

THE MIDDLE AMERICAN POPULATIONS OF THE  
CRESTED FLYCATCHER *MYIARCHUS TYRANNULUS*

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The flycatchers of the genus *Myiarchus* are a difficult taxonomic group within a family noted for its difficult genera, such as *Contopus*, *Elaenia*, and *Empidonax*. There are some 14 to 18 species of *Myiarchus* in the whole of temperate and tropical America, including the West Indies and the Galapagos archipelago. A remarkable uniformity of coloration, a lack of appreciable sexual dimorphism, and interspecific overlap in most mensural characters have led to considerable discrepancy in their systematic treatment. The diagnostic characters that have been used in the past to indicate relationships have often been inadequate and unreliable. The author has undertaken a revision of the genus, based in large measure on field studies of systematically critical breeding populations. This initial paper reports the findings relating to one geographically discrete group, the Middle American populations of the crested flycatchers of the species *Myiarchus tyrannulus*, with special emphasis on the status of the so-called Ometepe Flycatcher (*Myiarchus brachyurus*) of Central America. Consideration is given to the vocalizations which may serve to supplement morphological characters in discerning taxonomic relationships.

## HISTORICAL BACKGROUND

The crested flycatchers of México have had an eventful nomenclatural history which need not concern us here. Suffice it to say that the populations of eastern México are now known as *cooperi* (Deignan, 1949) and that *magister* applies to those of western México (see fig. 7 for ranges of forms considered here). The two forms were formerly considered as races of a distinct Mexican species, *Myiarchus mexicanus* (Nelson, 1904; Ridgway, 1907), until Hellmayr (1927), the Fourth Edition of the A.O.U. Check-list (1931) and Griscom (1932) "lumped" them with the geographically distinct and polytypic *Myiarchus tyrannulus* of South America and the Lesser Antilles. These Mexican populations have since been regarded by most workers as conspecific with the disjunct South American group, although not without question (Eisenmann, 1955:67). This author follows Hellmayr, but reserves critical judgment on the matter pending completion of field studies on the South American populations.

A new species of *Myiarchus* was described by Ridgway (1887) from Central America, within the area of the hiatus between the ranges of *mexicanus* and *tyrannulus*. He called this form *brachyurus* and, on the basis of its larger size and shorter tail, he considered it specifically distinct from *Myiarchus nuttingi* which he had described from the same region five years earlier. Allen (1892) contested this specific distinction, commenting that the supposed differences were more likely due to individual variation. This may have influenced Ridgway, who later (1907) reduced *brachyurus* to racial status under *nuttingi*. Nelson, in his monograph (1904), retained the species status of *brachyurus*. The specific distinction between *brachyurus* and *nuttingi* was clearly and adequately summarized by Bangs (1909) and this treatment has been followed by all subsequent workers.

Dickey and van Rossem (1938) were impressed with the apparent intermediacy of their El Salvador specimens between *brachyurus* of Nicaragua and Costa Rica and *tyrannulus* from México, stating that "there would now seem to be little doubt that it is simply a geographical form of *tyrannulus*." This treatment was accepted by Wetmore (1944) and later followed in the Fifth Edition of the A.O.U. Check-list (1957). In his manuscript for a forthcoming volume of Peters' Check-list, Zimmer likewise considered

*brachyurus* to be a Central American race of *tyrannulus*. Other workers have expressed uncertainty about its taxonomic status (Blake, 1953; Paynter, 1955). Rand and Traylor (1954) and the Mexican Check-list (Pac. Coast Avif., 1957) accorded it full species rank.

The most recent addition to the group of forms considered here was an insular population, *M. t. insularum*, described by Bond (1936) and known only from the Bay Islands of Honduras.

