IDENTIFICATION AND STATUS OF WOOD PEWEES (CONTOPUS) FROM THE GREAT PLAINS: WHAT ARE SIBLING SPECIES?

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ABSTRACT.—We used discriminant functions analysis to identify specimens of wood pewees (*Contopus*) from the Great Plains. Size and shape differences between *C. virens* and *C. sordidulus* are slight, but we found significant differences in multivariate space. Specimens from places where both species occur are not phenetically intermediate; hence we have no evidence of hybridization. Singing birds were morphologically like those of the species whose song they sang; hence we have no evidence of song switching. Our analyses show that *C. virens* occurs in summer as far west as Crockett Co., Texas; Morton Co., Kansas; and Phillips Co., Montana. *Contopus sordidulus* occurs in summer east to Phillips Co., Montana; it is a fairly common and regular migrant through extreme western Kansas.

The Eastern and Western wood pewees (Contopus virens and C. sordidulus) are difficult to separate both in the field and in the hand (Phillips et al. 1966:169-170, Browning 1977). The most conspicuous difference between the two-their distinctive primary songs—is of restricted use: the females do not sing; spring migrants sing rather infrequently and fall migrants probably do not sing at all; in collections, song type is rarely indicated on specimen labels. Additionally, the song may be partially or wholly learned and thus be an imperfect indicator of "kind" especially in sympatry (where individuals may have learned either both songs or the "wrong" one).

In practice, non-singing pewees are often identified "on geographical grounds," and indeed the largely allopatric distributions of the forms leaves this an expedient and acceptable solution in most cases. However, their ranges do overlap both where they winter in Central and South America (A.O.U. 1957) and in Mexico and the western Great Plains where they occur in passage. In the Great Plains they occur, sympatrically in some places, as uncommon breeders (Fig. 1; Short 1961, Barlow and Rising 1965, Godfrey 1966, Rising 1974). The apparent intermediacy of several specimens from western Kansas and Nebraska suggests that hybridization between the forms may occur in the Great Plains (Short 1961, Barlow and Rising 1965, Schueler and Rising 1976). To date, however, the identification of these specimens from the Great Plains has been imprecise.

For two reasons, we became interested in

determining whether or not these pewees hybridize. First, the answer would help us to understand the significance of bright display plumages of birds. Sibley (1957) argued that such plumages have evolved because they facilitate accurate species recognition and thus reduce hybridization. Rohwer et al. (1980), however, pointed out that hybridization seems to occur most commonly among individuals of both the most dimorphic and the brightest species. On the basis of feather color intermediacy, for example, it has been argued that buntings (Passerina), grosbeaks (Pheucticus) and orioles (Icterus) all hybridize rather commonly in the Great Plains (West 1962, Rising 1970, Emlen et al. 1975). But do these hybridize more commonly than less brightlycolored birds, or do they merely seem to hybridize more commonly because hybrids (intermediates) are more easily defined in species with distinctive plumages? Perhaps hybridization occurs in species that are similar in appearance such as chickadees (Parus), wood pewees, and crested flycatchers (Myiarchus), and we just do not recognize the intermediates. Second, Mayr and Short (1970:60) suggested that these two pewees are conspecific; information pertaining to mate selection in sympatry will clarify their genetic relationship. Our purposes are (1) to establish rigorous criteria for identification of specimens, and using these criteria (2) to identify, as accurately as possible, our pewee specimens from the Great Plains as well as to reassess earlier identifications (e.g., those in Barlow and Rising 1965, Rising 1974).

