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Review

Taxonomic Considerations in Listing Subspecies Under the U.S. Endangered Species Act

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Abstract: *The U.S. Endangered Species Act (ESA) allows listing of subspecies and other groupings below the rank of species. This provides the U.S. Fish and Wildlife Service and the National Marine Fisheries Service with a means to target the most critical unit in need of conservation. Although roughly one-quarter of listed taxa are subspecies, these management agencies are hindered by uncertainties about taxonomic standards during listing or delisting activities. In a review of taxonomic publications and societies, we found few subspecies lists and none that stated standardized criteria for determining subspecific taxa. Lack of criteria is attributed to a centuries-old debate over species and subspecies concepts. Nevertheless, the critical need to resolve this debate for ESA listings led us to propose that minimal biological criteria to define disjunct subspecies (legally or taxonomically) should include the discreteness and significance criteria of distinct population segments (as defined under the ESA). Our subspecies criteria are in stark contrast to that proposed by supporters of the phylogenetic species concept and provide a clear distinction between species and subspecies. Efforts to eliminate or reduce ambiguity associated with subspecies-level classifications will assist with ESA listing decisions. Thus, we urge professional taxonomic societies to publish and periodically update peer-reviewed species and subspecies lists. This effort must be paralleled throughout the world for efficient taxonomic conservation to take place.*

Keywords: distinct population segment, evolutionarily significant unit, IUCN Red List, nomenclature, taxonomy

Consideraciones Taxonómicas para Enlistar Subespecies en el Acta de Especies en Peligro de E. U. A.

Resumen: *El Acta de Especies en peligro de E. U. A. (AEP) permite el enlistado de subespecies y otras agrupaciones por debajo del nivel de especie. Esto proporciona medios al Servicio de Pesca y Vida Silvestre y al Servicio Nacional de Pesquerías Marinas para seleccionar la unidad más crítica que requiere ser conservada. Aunque casi la cuarta parte de los taxa enlistados son subespecies, estas agencias de gestión están limitadas por incertidumbres acerca de estándares taxonómicos durante las actividades de inclusión o remoción del listado. En una revisión de publicaciones y sociedades taxonómicas, encontramos pocas listas de subespecies y ninguna que definiera criterios estandarizados para la determinación de taxa subespecíficos. La carencia de criterios es atribuida a un debate, que lleva siglos, sobre los conceptos de especie y subespecie. Sin embargo, la crítica necesidad de resolver este debate para los listados de AEP nos llevó a proponer que los criterios biológicos mínimos para definir subespecies (legal o taxonómicamente) deben incluir los criterios de discreción y significancia de segmentos distintos de la población (tal como los define AEP). Nuestros criterios de*

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subespecie contrastan notablemente con los propuestos por los partidarios del concepto filogenético de especie y proporcionan una clara distinción entre especies y subespecies. Los esfuerzos para eliminar o reducir la ambigüedad asociada con las clasificaciones a nivel de subespecie contribuirán a la toma de decisiones del AEP. Por lo tanto, exhortamos a las sociedades taxonómicas profesionales para que publiquen, y periódicamente actualicen, listas de especies y subespecies revisadas por pares. Este esfuerzo debe ser imitado en todo el mundo para que se lleve a cabo una conservación taxonómica eficiente.

Palabras Clave: Lista Roja IUCN, nomenclatura, taxonomía, segmento distinto de la población, unidad evolutiva significativa

Introduction

Infraspecific taxa are important in discussions of biodiversity because they represent evolutionary potential within a species. Lists of taxonomic groupings are key to conservation efforts because they provide a foundation for identifying species, subspecies (i.e., taxa below the species level), and evolutionarily unique populations. Recognizing this, subspecific taxa are included in the World Conservation Union (IUCN) Red List of Threatened Species, appendices in the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), TRAFFIC (wildlife trade monitoring network), Brazil's Lista Nacional das Espécies da Fauna Brasileira Ameaçadas de Extinção, Canada's Species at Risk Act, Australia's Environmental Protection and Biodiversity Act, South Africa's Biodiversity Act, and others (http://eelink.net/~asilwildlife/legislat.shtml).

The U.S. Endangered Species Act of 1973 (ESA) also protects infraspecific taxa. Originally the ESA definition of *species* included "any subspecies of fish or wildlife or plants." In 1978, the ESA was amended so "species" encompassed "any distinct population segment (i.e., DPS) of any species of vertebrate fish or wildlife, which interbreeds when mature" (USFWS & NMFS 1996). Currently one-quarter of ESA-listed taxa have subspecific rank (Tables 1 & 2; Fig. 1).