#### MATERIALS AND METHODS

Populations in northern Sonora and southern Arizona were studied during the summers of 1956 and 1957, with aid from the American Philosophical Society (Grant No. 2152) and the Frank M. Chapman Memorial Fund. An expedition from April through June, 1959, co-sponsored by the National Science Foundation (Grant No. G-7083) and the American Museum of Natural History, provided first-hand knowledge of critical populations in Costa Rica, Nicaragua, El Salvador, Guatemala, and southern México, including Yucatán. I am much indebted to Colonel and Mrs. D. S. McChesney of Syracuse, New York, for contributing immeasurably to the success of this expedition.

Emphasis in these field studies was placed on collecting specimens of known sex, vocalizations, habitat preference, and mate preference. Tape recordings were made of representative vocalizations of each of the breeding populations visited, using a Mag-nemite recorder at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. These recordings involved 54 individuals of the forms being reported on here, ranging in locations from Costa Rica north to Arizona. All recordings were analyzed by ear in the laboratory, and subsequently over 300 representative vocal patterns were selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extent of geographical variation evident from this analysis.

Over 500 specimens of these forms have been examined. I am indebted to the following for the loan of specimens in their care: James Bond, Pierce Brodkorb, Herbert Friedmann, Thomas R. Howell, Philip S. Humphrey, Richard F. Johnston, George H. Lowery, Jr., Robert T. Orr, Kenneth C. Parkes, Raymond A. Paynter, Frank A. Pitelka, George M. Sutton, Harrison B. Tordoff, Melvin A. Traylor, Dwain W. Warner, and David A. West. Linear measurements, in millimeters, were taken as follows: wing, flattened; tail, from the insertion of the central rectrices; bill length, from the anterior margin of the nostril; width of fuscous stripe along medial side of shaft of outer rectrix, at the midpoint of the shaft. In diagramming statistical analyses, 1.3 times the standard deviation has been plotted on each side of the mean (forming a solid rectangle). Thus, when comparing two samples, non-overlap of the solid rectangles indicates that at least 90 per cent of the individuals of one sample are separable from 90 per cent of the individuals of the other sample with respect to the character being analyzed. Color nomenclature is that of Ridgway (1912). Color of mouth linings was noted in all fresh specimens and photographed in representative individuals.

#### ANALYSIS OF VARIABILITY

*Morphological variation.*—Complete descriptions of the plumage of all forms but *insularum* have been published by Nelson (1904) and Ridgway (1907). Special attention is called to Nelson's comments on the problems associated with the marked seasonal changes in plumage within this genus. Coloration of body plumage was found to be remarkably uniform among all but one of these forms and consequently of no value in discriminating between populations. The one exception to this uniformity is the insular population on the Bay Islands of Honduras. The three specimens collected by Bond

(1936) are all somewhat darker above than any mainland population of this group, particularly on the pileum. All fresh specimens examined (none of *insularum*) had mouth linings that were a pale to light ochraceous-buff.

The species of *Myiarchus* differ to some extent with regard to the amount of cinnamon-rufous in the rectrices. Ignorance of the degree of individual variation in this diagnostic character has led to some taxonomic confusion in the genus. Within the crested flycatchers of Middle America, rectrix pattern is the most geographically vari-

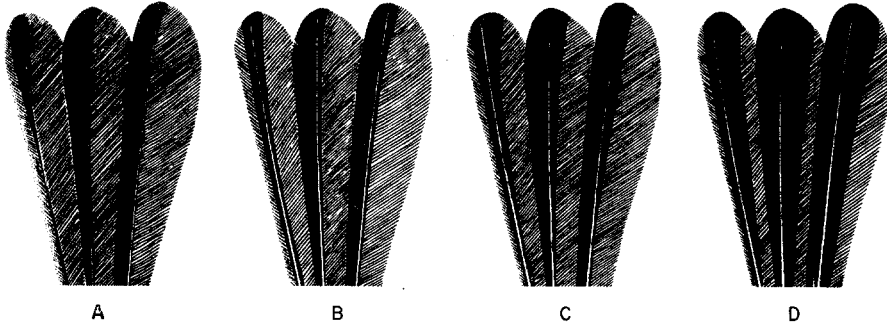


Fig. 1. Extremes in the width of the fuscous stripe of the three outer rectrices in samples of *Myiarchus tyrannulus brachyurus* (A and B), and in *M. t. magister*, *M. t. cooperi*, and *M. t. insularum* (C and D).