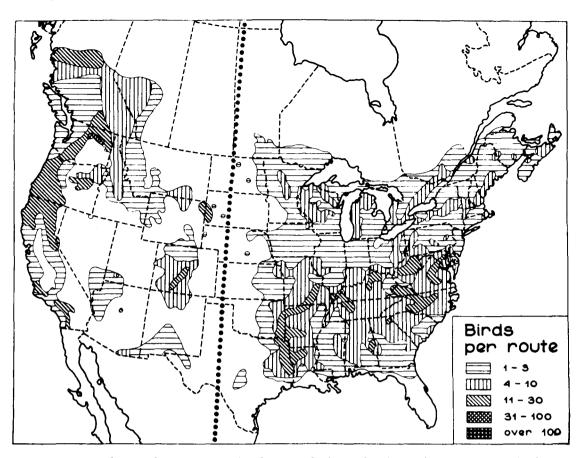


FIGURE 1. Map showing the approximate distribution and relative abundance of *Contopus virens* (to the east of the dotted line) and *C. sordidulus* (to the west). The data are the numbers of pewees found on randomly selected census routes (Robbins and Van Velzen 1974:173).

MATERIALS AND METHODS

In the summer of 1970 we collected three Contopus specimens from north-central Montana-a region where both species are of marginal occurrence (Fig. 1). These specimens were prepared as skin-and-skeletons (i.e., distal skeletal elements in the wing and leg on one side were left in the skin). In addition, D. M. Niles and S. A. Rohwer collected a Contopus from west Texas. This bird sang the song of C. virens but was taken within the range of C. sordidulus (Oberholser 1974). In the early summer of 1978 Rising collected eight migratory Contopus from western Kansas. Data on these specimens are in Table 1. A number of skin-only specimens also exist from the western Great Plains. For example, all of the specimens mentioned by Barlow and Rising (1965) and Rising (1974) were prepared as conventional skins. Data on these specimens are in Table 2.

To establish criteria for identifying skeletal material, we borrowed pewee skeletons from museums. Rising measured 31 features on each skeleton to the nearest 0.1 mm, with dial calipers: premaxillary length, depth and width; length of premaxilla from anterior edge of nostril; inter-narial and nasal bone widths; inter-orbital width; skull width, length and depth; gonial length; mandibular length and depth; coracoid and scapular lengths; width of base of scapula; length of furcular process; sternum length and width; keel length and depth; synsacrum width; maximal lengths of the femur, tibiotarsus, tarsometatarsus, humerus, ulna, carpometacarpus, and basal phalanx of digit II; and widths of the proximal and distal ends of humerus. Twenty-nine of these were measured as indicated in Robins and Schnell (1971); the others, "width of the proximal end of humerus" and "premaxillary width," were the maximal widths. These attributes were selected a priori as representative features (that could be readily measured on disarticulated skeletons) from different body regions and functional complexes. Of the breeding or presumed breeding specimens that we were able to measure, 32 were male C. virens, 33 male C. sordidulus, 22 female C. virens and 27 female C. sordidulus. In addition, we measured 2 specimens taken in October from Panama, 11 taken in May, June, and July from Mexico, and 8 (mentioned above) from western Kansas. Of the breeding birds, 19 male and 18 female C. virens specimens were from extreme eastern Kansas (especially Cherokee County) and 14 male and 14 female C. sordidulus were from southern Arizona (especially Cochise County). Most of these were collected by Rising and are known to have been breeding birds on the basis of gonad condition. Other specimens used in the reference samples were taken in mid-summer from regions where overlap is unknown and most were clearly breeding birds. One of these (ROM 115972) was taken 10 mi north of Bellburns, Newfoundland, 20 June 1972; it is the only specimen from that province.

Even though subtle average color differences exist between the species, we have not considered color-

