Conservation Genetics **1:** 67–76, 2000.

Questioning species realities

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Received 28 November 1999; accepted 25 April 2000

> "In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be free from the vain search for the undiscovered and undiscoverable essence of the term species."
>
> (Darwin 1859, p. 485)

Key words: mitochondrial DNA, phylogeny, phylogeography, speciation, species concepts, taxonomy

Introduction

A frequent outcome when studying complex biological systems is that data collected to test a specific hypothesis can be interpreted several ways, and interpretations can be influenced by the paradigm through which a given scientist views the world. A paradigm to which most biologists subscribe is that biological diversity can be meaningfully divided into least-common evolutionary denominators, called 'species'. Although delineating distinct species is often problematic, most biologists agree with Mayr (1957) that "the living world is comprised of more or less distinct entities which we call species." A contrasting view (the one to which we subscribe) is a recognition of more or less distinct clusters of organisms at varying biological scales, without assuming some fundamental and universal level of clustering that has evolutionary significance out of proportion to all other levels of clustering. This view from outside the species paradigm allows conclusions that depart significantly from those commonly advanced.

Taxonomic groups have historically been identified using morphological criteria, leaving uncertainty in some cases as to the validity and meaning of groups thus delineated. Within the last few decades, molecular techniques have provided a powerful new tool to independently evaluate the validity of taxonomic designations (although not without their own caveats). Many genetic studies have reexamined taxonomies formerly based exclusively on morphology, and have in some cases uncovered paraphyletic or polyphyletic groupings, thereby precipitating taxonomic rearrangement (e.g. de Jong 1998). Numerous genetic studies have also examined the validity of species designations in particular groups, in some cases confirming and in others refuting previous interpretations (e.g. Riddle and Hafner 1999). An extension of this approach, missing until recently, is the use of genetic data to evaluate the overarching concept of assigning groups of organisms to specific bins, most notably species.

Perhaps the first, and certainly the most ambitious attempt, to use genetic data for evaluating the validity of species as a concept has its basis in a series of reviews by Avise and colleagues (Avise and Walker 1998, 1999; Avise et al. 1998; Johns and Avise 1998). This series culminated in a paper titled *Species realities and numbers in sexual vertebrates: Perspectives from an asexually transmitted genome*, in which Avise and Walker (1999) used patterns of mitochondrial DNA (mtDNA) diversity to argue that "mtDNA data and traditional taxonomic assignments tend to converge on what therefore may be real biotic units in nature". Because this was the first major work of its kind, with important implications for evolution,

ecology, and conservation, its methods and conclusions deserve careful evaluation. Here, we provide a reanalysis of the data sets and methods used by Avise and colleagues, from which we conclude that mtDNA discontinuities do not closely match recognized taxonomic species.

This interpretation is ultimately independent of the class of genetic markers used to identify biotic discontinuities, and instead reflects what we perceive as fundamental flaws in the species paradigm. Recognition of these flaws would engender a broader consideration of how delineating distinct species fails to adequately capture the essence of biological diversity. We then discuss implications for two important goals of conservation biology – the identification of geographical regions and particular groups of organisms that warrant protection. Finally, we propose an alternative solution to the species problem. To attain this solution we suggest that biologists shift their focus from the elusive demarcation of species to more quantitative descriptions of variation within and among groups (or clusters) of organisms.

Reanalysis

Avise and Walker (1999) used published data to evaluate patterns of mtDNA diversity within 252 taxonomic species of vertebrates. Previous work by Johns and Avise (1998) had indicated that mtDNA differences among species were large, with approximately 90% of sister species pairs showing at least 2% sequence divergence. Many taxonomic species are therefore quite genetically distinct from each other, and have been evolving independently for a considerable length of time ($>$1,000,000 years). Remarkably, however, 56% of the species surveyed could be sub-divided into at least two "major intra-specific phylogroups", and 5% had three or more such phylogroups (Avise and Walker 1999). These phylogroups are envisioned as independently-evolving, historical lineages equivalent to taxonomic species in all ways, except presumably the magnitude of divergence (Avise and Walker 1998). The existence of distinct phylogroups within more than half of the surveyed species seems at odds with the conclusion that taxonomic species reliably unveil distinct evolutionary lineages.

Avise and Walker (1999) used data from three of their own recent reviews of the primary literature on mtDNA diversity within and among species (Avise and Walker 1998; Avise et al. 1998; Johns and Avise 1998). We reanalyzed the data in those reviews to see if we could bolster support for our interpretation or for that of Avise and Walker (1999). First, we generated cumulative frequency distributions of mtDNA sequence divergence between taxonomic sister species and between intra-specific phylogroups. Sequence divergence data used for this analysis was obtained from 277 sister species pairs and 183 phylogroup pairs of vertebrates (Table 1). These histograms were used in the spirit of analyses performed by Avise and colleagues to examine the degree of overlap in sequence divergence between inter-specific and intra-specific pairs. Second, we matched data for divergence among congeneric species [from Figures 1–4 in Johns and Avise (1998)] with data for divergence between conspecific phylogroups within each genus [from Table 2 in Avise and Walker (1998) and the Appendix of Avise et al. (1998)]. This second analysis was used to evaluate the degree to which divergence among phylogroups within a species differs from divergence among species in that genus.