Listing subspecific taxa is becoming increasingly controversial (Isaac et al. 2004; Zink 2004; Harris & Froufe 2005; Mallet et al. 2005) due to incongruencies between biological and legal criteria for recognizing and protecting subspecific taxa and because of the continuing debate among taxonomists regarding the validity of subspecies as a taxonomic unit (e.g., Zink et al. 2000; Ramey et al. 2005). This has been exacerbated by careless taxonomy in some cases (reviewed in Mayr & Ashlock 1991) and overapplication of the subspecies concept for species that attract human interest. Thus, the concept further fell out of favor when subspecies of notable species such as the leopard (*Panthera onca*; Larson 1997; Eizirik et al. 2001), Seaside Sparrow (*Ammodramus nigrescens*; Avise & Nelson 1989), and Redwing Blackbird (*Agelaius phoeniceus*; Williams et al. 2004) did not hold up under scrutiny.

Among taxonomists, definitions of subspecies are a source of considerable disagreement. This uncertainty is compounded in a conservation context when the specialized taxonomic expertise required to evaluate conflicting interpretations does not exist within management agencies responsible for listing species. Thus, management agencies need to be made aware of the best available science and policies that can relate biological criteria to legal requirements under the ESA.

To illustrate and understand the taxonomic information available to agencies evaluating subspecies for ESA listing we (1) reviewed subspecific definitions and concepts across taxonomic groups, (2) examined how subspecific taxa have been used in ESA listings, (3) reviewed variations in how taxonomists and management agencies use subspecific taxonomic groupings, (4) carried out discussions of issues related to subspecific listings with agency personnel responsible for ESA-related matters, and (5) devised recommendations on how taxonomists can better contribute to conservation under the ESA and other similar legislative entities around the world.

Subspecific Definitions and Concepts

Species are generally recognized as the fundamental units of taxonomy, but species concepts provide little assistance in recognizing taxa below the species level. For example, reliance of Mayr's (1963) biological species concept (BSC) on reproductive isolation between species might lead one to assume that partial reproductive isolation would be an appropriate criterion for subspecies recognition. Nevertheless, there is little evidence outside of *Drosophila* (e.g., Ayala et al. 1974) that this criterion has been routinely employed. Thus, in recent decades, taxonomists have applied subspecies names to geographic races without evidence of or reference to partial isolation. Under most phylogenetic species concepts (PSCs; Cracraft 1983), species are the smallest, irreducible, monophyletic units as measured by molecular markers. Any groupings within such species do not warrant taxonomic standing, so subspecies are not recognized.

Table 1. Species and subspecies listings by taxa under the U.S. Endangered Species Act as of October 2005.[a]

Taxon	*U.S. listings[b]*			*Species listed outside U.S.[c]*			*All listings*
	species	*subspecies*	*total*	*species*	*subspecies*	*total*	
Birds	53	40	93	145	39	184	277
Mammals	28	56	84	209	68	277	361
Fish	121	21	142	12	0	12	154
Herpetofauna	40	16	56	74	25	99	155
Invertebrates	141	15	156	2	1	3	159
Plants	617	125	742	3	0	3	745
Fungi (lichens)	2	0	2	0	0	0	2

[a]*Data summarized from http://www.fws.gov/endangered. Trinomials are considered subspecies, whereas those listed as binomials are considered species.*
[b]*Species were considered to be U.S. listings if the reported historic range included the United States and the listing included their entire range.*
[c]*Listings outside of the United States are principally CITES listings.*

The concept of infraspecific taxa has been used at least since Linnaeus' time (1753). Qualitative definitions have been proffered by Darwin (1896), who considered varieties to be incipient species, potentially evolving into full species; Mayr (1963), defined subspecies as "geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of the species"; and Frankham et al. (2002), who stated they were ". . . populations partway through the evolutionary process of divergence toward full speciation." Qualitative definitions have been criticized as arbitrary because some groups classified qualitatively as subspecies are not differentiated based on multiple characters (Wilson & Brown 1953; Mallet 2001).

Traditionally, subspecies have been defined by morphological traits or color variations, but recent critics are concerned that these traits may not reflect underlying genetic structure and phylogenies. This concern stems from recent work in which phylogenetic patterns of genetic variation were not concordant with some subspecies classifications defined by morphology (Zink 1989; Ball & Avise 1992; Zink et al. 2000; Zink 2004).