Museum/Number ^a	Sex	Date collected	Locality	Remarks
ROM 106613	M	3 June 1970	Montana: Toole Co., 5 mi E, 8 mi S Shelby	Not singing
ROM 106612	Σ	6 June 1970	Montana: Phillips Co., 1 mi S Dodson	Not singing
ROM 106746	M	7 June 1970	Montana: Phillips Co., 1 mi S Dodson	Song = sordidulus
KU 63883	Μ	13 June 1969	Texas: Crockett Co., 29 mi W Ozona (Pecos River Valley)	Song = virens
ROM 130128	ы	3 June 1978	Kansas: Seward Co., 8 mi NE Liberal	Not singing
ROM 130129	Μ	5 June 1978	Kansas: Morton Co., 8 mi N, 1 mi E Elkhart	Not singing
ROM 130130	н	5 June 1978	Kansas: Morton Co., 8 mi N, 1 mi E Elkhart	Not singing
ROM 130131	Μ	6 June 1978	Kansas: Wallace Co., 2 mi N, 3 mi W Sharon Spgs.	Not singing
ROM 130132	M	7 June 1978	Kansas: Wallace Co., 2 mi N, 3 mi W Sharon Spgs.	Not singing
ROM 130133	Ч	7 June 1978	Kansas: Wallace Co., 2 mi N, 3 mi W Sharon Spgs.	Not singing
ROM 130134	W	7 June 1978	Kansas: Wallace Co., 2 mi N, 3 mi W Sharon Spgs.	Song = sordidulus
ROM 130135	Μ	7 June 1978	Kansas: Wallace Co., 2 mi N, 3 mi W Sharon Spgs.	Song = sordidulus

TABLE 1. Specimens of Contopus collected from the central Great Plains and prepared as skins-and-skeletons.

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TABLE 2.

Museum/Number	Sex	Date collected	Locality	DF score	DF iden- tion ^a	Remarks ^a
KU 34189	Σ	6 August 1957	Kansas: Morton Co., 7½ mi N Elkhart	59.9	vir.	much fat; "sord." ^b
KU 45568	Σ	11 July 1964	Kansas: Morton Co., 7½ mi N Elkhart	68.1	sord.	testis 7×5 mm; "sord." ^b
KU 45639	Σ	7 June 1964	Kansas: Morton Co., 7½ mi N Elkhart	65.2	sord?	testis 7 mm; "sord." ^b
KU 45640	Σ	8 June 1964	Kansas: Morton Co., 7½ mi N Elkhart		sord?	testis 7 mm; "sord." ^b
KU 49249	Σ	11 June 1965	Kansas: Morton Co., 7½ mi N Elkhart		vir.	testis 9×5 mm; singing virens ^c
KU 57754	Σ	7 June 1967	Kansas: Stevens Co., 9 mi N, 7 mi W Hugoton	67.1	sord.	singing sord. ^c
KU 49248	M	27 June 1965	Kansas: Wallace Co., 2 mi N Sharon Spgs.	65.8	sord?	testis 3×2 mm; "intermediate" ^c
KU 63883	Σ	13 June 1969	Texas: Crockett Co., 29 mi W Ozona	61.1	vir.	skel. & song virens ^d
ROM 106612	Μ	6 June 1970	Montana: Phillips Co., 1 mi S Dodson	64.8	<u>م</u> .	skel. virens ^d
ROM 106746	Σ	7 June 1970	Montana: Phillips Co., 1 mi S Dodson	64.6	a.	skel. & song <i>sord.</i> ^d
ROM 106613	Σ		Montana: Toole Co., 5 mi E, 8 mi S Shelby	64.0	n.,	skel. virens ^d
KU 16626	ы	6 July 1927	Kansas: Morton Co., Elkhart	31.2	<u>л</u> .	"virens" ^b
KU 34187	ы	6 August 1957	Kansas: Morton Co., 7½ mi N Elkhart	31.2	a.	much fat; "virens"
KU 44567	ц	11 July 1964	Kansas: Morton Co., 7½ mi N Elkhart	32.6	sord.	"paired with 45568"; "virens"
KU 45641	ы	8 June 1964	Kansas: Stevens Co., 9 mi N, 7 mi W Hugoton	30.4	<u>م</u> . '	"sord."
KU 57751	Γ.	7 June 1967	Kansas: Stevens Co., 9 mi N, 7 mi W Hugoton		sord.	"sord."
KU 57752	ы	7 June 1967	Kansas: Stevens Co., 9 mi N, 7 mi W Hugoton		sord.	"sord."e
KU 57753	Ľ.	7 June 1967	Kansas: Stevens Co., 9 mi N, 7 mi W Hugoton	31.2	a.	"sord.""c
^a Abbreviations:	oir. =	Abbreviations: vir. = C. virens; sord. = C. sordidulus	ordidulus.			

