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LETTER

Current Topics in Avian Conservation Genetics with Special Reference to the Southwestern Willow Flycatcher

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Abstract: It is sometimes said that scientists are entitled to their own opinions but not their own set of facts. This suggests that application of the scientific method ought to lead to a single conclusion from a given set of data. However, sometimes scientists have conflicting opinions about which analytical methods are most appropriate or which subsets of existing data are most relevant, resulting in different conclusions. Thus, scientists might actually lay claim to different sets of facts. However, if a contrary conclusion is reached by selecting a subset of data, this conclusion should be carefully scrutinized to determine whether consideration of the full data set leads to different conclusions. This is important because conservation agencies are required to consider all of the best available data and make a decision based on them. Therefore, exploring reasons why different conclusions are reached from the same body of data has relevance for management of species. The purpose of this paper was to explore how two groups of researchers can examine the same data and reach opposite conclusions in the case of the taxonomy of the endangered subspecies Southwestern Willow Flycatcher (*Empidonax traillii extimus*). It was shown that use of subsets of data and characters rather than reliance on entire data sets can explain conflicting conclusions. It was recommended that agencies tasked with making conservation decisions rely on analyses that include all relevant molecular, ecological, behavioral, and morphological data, which in this case show that the subspecies is not valid, and hence its listing is likely not warranted.

Keywords: Endangered species act, Southwestern willow flycatcher, Subspecies, Mitochondrial DNA, Plumage coloration, Phylogeography.

INTRODUCTION

Decisions to list a species as threatened or endangered can draw on several sources of information, including population demography, habitat loss, taxonomy, and the genetic characteristics of the population considered at risk. It is also the case that some listing decisions can be reversed if the population, subspecies or species recovers, or it was subsequently determined that the original listing of a subspecies was unwarranted owing to “data error”. The latter occurs relatively frequently when subspecies, often named a century ago, are used at face value as valid taxa by listing agencies. In many cases, modern taxonomic methods find that such subspecies are not supported by analyses of modern genetic or morphological data [1, 2]. Unfortunately, in some cases, the subspecies are considered flagships upon which the preservation of an area is based. The coastal California Gnatcatcher (*Polioptila californica californica*) is one such subspecies, serving as a flagship for the Coastal Sage Scrub of southern California and northwestern Baja California, and there is vigorous debate as to its validity [3 - 6]. In this and other examples, different groups of scientists publish peer-reviewed papers that reach different conclusions from the same body of existing data, sometimes by differentially weighting particular pieces of evidence, or by excluding some evidence.

Contrary null hypotheses can play a role. For example, there is an argument from “negative evidence”, which in

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essence says no matter how many data sets document a lack of genetic or morphological differences among populations thought to be threatened or endangered, no decision can be made [6]. However, the theoretical expectation for populations that are connected by gene flow is that they will show no diagnostic differences, *e.g.*, they are not evolutionarily distinct units. Thus, the data showing no differences among subspecific taxa are in fact positive and support this null hypothesis [5]. Often, when data emerge that support this null expectation, critics ignore the conclusion by applying the “negative data” tag. Indeed, one cannot disprove a hypothesis of no differences, as it would require an infinite number of data sets. Thus, if multiple lines of evidence do not support a subspecies as valid, but others argue the evidence is “negative” or future studies might reveal diagnostic differences, a conundrum is created for agencies tasked with making decisions based on the best available data, and not waiting for some unknown point in the future when new data might emerge. For example, in a recent decision to retain the coastal California Gnatcatcher as Threatened under the U.S. Endangered Species Act [ESA; 7], the U.S. Fish and Wildlife Service essentially redefined the word “available” and called for additional data, rather than acting on what was available at the time. There were no “positive” data cited in support of the subspecies, and in effect they favored a subspecies taxonomy almost a century old despite modern evidence to the contrary. This of course sets a precedent for any listing agency to avoid decisions that are compatible with existing data if they are politically unfavorable, and defer to future data with unknown timeframes and conclusions under the “negative data paradigm”. In my opinion the USFWS acted in a way that is at odds with the intent of the phrase “best available commercial and scientific data” required by the ESA.

In this paper, conclusions reached from the same sets of data concerning the taxonomic distinctiveness of an endangered passerine bird of the American Southwest, the southwestern willow flycatcher (*Empidonax traillii extimus*) are compared. Many parallels exist with the coastal California Gnatcatcher. Analyses based on all relevant data show that the best available data do not support the taxon and it is recommended that agency decisions regarding listing or delisting are based on full data sets.