The only quantitative subspecies definition we found was the 75% rule (Amadon 1949; Patten & Unitt 2002) that states a subspecies is valid if 75% or more of a population is separable from all (or >99% of) members of the overlapping population. Although the 75% rule is more quantitative than other definitions, there is disagreement about the 75% threshold and the number of characters that should be used when comparing populations (Patten & Unitt 2002).

Despite all the criticisms, recent studies in which researchers used multiple criteria (e.g., morphological, behavioral, and genetic characters) have confirmed that many subspecies are evolutionarily definable entities (e.g., Gavin et al. 1999; Pasquet 1999; Haig et al. 2004). Thus, although subspecies definitions may have been too liberally applied by some early taxonomists, this does not invalidate the concept of subspecies as meaningful biological entities. Taxonomists continue to recognize and sometimes describe subspecies. More work is needed, however, to clarify this taxonomic concept to assist management agencies with identifying which entities are appropriate for providing regulatory protection. These efforts should focus on developing guidelines for how to reconcile multiple lines of evidence when evaluating the validity of a subspecies. One good example of this attempt is the recent British Ornithologists Union guidelines for defining subspecies in birds (Helbig et al. 2005) that considered PSCs and the BSC.

Variation in Subspecific Classifications across Taxa

In an extensive literature review, we found no universally accepted subspecies definition within or across taxa (Table 3). Furthermore, we found use of subspecies in modern taxonomy differed by taxonomic group. In general, more subspecies have been described for vertebrates and plants than the less-studied invertebrates and fungi, where most taxonomic studies remain focused at the species level. Defining subspecies is complicated by the biology of an organism and by a paucity of knowledge about the diversity in some groups. For example, some groups (e.g., birds) are better dispersers than others;

Table 2. Potential listing categories for various taxa under the U.S. Endangered Species Act.

Taxa	*Species*	*Subspecies/variety*	*DPS[a]*	*ESU[b]*
Birds	•	•	•	
Mammals	•	•	•	
Fish	•	•	•	•[c]
Herpetofauna	•	•	•	
Invertebrates	•	•		
Plants	•	•		
Lichens/fungi	•	•		

[a]*Distinct population segment.*
[b]*Evolutionarily significant unit.*
[c]*The ESU is used for DPSs of Pacific salmon.*

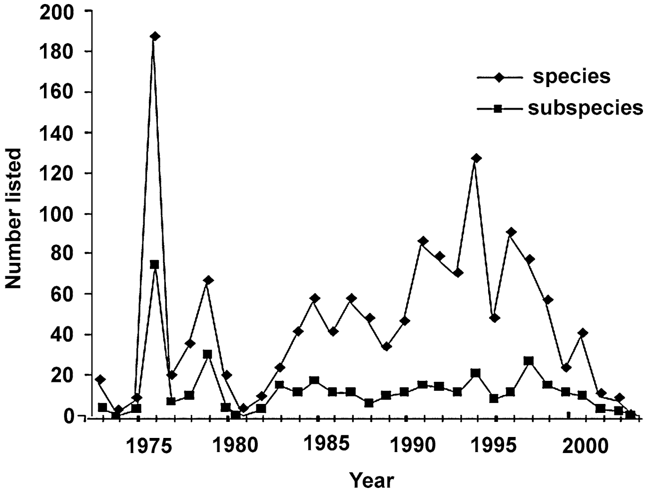

Figure 1. Number of species and subspecies listed by year under the U.S. Endangered Species Act as of October 2005.

hence, there may be fewer, less defined, or genetically differentiated avian subspecies than in less vagile taxa (e.g., amphibians). These factors and others result in an imbalance in how ESA protection can be applied across taxa.

Every taxonomic group has followed a similar evolution of ideas to resolve taxonomic questions. Historically, morphology and geography were used to separate taxa. Subsequently, BSC stimulated simplifications (i.e., lumping) at the species level and an enthusiasm for the use of subspecies level classifications to describe morphological variation within resulting polytypic species. Currently, taxonomists are struggling with how to incorporate results of modern molecular methods into their assessments that are based on various PSCs.

In the following we summarize taxon-specific use of subspecies rank, organizations that provide taxonomic standards or official lists of taxa, and the prevalence of subspecies listings under the ESA. Current species and subspecies numbers are presented in Table 3 for all taxa.