 ^b Barlow and Rising (1965).
^c Rising (1974).
^d Present study.

304 JAMES D. RISING AND FREDERICK W. SCHUELER

TABLE 3.	Discriminant funct	ion coefficients	for d	liserimination	among	Contopus groups.

	Discriminant function coefficients						
	Standa	urdized	Unstanda	ardized			
Variable	1	2	1	2			
Premaxillary length	0.073	0.249	0.09635	0.32711			
Premaxillary depth	0.133	-0.156	0.49570	-0.58248			
Internarial width	-0.101	0.248	-0.54157	1.32237			
Nasal bone width	-0.031	-0.379	-0.07022	-0.87137			
Skull width	-0.183	-0.188	-0.56252	-0.57576			
Skull depth	0.098	-0.207	0.30149	-0.63614			
Mandibular depth	0.151	-0.204	1.34346	-1.81945			
Scapular length	0.204	-0.287	0.28690	-0.40499			
Sternal width	0.101 /	-0.131	0.16008	-0.20683			
Synsacral width	-0.094	0.158	-0.29802	0.49873			
Tibiotarsal length	-0.150	-0.049	-0.23985	-0.07807			
Tarsometatarsal length	-0.171	-0.128	-0.39120	-0.29317			
Proximal end humerus width	0.278	-0.039	1.22183	-0.17045			
Distal end humerus width	0.203	0.246	0.88448	1.06927			
Carpometacarpal length	0.592	0.589	1.15812	1.15295			
Constant			-18.07437	8.52676			

ation here because: (1) the species overlap in coloration, especially where their ranges approach each other; and (2) the colors of specimens change greatly with age (Browning 1977). To identify the skins, we measured four variables (chord of longest wing feather, "wing length"; length of culmen from anterior edge of nostril; length of longest secondary, and length of longest rectrix, "tail length") on 193 specimens from the collections of the Royal Ontario Museum and the University of Kansas. We selected specimens from throughout the ranges of the species (with a bias for Ontario and eastern Kansas for C. virens), including some of C. sordidulus from the Yukon Territory, central Alberta, central Manitoba and New Mexico. Geographic variation in size is slight, at least north of Mexico (Browning 1977). Only adults that possessed all four features were measured. No attempt was made to compensate for feather wear (i.e., the actual feather lengths were entered), although badly worn specimens were avoided. All the birds used were taken in late spring or early summer so there should be no consistent bias; wear would thus contribute to the "error variance" in all groups.

To separate the four groups (males and females of the two species) as much as possible we used a stepwise discriminant functions analysis (DFA), in the Statistical Package for the Social Sciences (SPSS; Nie et al. 1975). In the analysis of the skeletal matrix, only the first 15 variables to enter in the DFA were used; thus there were more individuals in the smallest group than variables in the analysis. Unknowns (specimens from Montana; western Kansas; Ozona, Texas; Mexico; and Panama) were identified according to the criteria (selected features and their discriminant function coefficients) found to maximize the separation of these groups. Missing values (bones lost or broken) were estimated by regression analysis and specimens missing more than 4 of the 31 values were omitted from the analyses.

RESULTS AND DISCUSSION

SKELETAL ANALYSES

The 15 characters used to obtain a maximal separation and their discriminant function coefficients (DFCs) are listed in Table 3.