BACKGROUND

The southwestern willow flycatcher (hereafter SWWF) is part of a widely distributed and common species, the willow flycatcher (*E. traillii*). Partners in Flight estimate a North American population of *E. traillii* at 9,100,000 (<http://rmbo.org/pifpopestimates/Database.aspx>; accessed 10 June 2016), although the species is clearly not dense in the southwest where populations are considered to represent *E. t. extimus*, although these local populations are increasing [8]. The SWWF represents a distributional extreme in the American Southwest, where it inhabits riparian habitats. Concern over habitat loss and concomitant reduction in populations led to its listing as endangered under the U.S. ESA in 1995 [9]. A petition to delist the subspecies was filed [10].

Listing of the SWWF was based on the assumption that it is a valid taxonomic entity. Zink [11] analyzed existing data on mitochondrial DNA (mtDNA), plumage coloration, ecological niches, and song, and concluded that the Southwestern Willow Flycatcher is not a valid subspecies. That is, in the parlance of the ESA, the listing was based on original data error. If true, implications exist for its continued listing. Theimer *et al.* [12] argue that some of the data presented by Zink [11] support the subspecies. Thus, this represents an instance in which two groups of researchers examine the same data and come to different conclusions. This divergence of opinions is explored in this paper, and examined how differing interpretations of the ESA, and uses of subsets of data lead to apparently contrasting taxonomic conclusions.

Taxonomy, Range, and Interpreting the U.S. Endangered Species Act

The fundamental units that can be listed under the ESA are taxonomic categories, which have been notoriously labile and contentious. For example, many have argued the efficacy of the subspecies category, with some maintaining its value [13], others concluding that subspecies are rarely valid [14, 15]. Although this begs the question of whether subspecies *per se* are bad, or there are just bad subspecies, a majority of molecular studies support 50% of subspecies at best, mostly in tropical or island situations [2].

The taxonomy of the Willow Flycatcher was addressed by several authors [16 - 21]. The SWWF was described by Phillips [22] in 1948. Its description was based on subtle differences in coloration and measurements, although no statistical comparisons were presented in the original description [22]. The source accepted by most agencies and journals as the taxonomic authority for North American birds, is the Checklist produced by the American Ornithologists' Union (AOU; as of this writing, the AOU and the Cooper Ornithological Society have merged and will be known together as the American Ornithological Society (AOS)). This checklist listed subspecies until 1957, whereas

subsequent checklists included only species. It is important to note that although Phillips' (1948) description of the SWWF was in the Auk, the official publication of the AOU, the 1957 AOU Checklist [23] did not include it. That is, the AOU did not consider it a valid subspecies. However, the U. S. Fish and Wildlife Service considered it valid, despite conflicting scientific opinions [18, 20, 21].

Comparing opinions on the ranges of subspecies shows considerable disagreement among these authors. For example, Unitt [20] stated that "Phillips (1948) and Aldrich (1951) included southern California in the breeding range of *brewsteri*, but this study shows that instead *extimus* occupies this area." In my opinion, if the subspecies was a distinct evolutionary unit, it should be straightforward to define range boundaries.

It is important to consider how agencies interpret taxonomic categories relative to interpretations by researchers. Theimer *et al.* [12] cite a portion of a 1973 amendment to the ESA concerning taxonomic categories, which stated that protection could be applied to "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature". The Endangered Species Act in 1973 defined "species" to include "subspecies of fish or wildlife or plants and any other group of fish or wildlife of the same species or smaller taxa in common spatial arrangement that interbreed when mature." The U.S. Fish and Wildlife Service interpreted the definition to authorize the listing of populations, subspecies and species. In 1978, Congress clarified the definition of "species" to authorize the listing of "distinct population segments" of species of vertebrate species of fish or wildlife (16 U.S.C. § 1532(16)). The 1978 amendments limited the population listing authority to avoid trivializing the ESA by "protect[ing] peripheral populations," especially because "many common species are uncommon or rare at the edge of their range" [24]. In 1996, the U.S. Fish and Wildlife Service [25] interpreted the 1978 "distinct population segment" amendment to the definition of species to require a determination that a population is both (1) discrete in relation to the remainder of the species to which it belongs, and (2) significant to the species to which it belongs. As explained by the U.S. Fish and Wildlife Service: "Congress has instructed the Secretary to exercise this authority with regard to DPS's . . . sparingly and only when the biological evidence indicates that such action is warranted." (Senate Report 151, 96th Congress, 1st Session). The requirement that a DPS be significant is intended to carry out the expressed congressional intent that this authority be exercised sparingly as well as to concentrate efforts undertaken under the Act on avoiding important losses of genetic diversity (R. D. Thornton, pers. comm.). The measures of discreteness and significance serve decidedly different purposes in the policy. The interests of conserving genetic diversity would not be well served by efforts directed at insignificant units. Therefore, if a population segment is considered discrete under one or more of the above conditions, its biological and ecological significance will then be considered in light of Congressional guidance (see Senate Report 151, 96th Congress, 1st Session) that the authority to list DPS's be used sparingly while encouraging the conservation of genetic diversity" [25].