able aspect of plumage coloration. The breeding birds of Nicaragua and Costa Rica (*brachyurus*) have a consistently greater amount of rufous in the tail than do the other Middle American populations. The dark, fuscous stripe, when present, was never greater than 2 mm. wide (average, 1 mm.) in a sample of 78 specimens. Elsewhere, the fuscous stripe in a sample of 282 specimens from the remaining populations varied from 1.5 mm. to 6 mm. (average, 3.5 mm.) with no geographical trend apparent (see fig. 1). The

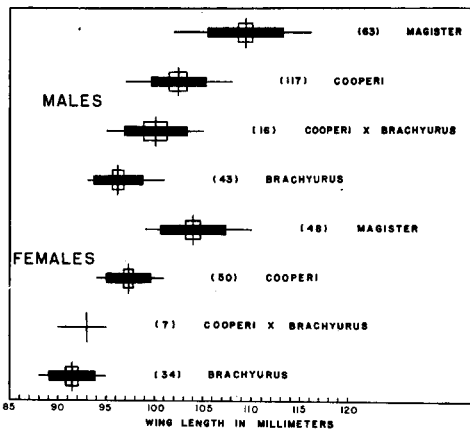


Fig. 2. Statistical analysis of wing length. Numbers in parenthesis indicate sample size. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.2 times the standard deviation.

breeding birds of the Pacific lowlands of El Salvador and Honduras have a rectrix pattern that is intermediate between the samples just mentioned. In a sample of 23 specimens, the width of the fuscous stripe varied from 1 to 4 mm. (average, 2 mm.) wide.

Wing length was the least variable, within populations, of the measurements taken (coefficient of variation from 1.82 to 2.73). The three mainland forms, *magister*, *cooperi*, and *brachyurus*, are well differentiated, and equally so, by wing length (fig. 2). The sample of *insularum*, although inadequate to include in the analyses of measurements, suggested no differentiation in size from *cooperi*. The breeding birds of El Salvador and southern Honduras have wing lengths that are intermediate between those of *cooperi* and *brachyurus*. No clinal variation was evident within the ranges of these forms.

Tail length was a somewhat more variable character than wing length (coefficient of variation from 2.34 to 3.64). The two Mexican forms, *magister* and *cooperi*, were less

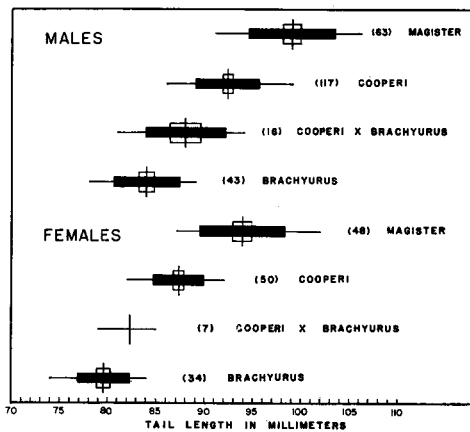


Fig. 3. Statistical analysis of tail length.

differentiated with respect to tail length than to wing length (fig. 3). Although Ridgway, in naming *brachyurus*, meant to denote a shorter tail relative to that of the Nicaraguan *nuttingi*, his name is even more appropriate when *brachyurus* is compared with *cooperi*. The population from Nicaragua and Costa Rica is significantly shorter tailed than the form to the north. As was the case with rectrix pattern and wing length, tail lengths of the birds of El Salvador and southern Honduras were intermediate between those of *cooperi* and *brachyurus*. Once again there was no clinal variation evident within populations.