If taxonomic species designations converge on mtDNA discontinuities, we would expect little overlap in the cumulative frequency distributions of sequence divergence within and between species. Thus, few phylogroup pairs should exceed the levels of sequence divergence that separate species (i.e. the line for phylogroups in our Figure 1 should approach zero before the line for species begins to fall below unity). This was not the case (Figure 1). For example, although 88% of bird sister species pairs exceeded 0.6% sequence divergence, 81% of bird phylogroup pairs also exceeded that level. Exceeding 2% sequence divergence were 66% of bird sister species pairs but also 37% of bird phylogroup pairs. Considerable overlap in the amount of divergence within and between species was also evident for each of the other taxa (Figure 1). We conclude that there is no clear separation and no single threshold level for mtDNA divergence that distinguishes species from phylogroups. Considerable overlap between the amount of genetic divergence between phylogroups and species is also evident in other, less-extensive, reviews (Vogler and DeSalle 1994; Klicka and Zink 1999; Riddle and Hafner 1999).

If taxonomic species designations converge on mtDNA discontinuities, we would also expect that divergence among phylogroups within species should be considerably less than divergence between that species' congeners in paired comparisons. Although this was sometimes the case, intra-specific diver-

Table 1. Characteristics of the data and sources used in our analysis, and by Avise and Walker (1999), to compare divergence between sister species ('Species') and phylogroup pairs ('Phylogroup'). Some species had more than two phylogroups, and so the total number of species from which phylogroup pair divergence was estimated is indicated in parentheses. Information includes the publication from which the data were obtained ('Source' – either Avise and Walker 1998, 'A & W', or Avise et al. 1998, 'A et al.'), the relevant table or figure in those publications ('Location'), the number of species or phylogroup pairs ('Pairs'), the type of mtDNA data used ('Data'), the number of phylogroup comparisons corrected for within phylogroup variation ('Corrected'), the number of control region studies included by Avise and colleagues ('Control region'), the number of species excluded because geographically divergent samples did not demonstrate major intra-specific phylogroups ('Excluded'), and the median level of sequence divergence

	Mammals		Birds		Herpetofauna		Fish	
	Species	Phylogroup	Species	Phylogroup	Species	Phylogroup	Species	Phylogroup
Source	A et al.[a]	A et al.	A & W[b]	A & W	A et al.[a]	A et al.	A et al.[a]	A et al.
Location	Figure 2a	Figure 2b	Figure 2a	Table 1	Figure 3a	Figure 3b	Figure 4a	Figure 4b
Pairs	92	72 (54)	35	37 (37)	42	47 (25)	108	26 (24)
Data	*cytb*[c]	>150 bp[d]	cytb[c]	>200 bp[d]	cytb[c]	>150 bp[d]	cytb[c]	>150 bp[d]
Corrected	0	?[e]	0	14	0	?[e]	0	?[e]
Control region[g]	0	9	0	2	0	2	0	1
Excluded	0	57[f]	0	26	0	37[f]	0	20[f]
Median divergence	6.4	2.6	5.6	3.1	6.1	3.1	4.1	2.6

[a]Data were originally compiled by Johns and Avise (1998). [b]Data were originally compiled by Klicka and Zink (1997). [c]A single sequence of the mitochondrial cytochrome *b* gene (the longest ⩾200 bp in GenBank, release 103.0) was used to represent each species (Johns and Avise 1998). [d]Various regions of the mtDNA genome were used (Avise and Walker 1998; Avise et al. 1998). [e]Some phylogroup pairs were corrected for within phylogroup variation but the number was not indicated by Avise and colleagues. [f]Excluded species were not reported in the publications, so we estimated them using the reported percentage of excluded species for all vertebrates combined (44%, Avise and Walker 1999). [g]The control region data are problematical because only a subset of control region studies were included by Avise and colleagues. It was not indicated by Avise and Walker (1999) if control region data were corrected for its faster rate of evolution. Owing to these cumulative ambiguities, we excluded control region sequence divergence data from our analysis.

gence often approached levels of inter-specific divergence (Figure 2). On average, intra-specific divergence was 44% as large as the average inter-specific divergence within the same genus, and 87% as large as the minimum inter-specific divergence. Divergence among phylogroups within species actually exceeded the minimum amount of divergence among congeners for 18 of 52 comparisons (35%). Thus, although taxonomic species often recognize large mtDNA discontinuities, they fail to recognize many other such discontinuities. In fact, phylogroups identified in genetic surveys are often later interpreted as cryptic species [Klicka and Zink (1999) report some examples].

