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## Old-school Taxonomy Versus Modern Biosystematics: Species-level Decisions in *Stelgidopteryx* and *Empidonax*

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The AOU Committee on Classification and Nomenclature (hereafter, "Check-list Committee" or "CLC") rejected Phillips' (1986) proposal of species status for "*Stelgidopteryx ridgwayi*," but accepted Johnson and Marten's (1988) conclusion that *Empidonax occidentalis* is a biologic species (AOU 1989). Phillips (1994) argued that the opposite decision was justified in each case. In this response I defend decisions of the Check-list Committee on both issues. I also present personal views on the function of the CLC, of which I am a member. My views do not necessarily coincide with those of other CLC members.

At the outset it should be emphasized that no two species-level problems in avian systematics are identical. Pairs of any taxa always differ in distribution, degree of interaction, patterns of morphologic vari-

ation, and ecologic requirements. The kinds and quality of available information pertinent to the solution of each problem also will differ from case to case. Furthermore, researchers, including members of the CLC, seldom agree precisely on the relative importance of different kinds of data, on methods of data evaluation, or on concepts of species and subspecies. Nothing prevents an individual investigator from holding any view he or she chooses for any particular group of birds. In decisions on taxonomic status, therefore, members of the CLC think and vote as individuals. For these reasons, decisions on the systematic status of different pairs of taxa rarely will be comparable.

Despite these complications, the CLC attempts to deliberate issues consistently and conservatively, thus

minimizing confusion resulting from nomenclatural change, while still allowing revision when the biologic situation so dictates. Thus, proposals potentially leading to taxonomic change in the formal AOU list should be supported by evidence gathered and analyzed according to modern standards.

With respect to "*S. ridgwayi*," the CLC unanimously agreed that Phillips' (1986) information was inadequate to support a taxonomic change (a judgment which by no means ruled out the possibility that "*S. ridgwayi*" is actually a species). Instead of careful lists and maps of certain nesting localities documented by specimens in reproductive condition, Phillips offered brief, highly generalized statements of breeding occurrence which are so riddled with uncertainty as to be essentially useless to anyone seeking areas of possible contact between "*S. ridgwayi*" and *S. serripennis*. Motzorongo, Veracruz (for "*S. ridgwayi*") is the only precise nesting locality provided for either species. Thus, documentation of supposed sympatry is lacking.

Furthermore, Phillips (1986) offered no quantitative appraisal of geographic variation, either of morphology (stated, without documentation, to be invariant) or color, of any taxon in *Stelgidopteryx*. For depth of furca ("longest minus central rectrices"), the only morphologic feature by which *S. ridgwayi* is said to show "little or no overlap" with other forms of *S. serripennis*, Phillips (1994:770) only gives extreme measurements in a key. He provides no sample sizes, sample means, standard deviations, or standard errors to enable interpretation of significance. The possibility of geographic variation in depth of furca is not mentioned let alone explored. Regarding voice, Phillips (1994:771) states that "This is apparently less important for species recognition in swallows than in flycatchers; that of *S. ridgwayi* is apparently unrecorded." Thus, Phillips obtained no tape recordings of vocalizations of these potential sibling species of swallows and, therefore, his account lacks audiospectrograms, data relevant to possible reproductive isolation. He described no fieldwork indicating familiarity with these swallow taxa in their natural setting. One searches in vain in Phillips' work for either data or analysis reflecting a modern treatment of variation that could support the recognition of *ridgwayi* as a distinct species, whatever its true biologic status.

In seeking the most complete information possible as a basis for sound taxonomic decisions, the Checklist Committee routinely encourages further study and such is definitely needed in *Stelgidopteryx*. Proper data on breeding distribution, possible sympatry, morphologic variation, vocalizations, and genetic variation should be sought in southern Mexico.

The data base used for the decision in the *E. difficilis* complex differed completely from that for the swallows. The flycatcher research included thorough, quantitative descriptions of morphology, color, voice, and allozymes, all analyzed with the most sophisti-

cated techniques available at the time of publication (Johnson 1980, Johnson and Marten 1988). Indeed, peers (Anonymous 1993) generously described the 1980 monograph as "perhaps the most detailed and comprehensive analysis of geographic variation in any group of birds, particularly in its integration of vocalizations with plumage, size, and shape . . ." Whether the merits of the work justify hype at this level remains questionable; suffice it to state that a shallow study it was not. My response to Phillips (1994) follows his numbered headings:

(1) *Characterization and distributions*.—Phillips states that "Johnson and Marten (1988) gave no morphologic definition, key, plate, difference in color, pattern, or structure, nor distribution in winter or migration. Even for the breeding season, they gave no distributions outside of a small area in or near California." This statement is both false and unfair because Johnson and Marten (1988) dealt only with genetic differentiation. All other information Phillips specifies as lacking, except for a plate and a key, both of which are generally useless in discriminating sibling species (unless they contain quantitative data on voice and genetic differentiation), is published in Johnson (1973, 1974, 1980).

