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Avian Subspecies and the U.S. Endangered Species Act

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CHAPTER 2

AVIAN SUBSPECIES AND THE U.S. ENDANGERED SPECIES ACT

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Abstract.—Scientific debate over identification of taxa below the species level has persisted for centuries. This issue can be especially problematic for avian species, because dispersal is often orders of magnitude greater than in other vertebrates, leaving genetic differences among groups proportionately smaller. While the debate lingers, management decisions, often with millions of dollars and potential extinctions resting on the outcome, are regularly made by agencies tasked with maintaining lists of threatened and endangered taxa. With outdated taxonomic treatments and no formal policy or guidelines for defining species or subspecies, agencies have no authority to cite in determining limits to species or subspecies ranges. Lack of guidance from professional organizations regarding taxonomic criteria and lists does not benefit these species of concern. Here, we describe how subspecies designations are evaluated under the Endangered Species Act, tradeoffs between maintaining the biological species concept in avian taxonomy versus adopting a phylogenetic species approach, and why it is imperative for scientific organizations to maintain updated taxonomic treatments regardless of the species concept they use.

Key words: biological species concept, distinct population segment, Endangered Species Act, phylogenetic species concept, species, subspecies.

Subespecies de Aves y el Acta de Especies Amenazadas de los Estados Unidos

Resumen.—El debate científico sobre la identificación de taxones por debajo del nivel de especie ha persistido por siglos. Este asunto puede ser especialmente problemático para las especies de aves, debido a que la dispersión en éstas con frecuencia es órdenes de magnitud mayor que en otros vertebrados, lo que conduce a que las diferencias entre grupos sean proporcionalmente más pequeñas. Mientras el debate continúa sin resolverse, las agencias que mantienen listas de taxones amenazados regularmente toman decisiones de manejo que ponen en juego millones de dólares y extinciones potenciales. Al contar con tratamientos taxonómicos desactualizados y al carecer de políticas o lineamientos formales para definir especies y subespecies, las agencias no tienen autoridades a las cuales citar al determinar los límites de las distribuciones de las especies y subespecies. La falta de guianza por parte de organizaciones profesionales con respecto a los criterios taxonómicos y a las listas no beneficia a las especies de interés en la conservación. En este trabajo, describimos cómo las designaciones de subespecies son evaluadas bajo el Acta de Especies Amenazadas, los compromisos entre mantener el concepto biológico de especie en la taxonomía de las aves versus adoptar un enfoque de especies filogenéticas, y por qué es imperativo que las organizaciones científicas mantengan tratamientos taxonómicos actualizados, independientemente del concepto de especie que utilicen.

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The subspecies concept may be "the most critical and disorderly area of modern systematic theory" (Wilson and Brown 1953:100), and debate over the existence and definition of subspecies will likely continue for years to come because of fundamental differences of opinion regarding species concepts and inherent difficulties in objectively determining intraspecific units. In the meantime, bird species worldwide face an extinction crisis of epic proportions (e.g., 2–3 times the prehuman rates of extinction; Brooke et al. 2008). This crisis results from factors such as anthropogenic habitat destruction, climate change, and introduction of invasive species. As a result, many government and nongovernmental conservation agencies around the globe seek to efficiently and effectively identify and prioritize taxonomic and conservation units eligible for protection (Table 1; Phillimore and Owens 2006). Garnett and Christidis (2007) summarized international endangered-species legislation and definitions of what taxonomic groups are eligible for listing under each system and found that it tends to be in the poorer countries, many of which are highly subspeciose, that subspecies assessments have not been undertaken. Some of those poorer countries rely exclusively or heavily on assessments by the International Union for the Conservation of Nature, which does not currently assess avian subspecies because of a lack of resources. However, in countries where these assessments are undertaken, subspecies taxonomy can have considerable influence on the allocation of limited conservation resources. To provide some perspective on this situation, we discuss below why subspecies designations matter for avian species listed under the U.S. Endangered Species Act. We consider the legal and conservation implications of avian taxonomists officially adopting either the biological species concept or a phylogenetic species concept.

Why Subspecies Matter under the Endangered Species Act

Subspecies have been eligible for protection since the inception of endangered species laws in the United States. In 1966, 13 of the 36 avian taxa listed under the 1966 Endangered Species Preservation Act were subspecies. Today, under the Endangered Species Act of 1973 (as amended, 16 U.S.C. 1531 et seq.), 40 of 90 avian taxa listed are subspecies, which represents one of the highest percentages (44%) of avian subspecies listings among national and international classification systems of imperiled species (Table 1). Yet most taxonomists are not aware of how subspecies designations affect the listing and recovery of populations under the Endangered Species Act, despite the fact that taxonomic descriptions often have real conservation consequences. To begin to understand the complexities of the issue, one must first appreciate what is eligible for listing under the Endangered Species Act below the species level and how those listings are affected by trinomial nomenclature.

