

A REASSESSMENT OF THE TAXONOMIC STATUS OF THE YELLOW-BILLED CUCKOO

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Two North American subspecies of the Yellow-billed Cuckoo (*Coccyzus americanus*) have been defined by a difference in size: a smaller eastern (*C. a. americanus*) and a larger western (*C. a. occidentalis*). This taxonomic treatment was proposed originally by Ridgway (1887) and later followed by other workers (Peters 1940, A.O.U. 1957, Oberholser 1974), though various authors have questioned the validity of this separation (Todd and Carriker 1922, Van Tyne and Sutton 1937, Mees 1970, Banks 1988).

The purpose of our investigation was to reexamine the taxonomic status of the Yellow-billed Cuckoo. We assessed behavioral and ecological differences between the two populations to determine whether they were correlated with morphological differences. Additionally, we wanted to determine the taxonomic identity of birds from New Mexico, western Texas, and adjacent Mexico.

MATERIALS AND METHODS

Richard C. Banks kindly provided all the raw measurements that he had taken for his analysis (Banks 1988). We measured 41 additional specimens by Banks' techniques. We divided the specimens into four geographic samples (west, east, Caribbean, and Texas and vicinity) and analyzed the sexes separately. We analyzed birds collected in western Texas, New Mexico, and adjacent Mexico separately because of the likelihood that they are intermediate between the eastern and western subspecies. We included tail length as one of the variables, measuring it on the 41 additional specimens and using it where available in Banks' data set.

We attempted to restrict our evaluation to breeding birds only. On the basis of the nesting chronology in Bent (1940), we used eastern specimens collected from 1 June through 15 August and western specimens collected from 1 June through 31 August only in our sample. Vagrant Yellow-billed Cuckoos are not uncommon, especially during spring and the early part of the breeding season (Gaines and Laymon 1984), so individuals collected away from breeding areas were excluded from the analysis. One bird was excluded because it had an abnormally small bill.

Specimens from eastern Texas east were combined into the eastern sample, while those from western New Mexico west were combined into the western sample. Specimens from eastern New Mexico, western Texas, and adjacent Mexico constituted a third group. In addition, our preliminary review of the data indicated there was the possibility that the Caribbean

birds were different enough from the eastern population to warrant being segregated from them, so we defined them as a fourth group.

We used Students' *t* test to compare means of measurements from adult eastern birds and western birds, each sex handled separately. We defined the difference between the means of two populations as being significant if the *t* test specified that the probability of their being the same was less than 0.05. Separate *t* tests for each sex compared eastern and western birds for differences in maxilla depth, bill length, wing length, and tail length.

All statistical analyses were done on an IBM PC XT computer by means of the Number Cruncher Statistical Package (Hintze 1987). Univariate statistics were computed by means of the descriptive statistics program and the unpaired *t* test program.

We performed a discriminant analysis on the data by using the discriminant analysis program. Discriminant function analysis distinguishes between two populations on the basis of several variables considered simultaneously. Using measurements obtained from members of two known populations, this program devises an equation, the discriminant function. For example, the discriminant function equation for eastern males was calculated from the data from all male specimens collected in the east. Applying the rule to measurements of an individual specimen yields a score that assigns the individual to one of the two populations. We used measurement of 256 western and 393 eastern Yellow-billed Cuckoos to derive a discriminant function for each sex and population that produced maximal separation between these samples on the basis of four variables (bill length, maxilla depth, tail length, and wing length). When not all measurements could be taken on a specimen, the program disregards all data from that specimen. Because of wear, tail measurements were often unreliable. Therefore, we ran the discriminant analysis first using all four variables, then using only three variables, bill length, maxilla depth, and wing length, to maximize sample size. The resulting functions were evaluated to yield discriminant scores for each individual in the two presumed populations. The discriminant function was tested for statistical significance with the Wilk's lambda test (Marascuilo and Levin 1983).

The discriminant functions for separating male eastern and western Yellow-billed Cuckoos are presented in Equation 1. Results for females are shown in Equation 2. When values (in millimeters) from an individual specimen are inserted into the eastern equation, a score greater than 0.5 suggests that the individual is from the eastern population, while a score less than 0.5 suggests that the bird originated from the western population. Similarly, when the western equation is used, if the score is more than 0.5, the individual would be classified as a western bird. We analyzed only the equations for eastern birds because the equations for western birds are a mirror image and thus provide no additional information. Finally, we figured the classification score: the percentage of Yellow-billed Cuckoos in each sample categorized as expected on the basis of range.