(2) *Structure*.—Johnson and Marten (1988) did not discuss *E. d. cineritius* for the obvious reason that their paper dealt with genetic differentiation, and no tissue of that form was available for molecular study. Johnson (1980:45), however, gave an elaborate analysis of wing shape, which proved that this subspecies "is relatively long-winged and falls out of the long Pacific Coastal trend," thus falsifying Phillips' (1994) claim that *E. d. cineritius* has a somewhat more rounded wing. Johnson (1980:114), while noting that available material of this form is generally worn, tentatively recognized it on the basis of paleness, "pending the accumulation of better specimens and sound recordings." The latter are now available (Howell and Cunnings 1992) and clearly show the vocal alliance of southern Baja birds with coastal forms to the north.

(3) *Color and size*.—*E. flavescens* differs profoundly in color from *E. occidentalis* as proved by a refined, quantitative analysis using reflectance spectrophotometry (Johnson 1980:52); plottings of the two forms barely overlap. Furthermore, our statement (Johnson and Marten 1988:177) that "Insular, coastal, and interior populations of the western United States . . . are strongly differentiated in size, color, voice, and preferred habitat" is true. Admittedly, all of these features are more different when coastal *E. difficilis* is compared with remote populations of *E. occidentalis* from the far interior. However, even where the two taxa occur in close proximity, such as in the Shasta and Warner regions of northern California, the break is abrupt. Note the statistically different means for length of primary 7, length of tail, cube root of body mass (weight), and brightness of breast color in samples representing Shasta and Warner (Johnson 1980:

TABLE 1. Measurements\* of adult males, first-year males, adult females, and first-year females in *Empidonax difficilis-occidentalis* complex. All were breeding birds.