Analytical hurdles in testing species realities

Avise and Walker's (1999) review sets an important precedent for the use of genetic data to evaluate species realities. Their methods therefore deserve careful consideration to identify any potential concerns that should be addressed in future studies. Avise and Walker (1999) are careful to mention potential sampling biases inherent in their data. Here we reiterate and elaborate on those biases, and discuss additional analytical concerns not addressed in their manuscript. Some of the identified biases would tend to increase and others decrease apparent concordance between traditional species and genetic discontinuities (all biases will increase inferential uncertainty). It will be important for future studies to reduce these biases or to at least evaluate their strength. We will start with the most general issues and work toward the more specific.

Avise and colleagues surveyed vertebrates, a group for which confusion as to species status is much lower than for other taxa. It is therefore discouraging that Johns and Avise (1998) found "rather poor equivalency of taxonomic rank across some of the Vertebrates". For example, they found that "surveyed avian taxa on average show significantly less genetic divergence than do same-rank taxa surveyed in other vertebrate groups . . . " If poor correspondence prevails among different vertebrate taxa, correspondence between vertebrates and other groups is certainly lower. The greater ambiguity and inconsistency encountered in defining species within groups such as eukaryotic algae, fungi, plants, marine invertebrates, nematodes, insect herbivores, and partheno-

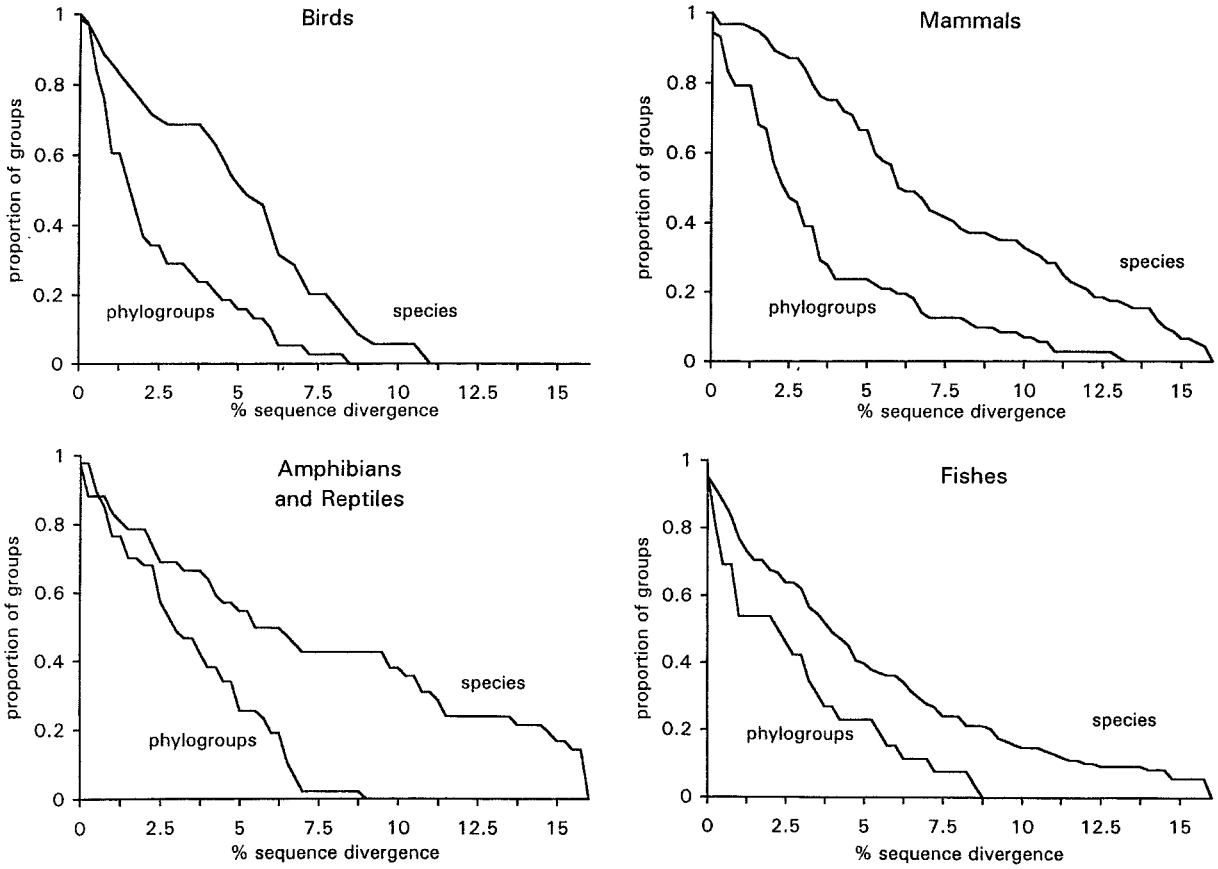

Figure 1. Proportions of sister species pairs and phylogroup pairs exceeding different levels of sequence divergence. Note the large amount of overlap in the distributions.

genic insects is apparent in the contributions to Claridge et al. (1997). The problem of non-equivalence of taxonomic rank among different types of organisms is discussed by Avise and Johns (1999), along with their proposed solution.