The populations of western México (*magister*) are significantly longer billed than the remaining forms; *cooperi* and *brachyurus* are not well differentiated by this character (fig. 4). Bill length was a highly variable character within populations (coefficient of variation of 2.51 to 5.31).

There is little sexual dimorphism in these forms. No consistent differences were noted between the sexes with regard to plumage coloration, including rectrix pattern. Males average larger in size throughout Middle American populations, but considerable overlap exists in all measurements. The most reliable dimorphism occurs in the length of the wing, with males averaging 5 mm. longer in all samples studied.

*Variation in vocalizations.*—In preliminary field studies made in Arizona in 1956–57, the author determined that the vocal repertoire of *magister* consisted of four basic patterns. Various combinations of these basic patterns were sometimes rendered, there-

by extending the apparent variety of the repertoire. The most distinctive of these patterns, that is, the one found to be most useful in distinguishing *magister* from the two sympatric species of *Myiarchus* in Arizona, is illustrated in the top row of spectrograms in figure 5. It is rendered with great intensity, may be heard at a considerable distance, and is not to be found in the repertoire of any other *Myiarchus* of North or Middle America. Spectrograms of the most distinctive vocal patterns of these other *Myiarchus* flycatchers are shown in figure 6 for comparative purposes.

Analysis of tape recordings made in 1959, from representative populations elsewhere in Middle America, reveals that this same basic repertoire is shared by all of the forms being considered here (see fig. 5). Geographical variation in these basic patterns was found to be no greater than the individual variation recorded within populations. The only consistent geographical variation, a slight rise in frequency from north to

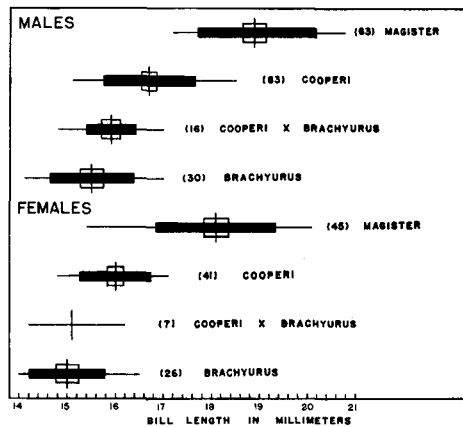


Fig. 4. Statistical analysis of bill length.

south, is probably correlated with body size. In the top row of spectrograms in figure 5, for example, the patterns of *brachyurus* at the left are at a somewhat higher frequency than those at the right, which are of the larger *cooperi* and *magister*.

By collecting specimens whose vocalizations were previously recorded on tape it was possible to demonstrate that both sexes of these Middle American forms render all of these basic vocal patterns, although the males tend to be more vociferous. Vocal patterns *per se* cannot be used, therefore, as a means of sexing birds in the field.

In view of the great morphological similarity among the species of *Myiarchus*, the homogeneity of the vocal repertoire and its distinctiveness from that of sibling species suggests that vocal characters may be important in species discrimination among these birds. Preliminary investigation supports this contention, but carefully controlled experiments are needed. A field experience in eastern Guatemala is a case in point. A search for *cooperi* breeding in this remote area led the author to clearings in the rain forest near Sebol, just south of the Peten border. A pair of *cooperi* was heard from beyond an impenetrable tangle of low vegetation. An initial playback of a recording of *M. tuberculifer*, a sympatric species, brought no response from the distant birds. But a second recording, made of *brachyurus* in Costa Rica, brought an immediate response. The pair of *cooperi* appeared and darted nervously about in the vicinity of the speaker. They were quite vociferous and were subsequently recorded and collected.