Sample area <sup>b</sup>	Adult males		First-year males		Adult females		First-year females	
	$\bar{x} \pm \text{SD} (n)$	CV	$\bar{x} \pm \text{SD} (n)$	CV	$\bar{x} \pm \text{SD} (n)$	CV	$\bar{x} \pm \text{SD} (n)$	CV
<b>Primary 10</b>								
Shasta	56.99 ± 1.17 (13)	2.05	54.72 ± 1.35 (5)	2.47	52.38 ± 1.21 (5)	2.31	51.80 ± 1.18 (3)	2.28
Siskiyou	59.54 ± 1.64 (17)	2.75	56.77 ± 0.79 (6)	1.39	54.81 ± 1.80 (8)	3.28	53.57 ± 2.01 (3)	3.75
Warner	60.70 ± 1.41 (27)	2.32	60.15 ± 0.53 (4)	0.88	56.62 ± 1.08 (10)	1.91	54.58 ± 1.79 (5)	3.28
<b>Primary 7</b>								
Shasta	66.11 ± 1.21 (13)	1.83	63.60 ± 1.53 (5)	2.41	61.30 ± 1.26 (5)	2.06	60.20 ± 0.62 (3)	1.03
Siskiyou	68.93 ± 1.50 (17)	2.18	65.07 ± 0.77 (6)	1.18	63.79 ± 1.76 (8)	2.76	62.07 ± 0.83 (3)	1.34
Warner	70.64 ± 1.42 (27)	2.01	68.80 ± 0.79 (4)	1.15	66.13 ± 0.89 (10)	1.35	63.98 ± 2.22 (5)	3.47
<b>Primary 4</b>								
Shasta	55.36 ± 0.89 (13)	1.61	54.78 ± 0.97 (5)	1.77	52.72 ± 1.40 (5)	2.66	51.83 ± 1.35 (3)	2.61
Siskiyou	57.86 ± 1.18 (17)	2.03	55.75 ± 0.89 (6)	1.60	54.13 ± 1.45 (8)	2.68	54.53 ± 1.68 (3)	3.08
Warner	58.89 ± 1.07 (27)	1.82	58.73 ± 0.67 (4)	1.14	56.40 ± 1.19 (10)	2.11	54.82 ± 2.21 (5)	4.03
<b>Tail Length</b>								
Shasta	58.55 ± 1.64 (13)	2.80	57.22 ± 1.54 (5)	2.69	55.70 ± 1.50 (5)	2.69	54.50 ± 2.19 (3)	4.02
Siskiyou	60.60 ± 1.27 (17)	2.10	58.12 ± 2.03 (6)	3.49	56.61 ± 1.73 (8)	3.06	55.57 ± 0.50 (3)	0.90
Warner	61.63 ± 1.56 (27)	2.53	59.20 ± 1.08 (4)	1.82	58.56 ± 1.43 (10)	2.44	56.70 ± 1.90 (5)	3.35
<b>Bill Length</b>								
Shasta	8.40 ± 0.34 (16)	4.05	8.48 ± 0.47 (5)	5.54	7.84 ± 0.38 (5)	4.85	8.00 ± 0.30 (3)	3.75
Siskiyou	8.31 ± 0.33 (17)	3.97	8.30 ± 0.38 (6)	4.58	8.45 ± 0.48 (8)	5.68	7.97 ± 0.38 (3)	4.77
Warner	8.40 ± 0.27 (32)	3.21	8.20 ± 0.22 (4)	2.68	8.47 ± 0.29 (10)	3.42	8.24 ± 0.17 (5)	2.06
<b>Bill Depth</b>								
Shasta	3.50 ± 0.14 (17)	4.00	3.44 ± 0.11 (5)	3.20	3.42 ± 0.11 (5)	3.22	3.37 ± 0.12 (3)	3.56
Siskiyou	3.59 ± 0.12 (17)	3.34	3.55 ± 0.10 (6)	2.82	3.63 ± 0.15 (8)	4.13	3.60 ± 0.17 (3)	4.72
Warner	3.60 ± 0.14 (31)	3.89	3.50 ± 0.18 (4)	5.14	3.62 ± 0.22 (5)	6.07	3.60 ± 0.08 (4)	2.22
<b>Bill Width</b>								
Shasta	5.10 ± 0.21 (16)	4.12	5.08 ± 0.22 (5)	4.33	5.06 ± 0.18 (5)	3.56	5.17 ± 0.21 (3)	4.06
Siskiyou	5.16 ± 0.14 (17)	2.71	5.15 ± 0.16 (6)	3.11	5.16 ± 0.19 (8)	3.68	5.20 ± 0.17 (3)	3.27
Warner	5.20 ± 0.18 (32)	3.46	5.10 ± 0.32 (4)	6.27	5.17 ± 0.20 (9)	3.87	5.14 ± 0.18 (5)	3.50
<b>Tarsus + toe</b>								
Shasta	25.90 ± 0.60 (18)	2.32	26.24 ± 0.48 (5)	1.83	25.10 ± 0.70 (5)	2.79	24.90 ± 0.46 (3)	1.85
Siskiyou	25.97 ± 0.67 (17)	2.58	25.55 ± 0.64 (6)	2.50	25.34 ± 0.73 (8)	2.88	25.13 ± 0.45 (3)	1.79
Warner	26.20 ± 0.72 (32)	2.75	26.23 ± 0.43 (4)	1.64	25.44 ± 0.55 (10)	2.16	25.40 ± 0.74 (4)	2.91
<b>Body mass</b>								
Shasta	10.5 ± 0.43 (18)	4.10	10.24 ± 0.43 (5)	4.20	10.83 ± 0.51 (4)	4.71	10.67 ± 0.75 (3)	7.03
Siskiyou	11.3 ± 0.64 (17)	5.65	10.73 ± 0.49 (6)	4.57	11.90 ± 0.62 (6)	5.21	11.17 ± 0.55 (3)	4.92
Warner	11.8 ± 0.43 (23)	3.64	12.3 (1)	—	11.00 ± 0.45 (8)	4.09	11.55 ± 0.61 (4)	5.28

\* See Johnson (1980:6-7) for methods of measurement.

<sup>b</sup> Shasta represents *E. d. difficilis*, Warner represents *E. o. bellmayri* and Siskiyou is a sympatric sample of both species.

figs. 8, 12, 20, and 21). Moreover, five of six variables of advertising song syllables also were statistically different between the same two regions (Johnson 1980: fig. 28). Even samples from as close as the two sides of the Cascade Mountains in southern Oregon (e.g. Rogue River and Crater Lake) differ significantly in length of primary 7 (Johnson 1980:fig. 8). Tables 1 and 2 summarize size and color data for Shasta (representing *E. difficilis*) and Warner (representing *E. occidentalis*). When sex and age groups are properly separated, the utility of length of primaries, length of tail, body mass, and brightness of breast in distin-

guishing the two species is readily evident. The three bill characters and the length of tarsus plus middle toe, as well as the dominant wavelength and purity of breast color, are less useful in this regard. For additional analysis of genetic data beyond Johnson and Marten (1988), see Barrowclough and Johnson (1988) where the distinction of *E. d. insulicola* is clearly shown.