Biases may arise owing to the subset of species selected for analysis. Avise and Walker (1999) point out that species with large geographic ranges are often chosen for phylogenetic analyses because they show the greatest potential for multiple historical units. Species with narrow ranges (and less expected intra-specific structure) may be underrepresented. This effect was compounded in Avise and Walker (1999) because they only considered studies with "multiple samples from widely spaced localities across significant portions of a species' range". However, the extent to which the geographical range of a group of organisms actually influences its potential for independent lineages has not been quantified.

An obvious bias can arise from limited sampling across a species' range (Avise and Walker 1999). The resources available to any genetic survey are limited, and sampling is usually restricted to a subset of the locations in which any particular species is found. Increased sampling from other locations would not decrease the amount of intra-specific genetic variation and might increase it substantially. This bias may have been reduced (to an unknown degree) in Avise and Walker (1999) through their aforementioned decision to only consider studies that sampled across much of a species' range. Of course their focus on studies over large geographic ranges makes their conclusion that 93% of the phylogroups "displayed a strong geographical orientation" less remarkable.

The types of studies excluded from a review is also an important consideration. For example, species for which data were available but for which major phylogroups were not detected (112 of 252 species)

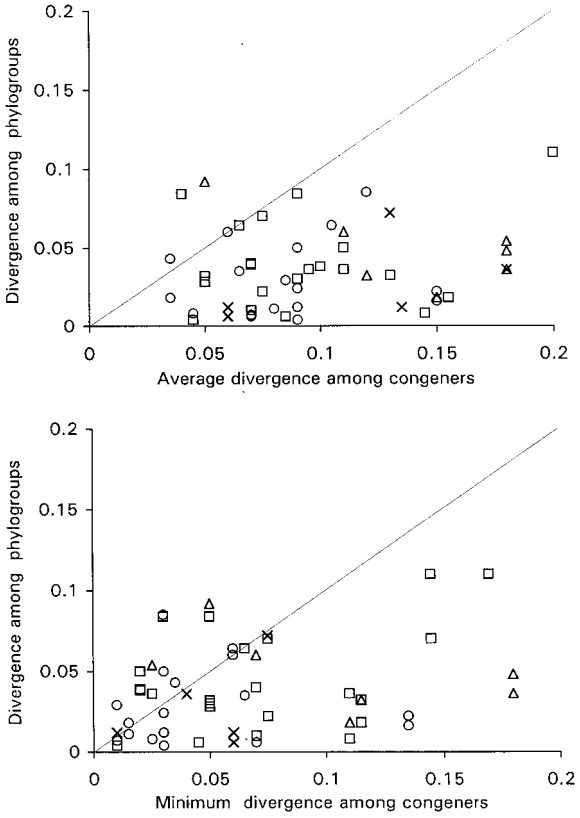

Figure 2. Amount of sequence divergence within conspecific phylogroups relative to the average (top panel) and minimum (bottom panel) amount of sequence divergence between that species and its congeners. Birds are represented by circles, mammals by squares, amphibians and reptiles by triangles, and fishes by crosses. The diagonal line is the isoline, where divergence between phylogroups is the same as that between species. Note that in many instances divergence within species approaches or exceeds divergence among congeners.

were excluded from the analysis of Avise and Walker (1999), and therefore from our own. (We did contact Dr Avise to inquire about these excluded studies but he indicated that records had not been kept of the specific studies that failed to detect phylogroups). Including these studies would perhaps have increased apparent cohesiveness of taxonomic species. Working at cross-purposes is the exclusion of studies that monitored the rapidly-evolving control region, "except where ancient and explicit divergence dates ... were proposed in the original publications" (Avise and Walker 1999). This policy was adopted "to avoid a focus on unduly shallow mtDNA clades that are of little interest in the current context ..." However, we feel these shallow clades will be important in the context of testing "whether biotic discontinuities ... bear resemblance in number and composition to the biological units currently recognized as taxonomic species" (Avise and Walker 1999).

Another concern is that phylogroups must be fairly distinctive to be recognized. In Avise and Walker (1999), phylogroups were identified "by relatively large genetic gaps between respective branches that received strong bootstrap support in an estimated mtDNA gene tree". Phylogroups identified in this manner typically "were distinguished consistently by at least 0.6% sequence divergence", which is equivalent to about 300,000 years of separation (assuming 2% sequence divergence per million years). This level of separation would exclude many groups that are highly divergent in morphology, ecology, behavior, and mate recognition. For example, many of the 300 or so endemic haplochromine cichlid fishes of Lake Victoria would not be recognized even as intra-specific phylogroups. Avise et al. (1998) acknowledged Lake Victoria fishes, and the existence of other "examples that depart radically from the vertebrate norm", but if taxonomists recognize species with very recent origins, genetic surveys designed to test species realities should also consider such groups. At a more fundamental level, young species are important for understanding the processes of diversification because they sometimes maintain their distinctiveness under the most difficult of circumstances – strict sympatry (Schluter 1996; Taylor 1999).