The Endangered Species Act allows listing of species, subspecies, and "distinct population segments" of vertebrates. The Endangered Species Act and its implementing regulations do not include "evolutionarily significant units" in their definition of units eligible for protection. The concept of using evolutionarily significant units for Endangered Species Act listings was first introduced in a National Marine Fisheries Service (NMFS) Policy on the Definition of Species under the Endangered Species Act (NMFS 1991). The policy on distinct population segments considers evolutionarily significant units to be equivalent to distinct population segments, but in listing species under the Endangered Species Act, evolutionarily significant units have been applied only to Pacific salmon and therefore are not applicable to avifauna.

It has also been argued that "significant portions of a species' range" are eligible for Endangered Species Act protections, because this phrase is included in the act's definitions of "threatened" and "endangered." However, there is no consensus on what a significant portion of a species' range is or on whether the entire species gets listed if only a significant portion of the range is at risk (see Vucetich et al. 2006; Waples et al. 2007a, b; Nelson et al. 2007; Office of the Solicitor 2007; D'Elia et al. 2008). Litigation on this point is ongoing.

Defining the significance of a population is also a key factor in determining eligibility for status as a distinct population segment (see below). Although distinct population segments can be population segments of either species or subspecies (U.S. Fish and Wildlife Service [USFWS] and NMFS 1996; Center for Biological Diversity v. USFWS, 9th Cir. 2008), because significance is evaluated against the taxon to which it belongs (per the policy on distinct population segments), subspecies designations play a critical role in the legitimacy of some distinct-population-segment designations. Without subspecific status, some distinct population segments simply would not meet the significance

Table 1. Classification systems for imperiled species and the number of avian species and subspecies listings under each system.

Classification system	Number of avian taxa listed	Allows subspecific listing?	Number of avian subspecies listed	Percentage of avian taxa listed as subspecies	Categories[a]
International					
CITES Appendices	1,455	Yes	17	1	Appendix I, II, and III
IUCN Red List	1,217	Yes	0	0	CE, E, V
NatureServe Conservation Status Assessments	225	Yes	128	57	CI, I, V
U.S. Endangered Species Act List of Endangered and Threatened Wildlife (International)	186	Yes	37	20	T, E
Australia					
Australia's Environment Protection and Biodiversity Conservation Act List of Threatened Fauna	108	Yes	55	51	CE, E, V
Brazil					
Lista Nacional das Espécies da Fauna Brasileira Ameaçadas de Extinção Grupo	160	Yes	44	28	CE, E, V
Canada					
Federal List of Widlife Species at Risk	53	Yes	19	36	E, T, SC
Costa Rica					
Lista de Especies de Aves con Poblaciones Reducidas y en Peligro de Extincion para Costa Rica (2005)	17	No	—	—	E
Europe					
European Union Birds Directive Species	193	Yes	18	9	Annex I species
Mexico					
Especies enlistadas en la NOM-059-SEMARNAT-2001 y de especies prioritarias	361	Yes	85	24	E, T, SSP
New Zealand					
New Zealand Threat Classification List	66	Yes	22	33	NC, E, V, SD
Panama					
Animales en Peligro de Extinción en Panamá	27	Yes	0	0	E
Peru					
Especies de Fauna Amenazada del Peru	108	No	—	—	CE, E, V
Russia					
Red Data Book for the Russian Federation (1997)	123	Yes	11	9	—
South Africa					
South Africa's Red List	32	Yes	0	0	CE, E, V, PS
United States					
U.S. Endangered Species Act List of Endangered and Threatened Wildlife (Candidates)	13	Yes	3	23	C
U.S. Endangered Species Act List of Endangered and Threatened Wildlife (Domestic)	90	Yes	40	44	T, E

[a] C = candidate, CE = critically endangered, CI = critically imperiled, E = endangered, I = imperiled, NC = nationally critical, PS = protected species, SC = special concern, SD = serious decline, SSP = subject to special protection, T = threatened, and V = vulnerable.

test of the policy (i.e., those populations that are significant to the subspecies but not to the more widely distributed species) and therefore would not merit the substantial protections provided under the Endangered Species Act.

The Endangered Species Act does not define distinct population segments. However, the USFWS and the NMFS (1996), the two agencies tasked with implementing the Endangered Species Act, established a joint formal policy interpreting what the Endangered Species Act means by distinct population segments. According to the policy, two tests must be satisfied for a population segment to qualify as a distinct population segment: discreteness of the population segment in relation to the remainder of the taxon and significance of the population segment to the taxon. If a population segment qualifies as a distinct population segment, the conservation status of that distinct population segment is evaluated to determine whether it is threatened or endangered.