Animals (Kingdom Animalia)

The Zoological Record, implemented via the International Council on Zoological Nomenclature (ICZN), is the most comprehensive list of animal names in the world (Table 3; www.biosis.org/products/zr/). The ICZN has no role in determining which species concepts are applied; however, it provides clear instructions on the formation of specific and subspecific names and has published nomenclatural changes since 1905. Changes in recognized names of taxa are printed in the *Quarterly Bulletin of Zoological Nomenclature* with commentary from the ICZN. Additionally, its *Official List of Names in Zoology and Works in Zoological Nomenclature* includes names of taxa and titles of works that have been the subject of their rulings. The ICZN recently proposed a Web-based register ("ZooBank") that identifies animal names and facilitates communication regarding their nomenclature (Polaszek 2005).

BIRDS (CLASS AVES)

Ornithologists have spent considerable effort refining and debating subspecies concepts (Wiens 1982). In the early twentieth century, Walter Rothschild and Ernst Hartert made extensive use of their geographic-based subspecies concept in numerous avian taxonomic publications (Mayr 1976; Rothschild 1983). However, following introduction of the BSC, 315 of the 607 North American bird species were reclassified as subspecies (AOU 1957; Mayr 1982). The American Ornithologists' Union (AOU) Committee on Classification and Nomenclature is the scientific body responsible for standardizing avian taxonomy in North America. The committee has published seven editions of its *Checklist of North American Birds* since 1896. Subspecies were included in the first four editions but have not been included since 1957 due to committee time

Table 3. Estimated numbers of worldwide and U.S. species per taxon and use of infraspecific categories in taxonomy.

	Species			
Taxon	*worldwide*	*U.S.*	*Infraspecific categories*	*Authority reference*
Birds	9,688	650	mostly subspecies	AOU 1998; globalforestwatch.org; bsc-eoc.org/avibase/avibase.jsp
Mammals	5,416	432	mostly subspecies	Wilson & Reeder 2005; globalforestwatch.org
Fish	24,600	2,428	subspecies but not often	Robins et al. 1991; Helfman et al. 1997
Amphibians	5,743	263	subspecies	globalamphibians.org; globalforestwatch.org
Reptiles	8,240	287	subspecies	reptile-database.org; globalforestwatch.org
Invertebrates	1,288,518	approximately 93,000	subspecies, varieties	Brusca & Brusca 2003; www.iczn.org
Plants	300,000	n/a	subspecies, varieties, forms	Greuter et al. 2000
Fungi	80,000–150,000 described	5–10,000	subspecies, varieties, forms	Kirk et al. 2001

constraints AOU (1998). Currently, 43% of ESA-listed birds are listed at the subspecific rank, emphasizing the importance of reliable avian subspecific taxonomy (Table 1).

Recent avian subspecies debates have been motivated by examples of genetic population structure that differed from morphology-based subspecies delineations (Zink 1989; Ball & Avise 1992; Zink et al. 2000; Zink 2004). Some ornithologists argue that historic classifications may not accurately reflect phylogeny because morphological differences do not always have a phylogenetically significant basis (Zink 2004). Others debate whether the subspecies concept has intrinsic value to avian classification (Smith & White 1956; Barrowclough 1982; Wiens 1982; Zink 2004). Yet a new consideration of avian subspecies worldwide indicates that 36% are phylogenetically distinct and that lack of distinctness is most pronounced in North American and European taxa, where much of the debate has taken place (Phillimore & Owens 2006).

MAMMALS (CLASS MAMMALIA)

Mammalian classification is listed in *Mammal Species of the World* (Wilson & Reeder 2005), which is updated every 10 years in a cooperative effort between the Association of Systematics Collections and the American Society of Mammalogists. Editors assume that systematic and nomenclatural decisions are the province of the professional research community, but they address conflicting opinions regarding taxonomy. Modern systematists suggest that some traditional mammalian subspecific designations based on minor geographic variations in size and/or color may not necessarily represent actual genetic differences. Conversely, cryptic taxa have been overlooked and denied status (Hershkovitz 1983; Smith & Patton 1988). Over two-thirds of ESA mammal listings are for subspecies (Table 1). Although this trend toward subspecies listing has been consistent over time, more-recent mammal listings have focused on DPSs (Fig. 1).