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Equation 1. Regression Equation for Discriminant Analysis of Male Yellow-billed Cuckoos

East: If $8.8315 + [\text{wing length } (-0.0184) + \text{tail length } (-0.006) + \text{bill length } (-0.1606) + \text{maxilla depth } (-0.2399)] > 0.5$, bird is likely of eastern origin; if < 0.5 , bird is likely of western origin

West: If $-7.8315 + [\text{wing length } (0.0184) + \text{tail length } (0.006) + \text{bill length } (0.1606) + \text{maxilla depth } (0.2399)] > 0.5$, bird is likely of western origin; if < 0.5 , bird is likely of eastern origin

Equation 2. Regression Equation for Discriminant Analysis of Female Yellow-billed Cuckoos

East: If $10.5013 + [\text{wing length } (-0.0195) + \text{tail length } (-0.0268) + \text{bill length } (-0.1279) + \text{maxilla depth } (-0.0836)] > 0.5$, bird is likely of eastern origin; if < 0.5 , bird is likely of western origin

West: If $-9.5013 + [\text{wing length } (0.0195) + \text{tail length } (0.0268) + \text{bill length } (0.1279) + \text{maxilla depth } (0.0836)] > 0.5$, bird is likely of western origin; if < 0.5 , bird is likely of eastern origin

RESULTS

Student's *t* Test

Western cuckoos of both sexes were significantly longer winged (males 4.45 mm, $t = -9.28$, $P < 0.00001$; females 5.71 mm, $t = -11.69$, $P < 0.00001$) than their eastern counterparts (Tables 1–3). Although some tail feathers were a little frayed, western males averaged 5.06 mm longer-tailed than eastern males ($t = -6.60$, $P < 0.00001$) (Tables 1 and 3). Mean tail lengths of females were 6.95 mm greater in western than in eastern specimens ($t = -8.33$, $P < 0.00001$) (Tables 2 and 3). Our *t* test results showed that bill length and maxilla depth were significantly greater in western than in eastern cuckoos among both males and females (Tables 1–3).

A comparison of cuckoos from the Caribbean and eastern North America indicated that males are similar in tail length, bill length, and maxilla depth but that Caribbean birds have significantly shorter wings ($t = 2.39$, $P < 0.02$) (Table 3). Female Caribbean birds had both wings ($t = 2.76$, $P < 0.05$) and tails ($t = 2.52$, $P < 0.05$) significantly shorter than did eastern birds (Table 3). Western Yellow-billed Cuckoo males were significantly larger than the Caribbean males in all four variables (Table 3). Female western specimens were larger in terms of wing length, tail length, and bill length but were not significantly different in maxilla depth (Table 3).

Males from eastern New Mexico, western Texas, and adjacent Mexico, were similar to eastern birds in wing length, tail length, and maxilla depth (Table 3). However, their bills were longer than those of eastern birds by a mean difference of 0.74 mm (Table 3). Similarly, females from this area had bills (by 0.53 mm) and wings (by 5.21 mm) significantly longer than those of eastern females (Table 3).

Western males were significantly larger in wing length, tail length, and maxilla depth than males from western Texas, eastern New Mexico, and adjacent Mexico, but were similar in bill length (Tables 1 and 3). Females from the western populations had longer wings, tails, and bills than those

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Table 1 Sample Sizes, Means, and Standard Deviations of Measurements (mm) of Male Yellow-billed Cuckoos from the East, West, Texas and Vicinity, and the Caribbean; Discriminant Function Scores for Males in the East and West

	<i>n</i>	<i>X</i>	S.D. ^a	Range
Wing length				
East	186	140.63	4.09	128.7–155.6
West	141	145.08	4.55	131.0–155.5
W. Texas & vicinity	18	140.89	3.84	132.3–147.8
Caribbean	20	138.32	4.37	130.0–151.0
Tail length				
East	152	138.43	4.93	125.4–152.0
West	87	143.49	6.85	124.6–166.6
W. Texas & vicinity	11	138.37	4.46	129.1–144.2
Caribbean	15	136.32	3.79	130.0–147.2
Bill length				
East	174	19.03	0.86	16.6–21.2
West	135	20.13	1.02	17.2–22.9
W. Texas & vicinity	16	19.84	0.81	18.2–21.1
Caribbean	20	19.05	0.75	17.7–20.8
Maxilla depth				
East	181	6.48	0.36	5.4– 7.5
West	141	6.66	0.44	5.6– 7.7
W. Texas & vicinity	17	6.42	0.43	5.8– 7.4
Caribbean	20	6.38	0.25	6.0– 6.9
Discriminant function score				
East	136	0.748	0.234 ^b	0.09–1.00
West	59	0.292	0.282 ^c	0.00–0.95

^aS.D., standard deviation

^bStandard error, 0.40

^cStandard error, 0.073

from Texas, New Mexico, and Mexico; however, maxilla depth was similar (Tables 2 and 3).