A population segment of a vertebrate species may be considered discrete by the USFWS if it satisfies either of the following conditions: (1) it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors; or (2) it is delimited by international governmental boundaries between which there are differences in control of exploitation, management of habitat, conservation status, or significant differences in regulatory mechanisms.

If a population is found to be discrete, it is evaluated for significance under the policy on distinct population segments on the basis of its importance to the taxon to which it belongs. This consideration may include, but is not limited to, the following: (1) persistence of the discrete population segment in an ecological setting unusual or unique to the taxon, (2) evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon, (3) evidence that the population represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historical range, or (4) evidence that the population differs markedly from other populations of the species or subspecies in its genetic characteristics. Thus, the policy on distinct population segments clearly contemplated the potential to conserve threatened or endangered populations that have a distinct evolutionary history from other populations of the same species or subspecies. This policy affords the USFWS substantial flexibility to ensure that distinct vertebrate populations are protected before the entire taxon is imperiled (Pennock and Dimmick 1997).

If a population segment is discrete and significant (i.e., it is a distinct population segment), its evaluation for endangered or threatened status is based on a thorough review of population numbers, trends, and threat factors that affect the population segment. Although the policy on distinct population segments has been upheld by several courts, individual listing decisions that rely on this policy remain heavily litigated and subject to policy interpretation regarding what qualifies as a discrete and significant population. Conversely, subspecific designations backed by taxonomic authorities are usually not subject to this kind of policy interpretation or litigation when they are kept current, because the courts generally defer to the scientific authority.

Listing Prioritization

Subspecific designations also come into play in prioritizing candidate species for listing under the Endangered Species Act and in prioritizing recovery planning. Currently, 2 of 11 candidate avian taxa are subspecies—Streaked Horned Lark (*Eremophila alpestris strigata*) and Red Knot (*Calidris canutus rufa*)—and >18% of all candidate taxa (46 of 247) are subspecies or varieties (see http://ecos.fws.gov/tess). The Endangered and Threatened Species Listing and Recovery Priority Guidelines (USFWS 1983) indicate that species will be afforded priority over subspecies in listing and recovery actions. Later, in its policy on distinct population segments (USFWS and NMFS 1996), the USFWS established that distinct population segments would be afforded the same considerations as subspecies, but when a subspecies and distinct population segments have the same numerical priority, the subspecies will generally receive higher priority.

Resolving Taxonomic Uncertainty in Conservation Decisions

Choices of what to conserve must often be made with regard to populations that are not completely separate from others, or when information regarding the relationships and degrees of distinction among populations is incomplete. Such decisions, although often difficult because of remaining uncertainties, are similar to decisions made in other contexts in which scientists have imperfect knowledge or where nature does not present clear boundaries (Hey et al. 2003). Thus, taxonomic decisions should not be viewed as fundamentally different from other conservation decisions that must be made regardless of uncertainties.

There are two error types described in conservation decisions (Woods and Morey 2008). The first type is an underprotection error, which in taxonomy means defining too few taxa to effectively conserve biodiversity (Skalski et al. 2008). This is a particular issue with island species for which the true species diversity is underestimated because similar taxa from different islands are lumped (Hazevoet 1996; Pratt and Pratt 2001; Pratt, this volume). The potential consequences of this error include loss of taxa and preclusion of conservation actions before species are critically endangered. The second type of error is overprotection: defining too many taxa, which can create excessive administrative costs and dilute conservation dollars.

There are potentially serious biological risks to flawed taxonomic splitting if it results in deleterious management. For example, erroneous delineation of subspecies or distinct population segments can delay or impede management actions to reestablish gene flow to an inbred population fragment that has become isolated because of habitat loss or other anthropogenic barriers. Although this could be overcome through intercrossing subspecies or distinct population segments (that are erroneously delineated) to rescue the inbred population fragment from local extinction, such intercrosses are rarely used and require the approval of the USFWS director (USFWS and NMFS 2000). In any case, the potential consequences of over- and underestimating the number of subspecies are economic losses, loss of conservation options because funds are misdirected, loss of scientific credibility, and loss of important components of biodiversity. Balancing these errors requires interpreting taxonomic descriptions in a manner similar to that used in other types of conservation decisions, which establish explicit criteria appropriate to the problem (Haig et al. 2006, Gippoliti and Amori 2007). Decisions will ultimately be made in the context of societal goals and the resources available. For example, a country or state with many resources and the strong support of citizens might be able to manage what would be considered dramatic overprotection by an entity that can only afford to try to keep portions of ecosystems from disappearing entirely.