FISHES (CLASSES CEPHALASPIDOMORPHI, CHONDRICHTHYES, MYXINI, AND OSTEICHTHYES)

Fishes are the most diverse vertebrate group at the species level, with approximately 24,600 formally recognized species globally (Helfman et al. 1997; Table 3). Subspecies classifications in fish are based most commonly on allopatry (Echelle 1991; Duvernell & Turner 1999). In this context, Linnaen trinomials applied to fishes are largely synonymous with geographic races. There is a wide disparity, however, in levels of molecular genetic divergence among conspecific taxa representing different subspecies. Some taxonomists argue against use of subspecies designations for fish because under a strict subspecies definition (e.g., a population in a particular region that is genetically distinguishable from other such populations and is capable of interbreeding with them), every isolated creek and pond could have a unique subspecies or species of fish (Mayden 1999).

The American Fisheries Society and the American Society of Ichthyologists and Herpetologists are the scientific bodies responsible for reviewing published taxonomic descriptions of fish and for compiling a standardized list of fish species, subspecies, and other infraspecific names for North American taxa (Nelson et al. 2004). Their joint Name of Fishes Committee *List of Species* does not list subspecies but acknowledges them in footnotes (e.g., subspecies of Pacific salmon, *Onchorynchus mykiss*). Thus, because subspecific classification has been used unevenly and often sparingly with fishes, it is correspondingly underrepresented in ESA listings. Only 15% of U.S. fish listings are targeted at the subspecific rank (Table 1). The USFWS and National Marine Fiseries Service (NMFS) have more often listed fish DPSs (NMFS uses an ESU concept to define DPSs of Pacific salmon; NMFS 1991) than subspecies. Consequently, 31% (44/142) of domestic fish listings are at the level of DPS.

REPTILES (CLASS REPTILIA) AND AMPHIBIANS (ORDERS ANURA, CAUDATA, AND GYMNOPHIONA)

In North America, the Society for the Study of Amphibians and Reptiles (SSAR) and the Center for North American Herpetology publish lists of scientific and standard herpetological names (Crother et al. 2000, 2003; Collins & Taggart 2002; Table 3). Both lists include subspecies. The SSAR list has been sanctioned by the major herpetological societies in North America (Stuart 2002). A review of the SSAR list (Crother et al. 2003) indicates that a similar number of species and subspecies have been identified in North America. The proportion of subdivided species within each genus ranges from 0% (crocodiles) to 56% (snakes), with up to 12 subspecies described per species.

Variation in the ratio of described species/subspecies under herpetofauna reflects the fact that the subspecies concept has fallen from favor in modern herptofauna systematics (D. Wake, personal communication). Currently, 29% of ESA herpetofaunal listings are for subspecies (Table 1). Whether this disproportionate listing of species reflects a greater need for conservation at the species level in herpetofauna or the influence of other factors (e.g., a disproportionate listing of taxa with relatively few recognized subspecies) is unclear.

INVERTEBRATES (PHYLA ANNELIDA, ARTHROPODA, BRACHIOPODA, BRYOZOA, CNIDARIA, CTENOPHORA, ECHINODERMATA, LORICEFERA, MOLLUSCA, NEMATODA, PHORONIDA, PLATYHELMINTHES, PORIFERA, AND ROTIFERA)

Invertebrates make up a vast paraphyletic group that includes approximately 96% of all described animal species (Table 3). Thus, multiple professional groups oversee their nomenclature. In North America, these groups include the Acarological Society of America (mites), American Malacological Society (molluscs), International Union for the Study of Social Insects (primarily Hymenoptera and some Isoptera), Orthopterists Society (grasshoppers), Crustacean Society (all crustaceans), Xerces Society (primarily butterflies), Lepidopterists Societies (butterflies), and Coleopterists Society (beetles).

Among invertebrates, fine-scale variation in morphological traits has most often been ascribed at the species rather than subspecies level. Combined with a lower overall amount of taxonomic knowledge, relatively few species or subspecies of invertebrates have been described compared with most vertebrate groups, except among butterflies (Wilson & Brown 1953; Brusca & Brusca 2003). Subspecific ESA listings have largely been restricted to more fully described taxa such as butterflies and freshwater mollusks.