Discriminant Analysis

The discriminant function scores, means, standard deviations, and ranges for eastern and western males and females are shown in Tables 1 and 2, respectively. Results are plotted in a histogram (Figure 1) that shows the separation of the two groups based on the discriminant function analysis. The results indicate that most birds (more than 70% for all populations) strongly exhibit the characteristics of their respective populations.

Because the figure is based on the equation derived for eastern birds (see Equations 1 and 2), a discriminant function score greater than 0.5 suggests that the bird is of eastern origin, whereas a score less than 0.5 suggests that the bird is from the western population. The discriminant function analysis yielded classification scores of 83.8% and 74.6% for eastern and western

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Table 2 Sample Sizes, Means, and Standard Deviations of Measurements (mm) of Female Yellow-billed Cuckoos from the East, West, Texas and Vicinity, and the Caribbean; Discriminant Function Scores for Females in the East and West

	<i>n</i>	<i>X</i>	S.D. ^a	Range
Wing length				
East	188	144.63	3.73	134.5–155.0
West	105	150.34	4.49	138.2–163.5
W. Texas & vicinity	16	147.17	5.00	133.7–157.6
Caribbean	16	141.96	3.34	134.8–146.8
Tail length				
East	132	141.84	4.92	130.1–155.2
West	53	148.79	5.65	133.2–161.6
W. Texas & vicinity	8	143.64	4.74	137.1–151.2
Caribbean	10	137.81	4.32	130.9–145.0
Bill length				
East	179	19.31	0.87	16.4–21.4
West	100	20.53	0.99	18.0–23.0
W. Texas & vicinity	16	19.84	0.91	17.9–22.3
Caribbean	14	19.34	0.71	18.4–20.6
Maxilla depth				
East	186	6.45	0.37	5.1–7.4
West	103	6.73	0.49	5.1–7.8
W. Texas & vicinity	16	6.53	0.32	5.6–6.9
Caribbean	15	6.57	0.33	6.1–7.2
Discriminant function scores				
East	120	0.786	0.261	0.02–1.00
West	48	0.184	0.212	0.00–0.95

^aS.D., standard deviation

^bStandard error, 0.048

^cStandard error, 0.061

Table 3 Student's *t* Test Values Comparing Measurements (mm) of Breeding Yellow-billed Cuckoos in Eastern and Western North America, West Texas and Vicinity, and the Caribbean

Comparison	Sex	Wing length	Tail length	Bill length	Bill depth
East vs West	M	-9.28 ^a	-6.60 ^a	-10.29 ^a	-4.19 ^a
	F	-11.69 ^a	-8.33 ^a	-10.74 ^a	-5.35 ^a
East vs Caribbean	M	2.39 ^a	1.61	0.08	1.21
	F	2.76 ^a	2.52 ^a	-0.15	-1.17
West vs Caribbean	M	-6.25 ^a	-3.94 ^a	-4.56 ^a	-2.83 ^a
	F	-7.17 ^a	-5.82 ^a	-4.34 ^a	-1.21
East vs w. Texas & vicinity	M	-0.26	0.04	-3.63 ^a	0.56
	F	-2.54 ^a	-1.01	-2.36 ^a	-0.77
West vs w. Texas & vicinity	M	-3.74 ^a	-2.41 ^a	-1.10	-2.11 ^a
	F	-2.60 ^a	-2.45 ^a	-2.61 ^a	-1.58