The type of genetic marker chosen for study may influence apparent concordance between taxonomic species and biotic discontinuities. Avise and Walker (1999) point out that mtDNA patterns will fail to reflect the degree of interbreeding if gene flow is male-biased. Another consideration is the potential for ancient mtDNA lineages to be maintained for long periods of time within interbreeding populations. These ancient lineages can then be sorted between smaller, recently-diverged populations, artificially increasing their apparent age and distinctiveness. Alternatively, two groups with similar mtDNA profiles can actually be independent if, for instance, mtDNA of one group has been "captured" in the other following an ancient hybridization event (Avise 1994). Finally, the typical length of mtDNA surveyed in the bird studies (and presumably in the other taxa) is only 500 bp, and this may be too short to firmly establish phylogenetic groups that originated less than 200,000 years ago (Avise and Walker 1998). We have illustrated the concerns associated with mtDNA because this is the only class of markers yet employed for test-

ing species realities. Other genetic markers will have their own sets of constraints.

Another bias can arise owing to adjustments for within-group variation – "When possible from the data provided, p (sequence divergence) values between major phylogroups (e.g., 'A' and 'B') were corrected for within-phylogroup variation according to the following formula: $p_{AB(net)} = p_{AB} - 0.5(p_A + p_B)$" (Avise et al. 1998; see also Avise and Walker 1998; Avise 1994, p. 96). In this manner, divergence between phylogroups was sometimes discounted by the amount of divergence within those phylogroups, and within-group divergence was often quite large (Avise and Walker 1999). The specific phylogroups subjected to these corrections were indicated for birds (14 of 38 phylogroups, Avise and Walker 1998) but not for the other taxa. The correction is not wrong in and of itself but the problem is that divergence was corrected in this manner for only some of the phylogroups, and divergence among species was not corrected using a similar procedure (only a single mtDNA sequence was used for each species, Johns and Avise 1998). Avise and Walker (1998) did ponder a similar correction to between-species sequence divergence, and concluded that its effects would be considerable. In short, the absolute amount of divergence between a considerable proportion of the phylogroups surveyed is higher than that reported by Avise and colleagues.

Recognizing that relative strengths of the various biases are unknown, Avise and Walker (1999) suggest that they "should partially cancel one another" and that current taxonomic species agree with mtDNA discontinuities "certainly within an order of magnitude". The first view seems premature in the absence of supportive analysis, and the second certainly leaves room for improvement. Given the large number of uncertainties in the data and analyses performed thus far, we (and Avise and Walker 1999) encourage further efforts to extend tests of species realities to larger data sets, other taxa, and to the use of additional analytical techniques.

Unsolvable problems with the concept of species

Whether or not a group of organisms is recognized as a distinct species is ultimately a dichotomous decision – yes or no. Notwithstanding the aesthetic simplicity of this approach, it remains burdened by unsolvable philosophical, theoretical, and empirical problems. These problems have been the subject of unremitting and escalating debate for centuries (Darwin 1859; Mayr 1957; Otte and Endler 1989; Mallet 1995; Claridge et al. 1997; Wheeler and Meier 1997; Howard and Berlocher 1998; Wilson 1999). Instead of revisiting these intricate and often convoluted exchanges, we wish to highlight two critical problems, the consideration of which hints at what we feel may be the only real solution. First, biologists are forced to decide, either explicitly or implicitly, what level of difference between two groups makes each worthy of its own species designation. Second, once species are identified, all are considered equal (except in phylogenetic weighting approaches, see below), despite the fact that they may vary by orders-of-magnitude in the amount of difference from their nearest relative.

Regardless of the operational species concept chosen (reviewed by Mayden 1997), biologists are forced to grapple with the vexing choice of what level of difference (or amount of isolation) makes a species. For example, the popular biological species concept (BSC) states that species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1940). If 100% reproductive isolation is used as a criterion for applying the BSC, identification of distinct species is relatively straightforward (although other problems remain). If this criterion was universally adopted, however, many current taxonomic species would no longer be recognized, owing to rampant hybridization and introgression in the wild (Arnold 1997). If some gene flow is permitted among species when applying the BSC (the approach taken by most modern biologists), a threshold amount of isolation necessary to discriminate between species must be assumed, and any such choice is largely arbitrary. Should two groups be considered separate species if they are 90% reproductively isolated, or if they are 10% reproductively isolated? Mayr (1996) suggested that species should be considered distinct as long as "clandestine hybridization" does not result in "the complete fusion of such species populations". But how does one determine 'complete fusion' without retreat to thresholds? Compounding the problem, the threshold chosen will vary widely among investigators.

