance of what we now term oversplitting:

> [Dr. Merriam] will do his work, if not in better shape, at least in a manner which will make it more readily understood by outsiders, if he proceeds on the theory that he is going to try to establish different species only when there are real fundamental differences, instead of cumbering up the books with hundreds of specific titles which will always be meaningless to any but a limited number of technical experts, and which, even to them, will often serve chiefly to obscure the relationships of the different animals by over-emphasis on minute points of variation. It is not a good thing to let the houses obscure the city. (Roosevelt 1897:880)

Despite the claims of various species-concept factions, conservation biology has flourished while this debate has continued (e.g., BirdLife International 2000, Norris and Pain 2002). Conservation units such as subspecies, evolutionarily significant units (ESUs), distinct population segments (DPSs), management units (MUs), and designatable units (DUs) have been developed to prioritize within-species diversity (ESA 1973; Ryder 1986; Moritz 1994, 1996; Green 2005; COSEWIC 2005). These units differ in their focus. For example, MUs represent sets of populations that are currently demographically independent, whereas ESUs are based on historically isolated sets of populations that together encompass the evolutionary diversity of a taxon (Moritz 1994). These subspecific units are not without their own inherent difficulties of definition (e.g., Paetkau 1999, Crandall et al. 2000), but they can provide a common, taxonomically largely neutral, ground—where, for example, the loaded term "species" can be ignored—upon which the majority of biologists can agree, regardless of species concepts. For example, Barrowclough and Flesness (1996) simply equated phylogenetic species with ESUs and discussed the latter to communicate more effectively with conservation biologists.

The collective job of conservation biologists, systematists, taxonomists, and wildlife managers is to recognize, conserve, and manage biological diversity from the population to the species level. These complex subjects of species concepts, geographic variation, differentiation, taxonomy, and hybridization play a central role in this business. But recognition of units, regardless of what we call them, can be accomplished. Assessment of these units' uniqueness and value are critical to future management and conservation, and they require the best scientific evidence available. Clearly, units for conservation priority can and have been developed and determined without major impediment from the species-concept debate and without scrapping current species concepts. Indeed, in looking forward, it seems that a BSC framework is more likely to prevail if only because it enhances stability (Agapow et al. 2004, Mace 2004). Regardless of species concepts and debates, however, we should recognize that an ever-growing body of data and an improved understanding of evolution are, in part, contributing to this effervescent front.

One area where the species-concept debate has potential to be detrimental is in the political arena. Issues regarding conservation of our planet's biodiversity are fertile battlegrounds for disagreement. Public and political support is germane to protecting populations and communities; conservation priorities are weighed against economic and political priorities. The public and politicians look to biologists to describe the organisms, populations, and higher units that need consideration. Public

or institutional debates often ensue, and often during these debates the science is questioned. For example, scientific debates over concepts in evolutionary biology have left an opening for religious agendas in the U.S. education system (e.g., the "intelligent design" movement). Scientific debate over the causes and effects of global warming has left an opening for governments to delay development or implementation of effective policies to address the problem. It is not unreasonable to consider that debates over species concepts might provide an opening for government agencies or pro-development forces to neglect or postpone costly conservation efforts until species concepts are resolved. Biologists should recognize the social dimension to this scientific issue and be prepared to stand united on the fact that global biodiversity losses are—and will likely continue to be—staggering, and that responsible management and conservation of this diversity is imperative. Our longstanding disagreement over species concepts should not become an impediment to these goals. We should be prepared to shelve the debate and agree on the importance of responsible conservation and management regardless of what labels are used to denote the focal unit(s). Hey et al. (2003) drew parallels between species uncertainties and medical diagnoses or major weather events such as droughts—all are areas where professionals deal with inherent uncertainties in matters of great importance to society, and the uncertainties in each can be explained.