Plants (Kingdom Plantae)

Botanical species concepts are numerous (Stuessy 1990; McDade 1995; Mayden 1997; Bachmann 1998; Rieseberg & Burke 2001). However, most plant taxa have been described based on a morphological (or Linnaean) species concept. Although subspecific concepts in plants have received less discussion than species concepts (but see Stuessy 1990; McDade 1995), subspecific taxa are frequently described. McDade (1995) found that of 104 contemporary monographs, 56% included infraspecific taxa. Authors generally utilized the rank of subspecies or variety (roughly equally) but not both. This suggests that although these concepts are technically different (Greuter et al. 2000), in practice they are being treated synonymously (McDade 1995; Table 3). Consequently, extension of the ESA's definition of species to include "variety" (USFWS 1978) appears congruent with current nomenclatural practice.

The naming of plants (and historically, fungi) is dictated by the International Code of Botanical Nomenclature (Greuter et al. 2000). The code provides a hierarchy (species, subspecies, variety, form) but no definitions to clarify ranks. There is no internationally recognized list of valid plant taxa, but the U.S. Department of Agriculture's PLANTS database (USDA NRCS 2006) is used to provide guidance for federal agencies. Many states have floras compiled that, although frequently out of date, provide a local authority on plants. The *Flora of North America* (1993+) is an ongoing, multi-volume project that has been partially published and is considered an authority on plant names for the United States.

In the United States, ESA authority to list DPSs and the ESA "take" prohibitions do not apply to plants (Table 2). The protections that do apply to plants cover only those that occur on federally owned land or are affected by a federal action. Thus, the ESA provides protection for plants to a more-limited extent than to animals. Of 745 plants listed by USFWS, 123 are for subspecies (including varieties; Table 1).

Kingdom Fungi

Fungus taxonomy is focused at the species level. Approximately 800 new fungus species names are cataloged in the *Index Fungorum* each year, but many are never reassessed after their original description. It is estimated that mycologists inadvertently redescribe known species at a rate of 2.5:1 (Hawksworth 1991). Given this error rate, the estimated number of described fungal species ranges from 80,060 to 150,000. It is widely accepted that there are 1.5 million species of fungi worldwide (Hawksworth 1991), which suggests that $<$10% of fungal species have been described.

The authoritative reference on fungal taxonomy is *The Dictionary of the Fungi* (Kirk et al. 2001), which is in its fifty-ninth year and ninth edition. This dictionary summarizes accumulated knowledge on all organisms studied by mycologists including lichens, mushrooms, slime molds, water molds, and yeasts. Criteria for delineating the three subspecific categories most commonly used in fungal taxonomy (subspecies, variety, form) are defined by individual monographers and vary among families and genera. The terms *subspecies* and *variety* appear to be used interchangeably (see *Index Fungorum*, www.indexfungorum.org). In many situations, however, the same infraspecific name is listed under the rank of subspecies and variety. Often the rank of subspecies is converted to the rank of variety in later taxonomic treatments, indicating either that most fungal taxonomists consider the ranks biologically equivalent or have not settled on criteria to define them. The uncertainty surrounding the number of described and actual fungi species suggests standardized criteria for designating subspecific ranks are unlikely to be defined in the near future.

There is no world or North American checklist for fungi, although establishment of MycoBank in 2004 (Hawksworth 2005; www.mycobank.org) is quickly filling that niche by providing online accession numbers to newly described taxa. Currently only two species of lichenized fungi (*Cladonia perforata*; *Gymnoderma lineare*) are listed under the ESA (USFWS 1993, 1995*a*). Future efforts related to listing fungi under the ESA should pay special attention to verifying names at the taxonomic rank of species, if not subspecies or variety.

Perspectives and Recommendations

Listing Subspecies

Listing subspecies under the ESA has increasingly become a source of conflict in science and policy. The complex processes involved in speciation (Dobzhansky 1937; Grant 1981; Coyne & Orr 2004) can make it difficult to define species or subspecies relationships as simply as stated in the applicable legislation. Although the scientific community has some level of comfort with the subjective nature of subspecies classification (Hey et al. 2003), agencies and the general public want subspecies criteria to be more quantitative or better defined so that conservation designations are applied more predictably. One potential criterion would favor adopting a PSC. They generally do not, however, recognize subspecies, and it would result in species-level recognition of smaller units. That is, subspecies would either be elevated to full species or not be recognized. This would lead to a proliferation of described species, most of which would occupy more-restricted ranges and thereby be more vulnerable to extinction and listing under the ESA. In addition, phylogenetic taxonomy presents its own methodological problems and is not universally accepted among biologists (Hudson & Coyne 2002; Avise 2004; Coyne & Orr 2004).

