

## **Subspecies are for Convenience**

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## CHAPTER 5

### SUBSPECIES ARE FOR CONVENIENCE

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**ABSTRACT.**—The century-long debate over the meaning and utility of the subspecies concept has produced spirited print but only superficial consensus. I suggest that genuine consensus about subspecies is an impossible goal, because trinomial epithets will inevitably be applied to a heterogeneous mix of evolutionary phenomena, thereby precluding genuine standardization of the concept. Populations that have intermediate levels of phenotypic differentiation and geographic isolation from one another often fall into a region I refer to as the “zone of art,” where even skilled experts can disagree about the validity of any one subspecific treatment. The trinomial system cannot accurately represent the kind of information now available about genetic and character variation across space. Instead, ever more accurate tools are being perfected for quantitative, standardized descriptions of variation. These analyses—not subspecies classifications—will keep providing new scientific insights into geographic variation. Even more important, those of us who propose, debate, set, or enforce scientifically based conservation policies need to recognize that trinomial nomenclature survives primarily as a tool of convenience that cannot be viewed as strict science and should not be called on to establish or resolve crucial policy issues such as endangered-species listings. I have described new subspecies myself, and I regard the concept as a useful convenience. However, I submit that art and judgment will always be involved in practice and that no one trinomial treatment can be scientifically proved to be the biologically correct one. In this context, the subspecies concept itself is simply too heterogeneous to be classified as strict science.

Key words: conservation, endangered species, differentiation, geographic variation, subspecies.

#### Las Subespecies Son por Conveniencia

**RESUMEN.**—El siglo de debate sobre el significado y la utilidad del concepto de subespecie ha producido escritos muy animados pero se ha llegado a un consenso sólo de modo superficial. Sugiero que alcanzar un consenso genuino sobre las subespecies es un objetivo imposible, porque los epítetos trinomiales serán aplicados inevitablemente a un conjunto heterogéneo de fenómenos evolutivos, lo que impide una estandarización genuina del concepto. Las poblaciones que tienen niveles intermedios de diferenciación fenotípica y aislamiento geográfico entre sí usualmente se ubican en una región a la que yo llamo como la “zona de arte,” donde incluso los expertos más hábiles pueden estar en desacuerdo sobre la validez del tratamiento de alguna subespecie. El sistema trinomial no puede representar de modo preciso el tipo de información disponible actualmente sobre la variación genética y en caracteres a lo largo del espacio. En cambio, las herramientas más precisas están siendo perfeccionadas para brindar descripciones cuantitativas estandarizadas de la variación. Estos análisis—no las clasificaciones de subespecies—van a seguir brindando nuevas visiones científicas sobre la variación geográfica. Incluso más importante, aquellos que proponen, debaten, fijan o hacen cumplir políticas de conservación con base científica necesitan reconocer que la nomenclatura trinomial sobrevive principalmente como una herramienta de conveniencia que no puede ser vista como ciencia estricta y que no debe ser utilizada para establecer o resolver la política de asuntos cruciales como el listado de especies amenazadas. Yo mismo he descrito nuevas subespecies y veo a este concepto como una conveniencia útil. Sin embargo, acepto que arte y juicio siempre estarán

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involucrados en la práctica y que ningún tratamiento trinomial puede ser probado de modo científico como el correcto biológicamente. En este contexto, el concepto mismo de subespecie es simplemente demasiado heterogéneo como para ser clasificado como ciencia estricta.

LIKE MOST QUESTIONS for which multiple correct answers exist, the century-long debate over the meaning and utility of the subspecies concept has produced spirited print but only superficial consensus. Naming subspecies codifies our recognition (traceable to Darwin) that species are neither static nor unitary across space and time. Few biologists dispute that understanding intraspecific geographic variation remains elemental to understanding evolution, or that naming distinguishable geographic units (whether as species or as subunits of species) facilitates conversations about them. Subspecific names provide convenient handles by which to describe, sort, store, retrieve, and discuss certain kinds of information about phenotypic geographic variation (Mayr 1982a). Beyond these generalizations, however, opinions about meaning and process associated with subspecies remain as diverse as ever (Haig et al. 2006; Haig and D'Elia, this volume; Winker, this volume). Indeed, diversity of opinion on the subspecies question has been amplified, not narrowed, by today's burgeoning access to genetic information about spatial variation within species and near-species.