Conservation biology has moved forward in three major ways, despite disagreement over species concepts: (1) top-down conservation, working with higher-level taxa to formulate conservation plans, or effectively implementing conservation at the ecosystem level by preserving communities that exhibit shared patterns of evolutionary history (e.g., Moritz 1996, Williams et al. 1997, Villaseñor et al. 2005, Brooks et al. 2006); (2) "coat-tails" conservation, in which management or preservation of particularly desirable organisms (e.g., old-growth trees, cranes, waterfowl) necessarily brings additional biodiversity along; and (3) redefining and proceduralizing the recognition of units on the population-to-species continuum. This area has moved forward well since Mayr's (1969) *Principles of Systematic Zoology*, and recent advances can be seen in Helbig et al. (2002), Patten and Unitt (2002), and Sites and Marshall (2004). In addition, ESUs, MUs, DPSs, and DUs have been brought to bear in conservation and management. Mace's (2004) suggestion and the demonstrated utility (e.g., Bulgin et al. 2003, Pruett et al. 2004, Barrowclough et al. 2005) of combining taxonomy–systematics and conservation biology to address issues in the biopolitical realm is a likely roadmap to success. Likewise, Moritz's (2002) suggestion to aim for protection of both the patterns of biodiversity and the processes that generate this diversity emphasizes a most sensible multidimensional aspect to the scientific basis of biological conservation. Finally, we should remember that congruence among multiple data sets will enhance acceptance of determinations regardless of the units under consideration.

Conclusions

Although there is little agreement on which species concept or suite of species concepts is best, we must acknowledge that the debate has helped guide speciation research and furthered our knowledge and understanding of evolutionary processes. Many advocates of a PSC have suggested complete abandonment of the BSC (e.g., Nixon and Wheeler 1990, Zink and McKitrick 1995, Cracraft 1997). In our opinion, this would be a grave mistake. In establishing and defending the BSC, biologists have contributed to our understanding of the process of speciation in sexually reproducing organisms, thus identifying mechanisms that lead to reproductive isolation. Similarly, extensive research on phylogenetic lineages under the framework of the PSC has increased our understanding of historical patterns of differentiation (Avise 2000a). Modern molecular evolutionary techniques are bridging the historical gap between population genetics and systematics, and both sides are beginning to realize how intimately related their fields are (Avise and Walker 1999, Avise 2000a). Undoubtedly, the strengths of each of these concepts are being applied to improve our understanding of biodiversity.

Cracraft (2000) did a service in pointing out the "my concept is best" phenomenon among the species-concept debaters. This strong and repeated trend in the debate emphasizes its political and subjective nature. Levin's (1979) view that species are essentially tools or abstract

constructs that we create to handle biodiversity is a useful insight. Endler (1989) discussed the use of different concepts for different aspects of the study of speciation, further strengthening the analogy to tools. Hey (2001) determined that the species problem is inherent in the clash between the human propensity to categorize and the desire among biologists to make the categorical bin of "species" concordant with an evolutionary group. Regardless of how future facets of the species-concept debate develop, we can be assured that it will continue; no imminent solution is likely (though see Hey [2006] on perceived progress). But we can learn from this debate and successfully continue both basic and applied research in biodiversity.

Within ornithology, the political and public landscapes still seem to be dominated by the BSC (e.g., del Hoyo et al. 1992–2005, AOU 1998, Dickinson 2003). However, this apparent stability in species concepts does not equal a rigidity in recognized species. Since the widespread adoption of the biological species concept, the number of recognized bird species has grown more rapidly than new species have been described (on the latter, see Banks 2004). Mayr (1946) estimated that there were 8,616 species of birds. Decades later, he raised that estimate to about 9,000 (Mayr 1982). Sibley and Monroe (1990) considered that there were 9,672 bird species, and Dickinson (2003) gave 9,721. Implementation of the BSC resulted in over-lumping (see Peters et al. 1934–1986), and as our understanding of species (and subspecies) limits has improved and more data have become available, many taxa treated as subspecies under the BSC have undergone taxonomic revision and are now recognized as species (compare Dickinson 2003 with Peters et al. 1934–1986; see also Haffer 1997). This trend of increasing numbers of recognized species will continue without a change in species concepts (all of the works cited here use the BSC), even if no more bird species new to science are described. A similar phenomenon has occurred in primate taxonomy (Mace 2004). The point is that continued study of diversity under the BSC is not stymied or frozen in time by adherence to that concept, and some of the complaints against it are being recognized and rectified.

As Hey (2001) pointed out, we have been without a consensus on how to define species over the entire history of evolutionary biology. Ongoing development of this field has probably occurred because our science has progressed toward a working solution that separates the semantic from the empirical aspects of understanding species, an approach explicitly recommended for continued progress (Hey et al. 2003). As major works in evolutionary biology continue to purposely use the BSC (e.g., Avise 2000a, West-Eberhard 2003, Coyne and Orr 2004), basic science is continuing without undue angst over this lack of consensus on what constitutes a species.

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