The lack of rigid definitions does not mean that currently described subspecies are not useful for defining populations worthy of ESA listings. For example, listings have included well-known and accepted subspecies such as Florida panther (*Felis concolor coryi*; USFWS 1967), Northern Spotted Owl (*Strix occidentalis caurina*; USFWS 1990), and Marbled Murrelet (*Brachyramphus marmoratus marmoratus*; USFWS 1992). Nevertheless, listing a poorly defined or invalid subspecies could have unwarranted economic impact on private landowners, developers, and other interests (Zink et al. 2000; Ramey et al. 2005). Clearly, the best possible methods must be used to assess taxonomy to avoid this problem. These assessments may have to be reevaluated periodically as techniques evolve, similar to adaptive management efforts in other types of biological management.

The ESA provides for protection of groups or populations to allow for the conservation of evolutionary potential within a species. This helps focus management efforts on vulnerable areas so that the entire species does not become endangered or threatened. Thus, subspecies and DPS listings will result in a far less long-term impact on stakeholders than listing entire species because they ensure evolutionary potential is preserved but do not invoke protections beyond what is needed for a specific population.

Resolution of Subspecies Taxonomy and ESA Listings

In view of the legal need to bring together taxonomy and the ESA, as well as provide greater consistency for describing subspecies within each of the major taxonomic groups, we need a unified set of criteria that are biologically and legally defensible under the ESA. Certainly, we need to assure these decisions occur unidirectionally (Bowen & Karl 1999). That is, conservation strategies should be influenced by taxonomy, but taxonomy cannot be influenced by conservation priorities.

We propose that, as a starting point for discussion about subspecies criteria, *minimal* biological requirements in most situations include two criteria based on discreteness of the population in relation to the remainder of the species to which it belongs and the biological significance of the population to the species. This is in contrast to "evolutionary significance," which implies more species-like relationships. In other words, if a taxonomic subspecies does not satisfy these criteria, then the biological legitimacy of the particular subspecies classification should be questioned. Modification of the discreteness criterion would be necessary to allow for cases where subspecies contact one another along a stable hybrid zone but maintain their taxonomic integrity elsewhere. Adopting these criteria would provide for consideration of multiple types of biological data, not just molecular genetic data, yet would still carry the requirement of defining differences. Satisfaction of these criteria, however, would not necessarily warrant subspecies recognition via a Linnaean trinomial.

The proposed minimum criteria are somewhat similar to the DPS criteria in that the DPS policy provides useful discussion and insight into a reasonable set of minimum criteria for evaluating potential designations for groups lacking prior serious taxonomic consideration. Nevertheless, there are distinct differences between DPSs and subspecies; in particular, the caveat that DPSs are not listed for plants and invertebrates whereas subspecies of these taxa can be listed. Further, subspecies are a taxonomic grouping whereas DPSs are a legal classification.

Our proposal takes a distinctly different tact than that proposed by supporters of the PSC. The requirement that a taxonomic subspecies should satisfy the phylogenetic species rids taxonomy of the term *subspecies* and uses only molecular data in assessment of taxonomy. This emphasis on establishing evolutionary distinctness does not resolve the subspecies issue; hence, it provides a narrow perspective not useful for ESA considerations of units below the species level. Furthermore, factors other than genetics need to be considered in understanding relationships below the species level.

New Subspecific Descriptions and Taxonomic Revisions Involving Subspecies

When describing new subspecies or revising subspecies taxonomy, detailed descriptions of concepts and criteria used to determine taxonomic relationships should accompany each proposed classification or reclassification published in the scientific literature. We recommend explicit description of the geographic distributions of taxa to clearly define their limits for agency management. Experts in each field are better able to judge the legitimacy of subspecies if the methodology, including the species concept used to determine classification, is stated explicitly in taxonomic publications.

Molecular genetic techniques will continue to be useful for evaluating subspecies designations. Nevertheless, the level and magnitude of genetic variation among and within well-documented closely related species should be described for the sake of comparison (Barrowclough & Flesness 1996; Fraser & Bernatchez 2001). It is important to recognize that although these tools excel at exploring historic reproductive isolation, they usually do not directly address adaptive divergence. Therefore, all else being equal, species with high dispersal rates will have fewer subspecies identified via molecular markers than species with lower rates of dispersal. Consequently, they will generally require additional information beyond molecular markers to justify designation of subspecies, such as evidence of local adaptation in spite of ongoing gene flow.