Here, I suggest that genuine consensus about subspecies treatments—and about the subspecies concept itself—is an impossible goal, because trinomial epithets will inevitably be applied to a heterogeneous mix of evolutionary phenomena. I further suggest that no special reasons exist to expect or demand standardization in the application of trinomial names, because this nomenclatural system cannot possibly represent accurately the kind of information now available about genetic and character variation across space. Ever more accurate tools are being perfected for quantitative, standardized descriptions of variation. Simply put, in the 21st century, we know too much to be bound by a 19th-century nomenclatural convention, however useful aspects of that convention may be in some contexts.

Most important, it is essential that we who propose, debate, set, or enforce conservation policies recognize that trinomial nomenclature persists primarily as a tool of convenience and that it cannot be treated as strict science, because no standardized method for diagnosing and naming discrete units of evolutionary differentiation can be equally meaningful across taxa. In this context, I concur with Crandall et al. (2000) that

management policies (including endangered species listings) should be derived directly and exclusively from ecologically and genetically relevant information about population distinctiveness, not from names. It is both tactically and ecologically inappropriate for conservation policies to be determined by subspecific taxonomy, because the latter is so famously subject to heterogeneous, often arbitrary, and inevitably fallible personal conventions of alpha taxonomists, nomenclature committees, reviewers, and editors.

#### TOOL OF CONVENIENCE: EASTERN TOWHEES AS A CASE EXAMPLE

Across the scrub and pine flatwoods of central Florida lives a distinctive form of Eastern Towhee (*Pipilo erythrophthalmus*). Compared to all other populations east of the Rocky Mountains, this form is smaller, longer-legged, duller, and has much less white on the back, wings, and tail. This Florida form also has pale, cream-colored, or whitish irides, whereas those of all other Eastern Towhees are dark red. The distinctive Florida form has a convenient and unambiguous handle: it is the "pale-eyed" form of Eastern Towhee, *Pipilo erythrophthalmus alleni*.

Greenlaw (1996) followed the American Ornithologists' Union (1957) in recognizing three other subspecies of Eastern Towhee. Interestingly, Greenlaw (1996:4) also noted that the "four-subspecies concept in Eastern Towhee may no longer be defensible," because outside of Florida, character variation is discordant, named taxa are only weakly differentiated from one another, and intermediate populations form broad geographic zones between any two of them. Greenlaw's reservations about the biological validity of these four taxa are justified, because none is fully discrete. Indeed, no two of them even represent the same kind of subspecies. The widespread nominate race has numerous plumage characters that vary gradually—but discordantly—over most of the species' breeding range; *P. e. canaster* "is a Gulf Coast extreme of geographic clines" (Greenlaw 1996:4); *P. e. rileyi* represents "strongly introgressed secondary contact between [the other two races] and pale-eyed *alleni* in Florida" (Greenlaw 1996:4–5); and *P. e. alleni* is a form so different from the others, and so uniform across the Florida peninsula,

that Greenlaw suggested genetic investigations to determine whether it is a "separate phylogenetic entity" (Greenlaw 1996:5).

Biologically justified as they are, Greenlaw's reservations do not discount the conveniences achieved by having four names, because these (1) generally distinguish four kinds of Eastern Towhees and (2) generally identify each with a geographic subset of the species' range. The fact that borders of these subsets are variously fuzzy does not negate the utility of lumping variation into a few discrete categories, as long as we recognize that these crude categories are for purposes of overview only. Often, they help us organize conversations about, and even initiate the study of, variation. But these categories are not, in and of themselves, appropriate units for biological analysis. For the latter, we have other tools at our disposal, as discussed below.

#### THE SUBSPECIES AS A TERM OF ART

Few tools in science are applied in as heterogeneous a manner as the subspecies concept, and the reason is simple. Evolutionary changes across space and time develop like snowflakes: no two are identical. The taxonomic consequences of this fact are diabolical. Because histories vary, and no two populations differentiate from one another in precisely the same way, any attempt to apply a single nomenclatural category to the process cannot help but encompass a diverse array of configurations, stages, and degrees of divergence.