Issues of taxonomic disagreement at the species and subspecies levels are handled on a case-by-case basis under the Endangered Species Act. Although neither the Endangered Species Act nor its implementing regulations dictate how the USFWS or NMFS must resolve taxonomic uncertainty, the preamble to the listing regulations, published in the *Federal Register* on February 27, 1980 (p. 13013), established that the Services "will rely on generally accepted lists of taxa [maintained by professional societies] when they are available." Because the USFWS and NMFS are also directed to make listing determinations solely on the basis of the best scientific and commercial data available, newer data from the scientific literature and information provided by professional taxonomists must be considered when a professional society's taxonomic treatment is not kept current (Center for Biological Diversity v. Lohn 2003, Western Washington District Court). This latter approach can consume considerable amounts of time and resources, place difficult and controversial taxonomic decisions in front of the USFWS and NMFS, and increase litigation risk. Thus, from this perspective, the onus is more appropriately placed on the taxonomic societies to maintain updated species and subspecies lists and criteria. If these lists are not maintained, the USFWS and NMFS may need to expend scarce resources for outcomes that result in either type of conservation decision error, with potential implications for the taxa in question. Recognizing the costs, timeliness, and importance of these taxonomic descriptions, perhaps agencies like the U.S. National Science Foundation could provide grants to major taxonomic societies to regularly update their treatments. This would formally involve independent experts, help resolve disputes in a timely manner, and highlight areas that need further research.

Although critical, taxonomic lists alone are not enough for resolving Endangered Species Act issues. Scientific societies can make significant contributions to policy deliberations by maintaining taxonomic lists and providing the rationale for their listing decisions. The American Ornithologists' Union's (AOU) updates to its check-list, which identify new information and why a certain course is being followed in response to it, are particularly valuable in that they provide the scientific basis for changes in entries (although subspecies revisions are not included at present, except when they are being raised to species status). When there are multiple taxonomic authorities with competing lists, providing such a rationale adds context to the content of the lists. This transparency, in turn, can help reduce the number of unwarranted Endangered Species Act petitions or legal challenges that arise from taxonomic disagreements.

Without input from taxonomic authorities, the USFWS, with its resources already stretched thin on many high-priority conservation needs, is forced to undertake resolutions of taxonomic disputes under regulatory and legal time constraints, sometimes operating in a politically charged atmosphere. Furthermore, without the backing of scientific organizations, the results of USFWS efforts are often called into question in court and are not always afforded the same deference given to taxonomic treatments by groups like the AOU. For example, in 2006, the 9th Circuit Court ruled that the USFWS failed to explain adequately why it reversed course after decades of recognition of the subspecies Western Sage Grouse (*Centrocercus urophasianus phaios*, now *C. minimus*; see Oyler-McCance et al., this volume) in making its 90-day not-substantial finding (Institute for Wildlife Protection v. Norton; 9th Circuit 2006). The decision rested on a conclusion that the Western Sage Grouse is not a valid subspecies. The court ruled that the USFWS did not explain the principles used to determine the validity of a subspecies classification and noted that the only taxonomist whom the USFWS consulted believed that, while the subspecies was weakly characterized, it would be wise to continue to recognize it. However, the court upheld the USFWS's determination that the petitioned population did not constitute a distinct population segment. The court remanded the finding to USFWS to revisit its 90-day finding. In a similar example with the opposite outcome (United States v. Guthrie, 50 F.3d 936; 11th Cir. 1995), the court ruled that the USFWS was not arbitrary and capricious in its finding that the Alabama Red-belly Turtle (*Pseudemys alabamensis*) was a valid species despite uncertainty regarding speciation from the Florida Red-belly Turtle (*P. nelsoni*). The court gave deference to the agency partly because the validity of the species designation was accepted by several taxonomic authorities (and published in their lists or books), notwithstanding a lack of complete certainty. Thus, in the absence of up-to-date taxonomic treatments, the USFWS not only bears the weight of generating an updated taxonomic synthesis but must also defend that synthesis and, if unsuccessful, may be forced to repeat analyses until the plaintiffs or the courts are satisfied.

Subspecific Taxonomic Rank versus Taxonomic Inflation

Scientific debate over species concepts and the identification of taxonomic groups below the species level continues (e.g., in this monograph). These taxonomic issues can be especially problematic for avian species because dispersal is often orders of magnitude greater than in other vertebrates, leaving differences among groups proportionately smaller (Haig et al. 2006). Although numerous species concepts have been proposed, the biological species concept is the current standard in avian taxonomy, and the phylogenetic species concept is the leading challenger. There are legal, administrative, and conservation costs and benefits to choosing one species definition over another for Endangered Species Act listing decisions. Below, we explore the implications of continuing to use the biological species concept versus adopting the phylogenetic species concept on Endangered Species Act listing activities for birds.