The standardized DFCs indicate the relative importance of the various features for discrimination, with the most important features having the largest coefficients (regardless of sign). Thus, carpometacarpal length (0.592) is the most, and nasal bone width (-0.031) the least, significant feature used in DF 1. There are two highly significant (P < 0.0001) DF axes (with four groups, as many as three would have been possible). The first (which explains 63.9% of the variation used in discrimination) essentially separates the sexes (Fig. 2), whereas, the second (34.5%) separates the species. The third is not significant and explains only 1.6% of the variation. The group centroids in the two-dimensional discriminant function space are given in Table 4. The predicated and actual group memberships are indicated in Table 5; 87% of the birds are correctly identified (cf. 25% if placement were random). Based on DF coefficients and group means (Tables 3 and 4) males have large values on DF 1, and thus have relatively long wings (carpometacarpal and

TABLE 4. Group means from discriminant functions analysis of *Contopus* skeletal specimens.^a

	Discriminant function			
Group	1	2		
C. virens males	0.936	-0.527		
C. virens females	-0.825	-1.220		
C. sordidulus males	0.559	0.772		
C. sordidulus females	-1.119	0.675		

^a The position of a specimen in the two-dimensional space is determined by the sum of the products of the original measurements and the appropriate unstandardized DF coefficients plus the constant (Table 3). These are the means for the reference specimens for these four groups.



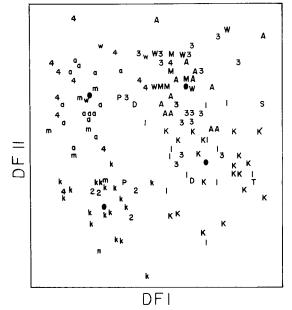


FIGURE 2. The positions of wood pewees in a space determined by DF 1 (Discriminant Function 1) and DF 2. Each letter shows the position of a specimen in the space; capital letters indicate the males and lower case letters the females. The K's show the positions of breeding birds from eastern Kansas; A's show the positions of breeding pewees from Arizona; W's show the positions of migratory pewees from western Kansas; M's show the birds from Mexico. The S is ROM 106613 from Shelby, Montana; the two D's are 105612 and 106746 from Dodson, Montana; T is KU 63883 from Ozona, Texas; and n is ROM 115972 from Newfoundland. Other birds are indicated by numbers, with 1 =male C. virens, 2 = female C. virens, 3 = male C. sordidulus, and 4 = female C. sordidulus. The four group centroids are indicated by dots.

scapular lengths; humeral and sternal widths) and short legs (tibiotarsal and tarsometatarsal lengths). Eastern Wood Pewees have low values on DF 2, and thus have narrow nasal bones, long wings and long and shallow bills. Measurements of bone width are disproportionately well represented (relative to the features originally measured which were mostly bone lengths): males tend to have wider bones associated with flight, and perhaps more gracile skulls.

Of the unknown specimens, all of those from western Kansas taken in June 1978 are identified as C. sordidulus. The specimen from near Ozona, Texas (singing C. virens) is identified as a male C. virens, as is ROM 106612 from Dodson, Montana; ROM 106746 (Dodson; singing C. sordidulus) is identified as C. sordidulus, and ROM 106613 (Shelby, Montana) is identified as C. virens, but is close to C. sordidulus (Fig. 2). Thus, all singing birds are "correctly" identified. Of 11 specimens from Mexico, 9 are identified as C. sordidulus. These are from Morelos (4 May and July, Oaxaca (late June), and Sonora (mid-May). The two identified as C. virens are both females, and are close to C. sordidulus; they are from Oaxaca. taken in June (KU 35908 and 38640). One of the Mexican pewees was identified as a male by the collector, but it clusters as a female. It is so far to the female side of the distribution that we judge that it was mis-sexed. Geographic variation may contribute to any difficulty we have in identifying these Mexican birds, especially if they represent Mexican breeding populations. We did not have known Mexican breeding material to include in our C. sordidulus reference sample, and size variation may occur among Mexican localities. The scatter of Kansas and Arizona specimens through their respective groups indicates that there is little size variation among the non-Mexican populations. The female from Newfoundland (though not entered as an "unknown") clusters as C. virens.