Heterogeneity of the subspecies as a taxonomic category has unavoidable consequences, two of which are especially relevant here. First, many different kinds and degrees of variation will always be lumped into this single taxonomic level, the most common of which are illustrated in Figure 1. For example, separate names (Fig. 1A, B) are routinely applied to widely allopatric populations, whether they differ grossly (uppermost) or barely (second from top) from one another, and also to parapatric populations, whether the contact zone is sharp (third from top) or gradual (third from bottom). Intermediate or hybrid populations often differ so much from those on either side that an additional subspecific name or names are proposed for these as well (Fig. 1C, D). The bottom two cases in Figure 1 illustrate two common nomenclatural treatments of a smoothly clinally variable species (not shown is a third option espoused by many: to recognize no subspecific distinctions at all, even to represent extreme points of clines). More

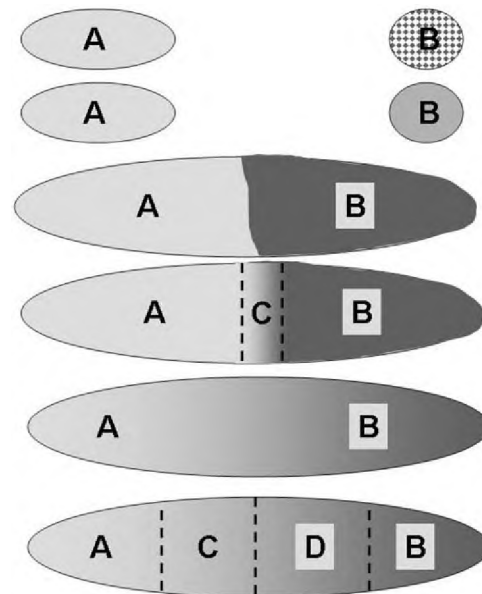


FIG. 1. Schematic examples of heterogeneity in most common applications of subspecies names (denoted here by A, B, C, and D) to geographically variable populations or taxa.

complex variation than is shown here (e.g., multiple discordant characters, variation along two dimensions, males and females showing different patterns, mix of isolated and continuous populations varying in different characters and degrees, etc.) is commonplace among widespread bird species. Taxonomists have dealt with this assortment by naming dozens of different kinds of subspecies. It is unfair to dismiss this historical heterogeneity as old fashioned or shoddy scientific practice (Patten, this volume; Winker, this volume). To the contrary, few such treatments can be proved incorrect, because the subspecies, including any quantitative rules used for "diagnosability" (Patten and Unitt 2002), is a human construct of convenience, not a biological entity that can be identified deductively and unambiguously.

Second, among birds at least, a large proportion of formally and usefully recognized subspecies will always be distinguished along arbitrarily demarcated geographic borders, or on the basis of arbitrarily defined levels of distinctiveness, or both. These features preclude standardization; hence, it will always be difficult (technically, impossible) to compare different species and their subspecies quantitatively and precisely for purposes of biological analysis or regulatory action (e.g., endangered-species listings; see below).

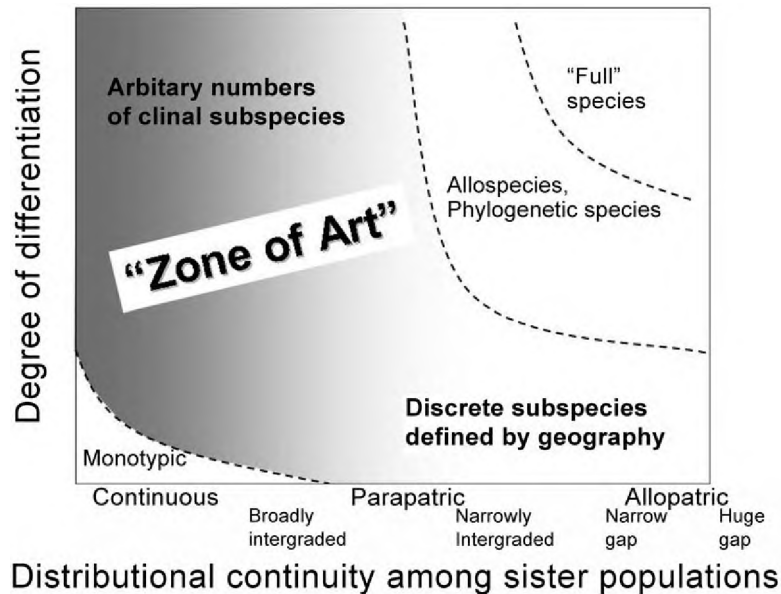


FIG. 2. Nomenclatural space for sister populations or taxa, visualized along two orthogonal axes: (1) degree of differentiation (phenotypic or genetic) and (2) distributional continuity between or among the taxa (adapted from Waples and Gaggiotti 2006).