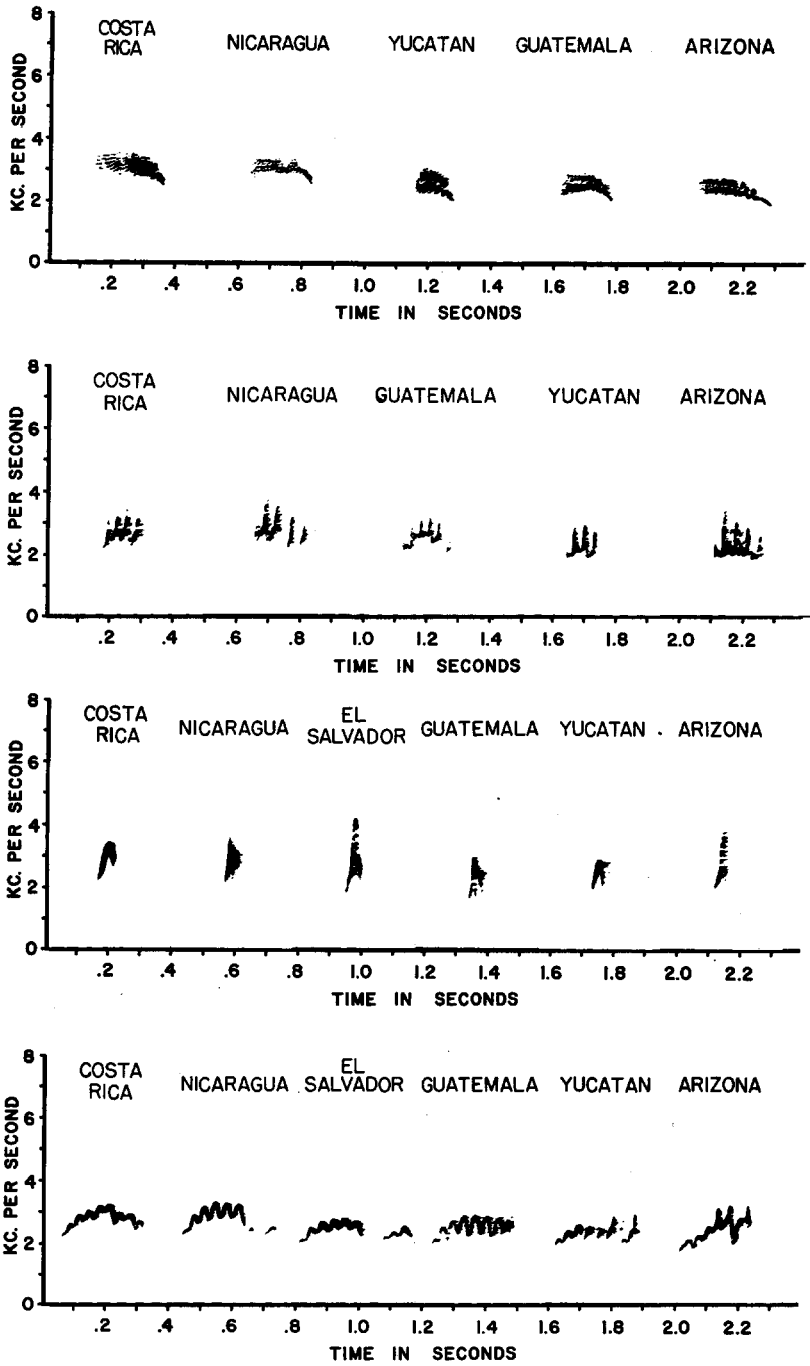


Fig. 5. Sound spectrograms of four vocal patterns characteristic of *Myiarchus tyrannulus* in Middle America.

GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION

The breeding ranges of the forms under consideration here are presented in figure 7. The distribution of *Myiarchus tyrannulus magister* is roughly coincident with the Lower Sonoran Zone of Arizona and Sonora and the Arid Tropical Zone of the Pacific lowlands of México. Although occurring casually throughout the desert-mesquite associations, tropical deciduous woodlands, and thorn forests, *magister* is most abundant among the giant cacti and riparian communities where it can find natural cavities or abandoned

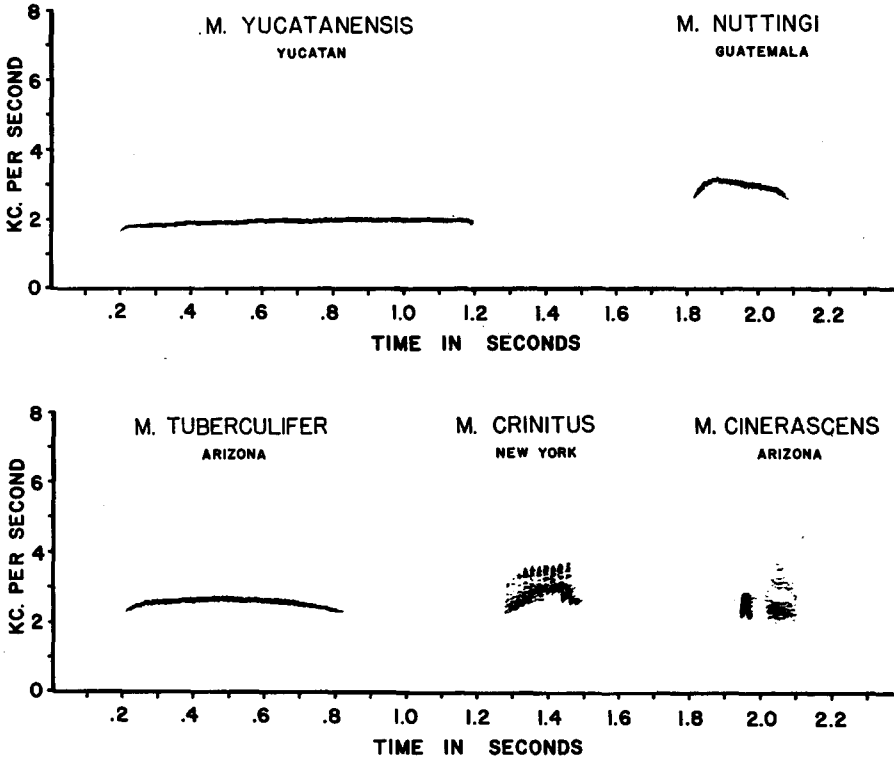


Fig. 6. Sound spectrograms of vocal patterns characteristic of five other species of *Myiarchus* occurring in Middle and North America.

woodpecker holes of substantial size for its nest sites. It has successfully colonized the Tres Marías Islands but without differentiation from the mainland population. The southernmost breeding specimens examined by the author that can unquestionably be assigned to this race were two males taken in the isthmus region of Oaxaca (U.S. Nat. Mus.). Breeding *tyrannulus* in the Pacific lowlands of the isthmus region are apparently of extremely local occurrence and gene exchange with *cooperi* is therefore restricted. In the northern part of its range, at least, *magister* is migratory. Two non-breeding specimens from coastal Chiapas (U.S. Nat. Mus.; Brodtkorb Coll.), obviously assignable to this race, suggest a limited winter movement south of the breeding range.

In the lowlands bordering the Gulf of México and the Caribbean, *M. t. cooperi* occupies a greater variety of habitats than the western Mexican race, ranging from mesquite and thorn forest in the north (most abundant in riparian communities) to clearings in tropical evergreen and rain forest in the south. The requirement for larger trees as nest sites is probably not as stringent in this smaller race, but its nesting habits are

otherwise identical. Although essentially a race of the Gulf lowlands, three breeding specimens from the isthmus region of Oaxaca (U.S. Nat. Mus.; Am. Mus. Nat. Hist.) are closer to *cooperi*. Intergradation with *magister* no doubt occurs in a limited area of eastern Oaxaca. The specimens taken by Edwards and Lea (1955) near Monserrate, Chiapas, are typical *cooperi* and constitute the only definite breeding record known to the author for the Pacific lowlands of Chiapas. However, a worn male taken in late April by Brodkorb (Univ. Mich. Mus. Zool. 102,605) near Pijijiapan, Chiapas, is also