In my opinion, Theimer *et al.* [12] misrepresent how the USFWS interpreted the DPS and misinterpret this part of the ESA and subsequent amendments. Specifically, contra Theimer *et al.* [12], the ESA does not state that "gene flow among adjoining populations will necessarily result in a complex boundary where genes and the phenotypic traits associated with them intergrade, making designations of subspecies and DPS boundaries difficult" [12]. Theimer *et al.* [12] further imply that the amendment means that "genes and phenotypic traits may move between adjoining subspecies at different rates and unequally in different directions, often yielding complex, indistinct boundaries between populations." Congress did not set forth such specific expectations for subspecies or DPSs, and it is important to recognize that these "predictions" stem from Theimer *et al.*'s [12] personal interpretation. It appears that this redefinition of the ESA was made by Theimer *et al.* [12] to fit the data for the specifics of the SWWF. In fact, all that the language of the 1973 amendment means is that there is interbreeding among individuals or populations within DPSs, not that separate DPSs or subspecies interbreed when mature.

Based on their idiosyncratic interpretation of Congressional intent in the 1973 amendment, Theimer *et al.* [12] conclude that the expectation is that "Within a subspecies boundary area, however, some traits should show a nonlinear break in frequency over geographic space (step clines) that would distinguish a subspecies boundary from the gradual, linear change in genetic and phenotypic frequencies (smooth clines) found in many species...". This too is language not found in the ESA or its amendments. Furthermore, what this statement does not point out is that this is the bane of past subspecies descriptions as it leaves open the possibility of describing a subspecies based on one or a small set of characters and ignoring conflicting information.

MATERIAL AND METHODOLOGY

Throughout their commentary Theimer *et al.* [12] select subsets of existing data or localities (or both) in their

attempt to garner support for *E. t. extimus*. In my opinion, the task is not to find some subset of characters that vary geographically in a particular way, but whether the subspecies exists in these data sets in the first place. Hence, I concentrate on analyses that include all characters and localities.

RESULTS AND DISCUSSION

Molecular Data and C-group Haplotypes

Theimer *et al.* [12] noted that Zink [11] plotted the relationship between latitude and the predicted C-group haplotypes, which Paxton *et al.* (2008) computed from joint consideration of latitude and elevation, rather than the actual frequency of these haplotypes. Paxton *et al.* [26] suggested that their predicted C-group frequencies (right-most column in their Table 1) better reflect the pattern of variation, but in their Figure 3, they instead plotted observed frequencies. Theimer *et al.* [12] claim that the latter plot reveals a step cline and their modeling suggests it is consistent with the boundaries some have proposed for *E. t. extimus*. I show both plots simultaneously (Fig. 1) and do not observe a discrete boundary in either plot. However, I would argue that in fact neither analysis is relevant. The “c-group” haplotypes include just 4 of 33 haplotypes found in that area. Because the entire mitochondrial genome (*e.g.*, all 33 haplotypes) is inherited as a single linkage group, there cannot be different signals in different regions of *Cytb* (or the entire mitogenome). Therefore, a more important question is whether a geographic signal consistent with subspecies limits is apparent in the entire *Cytb* data set.