Even the most careful taxonomists, examining the same data, often disagree with one another about how best to incorporate subspecific nomenclature to describe geographic variation within a widespread species. Disagreement occurs because, in most cases found in nature, no single subspecific treatment can be proven by a standardized algorithm to be the best, let alone the only, depiction of biologically meaningful and informative variation. The most obvious cases in point are subspecies names applied to various transitional stages or endpoints of clinal variation within continuously distributed populations (e.g., the Eastern Towhees discussed above), or even along step-clines that evolve among island or habitat archipelagoes. Both historically and in current practice, class Aves contains tens of thousands of such names (Dickinson 2003, Clements 2007).

Reviewing the question "What is a population," Waples and Gaggiotti (2006) elegantly visualized the well documented inverse relationship between population differentiation and degree of panmixia. I propose that in dividing species into discretely named taxa, taxonomists implicitly or explicitly invoke this relationship, and the exercise can be visualized along two axes (Fig. 2). One axis expresses the degree of divergence or differentiation—phenotypic, genetic, or both—among constituent sister populations. The other

axis describes the degree of geographic or distributional continuity among these populations. Monotypic species have mostly continuously distributed populations that cannot be distinguished from one another (i.e., very low values along both axes). At the other extreme (very high values along both axes), most well-differentiated and widely allopatric sister taxa today are recognized as full species. Just inside the full-species zone are allospecies, the component taxa of superspecies (Mayr 1963, Amadon 1966, Mayr and Short 1970). This zone incorporates most evolutionary units and taxonomic clusters regarded as phylogenetic species by some (e.g., Cracraft 1983, Nixon and Wheeler 1990). In such cases, which are often characterized by conspicuous differentiation among allopatric populations, geography renders moot the question of whether such forms could or would interbreed. Under the biological species concept, these cases are frequently treated as polytypic species (Mayr 1963) using trinomial nomenclature. As noted by many authors (e.g., Winker et al. 2007), neither of these two alternative treatments of well-differentiated allopatric populations is logically superior to the other. Whether they are called subspecies, allospecies, phylogenetic species, or even full species, treatment of well-differentiated sister taxa is biologically uncontroversial when they are allopatric.

BIOLOGICAL CORRECTNESS  
VERSUS THE ZONE OF ART

Often in nature, only slight phenotypic or genetic differences exist among sister populations, or populations differ from one another statistically but with substantial overlap among individuals. Where such populations are parapatric or allopatric, taxonomists historically have been tempted to name them as subspecies, and geography alone is sufficient to identify a given specimen to subspecies unambiguously (Fig. 2, lower right). Where populations are more continuously distributed, geographic differentiation commonly occurs clinally, either smoothly or along one or more steps. As in the Eastern Towhee case discussed above, clinal variation of different characters is often geographically discordant, which leads to a two-dimensional mosaic of phenotypes that grows increasingly complicated as more discordant characters are analyzed. Discordant geographic variation among characters within some widespread taxa may even be configured differently between males and females (e.g., Haffer and Fitzpatrick 1985). No taxonomic formulae or conventions exist for naming subspecies in such complex cases. Instead, the individual taxonomist is on his or her own—and in the case of birds, taxonomists have exercised this liberty for 150 years. This portion of the divergence—continuity spectrum can be referred to as the “zone of art,” because imagination, creativity, sample-size constraints, and local geographic idiosyncrasies play as much of a role in delimiting subspecies as could any strict, scientifically based rule. This, fundamentally, was Greenlaw’s observation about dividing Eastern Towhees north of the Florida peninsula into three subspecies: populations could be categorized in any number of ways, and no solution is intrinsically better or more biologically correct than any other. As visualized in Figure 2, the zone of art encompasses a broad range of situations within which multiple subspecific treatments are approximately equally defensible. Indeed, some authors argue that no subspecies should be recognized in such cases because broad intergradation or clinal differentiation occurs without obvious breaks or discontinuities. It is impractical to imagine that the zone of art can ever be fully resolved on biological grounds. Such fuzziness, however, does not negate the everyday utility of applying names to extreme variants and easily diagnosable units within this zone.