Biological Species Concept

The biological species concept defines a species as a group of interbreeding or potentially interbreeding natural populations separated from other such groups by intrinsic (genetically fixed) barriers to gene flow (Mayr 1942a, 2000a, b). The biological species concept is the most universally accepted species definition, but it is not without its critics. For example, problems arise when there is gradual evolution of reproductive isolation and discrete population entities are difficult to identify (González-Forero 2009, Irwin 2009, and many others). However, there are benefits to using this approach, including the relative ease with which a species can be identified.

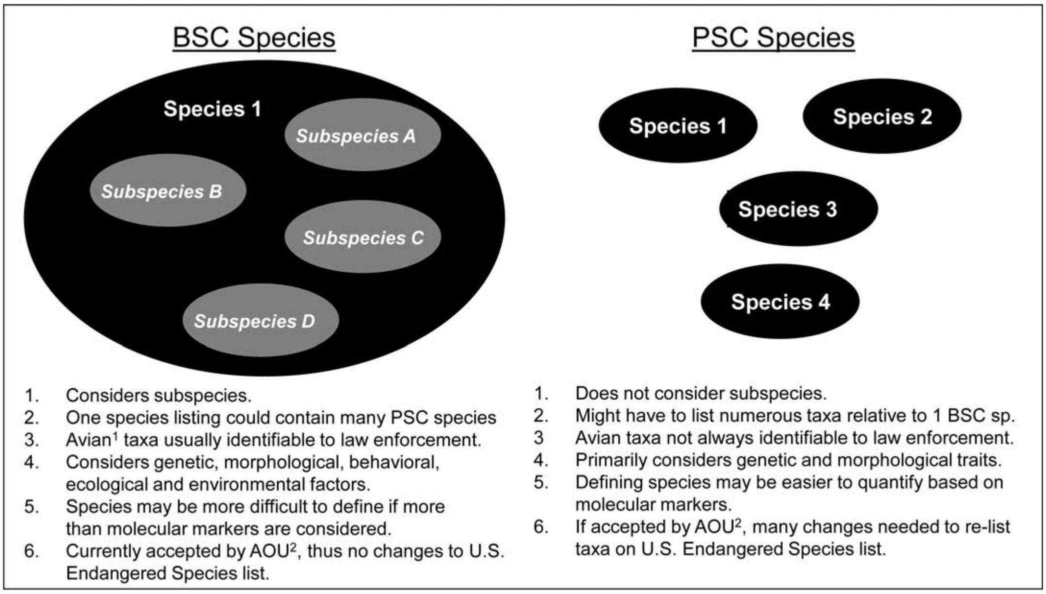
The biological species concept includes the concept of subspecies, defined by Avise and Ball (1990) as groups of actually or potentially interbreeding populations (normally allopatric) that are genealogically highly distinctive but reproductively compatible with other such groups. Criteria for determining subspecies have never been universally defined (reviewed in Haig et al.

2006); however, one definition, the 75% rule (Amadon 1949, Patten and Unitt 2002), states that a subspecies is valid if 75% or more of a population is separable from all (or >99%) members of the adjacent 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 and Unitt 2002; James, this volume; Haig and Winker, this volume). Another criterion for subspecies is that of reciprocal monophyly (Avise 2000), which has been endorsed by Zink (2004), although the same criterion is used to define species under the phylogenetic species concept. Thus, there is debate about the appropriateness of using reciprocal monophyly for both species and subspecies concepts (Goldstein et al. 2000).

Continued use of the biological species concept in avian taxonomy means that subspecies listings under the Endangered Species Act can be maintained (Fig. 1). No changes to subspecies means that the USFWS can focus on conservation priorities such as reducing the backlog of candidates, rather than administrative corrections to listings. Figure 1 illustrates the implications for implementing (or not) these ideas for avian species. There are two additional outcomes not portrayed in the figure: (1) that both methods define the same species, or (2) that the biological species concept defines more species than the phylogenetic species concept. The latter is particularly likely for recently derived species in which differentiation is driven by disruptive selection. However, the scenario portrayed is what we believe to be most likely for the vast majority of bird species.

Phylogenetic Species Concept

An overarching phylogenetic species concept has yet to be definitively described (Coyne and Orr 2004), but some definitions have stated that species are the least inclusive taxon recognized in a phylogenetic classification (Hennig 1966, Wheeler and Platnick 2000) or that species are the smallest diagnosable clusters of organisms, distinct from other such clusters, within which there are parental patterns of ancestry and descent (Cracraft 1983). Although the phylogenetic species concept can include other criteria, such as morphology and song, molecular markers are



[1]Most other taxa as well, however there are some cryptic species/subspecies that could be difficult.