Scatter plots of pairs of distinguishing characters (e.g. lengths of primaries 10 and 4) clearly separate all specimens of adult males from Shasta and Warner (Fig. 1A). Note that for the latter character the two populations do not overlap. Similarly, values for body

TABLE 2. Colorimetric data for breeding individuals in *Empidonax difficilis-occidentalis* complex (sex-age groups combined). See Johnson (1980:7) for methods of measurement.

Sample area	$\bar{x} \pm SD (n)$	CV
<b>Dominant wavelength of breast (<math>\lambda_d</math>)</b>		
Shasta	575.9 $\pm$ 0.65 (19)	0.11
Siskiyou	576.3 $\pm$ 0.70 (18)	0.12
Warner	576.4 $\pm$ 0.36 (27)	0.06
<b>Purity of breast (P)</b>		
Shasta	32.9 $\pm$ 3.55 (19)	10.79
Siskiyou	32.8 $\pm$ 3.64 (18)	11.10
Warner	33.8 $\pm$ 3.42 (27)	10.12
<b>Brightness of breast (Y)</b>		
Shasta	21.9 $\pm$ 1.82 (19)	8.31
Siskiyou	19.7 $\pm$ 2.61 (18)	13.25
Warner	18.4 $\pm$ 1.51 (27)	8.21

mass versus brightness of breast separate completely in a scatter diagram comparing Shasta and Warner (Fig. 1B). These data, among others, disprove the claim of Phillips (1994) and authors he cites of "vast areas of morphological (size) intergradation." It is important to emphasize that morphologic differences are not necessary to establish species status. After all, sibling species do not evolve for the purpose of being identified by taxonomists.

As Phillips (1994:770) states, my finding of an abrupt shift in size, song, and habitat in northern California and southern Oregon "was directly contrary to all earlier revisers" and the reason is obvious. Earlier taxonomists, including Phillips, routinely ignored two serious problems: age differentiation and late spring migration. First, because adults and first-year birds differ strongly in size (Johnson 1974:118-123), age groups in the *E. difficilis* complex must be separated in any taxonomic analysis. Thus, earlier researchers often incorrectly identified smaller, first-year individuals of forms that are larger as adults (e.g. *E. occidentalis*) as members of smaller forms (e.g. *E. difficilis*). Second, because in many regions of western North America spring migrants are still moving north (often even into mid-June) while local populations in this complex are already nesting at the same sites, supposed "breeding" samples often are contaminated with migrants. Thus, genuine nesting samples should be comprised only of specimens with accurate reproductive data, a standard routinely ignored in the past. Table 1 of Phillips (1994) thus represents a return to the dark ages of *E. difficilis* systematics. Although this table expressly excludes immatures (young in summer or fall), Phillips fails to separate first-year birds from adults. Furthermore, his midlatitude samples probably included migrants because reproductive condition was not noted for any specimens from which these miscellaneous measurements were compiled.

Furthermore, sample sizes are unstated and no statistics accompany his raw figures. See Johnson (1980) for a continentwide analysis of size variation based on large samples of correctly aged and sexed specimens, all in reproductive condition.

(4) *Nesting*.—Similarity or difference of nests is not necessarily related to species status.

(5) *Voice*.—This section in Phillips (1994) is entirely misleading. As I have described in detail (Johnson 1980:61-67), advertising songs of *E. difficilis* and *E. occidentalis* differ profoundly when relatively remote populations are compared (e.g. coastal California vs. northern Utah). Where the nesting distributions of the two taxa approach more closely, for example in the vicinity of the Cascade Mountains of northern California and southern Oregon, the songs approach in structure but do not overlap (Johnson 1980:fig. 28). In particular, the final syllable remains as "low-high" in sequence in *E. difficilis* and "high-low" in *E. occidentalis*, a difference audible in the field at sympatric localities in the Siskiyou region of northern California. Furthermore, male position notes differ obviously, from a typical sinusoidal, "boat-shaped," or "ladle-shaped" note in coastal *E. difficilis* to a steeply-rising, two-parted note in *E. occidentalis* of the far interior (Johnson 1980:68-70). Position notes are mixed in shape in populations of *E. occidentalis* in the Siskiyou region, Warner Mountains, and on the east side of the Cascade Mountains in Oregon. Here, at least some individual males can deliver both sinusoidal notes and steeply-rising notes (some of the latter occasionally are two-parted), despite their consistently interior advertising songs with the high-low third syllable. Some of the variability in the Siskiyou region is probably a result of sympatry (see below). The presence of "bilingual" individuals with regard to male position notes in this region is more difficult to explain. Although hybridization could be involved at least to a limited degree, such would be more convincingly indicated by a single style of note, a note somewhat intermediate in shape between the deeply-curved and steeply-rising types observed. Instead, the occurrence of both types of position notes may reflect possible mixed ancestry of populations now stabilized as *E. occidentalis hellmayri* in the northwestern portion of its range. I have never heard the two-parted note in coastal populations or the sinusoidal note in the far interior of the western United States. Vocal intermediacy is clearly not shown by populations of the two taxa in northern California and southern Oregon.