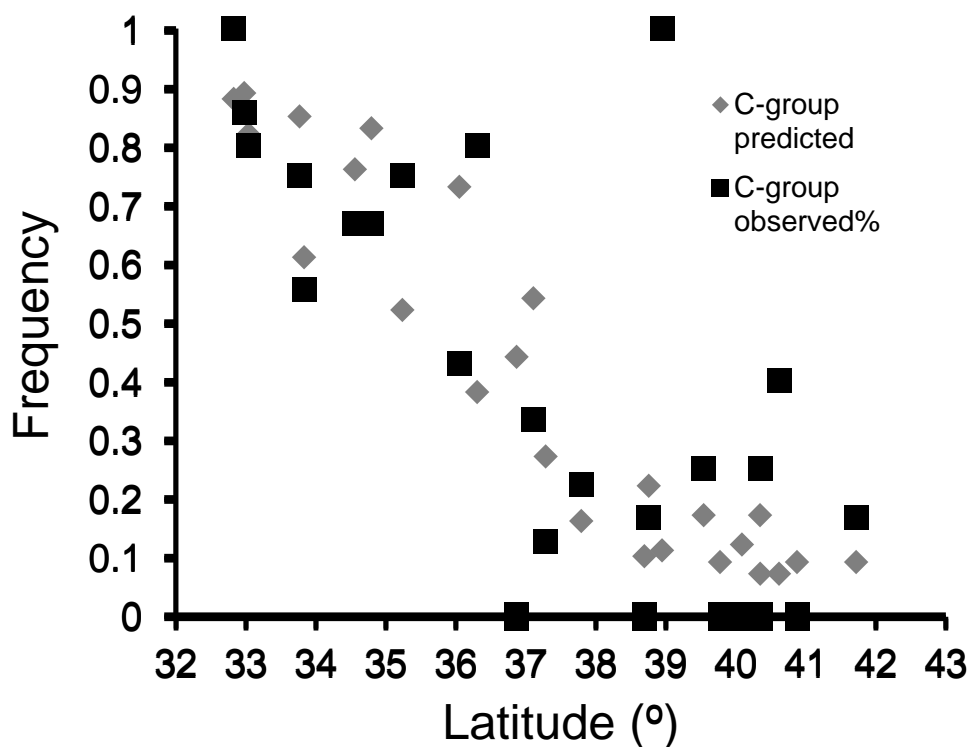


Fig. (1). Plot of C-group haplotypes that were adjusted by Paxton *et al.* [26] using a function of latitude and elevation, and raw values (C-group observed). With the exception of one outlier, the two plots suggest no step-cline between *E. t. adastus* and *E. t. extimus*.

Zink [11] performed but did not show a phylogenetic analysis of 93 mtDNA *Cytb* haplotypes deposited in Genbank, but not analyzed by, E. Paxton. According to Paxton *et al.* [27], these haplotypes came from breeding birds sampled in New York, Tennessee, Illinois, North Carolina, Virginia, North Dakota, South Dakota, Minnesota, and Maryland, Washington, Oregon, and California. The 93 Genbank haplotypes include those used by Paxton *et al.* [26]. Given

Theimer *et al.*'s [12] concern, Fig. (2) shows that there is no support for *E. t. extimus*, or any other subspecies.