[2]AOU refers to AOU Committee on Classification and Nomenclature.

Fig. 1. Considerations for Endangered Species Act listing of avian taxa under the biological species concept versus the phylogenetic species concept. See text for discussion of further outcomes of either scenario.

currently the prime source used in defining species under the criterion of reciprocal monophyly. The phylogenetic species concept generally addresses issues at the species level; however, the Committee on Phylogenetic Nomenclature currently accepts subspecies designations as long as they are not used as a rank (Dayrat et al. 2008).

Proponents of using the phylogenetic species concept in avian taxonomy argue that the major benefit of adopting it would be long-term benefits in that a relatively simple, arguably objective methodology would be in place to resolve species-level issues. For example, Zink (2004) suggested that this is necessary if we are to move beyond arguing over defining a listable unit and actually do something of conservation value. Although this argument has some merit, the major issue with the phylogenetic species concept is that it mistakes diagnosability for biological importance, something that is meaningful only to humans.

Under the phylogenetic species concept, many species based on the biological species concept would be split into two or more species (i.e., many subspecies would become full species). By some estimates, there would be 48% more species among all taxa (and no subspecies) if the phylogenetic species concept were used over the biological species concept (Agapow et al. 2004). Dillon and Fjeldså (2005) compared the numbers of bird species recognized in sub-Saharan Africa under the biological species concept and phylogenetic species concept and found ~33% more under the phylogenetic species concept, but patterns of endemism and diversity remained unchanged. Zink (2004) stated that for birds there could be as many as 100% more species. This taxonomic inflation results not only in the detection of new species but also in a greater proportion that are endangered because of a reduction in their range (Harris and Froufe 2004, Isaac et al. 2004, Padial and De la Riva 2006). However, taxonomic inflation does not necessarily correlate with inflation in endangered species lists where subspecies and populations (e.g., distinct population segments) are already eligible for protection, as in the case of the Endangered Species Act. Conversely, endangered species lists that are limited to, or biased toward, full species protection (e.g., IUCN Red List) would be affected by taxonomic inflation if the phylogenetic species concept were adopted (Garnett and Christidis 2007). The challenge is to weigh the costs and benefits (scientific, biological, economic, and political) of these scenarios and understand the consequences of this choice.

Adoption of the phylogenetic species concept by the AOU Committee on Classification and Nomenclature would be relatively benign for many species, such as the Spotted Owl (*Strix occidentalis*), in which subspecies are genetically distinct and would likely be considered full species under the phylogenetic species concept (Haig et al. 2004 Funk et al. 2008). Most island subspecies would likely find support as full species under the phylogenetic species concept, especially those on remote islands such as Hawaii, where separation of the subspecies from conspecifics occurred long ago and where there is little or no interbreeding (Pratt, this volume). This is significant, because island species make up 42.5% of the subspecies currently listed under the Endangered Species Act (30% are from Hawaii or other remote South Pacific islands; Table 2). Some mainland subspecies that are in close proximity (e.g., the three southern California Clapper Rails that are listed; see Fleischer et al. 1995; Table 2) would likely not be recognized under the phylogenetic species concept, because of a recent common ancestor, occasional interbreeding, or both, resulting in low levels of genetic differentiation.

Although the phylogenetic species concept could potentially double the number of recognized bird species, this might not be problematic for Endangered Species Act implementation because subspecies would be eliminated and populations below subspecies are already eligible for protection (provided that they meet distinct-population-segment criteria). Thus, the net change in listable entities under the Endangered Species Act might not change substantially under the phylogenetic species concept. However, there is considerable uncertainty regarding what the taxonomic landscape would look like under the phylogenetic species concept, and uncertainty can cause confusion in agencies tasked with maintaining the lists as well as among conservation partners that rely on these lists for management decisions (Funk et al. 2007). The impact on conservation of threatened and endangered species under the Endangered Species Act could be significant if many species based on the phylogenetic species concept were identified outside the bounds of currently identified subspecies or distinct population segments.

Regardless of which taxa are maintained, split, or no longer recognized under the phylogenetic

Table 2. Avian subspecies as listed under the U.S. Endangered Species Act (E = Endangered, T = threatened).