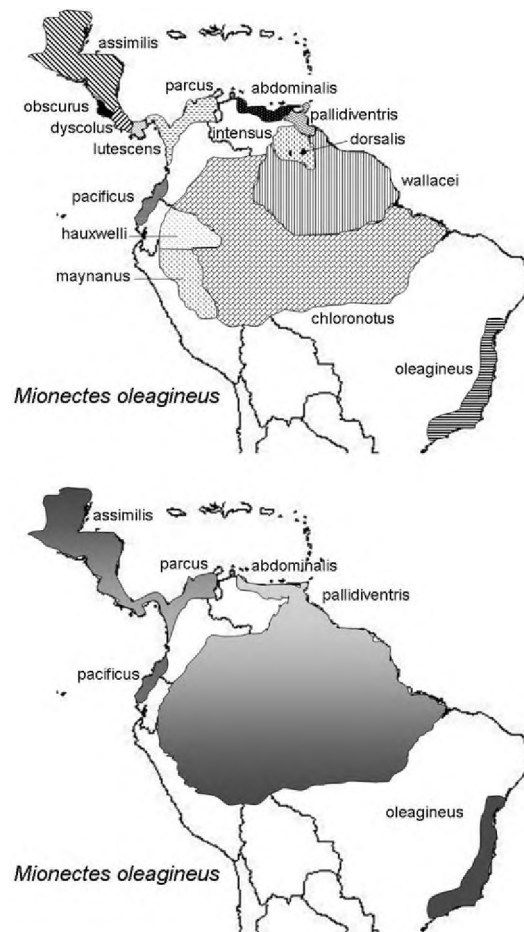


FIG. 3. Traditional (upper) and recently revised (lower) subspecies treatments of the Ochre-bellied Flycatcher (*Mionectes oleagineus*), a species that is remarkably uniform in phenotype and behavior across most of its range. Upper diagram shows published ranges of 15 poorly defined subspecies (Traylor 1979). Lower diagram identifies seven geographic regions where subtle clinal variation reaches endpoints (Fitzpatrick 2004).

Countless examples of the zone of art exist among widely distributed bird species, from the 200+ purported subspecies of Canada Goose (*Branta canadensis*; Hanson 2006) and 22 named subspecies of Northern Bobwhite (*Colinus virginianus*; Brennan 1999) to the 15 described subspecies of Ochre-bellied Flycatcher (*Mionectes oleagineus*; Traylor 1979). In the latter case—a widespread, dull ochraceous-green tyrant flycatcher of Middle and South America (Fig. 3)—most individuals literally cannot be assigned unambiguously to

subspecies without precise data on where the specimen was collected (appropriately, subspecies names in this species translate to such words as “obscure,” “similar,” “inseparable,” “intense,” “poor,” “pale-bellied,” “yellowish,” “greenish,” and “olive”). I simplified the subspecific taxonomy of this species to seven names (Fitzpatrick 2004), but perhaps a better case could be made that the entire complex represents a broad cline from somewhat darker, greener, and diffusely streaked birds in Middle America south to the paler, ochraceous-bellied, unstreaked examples of the Amazon Basin and southeastern Brazil. Such a treatment might be reduced to just two names, applied to opposite ends of the cline. Even more important in the present context, no phenotypically based nomenclature would capture the complex phylogeographic history suggested by recent molecular analysis of this species in Amazonia (Miller et al. 2008). My points here are (1) that no one subspecific treatment, including mine, can be demonstrated to be the correct one on biological grounds; and (2) that detailed information about genetic variation and population histories, as revealed by modern studies, transcends the scientific utility of any particular naming convention we might apply (see below).

#### SUPERIOR TOOLS ABOUND FOR ANALYZING VARIATION

Trinomial nomenclature entered ornithology in the mid-19th century, before Darwin and Wallace identified natural selection as a basis for geographic variation and a full century before Wright elucidated the role of genetic drift. Identifying bins for conveniently cataloguing intraspecific variation remains in vogue (e.g., Howard and Moore 2003, Clements 2007, del Hoyo et al. 2008, and several of the chapters in this volume), but the range of methods, questions, and outputs in the scientific study of geographic variation have vastly superseded those accommodated by trinomial nomenclature. Today, opportunities abound for detailed analyses of variation using quantitative comparisons of both phenotypic and genetic variation among populations across space. A plethora of tools exists for such analyses, including multivariate and spatial statistics (Maurer 1994), phylogeography (Avice 2000, 2004, 2006), coalescent theory (Wakeley 2006), and even historical demography (Rogers and Harpending 1992, Drummond et al. 2005). These modern tools