There is more variation between sexes than between species. In our samples the interspecific differences between the fe-

TABLE 5. Percentages of male and female *Contopus* in reference samples correctly identified by discriminant function criteria.^a

Actual group			Predicted group					
			vi	rens	sordi	dulus		
Species	Sex	n	M	F	М	F		
C. virens	М	32	84.4%	0.0%	15.6%	0.0%		
C. virens	F	22	0.0	100.0	0.0	0.0		
C. sordidulus	М	33	15.2	0.0	81.8	3.0		
C. sordidulus	F	27	0.0	3.7	11.1	85.2		

^a Total percentage correctly classified = 86.8%. Total C. virens identified as C. virens = 90.7%. Total C. sordidulus identified as C. sordidulus = 90.0%. Total males (species pooled) identified as males = 98.5%. Total females identified as females = 93.9%.

· · · · · · · · · · · · · · · · · · ·	Mean ^a	n	SE ^b	Range	Discriminan weight	
Wing length					_	
C. sordidulus (male)	87.1	56	0.257	82.2-91.4	1 1019	
C. virens (male)	84.0	43	0.313	77.6 - 88.1	1.1013	
C. sordidulus (female)	82.2	54	0.286	77.6-87.6	0.6503	
C. virens (female)	79.8	40	0.409	74.6 - 85.9	0.050	
Tail length						
C. sordidulus (male)	66.0	56	0.354	60.3 - 73.5	0 4597	
C. virens (male)	65.7	43	0.340	61.1 - 71.3	-0.4587	
C. sordidulus (female)	63.1	54	0.365	54.5 - 69.0	-0.3345	
C. virens (female)	63.5°	40	0.430	55.2 - 69.0	-0.3345	

TABLE 6. Statistics for measurements on study skins of 193 Contopus specimens.

^a Vertical lines connect means that are in statistically homogeneous sets (P < 0.05). ^b SE = standard error (of mean). ^c These data are significantly skewed to the left ($g_1 = -0.878$; P < 0.02) and leptokurtotic ($g_2 = 1.496$; P < 0.04). All others are normally distributed.

males are greater than between the males, and sexual dimorphism might be slightly more marked in C. virens than in C. sordidulus (Fig. 2).

STUDY SKIN ANALYSIS

The DFA revealed that lengths of secondary remiges and the culmen contributed nothing to or even obfuscated species separation, so our discrimination of study skins is based on just wing and tail lengths (Table 6). The separation of C. virens and C. sordidulus using the DFA of the two measurements of study skins is poor: 18% of the 43 reference C. virens males are misidentified, as are 12% of the 56 C. sordidulus males. 14% of the 54 C. sordidulus females and 35% of the 40 C. virens females. Nonetheless, these data provide the best currently available mensural criteria for identifying study skins of these forms.

Table 2 summarizes the results of the analysis of the study skins. The only deviation from Barlow and Rising's (1965) identifications (theirs are given in the "remarks" column of Table 2) of consequence involves KU 44567 which was apparently mated to C. sordidulus KU 45568. Barlow and Rising identified this bird as C. virens, whereas our analysis indicates that it is clearly C. sordidulus. Their identification was based on general coloration and wing length. We view all identifications of these skins with caution. Both of these birds could have been C. sordidulus (as our present analysis shows), and inasmuch as they both contained moderate fat, they could have been either early autumnal migrants (notwithstanding the male's 7×5 mm testis), or a breeding pair of C. sordidulus from southwestern Kansas. A male C. virens, KU 49249, was apparently breeding at the Elkhart locality.

Considering all of the western Kansas birds, we conclude that C. sordidulus is a regular migrant through that region and perhaps breeds rarely there; C. virens is probably an uncommon breeding species there. Two ROM specimens from Manitoba (Gypsumville; Riding Mountain) previously identified as C. sordidulus are confirmed as C. sordidulus in this analysis. Manitoba is the eastern extreme of this species' range and is a region where the two occur sympatrically (Godfrey 1966). The Ozona male C. virens is confirmed as C. virens; the three Montana specimens are intermediate (Table 2).