Common name	Scientific name	Listing status	Year listed	Island subspecies?	Listing citation
Akepa, Hawaii (honeycreeper)	*Loxops coccineus coccineus*	E	1970	Yes	35 FR 16047
Akepa, Maui (honeycreeper)	*Loxops coccineus ochraceus*	E	1970	Yes	35 FR 16047
Bobwhite, masked (quail)	*Colinus virginianus ridgwayi*	E	1967	No	32 FR 4001
Caracara, Audubon's crested	*Polyborus plancus audubonii*	T	1987	No	52 FR 25229
Coot, Hawaiian	*Fulica americana alai*	E	1970	Yes	35 FR 16047
Crane, Mississippi sandhill	*Grus canadensis pulla*	E	1973	No	38 FR 14678
Elepaio, Oahu	*Chasiempis sandwichensis ibidis*	E	2000	Yes	65 FR 20760
Falcon, northern aplomado	*Falco femoralis septentrionalis*	E	1986	No	51 FR 6686
Flycatcher, southwestern willow	*Empidonax traillii extimus*	E	1995	No	60 FR 10693
Gnatcatcher, coastal California	*Polioptila californica californica*	T	1993	No	58 FR 16742
Hawk, Puerto Rican broad-winged	*Buteo platypterus brunnescens*	E	1994	Yes	59 FR 46710
Hawk, Puerto Rican sharp-shinned	*Accipiter striatus venator*	E	1994	Yes	59 FR 46710
Kingfisher, Guam Micronesian	*Halcyon cinnamomina cinnamomina*	E	1984	Yes	49 FR 33881
Kite, Everglade snail	*Rostrhamus sociabilis plumbeus*	E	1967	No	32 FR 4001
Millerbird, Nihoa	*Acrocephalus familiaris kingi*	E	1967	Yes	32 FR 4001
Moorhen, Hawaiian common	*Gallinula chloropus sandvicensis*	E	1967	Yes	32 FR 4001
Moorhen, Mariana common	*Gallinula chloropus guami*	E	1984	Yes	49 FR 33881
Owl, Mexican spotted	*Strix occidentalis lucida*	T	1993	No	58 FR 14248
Owl, northern spotted	*Strix occidentalis caurina*	T	1990	No	55 FR 26114
Petrel, Hawaiian dark-rumped	*Pterodroma phaeopygia sandwichensis*	E	1967	No[a]	32 FR 4001
Pigeon, Puerto Rican plain	*Columba inornata wetmorei*	E	1970	Yes	35 FR 16047
Plover, western snowy	*Charadrius alexandrinus nivosus*	T	1993	No	58 FR 12864
Prairie-chicken, Attwater's greater	*Tympanuchus cupido attwateri*	E	1967	No	32 FR 4001
Rail, California clapper	*Rallus longirostris obsoletus*	E	1970	No	35 FR 16047
Rail, light-footed clapper	*Rallus longirostris levipes*	E	1970	No	35 FR 16047
Rail, Yuma clapper	*Rallus longirostris yumanensis*	E	1967	No	32 FR 4001
Shearwater, Newell's Townsend's	*Puffinus auricularis newelli*	T	1975	No[a]	40 FR 44149
Shrike, San Clemente loggerhead	*Lanius ludovicianus mearnsi*	E	1977	Yes	42 FR 40682
Sparrow, Cape Sable seaside	*Ammodramus maritimus mirabilis*	E	1967	No	32 FR 4001
Sparrow, Florida grasshopper	*Ammodramus savannarum floridanus*	E	1986	No	51 FR 27492
Sparrow, San Clemente sage	*Amphispiza belli clementeae*	T	1977	Yes	42 FR 40682
Stilt, Hawaiian	*Himantopus mexicanus knudseni*	E	1970	Yes	35 FR 16047
Swiftlet, Mariana gray	*Aerodramus vanikorensis bartschi*	E	1984	Yes	49 FR 33881
Tern, California least	*Sterna antillarum browni*	E	1970	No	35 FR 8491
Tern, roseate[b]	*Sterna dougallii dougallii*	E/T	1987	No	52 FR 42064
Thrush, Molokai	*Myadestes lanaiensis rutha*	E	1970	Yes	35 FR 16047
Towhee, Inyo California	*Pipilo crissalis eremophilus*	T	1987	No	52 FR 28780
Vireo, least Bell's	*Vireo bellii pusillus*	E	1986	No	51 FR 16474
White-eye, bridled	*Zosterops conspicillatus conspicillatus*	E	1984	Yes	49 FR 33881

[a]Pelagic birds that nest on islands.
[b]The Roseate Tern is listed as two distinct population segments. The north Atlantic Coast population is listed as endangered and the other populations in the Western Hemisphere are listed as threatened.