promote sophisticated scientific inquiry by providing detailed data at multiple scales, involving geographic variation at all stages of differentiation and speciation. By contrast, subspecies taxonomy provides, at best, a blurry lens through which to attempt to draw inferences about microevolutionary pattern and process. At worst, subspecies are treated as ends in themselves, thereby distracting us from more rigorous and illuminating analyses of this subject. No amount of statistical rigor, including a 75% rule (for discussion of this convention, see Patten, this volume), can change the fact that judgment must always be applied to subspecies treatments. Even the term “diagnosability” (Patten and Unitt 2002) is demonstrably malleable, because we can always add more characters, diversify statistical tools, or debate and change our acceptable criteria for diagnosis. The subspecies applies to such a range of intermediate situations that no single correct algorithm exists to represent these intermediates using the trinomial tool.

#### SUBSPECIES STATUS IS A POOR GUIDE FOR CONSERVATION PRIORITIES

It is, at long last, axiomatic that long-term conservation of biological diversity demands protection of natural variation at the infraspecific level. The subspecies, however, is at best a very poor proxy for this variation (Wayne and Morin 2004). It is high time that individuals and agencies involved in setting conservation priorities or policies (including local, state, and federal listing decisions) acknowledge the inherent heterogeneity and subjectivity of the subspecies concept and embrace more rigorous analyses of distinctiveness (including ecological distinctiveness) in establishing priorities and setting policies. Although trinomial nomenclature sometimes offers first-order clues about population distinctiveness, this naming system was never designed as a substitute for objective measurement and comparative assessment of the morphological, ecological, behavioral, genetic, and evolutionary data required for pursuing rational conservation policy today (Crandall et al. 2000, Moritz 2002). Despite the fact that the U.S. Endangered Species Act specifically allows for listing of “distinct population segments” that are not described subspecies, listing decisions routinely incorporate, and often hinge upon, debates about the validity of a particular

subspecific name (such a case is discussed below) rather than more biologically relevant questions (Haig et al. 2006).

Reliance on subspecies classifications as a proxy for delineating conservation units is misleading on at least two grounds. First, by partitioning complex and often discordant patterns of phenotypic and genetic variation into discrete entities, often using only a limited number of characters, subspecies nomenclature usually simplifies, and often grossly misrepresents, both the amount of variation and its geographic complexity. Modern geospatial statistical tools such as spline, spline regression, and step-regression (e.g., Skalski et al. 2008) allow biologists to detect, demonstrate, and interpret clines, step clines, local peaks of character divergence, and discordant character variation using multiple data sets, objective algorithms, and replicable procedures. Second, when it comes to proposing or recognizing subspecies names within geographically variable species, expert opinions often contradict one another. I suggest that this cannot be avoided, because multiple trinomial solutions—especially within the zone of art—can be approximately equally correct on biological grounds (see above). Because equivocal cases and contradictory treatments are common, conservation agencies run the risk of straying from otherwise warranted findings of population distinctiveness (Haig and D’Elia, this volume) by adhering to any single subspecific treatment. Instead, to ensure a sound biological footing, listing decisions and conservation priorities should be based on explicit and thorough analyses of ecological, behavioral, morphological, and genetic data. Trinomial epithets, whether historical or recent, can help guide these studies, but they should not—as they still so often do—replace them.

Failure to list the virtually isolated “San Diego” population of Cactus Wrens (*Campylorhynchus brunneicapillus*) in southern California provides an example of how undue reliance on the subspecies concept leads to erroneous conservation decisions. In 1990, the U.S. Fish and Wildlife Service (USFWS) received a petition to list as endangered a described subspecies of Cactus Wren (*C. b. sandiegensis*; Rea and Weaver 1990), on the grounds that this rapidly disappearing population represented a “distinct population segment” as defined by the Endangered Species Act (for definitions and discussion of this feature of the Endangered Species Act, see Haig and D’Elia,

this volume). In its published finding not to list (Beattie 1994), the USFWS stated the following:

The American Ornithologists’ Union Committee on Classification and Nomenclature did not recognize the San Diego cactus wren . . . as a subspecies of the cactus wren. . . . Since the conclusion of the committee is that *C. b. sandiegensis* likely only represents an intermediate form between two recognized subspecies of cactus wren, it is not currently under consideration for addition to the Federal List of Endangered and Threatened Wildlife and Plants.