Recent work emphasizes that adaptive divergence can take place despite gene flow (Wu 2001; Beaumont & Balding 2004). It is, therefore, important to use multiple sources of information when evaluating a taxon's status including tools that address the questions of reproductive isolation, adaptive divergence, and spatial patterns of local adaptation (Crandall et al. 2001; Fraser & Bernatchez 2001). Because it will often be impossible to clearly show adaptive divergence among populations (with translocation, common-garden experiments, or population-genomic approaches), significant differences in phenotypes (e.g., morphology, behavior, life history, or ecology) and environments may reflect local adaptation and should be used in listing decisions when harder scientific evidence for local adaptation would be too difficult or expensive to acquire. Thus, higher levels of confidence can be obtained in classifications based on the concurrence of multiple morphological, molecular, ecological, behavioral, and/or physiological characters.

Whatever criteria are accepted, professional taxonomic societies and journal editors need to adopt statements describing the range of currently acceptable taxonomic standards and concepts so that agencies preparing ESA listings have the proper peer-reviewed criteria to judge professional taxonomic decisions. We further recommend expert nomenclatural and taxonomic committees create and update accurate species and subspecies lists. The resulting lists could then be globally standardized and made accessible on the Internet through hosts such as the Global Biodiversity Information Facility (www.gbif.org/) or the National Biological Inventory Substructure (www.nbii.gov/index.html).

New ESA Subspecific Listings

The published final rules for endangered and threatened subspecies demonstrate that USFWS and NMFS use (and need) peer-reviewed publications, taxonomic checklists provided by professional societies, and comments from independent scientists and expert panels when evaluating taxonomic status. Therefore, USFWS and NMFS biologists actively seek professional comments when rules are under review, yet sometimes find limited published information or few taxonomists who specialize in that species, groups of species, or techniques used to classify subspecies. Consequently, numerous listings require extended internal reviews of taxonomic status by USFWS or NMFS because published information was either contradictory or not available. In some cases these agencies must evaluate highly esoteric disagreements among respected scientific experts with little expertise of their own (e.g., USFWS 2005). An example is the final rule for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). It stated that "the Service reviewed the information and found a majority opinion that *E. t. extimus* is a valid subspecies. . ." (USFWS 1995*b*). Although some degree of interpretation of what is the "best available" scientific information will always be required of management agencies when making listing decisions, the scientific community can help ensure that interpretation of taxonomy is solely a scientific endeavor.

Taxonomists can make a more significant contribution to conservation by developing an understanding of ESA policy (or the appropriate policies of their country) and regulatory requirements for listing species under the ESA. This will help taxonomists understand the nature of taxonomic challenges faced by agency biologists and provide directions for future research. Thus, the key is to provide scientists with enough practical background so they can understand consequences of different biological conclusions without making them advocates or encouraging them to blur boundaries between science and policy. Of course, these professionals must maintain an independence from the conservation implications of their work. Thus, we reemphasize the point that the relationship between conservation and taxonomy must be unidirectional (Bowen & Karl 1999).

Professional societies can reduce taxonomic uncertainty by working with USFWS and NMFS to identify old listings that may need taxonomic updating. This will facilitate research that can clarify these issues through the use of modern tools. An adaptive management strategy for dealing with taxonomy will keep taxonomy and listings up to date in view of the latest technology. Furthermore, it would be a major contribution to conservation if professional societies maintained a list of members who are qualified to make taxonomic evaluations or to participate in panels to evaluate special taxonomic cases for subspecies that are subjects of listing action or likely to become so. Peer-reviewed assessments of particular issues conducted by independent professional societies or their members will lend credibility to conclusions about taxonomy for the management agencies.

Conclusions

The ESA's protection of biodiversity through listing at the level of taxonomic species and subspecies provides taxonomists with a unique and challenging opportunity. Efforts to eliminate or reduce ambiguity associated with subspecies-level classifications will assist with ESA listing decisions and facilitate better identification of relationships among taxa by taxonomists. Although their general application extends worldwide, our recommendations may appear fairly U.S.A.-centric. To our knowledge, these taxonomic issues have weighed more heavily in the United States than in countries without the legislative ability to protect subspecies, with newer legislation, and those with fewer penalties for violation. Nevertheless, efforts to list subspecies under (for example) CITES or the IUCN Red List of Threatened Species already call for better clarification of taxa. We hope professional societies throughout the world can see this as a global issue and participate in this important effort toward taxonomic clarification.

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