species concept, removal of subspecific taxonomy would compel the USFWS to reexamine the listing of 33 avian subspecies that are currently listed nationally, 37 that are listed internationally, and 3 that are candidates for protection (Table 2). All subspecies currently listed would have to undergo a technical correction at a minimum, which would be relatively easy for those subspecies that were simply made species. However, there are likely to be cases in which elimination of subspecies would force expanded reviews, cause changes to critical habitat designations, or invite new petitions or litigation. This could be costly, even if it represented a fraction of the subspecies listed, because of the administrative complexities associated with adding a species to the list. Conversely, the AOU's adoption of the phylogenetic species concept would not absolve the USFWS of their responsibility to address avian subspecies, because subspecies are explicitly included among entities eligible for protection under the Endangered Species Act (USFWS and NMFS 1980; Endangered Species Act, section 3). Furthermore, unless the AOU or some other taxonomic authority maintains a standing review process, USFWS will always be liable for evaluating new information for taxa on the AOU's check-list. Absent new information, taxa on AOU lists would not be immune from Endangered Species Act challenges.

Each species listing requires publication of a proposed rule, peer review, solicitation of public comments, and publication of a final rule (USFWS and NMFS 1980). Listing rules published in the Federal Register require review and signatures from approximately 10 to 20 biologists and managers in the USFWS, regional and federal office legal council, and the signature of the regional director, director of USFWS, and high-level officials at the Department of the Interior. Costs of developing and publishing proposed and final listing rules can vary widely depending on the number of offices involved and the complexity of the species (e.g., narrow endemics are generally less costly than wide-ranging species that span several USFWS regions); however, totals of approximately $300,000 are typical, with the cost approaching $400,000 if designation of critical habitat is included and exceeding $1 million for wide-ranging controversial species (USFWS unpublished document entitled *Listing and Critical Habitat Allocation Methodology*). It is important to note that these are the administrative costs associated with assessing a species' status and critical habitat, publishing documents in the *Federal Register*, holding public meetings, and responding to public input. These costs do not include any on-the-ground conservation.

The added workload associated with adoption of the phylogenetic species concept, without concomitant funding, would be added to the already sizeable backlog of USFWS listing and critical habitat decisions, further delaying listing for ~250 species (or subspecific units) that are on the candidate list (i.e., species, subspecies, or distinct population segments that the USFWS has already determined warrant a position on the List of Endangered and Threatened Wildlife, but for which it did not have funding to propose listing; see http://ecos.fws.gov/tess_public/). Subspecies would have to be reexamined for listing as either a species or some other entity such as a distinct population segment or a significant portion of the species' range. This would have large transaction and opportunity costs, the former because of the enormous administrative task of updating lists, maps, and regulations and the latter because the money used to navigate the administrative updating could have been spent implementing on-the-ground conservation (Garnett and Christidis 2007). Finally, this taxonomic inflation might be perceived by some as motivated solely by conservation purposes and a form of bureaucratic mischief (*sensu* O'Brien and Mayr 1991), scientific dishonesty (Garnett and Christidis 2007), or professional legerdemain (Winker et al. 2007).

A Complex Philosophical Dilemma

Scientific discourse regarding issues as basic as the definition of a species will continue. Ultimately, the quest to determine and relate biological findings should not be stymied by political implications. No species concept is perfect (Winker et al. 2007); however, it would be useful to decision-makers if scientific uncertainty and the conservation consequences were explicitly stated by scientists when making a specific taxonomic proposal (Haig et al. 2006). Discussing the impact of choosing one species definition over another in view of the conservation implications is fraught with multidimensional philosophical conflicts (Mace 2004). However, as with many complicated situations, not making a decision is a decision. For example, if the phylogenetic species concept were adopted by the IUCN, the Red List would need to be updated to address those newly identified full species. This could take resources away from other high-priority conservation actions, including the protection of currently recognized full species. More subspeciose countries with fewer resources for conservation might be challenged to manage the protection and rehabilitation of an increased number of listed taxa (Table 1).

Conservation efforts will be more effective and less costly if they are initiated before an entire taxon has become critically endangered. Planning ahead is critical from a biological perspective in order to avoid irretrievable losses of heritable adaptations to local and regional conditions. Subspecies groupings, phylogenetic species, distinct population segments, or evolutionarily significant units can help target and prioritize protection for these populations that are geographically disjunct or morphologically unique.

Whatever species concept is accepted, scientists must operationally define the species concept and subspecies definition they used in their work so that USFWS and other conservation agencies understand the criteria by which results were judged (Helbig et al. 2002, Agapow et al. 2004, Haig et al. 2006, Fallon 2007). Clearly stating criteria for taxonomic identification will facilitate comparisons with similar taxa when undertaking listing, recovery, and status assessments. North American ornithologists have been leaders in this effort in the past (AOU 1957, 1998); however, there is a critical need to update this work at the subspecific level on a regular basis.

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