Finally, the song of *E. d. cineritius*, rather than being "the most distinctive" (Phillips 1994:771), has now been shown through audiospectrographic analysis (Howell and Cannings 1992) to be extremely similar to that of *E. d. difficilis* to the north.

(6) *Sympatry*.—Elsewhere (Johnson 1980:64), I published spectrograms that demonstrate trenchant differences in the advertising songs of *E. occidentalis* and *E. flavescens*, thus arguing for the species status of

TABLE 3. Data from specimens collected in the Siskiyou Region, northern California, listed by sex and then in ascending order of discriminant scores and grouped based on probable identity.

NKJ no.	Age	Conads	Locality	Date	Primary				Tail length	Bill			Tarsus + toe	Body mass	DF <sup>a</sup>
					10	7	4	4		Length	Depth	Width			
<b>Male <i>E. o. hellmayri</i></b>															
1876	Ad.	6 x 4 mm	Shovel Cr.	6 June 1964	61.5	70.5	59.8	60.5	8.8	3.6	5.3	25.8	12.0	-0.471	
1877	Ad.	6 x 4 mm	Shovel Cr.	6 June 1964	61.5	71.5	60.1	63.1	8.2	3.7	5.3	26.9	12.5	-0.122	
2751	Ad.	6 x 4 mm	Ike's Cr.	1 June 1968	61.8	70.6	58.8	62.6	8.6	3.7	5.3	26.2	12.5	-0.050	
1880	Ad.	6 x 3 mm	Shovel Cr.	7 June 1964	59.1	69.4	58.3	60.8	8.1	3.5	5.0	26.6	11.8	0.059	
2743	Ad.	5 x 3 mm	Shovel Cr.	31 May 1968	61.4	71.1	58.7	61.7	8.1	3.4	5.1	26.4	10.8	0.199	
4628	Ad.	7 x 4 mm	Shovel Cr.	19 June 1981	60.4	69.8	57.4	61.4	8.5	3.6	5.2	26.2	11.5	0.225	
4626	Ad.	6 x 2 mm	Shovel Cr.	18 June 1981	58.4	68.2	57.2	58.8	8.4	3.7	5.2	25.9	11.8	0.280	
4624	Ad.	6 x 3 mm	Shovel Cr.	18 June 1981	57.4	67.8	58.9	59.2	8.0	3.4	5.3	24.5	10.9	0.310 <sup>b</sup>	
4617	Ad.	5 x 3 mm	Harris Cr.	16 June 1981	62.0	69.5	58.4	61.3	7.6	3.5	5.0	25.9	11.1	0.377	
4618	Ad.	7 x 4 mm	Harris Cr.	16 June 1981	59.7	68.5	57.4	60.3	8.3	3.5	5.1	25.3	11.0	0.378	
<b>Male indeterminate<sup>c</sup></b>															
2748	Ad.	6 x 3 mm	Ike's Cr.	1 June 1968	60.0	69.5	57.4	60.7	8.3	3.7	5.1	25.1	10.8	0.515	
1879	FY	7 x 3 mm	Shovel Cr.	7 June 1964	57.4	65.0	56.4	58.3	8.7	3.6	5.2	25.8	11.4	0.585	
2752	Ad.	6 x 3 mm	Ike's Cr.	1 June 1968	59.0	67.2	56.6	59.0	8.2	3.5	4.9	27.1	10.9	0.656	
4623	Ad.	6 x 3 mm	Shovel Cr.	18 June 1981	58.5	69.3	58.4	61.0	7.9	3.6	5.4	26.4	10.6	0.659	
4616	Ad.	6 x 3 mm	Harris Cr.	16 June 1981	57.3	67.0	56.4	60.2	8.8	3.8	5.2	25.6	11.3	0.703	
<b>Male <i>E. d. difficilis</i></b>															
2741	Ad.	5 x 3 mm	Shovel Cr.	31 May 1968	57.8	67.4	56.8	60.5	8.2	3.5	5.0	25.8	10.2	0.753 <sup>d</sup>	
2745	Ad.	5 x 3 mm	Shovel Cr.	31 May 1968	58.5	66.6	56.2	58.4	8.7	3.6	5.2	25.4	11.4	0.828	
2746	Ad.	6 x 3 mm	Shovel Cr.	1 June 1968	57.8	67.9	56.6	60.7	8.6	3.7	5.2	26.4	11.3	0.859	
4630	FY	7 x 3 mm	Shovel Cr.	19 June 1981	56.2	65.9	56.4	58.8	8.1	3.4	4.9	24.5	10.2	0.940 <sup>e</sup>	
4620	FY	5 x 3 mm	Ike's Cr.	17 June 1981	57.7	65.8	55.9	58.4	7.8	3.6	5.1	26.3	11.1	0.956 <sup>f</sup>	
4629	FY	5 x 3 mm	Shovel Cr.	19 June 1981	57.3	65.3	56.4	60.6	8.5	3.5	5.4	25.7	10.6	0.970	
4622	FY	6 x 3 mm	Ike's Cr.	17 June 1981	55.8	64.5	55.2	58.2	8.7	3.7	5.2	25.1	10.9	0.978	
2744	FY	5 x 3 mm	Shovel Cr.	31 May 1968	56.2	63.9	54.2	54.4	8.0	3.5	5.1	25.9	10.2	1.052	
<b>Female <i>E. o. hellmayri</i></b>															
CWB 709 <sup>g</sup>	Ad.	Ova Enl.	Shovel Cr.	7 June 1964	60.7	68.7	57.4	59.0	8.4	3.6	5.1	24.8	11.8	-13.105	
4625	Ad.	Ova Enl.	Shovel Cr.	18 June 1981	56.0	66.0	56.2	58.1	8.6	3.6	5.2	24.2	11.5	-4.969 <sup>b</sup>	
2749	Ad.	Ova Enl.	Ike's Cr.	1 June 1968	56.4	64.8	53.9	55.1	8.7	3.7	5.2	26.4	12.4	-2.966	
4615	Ad.	Ova Enl.	Harris Cr.	15 June 1981	57.4	66.0	56.2	59.7	9.0	3.7	5.3	25.5	12.9	-2.354	
2747	Ad.	Laying	Ike's Cr.	1 June 1968	55.9	64.4	54.7	56.6	8.5	3.9	5.3	25.6	13.9	-0.971	