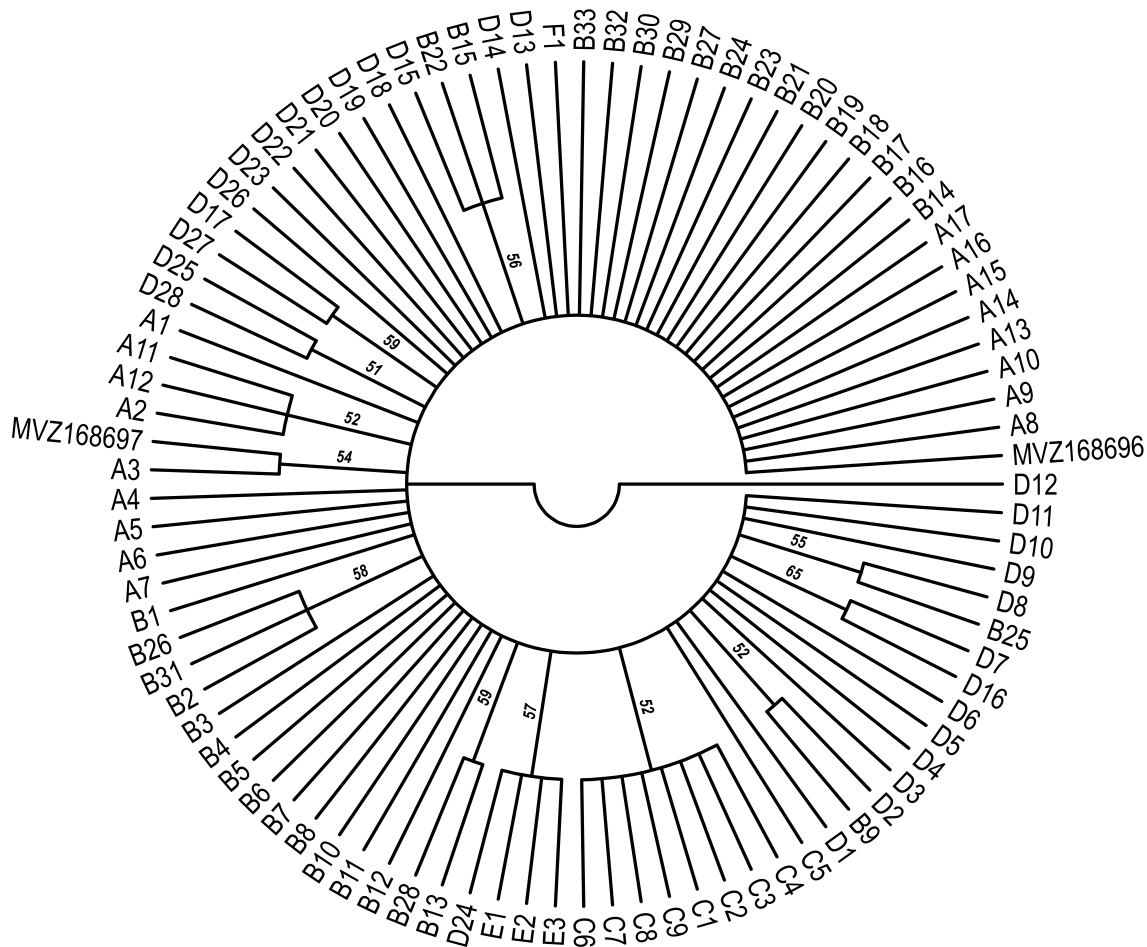


Fig. (2). Topology of bootstrap (1000 replications) neighbor-joining tree constructed with Mega6 [37] of 93 *Cytb* haplotypes for Willow Flycatcher deposited in Genbank (distance measure p-distance), rooted with *E. alnorum*. Haplotype codes are from [26, 27]. A haplotype followed by an “e” indicates it was found in a population assigned by Paxton *et al.* [26] to *E. t. extimus*, and “a” to *E. t. adastus*, and “e,a” represents a haplotype found in individuals of both subspecies. Although it is not possible to determine the geographic location of other haplotypes (the two MVZ specimens were collected by the author in Minnesota), they were found in breeding individuals taken throughout the range and representing all subspecies [27]. No node received > 60% bootstrap support (those with 50-60% support were groups of two or three haplotypes), showing that none of the four subspecies could be supported irrespective of the geographic locality or subspecies.

Subsampling data can lead to biased interpretations. For example, Figure 2C of Theimer *et al.* [12] shows a cline analysis for 8 populations, but has a potential flaw because it suggests that the haplotype groups A, B, C, and D are homogeneous. In Fig. (2), it can be seen that the haplotypes from the four haplotype groups are not clades, which is an assumption in the cline analysis by Theimer *et al.* [12]; violation of this assumption negates their conclusion. More importantly, in Fig. (3), I show the figure from Paxton [28, his Figure 2] in which the subspecies membership of the different haplotypes is indicated. In the inset, it can be seen that Theimer *et al.* [12] have removed information identifying taxonomic membership, which in my opinion is a deliberately misleading omission. Like the tree in Fig. (2), it shows that none of the main groups map onto subspecies. I agree that there is geographic variation, but I do not agree that there is support for a taxonomic boundary indicated by the center of a cline through a subsample of the samples. In any case of geographic variation, one will be able to find the center of a cline, but that is not the same as documenting the existence of a discrete taxon.