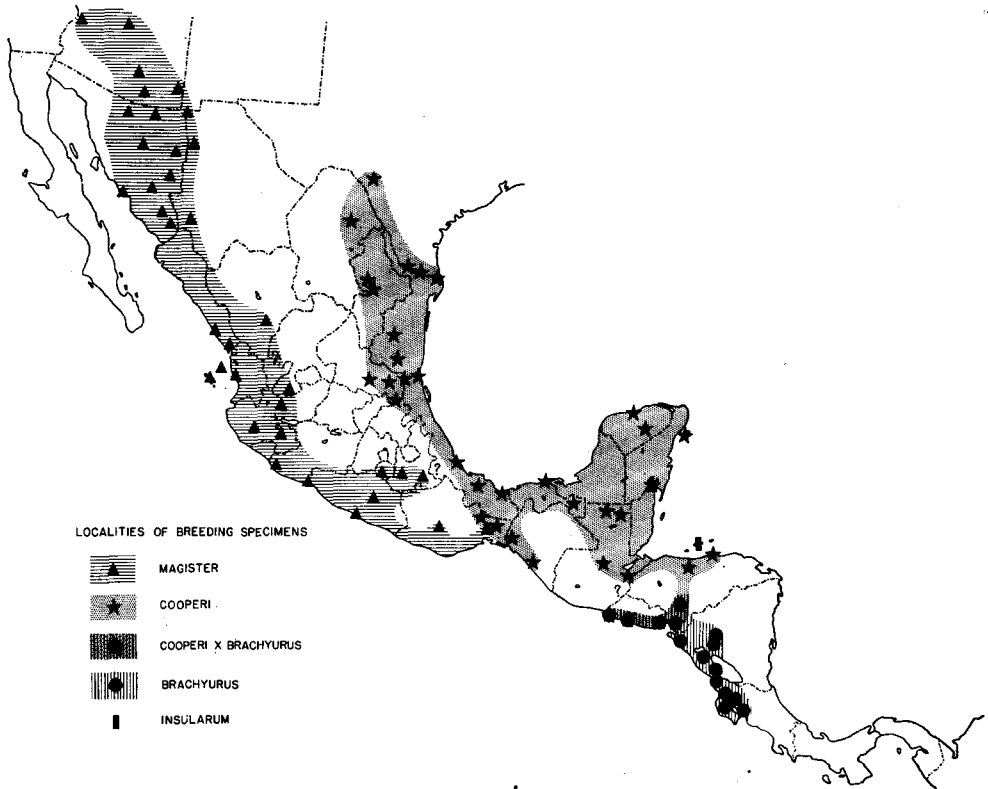


Fig. 7. Breeding range of *Myiarchus tyrannulus* in Middle America, as indicated by localities of specimens examined.

typical *cooperi* and suggests that the race may breed locally at least that far south in the Pacific drainage. Its absence as a breeding bird in the Pacific lowlands of Guatemala was reported by Griscom (1932) and substantiated by the author in 1959, thus creating an interesting hiatus in the breeding range of the species along the Pacific drainage (see fig. 7). The race has successfully colonized Cozumel Island off Quintana Roo but without differentiating from the mainland population.

The southeastermost breeding records of *cooperi* known to the author for the Caribbean lowlands are from northern Honduras: two juveniles (Carnegie Museum) collected by Twomey in June near Coyoles, and a molting female (U.S. Nat. Mus.) taken at Trujillo in September. The race is migratory in the northern part of its range. In winter, it is rather widely distributed throughout Guatemala, including the Pacific drainage. The southernmost wintering specimens are from El Salvador (Dickey Coll.; Mus. Vert. Zool.; Chicago Nat. Hist. Mus.).