Many taxonomists favor variants of the phylogenetic species concept (PSC) which defines species as the "smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983; Vogler and DeSalle

1994). The PSC, however, provides no reprieve from the arbitrary nature of species delineation because some threshold level of difference must still be adopted (with enough traits all individuals are diagnosable from each other, Avise 1994). Either that or the analysis must be restricted to a subset of possible traits, and the resulting diagnostic characters will vary widely and often arbitrarily, making it difficult to equate species counts and identities across even closely related taxa. Even if universal diagnosable criteria could be agreed upon, the resulting collection of 'species' would have no biological meaning other than their separation based on the chosen characters (Mallet 1995). Some purveyors of the PSC profess to not assume that species are real entities but nevertheless use the method for delineating distinct groups that merit conservation (Goldstein et al. 2000), an approach that does not obviate either of the major problems discussed herein (it simply removes the term species from discussion). The arbitrary nature of diagnostic criteria such as specific characters or thresholds is a problem universal to operational species concepts.

The amount of difference between taxonomic species (and at other taxonomic levels) in various genetic or phenotypic traits is often very large. For example, 25 of the 109 sister species of birds we considered showed less than 2% sequence divergence, whereas 11 of the pairs showed greater than 10% sequence divergence (Figure 1). The dichotomous nature of species delineation ignores quantitative differences between species, and effectively considers all equally distinctive. Thus, any study comparing species numbers among taxa, geographical regions, or time periods obscures the fact that biological diversity is poorly quantified simply by counting the number of taxonomic species. Comparative studies would certainly benefit from the adoption of a standardized temporal scheme for defining hierarchical taxonomic levels (e.g., Avise and Johns 1999) but such a scheme remains compromised by the need to choose and apply thresholds.

Conservation implications

Conservation biologists often proceed by gathering information designed to address several immediate and long term goals. One goal is the identification of geographical regions that warrant exceptional efforts at protection (e.g. Peterson and Navarro-Sigüenza 1999). These areas may contain extraordinary levels of biological diversity or provide succor for types of organisms not found elsewhere. A second major goal is the winnowing of complexes of closely related organisms into groups that would merit focused conservation efforts and those that would not (e.g. Vogler and DeSalle 1994). Both of these goals currently rely heavily on the identification or enumeration of distinct species or subspecific groups, and are therefore impacted by the operational and theoretical problems discussed above.

Scientific and popular pulpits used to appeal for the protection of particular geographical localities typically resort to superlatives based on counts of species, especially endemics (e.g. Wilson 1992). The conservation of areas with exceptional levels of irreplaceable biological diversity should indeed be a priority but decisions made by prioritizing regions based on species counts may not be the best approach (although it provides useful stop-gap information). Lurking beneath substantial operational difficulties, such as non-equivalence of species counts obtained using different concepts (e.g. BSC vs. PSC, Peterson and Navarro-Sigüenza 1999), are more fundamental problems. For example, some regions may contain many closely related species whereas others contain fewer but more diverse species. Counting genera or families is one attempt to circumvent this concern but becomes increasingly sensitive to the arbitrary nature of higher-level taxonomic categories, and ignores the extent of diversity within those categories.

A few inspired attempts have been made to quantify diversity at less inclusive levels of biological organization, such as Hughes et al. (1997) for 'populations'. These attempts are unfortunately still limited because they must likewise assume a threshold level of difference (Hughes et al. used statistical significance), and then the actual amount of difference among populations exceeding the threshold is ignored. It has been suggested that 'phylogeographic ESUs' are an improvement over species as measures of biological diversity (Riddle and Hafner 1999), but ESUs remain hampered with the same two fundamental problems we have discussed for species concepts. Mallet's (1995) 'genotypic cluster' view of biological diversity is a step in the right direction but it does not go far enough. Mallet's focus remains on identifying distinct clusters of organisms, which is important, but once clusters are identified the actual amount of difference among them is forgotten. Biologists need to take the next step and divorce themselves from the idea of

discrete, equal bins into which organisms must be forced, and begin to emphasize the level of variation within and among groups of organisms.

The status that humans confer on a particular group of organisms under consideration for conservation often hinges on whether or not that group has somehow crossed an unseen threshold and become a species, evolutionarily significant unit (ESU), management unit, or stock (Moritz 1994). The need to identify discrete groups deserving conservation has it roots in natural history but has been promulgated beyond all biological reality in the legal arena surrounding the US Endangered Species Act (Waples 1991; Pennock and Dimmick 1997; Waples 1998). In this arena, the chosen criteria for delineating a species or ESU becomes of critical importance to their future welfare. Our illustration that operational thresholds for species designation are arbitrary, inconsistent among genetic (or phenotypic) markers, and not comparable across taxa, suggests that important groups of organisms will remain unacknowledged and therefore forever outside the umbrella of attempted protection.