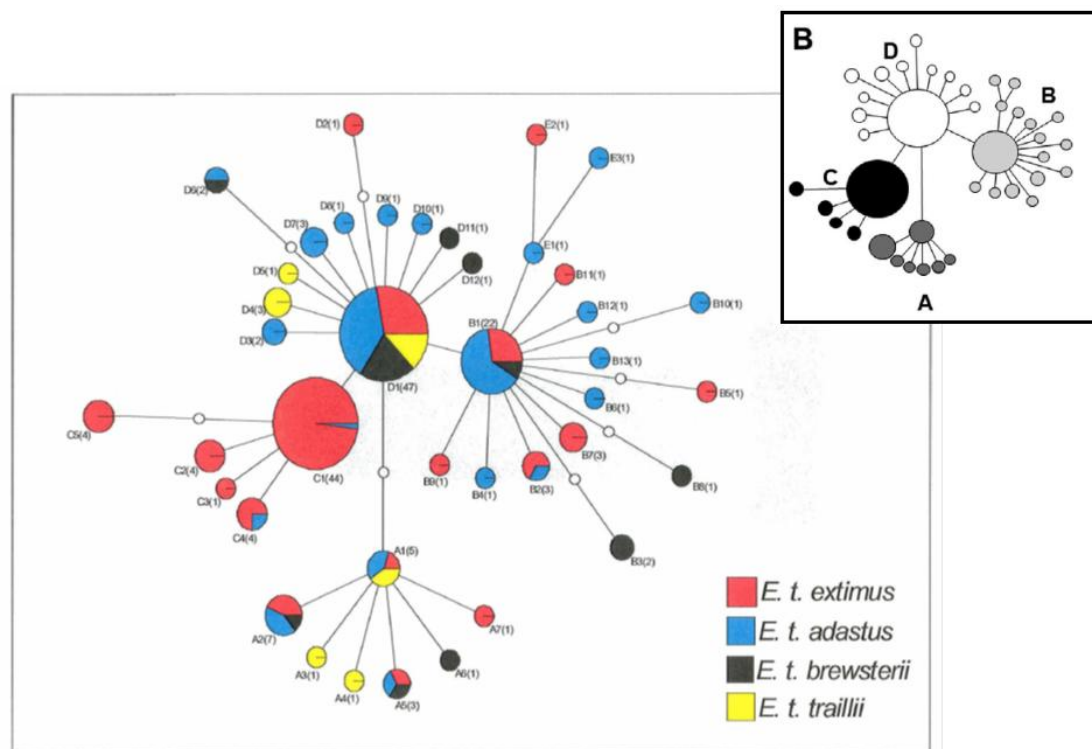


Fig. (3). Network showing relationships among Cytb haplotypes of four subspecies of Willow Flycatcher (from [28]). The color codes indicate that no subspecies is distinct, even at a level of 75%. The inset shows part of Theimer *et al.*'s [12] Fig. (2C), where they reproduce the network from [28] without revealing the mismatch between the network and subspecies.

A different way to address whether the Cytb data supports *E. t. extimus* is to evaluate it under the 75% rule [29, 30], which Theimer *et al.* [12] suggest as a viable approach. From the geographic distribution of haplotypes shown in Table 2 in Paxton *et al.* [26], I determined that 12.4% (18 of 145) of individuals could be unambiguously identified as coming from one of the 13 sites representing *E. t. extimus* (CAVE, ROOS, SAPE, GILA, GICL, ALPI, ZUNI, LOCI, TOPO, SEEG, SHIP MCSP, AZUL). By considering only the seven localities within the core of the range (CAVE, ROOS, SAPE, GILA, GICL, ALPI, ZUNI), the value drops to 6/145 (4.1%). These values fall well short of the 75% needed to support a subspecies according to 75% Rule [30]. The contrast between these two groupings shows that although geographic variation exists, there is no discrete boundary. It should also be noted that there is no statistical confidence intervals associated with this “75%” rule.

I repeat Paxton *et al.*'s [26] conclusion “We found no fixed differences between the two subspecies from either cytochrome-*b* haplotypes (Table 2) or AFLP polymorphic loci that would allow us to unambiguously distinguish individuals of one subspecies from the other.” I agree, and the genetic data fail to provide diagnostic or 75% support.

Morphology

Theimer *et al.* [12] select characters and localities that might support a subspecies irrespective of the pattern of variation in the other characters. They show results of cline analyses that show a cline centered over the approximate boundary used for *E. t. adastus* and *E. t. extimus*. I disagree that this represents best practices. The existence of geographic variation is established, the question is whether the subspecies qualifies as a taxon. In my earlier paper, I showed a PCA plot with all individuals and characters included, and there is clearly no support for subspecies, at the 75% level or any other level. It can be misleading to choose only characters that support one particular view or another [6].

I performed a discriminant function analysis of all six of the date-transformed color characters to evaluate support for subspecies. Again, there is no support for distinct subspecies considering all localities and characters. In terms of the

75% rule, no subspecies are supported either (Fig. 4).