TABLE 3. Continued.

NKJ no.	Age	Gonads	Locality	Date	Primary			Tail length	Bill			Tarsus + toe	Body mass	DF <sup>a</sup>
					10	7	4		Length	Depth	Width			
<b>Female indeterminate<sup>c</sup></b>														
4627	Ad.	Laying	Shovel Cr.	19 June 1981	52.9	62.5	53.1	54.8	8.0	3.6	5.4	24.6	13.2	0.595
2742	Ad.	Laying	Shovel Cr.	31 May 1968	53.4	63.1	53.4	57.2	7.5	3.5	4.8	25.9	11.7	2.739 <sup>d</sup>
4631	FY	At nest	Shovel Cr.	19 June 1981	53.3	61.8	52.7	55.5	8.4	3.8	5.4	24.7	10.8	2.838 <sup>e</sup>
<b>Female <i>E. d. difficilis</i></b>														
2753	Ad.	Ova 1 mm	Ike's Cr.	1 June 1968	53.7	61.7	52.3	54.8	8.7	3.6	5.1	25.5	11.6	4.106
4621	FY	At nest	Ike's Cr.	17 June 1981	53.3	61.8	52.7	56.1	7.7	3.5	5.1	25.1	11.8	4.847 <sup>f</sup>
2750	Ad.	Ova Enl.	Ike's Cr.	1 June 1968	52.8	61.8	53.2	56.6	8.6	3.4	5.0	26.0	11.3	7.671
4619	FY	At nest	Harris Cr.	16 June 1981	51.7	61.4	54.9	55.1	7.8	3.5	5.1	25.6	10.9	9.683

<sup>a</sup> Ranges of discriminant function (DF) scores calculated for reference samples: Shasta males, 4.196 to 1.082; Shasta females, 0.757 to 1.082; Warner males, -0.240 to 0.355; Warner females, -5.471 to -0.891.