One possible solution to the difficulty of identifying groups warranting conservation is to allocate resources in quantitative proportion to the level of distinction of each group (as well as the nature and intensity of the threat to their persistence). In this fashion, all groups would be considered meritorious of protection, and the level of protection they received would be in proportion to their distinctiveness. This approach could be modified to consider the degree of hybridization and introgression among groups, an issue that has been a traditional bane of the ESA (Arnold 1997). For example, the distinctiveness of each group could be discounted by the amount of introgression with other groups, weighted by the distinctiveness of those other groups.

The development of phylogenetic approaches to conservation, which weight species in one way or another by their distinctiveness have been described by several authors (e.g. Vane-Wright et al. 1991; Crozier 1992; Faith 1992; reviewed by Faith 1994; Krajewski 1994; Crozier 1997). Modifications to these approaches could be used to identify geographical regions warranting protection, as well as unique groups of organisms that merit focused conservation efforts. Phylogenetic methods still have some problems, however, including non-equivalence of different weighting procedures, inconsistencies between character sets, and a continued dependence on the reliable and consistent identification of species (Krajewski 1994; Crozier 1997). The last of these problems is the most critical in the present context, owing to the aforementioned ambiguities in species delineation, and the tendency to ignore within-group variation.

Quality in quantity – a promising direction

Any system of biological classification that partitions organisms into distinct species or ESUs (i.e., *any* species concept) fails to capture the essence of biological diversity. In the time of Linnaeus, species designations were a crucial contribution to natural history because they allowed biologists to communicate using a common currency. Now, however, it should be recognized that strict adherence to the species paradigm may actually be impeding progress in conservation and other areas of biology. We are joined in this view by a small chorus of philosophers and biologists (see Wilson 1999). We advocate replacement of the current artificial view of life with a system that describes groups of organisms based on the amount that they differ from other groups. Full description and justification of such a system must be left for future analyses. Here, we merely wish to introduce the germ of an idea that the species paradigm can be profitably replaced with a system based on the quantitative description of variation within and among groups (or clusters) of organisms.

Abandoning the concept of species and replacing it with a new system would ultimately constitute a radical change in the way biological organization is conceptualized, but the implementation of such a system would not be as painful as it might appear. The change could initially entail specifying the amount of difference in various traits (e.g. mtDNA, nuclear DNA, morphology) among recognized groups of organisms at various hierarchical levels (e.g. genera, species, subspecies, or populations in the current system). Measuring biological diversity could involve quantifying total diversity for various genetic and phenotypic traits within and among geographical regions or taxonomic groups. Studies of ‘speciation’ could be recast as studies of the evolution of reproductive isolation, and of genetic and phenotypic divergence (e.g. how much isolation or divergence over how long a period). Comparative studies (e.g. sister-species comparisons) could be replaced with comparisons of nearest-neighbor clusters in genetic space, and could incorporate the amount of difference between the clusters. Many of our suggestions are consistent

with an earlier recommendation for a standardized temporal scheme of biological classification (Avise and Johns 1999), however that method differs conceptually from ours in its dependence on the identification of discrete bins for organisms.

The suggested resolution we have superficially sketched here will certainly raise numerous questions. For example, what traits should be used to identify and quantify continuous variation among groups? Many, we hope, perhaps in a multivariate representation of axes combining correlated traits. How would the groups be identified, either before or during analysis? Many groups should appear as emergent properties of the data, and in our approach these groups need not be considered discrete – the degree of overlap can be quantified. What should be done when different markers or traits are in disagreement as to the strength of group identity? Perhaps they should all be retained as useful descriptors of group distinctiveness. We do not propose that these answers are definitive. Nor do we yet have answers to many other questions, some of which have yet to be posed. Instead, we would like to extend a pluralistic appeal to the community of biologists to help us further explore what we feel is a promising line of inquiry.

Acknowledgements

Our views were shaped during discussions with our friends and colleagues at the University of British Columbia, particularly Art Poon, Dolph Schluter, and Eric Taylor. Various manuscript iterations were read by Jenny Boughman, Howard Rundle, Eric Taylor, and an anonymous reviewer. Positive reinforcement was provided by persistent entreaties from the lead author's word processing spell-checker that 'speciation' be replaced with 'speculation'. A. P. Hendry was supported by a Natural Sciences and Engineering Council of Canada Postdoctoral Fellowship.

References

Arnold ML (1997) *Natural Hybridization and Evolution*. Oxford University Press, Oxford.

Avise JC (1994) *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York.

Avise JC, Johns GC (1999) Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl. Acad. Sci.*, **96**, 7358–7363.

Avise JC, Walker D (1998) Species durations and Pleistocene effects on vertebrate phylogeography. *Proc. R. Soc. London Ser. B*, **265**, 457–463.