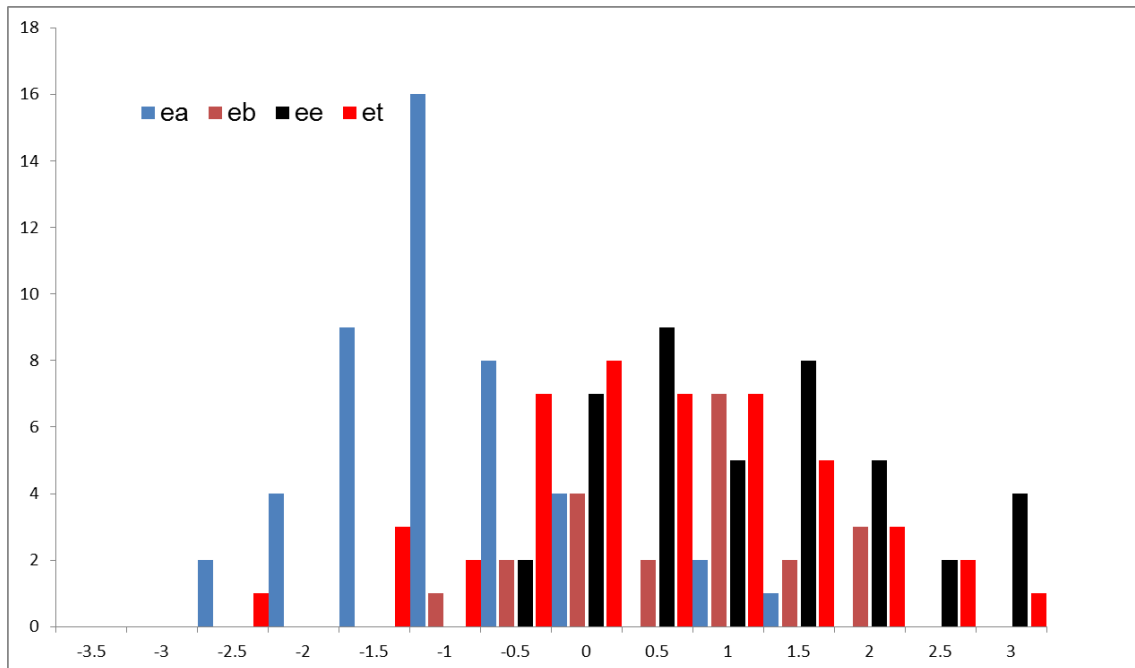


Fig. (4). Plot of individual's scores on Discriminant Function 1 based on six date-corrected coloration characters from [38] showing no example of a subspecies in which 75% of the individuals are distinct from 99% of the other individuals.

Niche Modeling

Neither the listing decision nor the subspecies description of *E. t. extimus* included tests for differences in ecological parameters. I performed a coarse-grained, but standard (*e.g.*, [31]) test of niche divergence to determine if there might be support for the subspecies in ecological data, given that the USFWS can use such data in listing decisions especially for a DPS. I included standard caveats about the role of ecological variables. Theimer *et al.* [12] provided a critique of my analysis that could invalidate many published studies (*e.g.*, [32]) if found to be general. But, they instead constructed a refined test, based on reduced sampling, that they (pg. 293) claim provides “weak evidence of niche partitioning between flycatcher subspecies...”. This does not provide strong evidence that the subspecies is ecologically discrete, especially considering they did not test *E. t. extimus* with samples to the east (*E. t. traillii*) and west (*E. t. brewsteri*). If the standard for recognizing subspecies is “weak evidence” of ecological divergence, then nearly all allopatric populations will be candidates for protection, an untenable stance scientifically and politically. Lastly, if a one group of flycatchers does not differ ecologically from geographically adjacent populations of the Yellow Warbler (*S. petechia*) then it is unlikely that two conspecific flycatcher populations would differ. The latter test, therefore, is specious.

Song

Theimer *et al.* [12] take subsets of the song data [33] and conclude that there is support for *E. t. extimus*. I maintain that the song data suggest geographic variation but are not definitive for subspecies delimitation.

Missing Subspecies Boundaries

Most assessments of subspecies limits include samples from all relevant forms (*e.g.*, [34]). To date, only the Cytb tree (Fig. 2) provides such an assessment, and even then, there are unsampled regions. Theimer *et al.* (2016) base their assertion of the significance of *E. t. extimus* primarily on comparisons of it with its northern counterpart, *E. t. adastus*, while discounting the significance of whether it is also distinct from *E. t. traillii* to the east and *E. t. brewsteri* in the west. I found that many specimens in Fig. (2) representing *E. t. traillii* from eastern North America (data not shown) were classified as *E. t. extimus*. Thus, it is possible that the latter two subspecies constitute a single unit, which is not threatened or endangered. A modern thorough study of the entire species is required, but their reanalysis provides no support for the subspecies.