^a*P* < 0.05

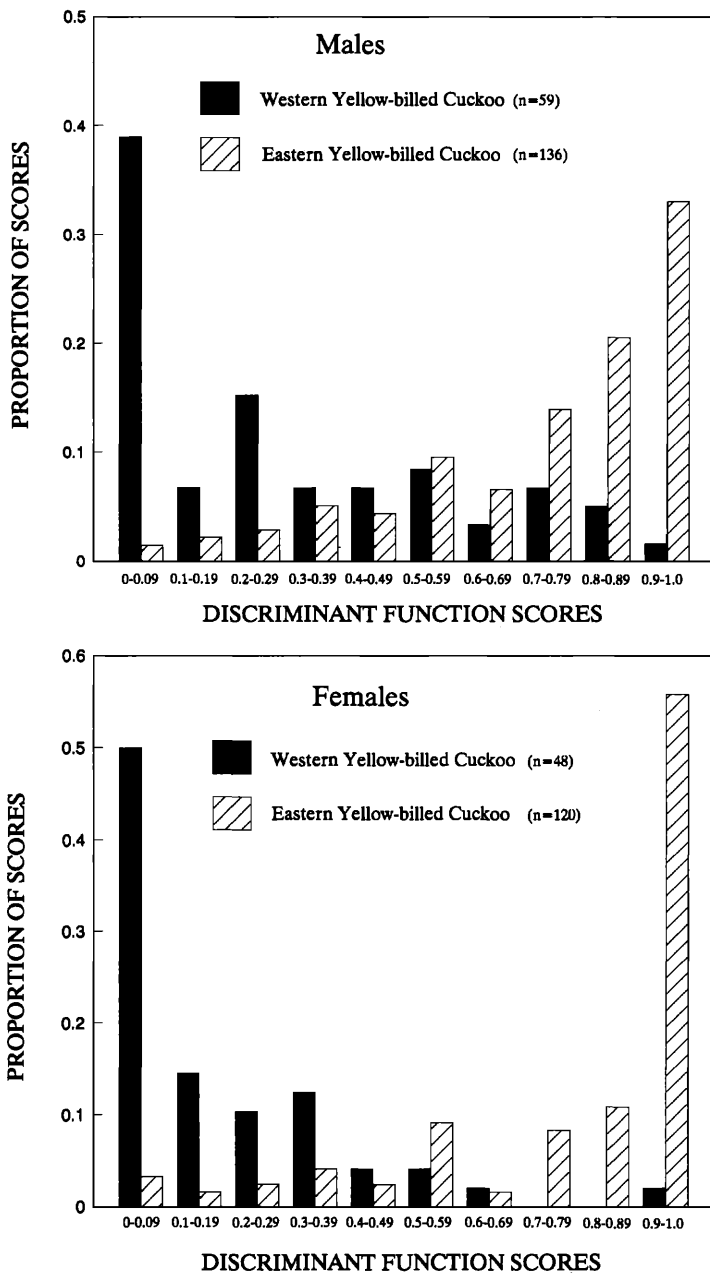


Figure 1. Discriminant function scores for male and female western and eastern Yellow-billed Cuckoos.

Table 4 Percentage of Correctly Categorized Individuals Based on Discriminant Function Analysis of Measurements^a of Yellow-billed Cuckoos from Eastern and Western North America^b

	Males	Females
<i>n</i>	195	168
East	83.8%	89.6%
West	74.6%	85.8%
Wilk's lambda	0.643	0.641
<i>F</i> ^c	53.58 ^a	47.61 ^a

^aAll four variables (wing length, tail length, bill length, and maxilla depth)

^bExcluding the Caribbean and west Texas and vicinity

^c $P < 0.001$ for *F* statistic

males, respectively, when all four variables were used (Table 4). Females had a higher probability of being correctly categorized than did males (Table 4): 89.6% of eastern and 85.8% of western females were correctly categorized. The Wilk's lambda test showed that the discriminant function score was significant ($P < 0.001$) (Table 4).

DISCUSSION

Taxonomy

Ridgway (1887) segregated Yellow-billed Cuckoos into two subspecies on the basis of the western birds' being "larger, with proportionately larger and stouter bills" as evidenced by differences in mean measurements of 1.5 mm in culmen length, 1.5 mm in bill depth, 6 mm in wing length, and 13 mm in tail length. Banks (1988) detected no consistent variation in color of the plumage. Moreover, he found that measurements of the maxilla depth, the length of the culmen, and the length of the wing of western and eastern birds were not significantly different. From this analysis he concluded that geographic variation in Yellow-billed Cuckoos is insufficient to warrant a division into two subspecies.

Contra Banks (1988), we found statistically significant differences between eastern and western birds in all variables examined (wing length, tail length, bill length, and maxilla depth). Banks (1990) recently reviewed his data and found that his original statistical analyses were incorrectly done and that there were statistically significant differences in these variables; however, the correction did not alter his view that the populations are not different enough to warrant recognition as subspecies (Banks 1990). Banks examined only one variable at a time and concluded that no single variable could separate eastern and western birds to subspecies.