<sup>b</sup> Four mated pairs indicated by superscripts b-b', d-d', e-e', and f-f'.

<sup>c</sup> Specimens categorized as "indeterminate" represent either *E. d. difficilis* or *E. o. hellmayri* within their normal range of variation. F, hybrids, backcrosses, or a combination of these four categories.

<sup>d</sup> C. W. Brown no. 709 (=MVZ no. 152634), although labelled as female with brood patch and yellow ovum 6 mm in diameter, is unusually large for that sex and has wing shape more typical of male. Data for this individual included for sake of completeness, but omitted from Table 1. All other specimens listed in this table collected by author.

these taxa despite their allopatric nesting distributions (Johnson 1980:111, 138).

Phillips (1994) questions the conclusion (Johnson and Marten 1988) that *E. d. difficilis* and *E. "d." hellmayri* breed sympatrically and mate assortatively in the Siskiyou region of northern California and, therefore, should be regarded as biologic species. In retrospect, the presentation of data from the Siskiyou region as a single population, rather than of overlapping, mixed populations, with regard to size (Johnson 1980) and genetic structure (Johnson and Marten 1988) admittedly rendered the data more difficult to analyze and probably contributed to Phillips' (1994) misinterpretations. Therefore, raw measurement data and discriminant scores for individual specimens are presented here (Table 3). The sample is larger (23 males and 12 females) than discussed by Johnson (1980) or Johnson and Marten (1988) because those papers excluded data from nine first-year birds and one adult female whose sex I initially questioned (see footnote to Table 3). Note that the discriminant scores from Siskiyou span the entire range of scores for both the Warner and Shasta samples (Johnson and Marten 1988: 187). Phillips' (1994:table 2) reanalysis of scores published earlier also clearly demonstrates the remarkably broad range of values seen in the Siskiyou sample.

High values for coefficients of variation (CV) can also reveal heterogeneity in samples (Mayr 1969:170). In adult males and females, for which samples are reasonably large, lengths of primaries 10, 7, and 4, length of tail, body mass, and brightness of breast color, features useful in distinguishing the two species, showed higher CVs for Siskiyou than for either Shasta or Warner in 9 of 10 comparisons (Table 1). The CV for brightness of breast color was exceptionally large in the Siskiyou sample (Table 2), suggesting that it was derived from a mixed population.

Finally, comparison of pairs of measurements from Siskiyou with reference samples from Shasta and Warner again demonstrates the mixed character of the former population (Fig. 1). For length of primary 10 versus length of primary 4, observe that 14 of 17 Siskiyou birds (82%) fall within either reference ellipse and that the three values outside the two ellipses are so close as to be reasonably viewed as representing normal variation (Fig. 1A). No cloud of points between Shasta and Warner that could suggest intermediacy of the Siskiyou sample is evident. Even more strikingly, in the plot of body mass versus brightness of breast color (Fig. 1B) values for Siskiyou span the entire range shown by Shasta and Warner. All of these lines of evidence lead to the conclusion that *E. difficilis* and *E. occidentalis* are sympatric in the Siskiyou region.

*Concluding remarks.*—Phillips (1994) also laments what he perceives as the dramatic deterioration of 20th-century ornithology. I concur, with regard to certain important trends that directly suppress avian systematics: the increasingly serious interference with