As a member of the referenced AOU committee at the time, I can attest that (1) the committee considered the validity of *C. b. sandiegensis* reluctantly, during a previously scheduled meeting at the U.S. National Museum; (2) we spent less than an hour on the question; (3) we examined a total of about 20 Cactus Wren specimens representing several subspecies, including only a few of the focal taxon; (4) we concluded that *C. b. sandiegensis* appeared to differ from both of the subspecies that surrounded it (*C. b. couesi* of the southwestern United States and adjacent mainland Mexico, and *C. b. bryanti* from San Diego County, California, south to northern Baja California); and (5) plumage characters of *C. b. sandiegensis* appeared to be intermediate between the two much more widespread subspecies, each of which appeared to be uniform across their much larger ranges.

Our analysis was not a scientific study of the distinctiveness of a population, and we did not submit our findings to be peer-reviewed or published, as had Rea and Weaver (1990). Our casual conclusion about the intermediacy of *C. b. sandiegensis* was conveyed as such in a letter to the USFWS by the committee chairman. Such determinations represent willing, if informal, participation in the zone of art (Fig. 2), and they abound in the history of ornithological taxonomy. Countless hundreds, perhaps thousands, of the world’s named avian subspecies today represent exactly the same level of population distinctiveness as *C. b. sandiegensis*. Identifying such intermediates as subspecies is neither correct nor incorrect but is simply a point of view, given available data—a convenient handle. What was incorrect was citing the committee’s conclusion as a fundamental reason for not considering this named population as a candidate for listing. As it turns out, mtDNA studies eventually revealed genetic uniqueness within this named form (Eggert 1996), yet this



rapidly disappearing population is still not federally listed. The California Department of Game and Fish recently identified *C. b. sandiegensis* as a “species of special concern” (Unitt 2008).

Most important, subspecies or not, localized Cactus Wren populations are well-documented indicators of a vegetative formation that is unique in North America, the cactus scrubs of southern coastal California (Rea and Weaver 1990, Solek and Szijj 2004). In this context, the status of *C. b. sandiegensis* as a valid subspecies is moot: these populations are well separated geographically and ecologically from other Cactus Wrens, thus fulfilling another of the criteria for designation as a distinct population segment (Haig and D’Elia, this volume). Both the habitat and its wrens have been catastrophically reduced by residential and commercial development and by unnaturally high frequency and severity of wildfires. As a consequence, survival of the coastal Cactus Wren is considered one of the greatest challenges in bird conservation for southern California (Unitt 2004). Section 2(B) of the Endangered Species Act specifies that the purposes of the act include “to protect the ecosystems upon which endangered species and threatened species depend.” Protection of coastal cactus scrubs in southern California continues to be impeded by failure of the USFWS to give standing to the habitat’s signature bird species. This failure originated from undue focus on the subspecies question. Equivocal validity of the name (about which legitimate debate will continue) became a red herring diverting attention from ecological distinctiveness and conservation importance of this population. Listing should be driven by the latter.

#### RECOMMENDATION: USE SUBSPECIES AS A CONVENIENT TOOL

By any of the current definitions, species are biological entities. By contrast, subspecies have been human constructions since they were first used in the 19th century. Our innate desire to name things that we see motivates us to apply

unique names to each of the variants that we detect within species. This is a useful habit, because recognizing different identifiable types helps draw attention to natural variation. Naming these variants facilitates conversation about them, encourages naturalists to recognize geographically distinct populations in the field, and—as emphasized without embarrassment by Mayr (1982a)—helps museum curators sort specimens to organize variants into categories for inspection and analysis. Persistence of the subspecies as a tool of convenience, however, must neither be confused with, nor stand in the way of, more precise, scientific, and ultimately useful methods of describing, analyzing, interpreting, and conserving geographic variation within species.

When it comes to conservation policies (e.g., prioritizing habitat for preservation, preparing listing petitions, making listing decisions, reviewing listings, or developing recovery plans), I view it as imperative that we refrain from placing too much weight on trinomial nomenclature. Not all biologically important or ecologically informative variation has been described in the form of subspecies, nor could it be. By the same token, described subspecies differ spectacularly in the respective levels of scientific rigor with which they were described, and in the biological meaning that underlies their trinomial names. Subspecific nomenclature is convenient but idiosyncratic. Subspecies should be used as just one, very fallible, clue in triggering more rigorous approaches to the careful evaluation of population distinctiveness, especially for purposes of establishing conservation priorities or actions.

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