Discriminant function analysis has been used previously to help define subspecies. Storer (1989) reported that the tremblers (*Cinlocerthia*) on

Dominica and St. Vincent islands warranted subspecific recognition based on his discriminant function analysis and differences in plumage color. Males on Dominica were correctly categorized 87.7% of the time and those on St. Vincent 95.0% of the time. Females from Dominica and St. Vincent were properly categorized 80.0% and 64.7% of the time, respectively (Storer 1989). The level of correct categorization of eastern and western cuckoos is similar to that of the Guadeloupe/Dominica populations recognized by Storer (1989) as subspecies. Although the level of differentiation in cuckoo populations is not as strong as that for tremblers, in our view the differences are substantial enough to support subspecific recognition.

Behavior and Ecology

In birds, subspecies are defined by differences in the color and pattern of the plumage and/or differences in the size and proportion of various body parts, when these differences are believed to be genetically based. Intraspecific differences in other aspects of a species' biology, such as vocalizations, breeding and molt chronology, and migratory behavior, may coincide with these physical differences, implying substantial genetic divergence (Johnson 1980, Lanyon 1982, Robbins et al. 1986, Unitt 1987).

From egg date records (Bent 1940), it is clear that eastern Yellow-billed Cuckoos begin breeding considerably earlier than their western counterparts. For example, in eastern Texas eggs have been noted as early as 24 March and as late as 30 June ($n = 34$), with the majority ($n = 26$) between 6 May to 6 June. In Illinois, eggs were noted from 20 May to 19 July ($n = 39$), with about 50% from 4 to 26 June. Egg dates for New York range from 24 May to 19 August ($n = 23$), with about 50% concentrated from 4 to 11 June. In contrast, in California, eggs have been observed from 15 May until 20 August ($n = 55$), with 51% from 17 June to 10 July. In Arizona, egg dates range from 28 June to 24 August ($n = 13$). Brandt (1951) observed that the height of the nesting season for cuckoos along the San Pedro River, Arizona, was 10–15 July and observed the earliest fresh eggs on 24 June. Incubation in three nests in Arizona commenced on 29 and 30 July and 6 August (Hamilton and Hamilton 1965). Clearly, breeding of the eastern Yellow-billed Cuckoo begins earlier with most clutches laid 2 weeks to 3 months before those of the western birds, depending on the area. For the eastern cuckoo, nesting begins later in more northern than in more southern locations, as is expected in a migratory species. Such a difference is not evident in the western Yellow-billed Cuckoo.

Dates of migration of eastern and western cuckoos also differ. Oberholser (1974) noted that in eastern Texas birds arrived from April to late May, but in the Trans-Pecos (west Texas) area, cuckoos were first observed from May to mid-June. This distinction corresponds with Oberholser's belief that Yellow-billed Cuckoos in west Texas were the western subspecies and those throughout the remainder of the state were the eastern subspecies.

In Florida, Yellow-billed Cuckoos usually are first seen in late March or early April and depart in autumn from late October to mid-November (Sprunt 1954). Transient and summer residents have been noted in Oklahoma from 17 April to 13 October (Sutton 1967). Farther north, cuckoos

seldom arrive in Pennsylvania before the second week in May (average date 12 May) and usually remain until late September (Todd 1940). In contrast, Yellow-billed Cuckoos in California arrive on the breeding grounds occasionally as early as late May, but most frequently in June or early July (Laymon and Halterman 1987a,b). In Arizona, the Yellow-billed Cuckoo is found from the first week in June through September (Phillips et al. 1964).

In California and Arizona, breeding habitats of Yellow-billed Cuckoos include wooded rivers and creeks in the Lower and Upper Sonoran and Transition zones. The riparian forests selected by cuckoos tend to have tall, mature stands of cottonwood (*Populus* spp.) and willows (*Salix* spp.). Dense stands of mesquite (*Prosopis* spp.) and tamarisk (*Tamarix* spp.) are seldom used (Groschupf 1987, Gaines and Laymon 1984).

In the Pecos Valley, New Mexico, Yellow-billed Cuckoos are said to be unusual because they nest not only in cottonwoods and willows but also regularly in dense tamarisks (Howe 1986). In contrast, cuckoos avoid tamarisk in other locations such as Arizona (Ohmart and Anderson 1982), the middle Rio Grande Valley in New Mexico (Hink and Ohmart 1984, Howe 1986), and California (Gaines and Laymon 1984).