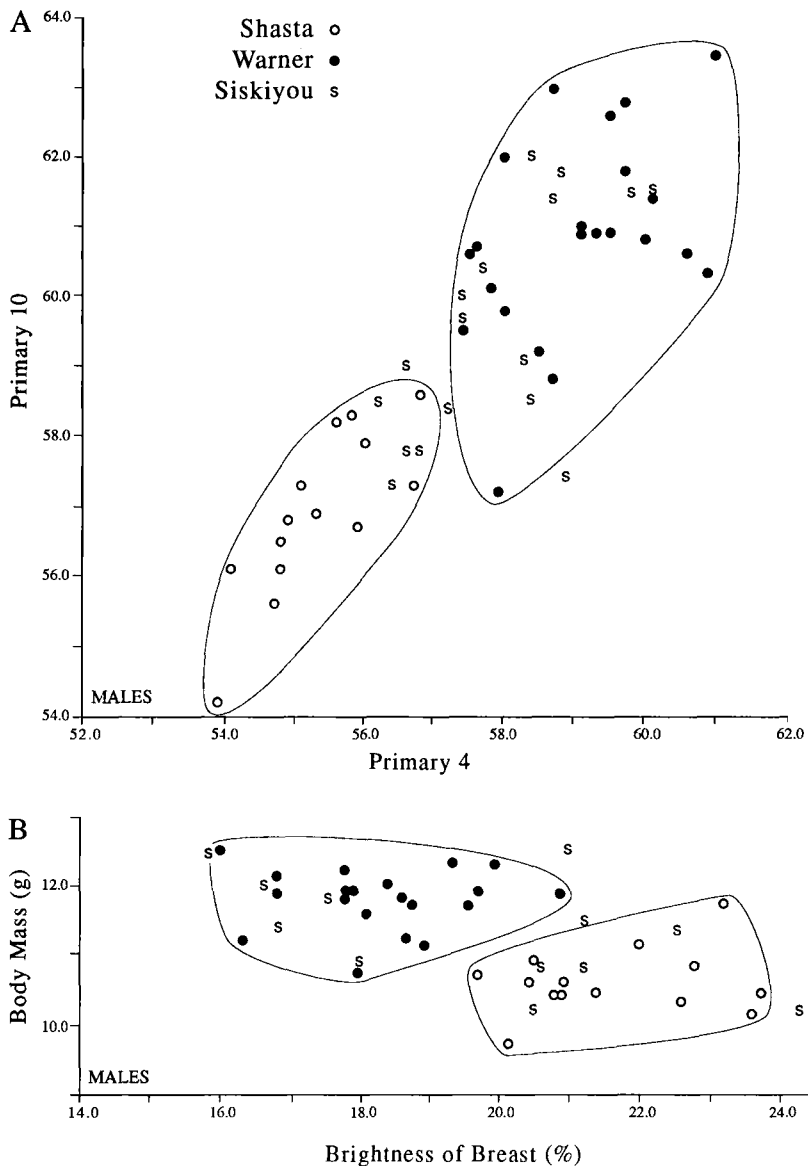


Fig. 1. Scatter diagrams in which circles represent specimens of *E. d. difficilis* from Shasta, dots represent specimens of *E. o. hellmayri* from Warner, and each "S" represents specimen in mixed, sympatric sample from Siskiyou. (A) Length of primary 10 plotted against length of primary 4; (B) body mass plotted against percentage brightness of breast plumage.

judicious specimen collecting (spearheaded by animal "rights" zealots and others); the abolition of major curatorial positions in ornithology (in recent years at the British Museum [Natural History], San Diego Natural History Museum, Los Angeles County Museum of Natural History, University of California, Los Angeles, and the Canadian Museum of Nature, Ottawa); the generally wretched financial support for collections; and the commonplace acceptance of shoddy

evidence for geographic occurrence. Although Phillips (1994) specifies none of these in his commentary, as a taxonomist he would doubtless agree that they are serious concerns.

With regard to the points he does emphasize, however, the opposite is true. Rather than being in decline, avian biology today is as vigorous as any discipline of natural science. His assertion that current researchers lack dedication is absurd. Only those who

have attempted large-scale, multidisciplinary studies of wild birds, using field, museum, and laboratory approaches, can truly appreciate the labor required and the benefits gained. In contrast, those who have never conducted modern research in avian systematics are in a poor position to criticize investigations that continue to breathe life and excitement into enduring problems by combining carefully selected traditional methods with current technology.

Finally, Phillips (1994:772) forecasts that "application of allozyme and other genetic differences to species' names would threaten the stability of our international nomenclature, since no such data were available when the animals were named." To the contrary, type specimens of birds used as the basis for the original names carry a storehouse of genetic information preserved in the DNA of their skins and feathers. The techniques of molecular evolution already have been applied successfully to reveal the sequence of mitochondrial DNA (mtDNA) bases in old museum specimens of small mammals (Thomas et al. 1990) and in material as limited as single human hairs (Vigilant et al. 1989). DNA has been isolated and amplified from small pieces of flight feathers (Ellegren 1992), and several currently active laboratories have obtained legible mtDNA sequences from bits of skin and feathers from old specimens.

Thus, we can anticipate broadscale future applications of molecular markers to a host of problems in avian systematics at all levels, ranging from the identification of song and call types of old and silent specimens of sibling species of flycatchers (*Empidonax*, *Tyrannus*, *Elaenia*) and crossbills (*Loxia*), and correct allocation to breeding populations of migrant and wintering specimens, to clarification of family and ordinal relationships. Material of extinct taxa also can be analyzed (Thomas et al. 1989, Herrmann and Hummel 1993). Indeed, the future of molecular evolution is so promising as to justify the prediction that the next 10 to 20 years will witness more truly dependable advances in our knowledge of the systematics and evolution of organisms than occurred in all of the preceding century.

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