Distinct Population Segments

Theimer *et al.* [12] mention the category of Distinct Population Segment (DPS). The DPS category was introduced to biologists in the ESA, whereas at the time, most effort was directed at the “evolutionarily significant unit” and “management unit” in addition to subspecies [35]. As noted above, a DPS must be distinct and significant to the species. Because Congress directed the United States Fish and Wildlife Service to use the DPS category sparingly it would be in my opinion hard to reconcile Congressional direction with the weak, at best, evidence supporting *E. t. extimus*. In any event, the southwestern Willow Flycatcher is not listed as a DPS, rather as a subspecies. To list *E. t. extimus* as a DPS would require delisting the subspecies, and the filing a petition for listing it as a DPS. In my opinion, the data fail to support the distinctiveness of the SWWF as a DPS, and hence it is not relevant to pursue discussion of its significance to the species.

Politics of Publishing on Conservation Topics

A reviewer of this manuscript remarked that it should be “submitted as a response to Theimer *et al.*'s paper to Condor, where the debate was initiated ... and should continue”. Indeed, the editor of The Condor: Ornithological Applications, declined to consider reviewing the manuscript, invoking a policy put in place after the Zink [11] paper was submitted that states that authors of Commentaries (*e.g.*, [11]) “will not typically be offered [the] opportunity” to respond to a Commentary addressing their original piece. An appeal to the editor and the AOU/COS Joint Publications Advisory Committee was declined with the comment that “there is no higher authority than the Editor”. This policy leaves open the possibility for editorial bias or prejudice. Although Zink [11] does not obviously fit the criteria for a “Commentary” as opposed to a “Research Article” (<http://www.editorialmanager.com/condor/default.aspx>), it was published by the editor as a Commentary. Thus, adherence to journal policy, and not scientific content (or a decision based on peer-review), delayed continued and timely discussion on the taxonomy of the southwestern willow flycatcher, which is currently being considered by the U.S. Fish and Wildlife Service in light of an ESA delisting petition filed during the time these papers were published and the current manuscript was submitted.

CONCLUSION

Theimer *et al.* [12] concluded that “we do not agree that currently available data fail to support the subspecies status of the endangered Southwestern Willow Flycatcher or its protection under the Endangered Species Act”. I believe that there is considerable evidence to the contrary, and in my opinion their conclusions stem from using an idiosyncratic interpretation of the ESA and subsets of the data. Analyses of the entire *Cytb* and morphological data sets do not meet the criteria stated by Theimer *et al.* [12] for a valid subspecies. Ecological and behavioral (song) support is weak at best, by their own admission. For a subspecies or any geographically defined unit to qualify as a listable unit under the ESA, it ought to be unambiguously differentiated. I agree that geographic variation exists and that the SWWF is the end of a clinal pattern of variation, but in my opinion, it does not meet the expectation stated by the USFWS that taxa listed under the ESA are evolutionarily significant. Some might consider the evidence suggesting a lack of distinctiveness as “negative” [6]. However, a lack of historical barriers to gene flow leads to the prediction that there will be no discrete character differences, which the analyses positively support. Thus, this is not a negative result, rather a confirmation of a particular evolutionary history of SWWF.

The SWWF refers to populations at the periphery of an otherwise common and widespread species that are clinally linked with the rest of the populations in North America, where it is not listed. Protection for the riparian habitats that the flycatcher inhabits is important, but in my opinion reliance on taxonomy of the last century falls short of needed support for using the SWWF as a flagship [4, 15]. Remsen [1] expressed a similar sentiment: “Is it any wonder, therefore, that the roster of formal subspecies, most described before the advent of statistical methods in ornithology, contains many names that refer only to arbitrary points on clines, average differences between populations, or zones of intergradation (as in *T. c. “connectens”* in Isler *et al.* 2005), rather than to discrete entities?” I believe that the AOU Checklist Committee [23], the recognized taxonomic authority for subspecific variation in North America, was correct in excluding the southwestern willow flycatcher as a valid subspecies.

Perhaps a next-generation sequencing approach Harvey MG *et al.* [36] or a range-wide, thorough morphological assessment might find support for subspecies that is not supported by existing data sets. But the fact remains that the best available evidence, analyzed in full, is not supportive of *E. t. extimus*. I urge agencies tasked with making listing decisions to base those decisions on analyses that use all available data sets and not subsets of them.

CONFLICT OF INTEREST

The author confirms that this article content has no conflict of interest. The author wrote this paper while funded as a faculty member of UNL but received no other funding to aid in the development or writing of this paper. I followed the Code of Ethics and Standards for Professional Conduct as outlined and adopted by The Wildlife Society.

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