Prior to the late 1920s cuckoos bred in towns along the Pecos River such as Roswell, Artesia, and Carlsbad (Bailey 1928). In these situations, the cuckoos probably selected elms (*Ulmus* spp.) and other exotic tree species for nesting (Howe 1986). By the 1920s tamarisk was well established and cuckoos began nesting in it (Hildebrandt and Ohmart 1982, Howe 1986). Currently cuckoos also use planted cottonwoods in this area for nesting. Bent (1940) noted that the eastern Yellow-billed Cuckoo originally may have been a woodland bird but has learned to use urban environments, where it finds an abundant food supply in shade trees, orchards, and gardens; it is seldom seen in dense woods.

Of the 30 specimens we examined from the Pecos River and Rio Grande, 12 of the 19 from the Rio Grande upstream of Big Bend were scored as western by the discriminant function, whereas 9 of 11 from the Pecos and Rio Grande rivers downstream of Big Bend were scored as eastern by the discriminant function. The discriminant analysis predictions agreed on 70% of the 30 cuckoos, showing a high degree of predictability within the zone of overlap. Of the 9 cuckoos for which the geographic and discriminant analysis predictors did not agree, 7 were "eastern" birds found in the west and only 2 were "western" birds found in the east. Eastern birds may be moving west from the Pecos River Valley at a rate greater than that at which western birds are moving east. The data suggest that this area is a zone of contact between eastern and western Yellow-billed Cuckoos and that continuing urban development, expansion of tamarisk, and seemingly more general breeding habitat requirements may be facilitating the gradual movement of eastern birds west.

The proclivity of western Yellow-billed Cuckoos to arrive on the breeding grounds at any time from the last week in May to the first week in July complicates the matter of judging what is truly a breeding individual. Vagrancy is also a difficult problem to address. Information from other species suggests that it is very likely that many, if not most, cuckoos found on the coast and at desert oases in California from mid-May to late June

and from September to November are of eastern origin. But no specimens of these are available with which this hypothesis could be tested.

Our field work suggests a difference in bill color between live eastern and western cuckoos, eastern birds having yellow bills and western birds having orange bills. These differences are not detectable in older museum specimens, in which the color of the bill fades. Existing tape recordings suggest a possible difference in call and song. Descriptions in the literature and our field work indicate a difference in juvenal plumage: young cuckoos in California have all-black bills for at least three weeks after leaving the nest, whereas juveniles in the east are said to have yellow bills (Oberholser 1974).

CONCLUSIONS

We believe that further study of geographical variation in call, bill color, and genetics of the Yellow-billed Cuckoo is warranted. Because the western Yellow-billed Cuckoo is endangered in most of its range, such a study will have to be restricted to live birds. Because the recognition of the subspecies on the basis of measurements of existing specimens is equivocal and because the apparent differences in calls and bill color need further study, we recommend that the two subspecies of Yellow-billed Cuckoos be retained until such a study is completed. The western Yellow-billed Cuckoo was denied protection under the Endangered Species Act as a result of the taxonomic recommendation by Banks (1988). But because the western cuckoo is so critically endangered (Gaines and Laymon 1984, Laymon and Halterman 1987c), we believe that changes in its classification should be made only after the best possible study.

SUMMARY

We analyzed measurements of 750 museum specimens of eastern (*Coccyzus americanus americanus*) and western (*C. a. occidentalis*) Yellow-billed Cuckoos to determine if recognition of the two subspecies should be maintained. Student's *t* tests of differences in wing length, tail length, bill length, and maxilla depth revealed statistically significant differences between the smaller eastern and larger western birds. A discriminant function analysis correctly categorized 83.8% of males in the east and 74.6% of those in the west, 89.6% of females in the east and 85.8% of those in the west, and we believe that this level of differentiation is sufficient to warrant retention of the two subspecies. These physical differences coincide with earlier migration and breeding and more generalized selection of breeding habitat (including urban development) by the eastern population. Western Texas, eastern New Mexico, and adjacent Mexico is a zone of overlap or intergradation between the eastern and western subspecies, and the eastern Yellow-billed Cuckoo is apparently expanding its range west from the Pecos River valley into the Rio Grande valley, New Mexico. Apparent differences between the eastern and western subspecies in calls and color of the bill of both adults and juveniles warrant further study.

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