The author has no knowledge of the voice, habits, or ecology of *M. t. insularum* on the Bay Islands of Honduras. It is clearly allied to *cooperi*, from which it differs only in a darkening of the upper parts. That even this degree of differentiation should have occurred is of interest in view of the lack of differentiation in insular populations of *magister* on the Tres Mariás and of *cooperi* on Cozumel.

The breeding birds of southern Honduras and of the Pacific coast of El Salvador and Honduras are morphologically intermediate between *cooperi* and *brachyurus* (see figs. 2 to 4). Gene exchange between this intermediate population and typical *cooperi* is probably accomplished via the Honduras depression (Carr, 1950) which connects the Caribbean and Pacific lowlands, and this population is contiguous on the south with typical *brachyurus*. The westernmost specimens in this intermediate population were collected by van Rossem (Dickey Collection; Chicago Nat. Hist. Mus.) in extreme western El Salvador. The absence of *tyrannulus* in the Pacific lowlands of Guatemala has already been discussed. The controversial specimen of "*brachyurus*" from Tonalá, Chiapas (U.S. Nat. Mus. 147638) is a female *cooperi*.

Aside from its morphological intermediacy, this rather small breeding population is of interest because of its apparent ecological restriction, in the coastal plain, to mangrove communities (Dickey and van Rossem, 1938; Rand and Traylor, 1954, and confirmed by the author in 1959). It is curious that there should be so much seemingly suitable habitat for *M. tyrannulus* unoccupied in this region—habitat of a type in which *brachyurus* breeds commonly only a short distance to the south in Nicaragua. There is no evidence of a comparable ecological restriction in any other Middle American population of *tyrannulus*. There is apparently some movement of these birds inland during the fall and winter (Dickey and van Rossem, 1938).

The geographically limited but well-defined race *M. t. brachyurus* is the resident population of the tropical, deciduous woodland of western Nicaragua and northwestern Costa Rica. No specimens are known from south of the Gulf of Nicoya, where the vegetation changes rather abruptly under the influence of a much greater rainfall. The nesting and foraging habits of this smallest Middle American race appear to be identical with those of the larger Mexican forms.

#### SUMMARY AND CONCLUSIONS

This paper is a report on one geographically discrete group of the flycatchers of the genus *Myiarchus*, the Middle American populations of *Myiarchus tyrannulus*. Special emphasis is placed on the status of *brachyurus*, the Ometepe Flycatcher of Central America, which is shown to be a race of *Myiarchus tyrannulus*. Spectrographic analysis of vocalizations is used to supplement morphological characters.

Plumage coloration was found to be remarkably uniform among all populations considered, with geographical variation evident only with respect to rectrix patterns and a darkening of the upper parts of an insular race. The breeding birds of Nicaragua and Costa Rica, the form *brachyurus*, differ from all other populations in having significantly larger amounts of cinnamon-rufous in the tail.

The three mainland forms (*magister*, *cooperi*, and *brachyurus*) are well differentiated with regard to wing and tail length, but less so with regard to bill length. The breeding birds of the Pacific lowlands of El Salvador and Honduras are intermediate between *cooperi* and *brachyurus* in rectrix pattern and size. Sexual dimorphism is limited in all populations and consists of slightly larger average size in males.

All populations considered, including *brachyurus*, share the same basic repertoire of vocalizations, which differs substantially from that of the other flycatchers of the

genus *Myiarchus* of North and Middle America. Preliminary investigation suggests that vocal characters may be important in species discrimination among these birds.

Four races of *Myiarchus tyrannulus* are recognized for Middle America, and a discussion of the geographical and ecological limits of their distribution is included. The hiatus in the breeding range on the Pacific drainage of Chiapas and Guatemala and the ecological restriction of the breeding birds of El Salvador and southern Honduras to mangrove communities are unexplained aspects of the distribution of the species.

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