Avise JC, Walker D (1999) Species realities and numbers in sexual vertebrates: Perspectives from an asexually transmitted genome. *Proc. Natl. Acad. Sci. USA*, **96**, 992–995.

Avise JC, Walker D, Johns GC (1998) Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. London Ser. B*, **265**, 1707–1712.

Claridge MF, Dawah HA, Wilson MR (1997) *Species: The Units of Biodiversity*. Chapman & Hall, New York.

Cracraft J (1983) Species concepts and speciation analysis. In: *Current Ornithology* (ed. Johnston R), pp. 159–187. Plenum Press, New York.

Crozier RH (1992) Genetic diversity and the agony of choice. *Biol. Cons.*, **61**, 11–15.

Crozier RH (1997) Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. *Annu. Rev. Ecol. Syst.*, **28**, 243–268.

Darwin C (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London.

de Jong WW (1998) Molecules remodel the mammalian tree. *Trends Ecol. Evol.*, **13**, 270–275.

Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol. Cons.*, **61**, 1–10.

Faith DP (1994) Phylogenetic pattern and the quantification of organismal biodiversity. *Phil. Trans. R. Soc. Lond. B.*, **345**, 45–58.

Goldstein PZ, DeSalle R, Amato G, Vogler AP (2000) Conservation genetics at the species boundary. *Cons. Biol.*, **14**, 120–131.

Howard DJ, Berlocher SH (1998) *Endless Forms: Species and Speciation*. Oxford University Press, Oxford.

Hughes JB, Daily GC, Ehrlich PR (1997) Population diversity: its extent and extinction. *Science*, **278**, 689–692.

Johns GC, Avise JC (1998) A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Mol. Biol. Evol.*, **15**, 1481–1490.

Klicka J, Zink RM (1997) The importance of recent Ice Ages in speciation: a failed paradigm. *Science*, **277**, 1666–1669.

Klicka J, Zink RM (1999) Pleistocene effects on North American songbird evolution. *Proc. R. Soc. London Ser. B*, **266**, 695–700.

Krajewski C (1994) Phylogenetic measures of biodiversity: a comparison and critique. *Biol. Cons.*, **69**, 33–39.

Mallet J (1995) A species definition for the modern synthesis. *Trends Ecol. Evol.*, **10**, 294–299.

Mayden RL (1997) A heirarchy of species concepts: the denouement in the saga of the species problem. In: *Species: The Units of Biodiversity* (eds. Claridge MF, Dawah HA, Wilson MR), pp. 381–424. Chapman & Hall, New York.

Mayr E (1940) Speciation phenomena in birds. *Am. Nat.*, **74**, 249–278.

Mayr E (1957) Species concepts and definitions. In: *The Species Problem* (ed. Mayr E), pp. 1–22. American Association for the Advancement of Science, Washington.

Mayr E (1996) What is a species, and What is not? *Philos. Sci.*, **63**, 262–277.

Moritz C (1994) Defining 'evolutionarily significant units' for conservation. *Trends Ecol. Evol.*, **9**, 373–375.

Otte D, Endler JA (1989)*Speciation and Its Consequences*. Sinauer Associates Inc., Sunderland.

Pennock DS, Dimmick WW (1997) Critique of the evolutionary significant unit as a definition for "distinct population segments" under the U.S. Endangered Species Act. *Cons. Biol.*, **11**, 611–619.

Peterson AT, Navarro-Sigüenza AG (1999) Alternative species concepts as bases for determining priority conservation areas. *Cons. Biol.*, **13**, 427–431.

Riddle BR, Hafner DJ (1999) Species as units of analysis in ecology and biogeography: time to take the blinders off. *Global Ecol. Biogeogr.*, **8**, 433–441.

Schluter, D (1996) Ecological speciation in postglacial fishes. *Phil. Trans. R. Soc. Lond. Ser. B*, **351**, 807–814.

Taylor EB (1999) Species pairs of north temperate freshwater fishes: evolution, taxonomy, and conservation. *Rev. Fish Biol. Fisheries*, **9**, 299–324.

Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect?-Systematics and the agony of choice. *Biol. Cons.*, **55**, 235–254.

Vogler AP, DeSalle AP (1994) Diagnosing units of conservation management. *Cons. Biol.*, **8**, 354–363.

Waples RS (1991) Pacific salmon, *Oncorhynchus spp.*, and the definition of “species” under the Endangered Species Act. *Mar. Fisheries Rev.*, **53**, 11–22.

Waples RS (1998) Evolutionarily significant units, distinct population segments, and the Endangered Species Act: reply to Pennock and Dimmick. *Cons. Biol.*, **12**, 718–721.

Wilson EO (1992) *The Diversity of Life*. W. W. Norton and Company, New York.

Wilson RA (1999) *Species*. The MIT Press, Cambridge.

Wheeler QD, Meier R (1997) *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press, New York.