The criteria we have found for skin identification might prove useful to curators and bird-banders, at least for approximate identifications (Tables 6 and 7). We sought to use our criteria to identify a bird collected at Cumberland House, Saskatchewan in June 1827. This specimen, now lost, was the type of Tyrannula richardsonii (Swainson and Richardson 1831) which, if a Western Wood Pewee, would be the type of that taxon (i.e., Contopus richardsonii). Among the measurements given by Swainson and Richardson are wing length (3 inches, 3 lines, or ca. 82.6 mm) and tail length (2 inches, 9 lines, or 69.6 mm). The sex of the specimen was not indicated. If it were a male, we could find its position in our discriminant space as the sum of the products of these two measurements and their unstandardized discriminant function coefficients (Table 6), i.e., $82.6 \times 1.1013 + 69.6 \times$ -0.4587 = 59.04. Comparing this value with the ranges given in Table 7, this specimen is well within the range of C. virens but not that of C. sordidulus. If a female, its score is 30.43 ($82.6 \times 0.6503 + 69.6 \times$ -0.3345), and it could be either species. A female with so long a tail (Table 6), is un-

TABLE 7. Statistics for discriminant functions scores for Contopus based on two feather measurements.^a

Group	Mean	n	SE	Range	Mean ± 2 SD ^b
C. virens males	62.4	43	0.296	65.4-65.8	66.3-58.5
C. sordidulus males	65.7	56	0.226	61.7-69.3	69.0-62.3
C. virens females	29.9	40	0.209	25.7 - 32.4	32.5 - 27.2
C. sordidulus females	31.5	54	0.173	29.0 - 35.1	29.0 - 34.1

^a The discriminant function score for an individual is the sum of the products of the character measurements and their discriminant weights (Table 6). Here, for a male multiply the wing length by 1.1013 and add the tail length times -0.4587.
^b 95% of the individuals in the samples fall between these values.

likely. For a number of reasons Phillips and Parkes (1955) considered the identity of this specimen to be in doubt. They argued that the wing formula is that of an Eastern Phoebe (*Sayornis phoebe*). We conclude that if Swainson and Richardson's bird were a *Contopus*, it must have been a male *C. virens*.

CONCLUSIONS

We find no good evidence for hybridization between the Eastern and Western wood pewees. Nevertheless, owing to the great similarity between them and the small number of specimens available from areas of sympatry, the possibility of hybridization cannot be altogether ruled out. The songs of the forms are sustained as being good species-specific characteristics even in sympatry: each specimen of known song type clusters phenetically with birds of the species whose song it sang.

Eastern Wood Pewees probably breed in western Newfoundland, and locally west to Morton Co., in Kansas, Crockett Co., in Texas, and Phillips Co., in Montana. At the sites in Texas and Montana, they occur sympatrically with Western Wood Pewees; sympatry in central Manitoba and (probably) in east-central Saskatchewan is sustained; sympatry might occur in southwestern Kansas. Ecological differences of the two in sympatry are unknown; if any exist they must be slight.

Western Wood Pewees are fairly common migrants in far western Kansas, occurring there through the first eight days of June (often singing) and again in early July through early August (not singing). The consistency of the records for early June (several different years), and the absence of records from later in the month, supports the interpretation of these birds as migrants. The gonadal condition of these specimens does not indicate breeding. Although this study does not provide a rigorous test, it yields no evidence for interpopulational within-species size variation of these pewees, at least north of Mexico.

WHAT ARE SIBLING SPECIES?

Sibling species are species that are not easily separated by conventional means—they are defined as morphologically similar or identical populations that are reproductively isolated (Mayr 1963). They are termed (more appropriately) cryptic species by Ross (1974). How similar species must be to qualify as sibling species is a subjective (and often a historically influenced) decision. If, given new information, a taxonomist splits a species, the new species (fragments of the old) will be called sibling species. Long recognized, but equally similar species, are less likely to be called siblings.

We suggest that sibling species could be more objectively defined as species in which the within-species phenetic variation of one or both of the species exceeds the phenetic variation between them when among-group differences are assessed in a manner (such as DFA) that maximizes group separation. Phenetic similarity is similarity based on an unweighted assessment of all available characters (Sneath and Sokal 1973); two species could only be sibling species with regard to given character sets (i.e., they could be morphological sibling species, behavioral sibling species, or both). Thus, the two wood pewees are morphological sibling species because the axis that explains the greatest amount of among-group variation separates within-species phena (in this case the sexes). They would not, however, be vocal sibling species (in recognition of which ornithologists, and seemingly the birds themselves, have long treated them as distinct).

We like this definition because it encourages precise statements of similarity between species and defines the degree of similarity that exists between sibling species. Using the term in this way emphasizes similarity among species where taxonomists have traditionally stressed dissimilarity; it identifies similarities in adaptive complexes rather than focusing on "isolat-

ing mechanisms." We might find, for example, that Lincoln's and Song sparrows (Melospiza lincolnii and M. melodia) are morphological sibling species, but because the plumage differences between them have been recognized for a long time, their similarities have remained obscure. From this study we have confirmed that even in size and shape, Eastern and Western wood pewees are very similar birds. From ecological theory we probably would predict that they could not occur together, or would do so at some mutual cost, unless they share resources. On morphological grounds we would expect that there is a greater ecological difference between sexes (e.g., members of a pair) than between species.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. Fifth ed. Am. Ornithol. Union, Baltimore.
- BARLOW, J. C., AND J. D. RISING. 1965. The summer status of wood pewees in southwestern Kansas. Bull. Kans. Ornithol. Soc. 16:14–16.
- BROWNING, M. R. 1977. Geographic variation in *Contopus sordidulus* and *C. virens* north of Mexico. Great Basin Nat. 37:453–456.
- EMLEN, S. T., J. D. RISING, AND W. L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87:145–179.
- GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Can. Bull. 203.

- MAYR, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, MA.
- MAYR, E., AND L. L. SHORT. 1970. Species taxa of North American birds. Publ. Nuttall Ornithol. Club 9.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBREN-NER, AND D. H. BENT. 1975. SPSS/Statistical package for the social sciences. Second ed. Mc-Graw-Hill, New York.
- OBERHOLSER, H. C. 1974. The bird life of Texas. Vol. II. Univ. Texas Press, Austin.
- PHILLIPS, A. R., M. A. HOWE, AND W. E. LANYON. 1966. Identification of the flycatchers of eastern North America, with special emphasis on the Genus *Empidonax*. Bird-Banding 37:153–171.
- PHILLIPS, A. R., AND K. C. PARKES. 1955. Taxonomic comments on the Western Wood Pewee. Condor 57:244-246.
- RISING, J. D. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.
- RISING, J. D. 1974. The status and faunal affinities of the summer birds of western Kansas. Univ. Kans. Sci. Bull. 50:347-388.
- ROBBINS, C. S., AND W. T. VAN VELZEN. 1974. Progress report on the North American breeding bird survey. Acta Ornithol. 14:170–191.
- ROBINS, J. D., AND G. D. SCHNELL. 1971. Skeletal analysis of the *Ammodramus-Ammospiza* grassland sparrow complex: a numerical taxonomic study. Auk 88:567–590.
- ROHWER, S. A., S. D. FRETWELL, AND D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Am. Nat. 115:400-437.
- Ross, H. H. 1974. Biological systematics. Addison-Wesley Publ., Reading, MA.
- SCHUELER, F. W., AND J. D. RISING. 1976. Phenetic evidence of natural hybridization. Syst. Zool. 25:283-289.
- SHORT, L. L., JR. 1961. Notes on bird distribution in the central Plains. Nebr. Bird Rev. 29:2–22.
- SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual selection and hybridization in birds. Condor 59:166–191.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman, San Francisco.
- SWAINSON, W., AND J. RICHARDSON. 1831. Fauna Boreali-Americana. Vol. 2. J. Murray Publ., London.

WEST, D. A. 1962. Hybridization in grosbeaks (*Pheuc-ticus*) of the Great Plains. Auk 79:399–424.

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