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SPECIFIC LIMITS AND DISTRIBUTION OF ASH-THROATED AND NUTTING FLYCATCHERS

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This is the second in a series of reports on the genus *Myiarchus*, one of the most difficult genera of tyrannid flycatchers. An initial paper (Lanyon, 1960a) treated the Middle American populations of the crested flycatchers of the species *Myiarchus tyrannulus*. The findings here relate to the controversial relationship between the Ash-throated Flycatcher, *Myiarchus cinerascens* (Lawrence), of western United States and México and the Nutting Flycatcher, *Myiarchus nuttingi* Ridgway, of Middle America.

HISTORICAL BACKGROUND

A review of the fluctuating climate of taxonomic opinion that has characterized this particular complex within the genus will serve to indicate (1) the desirability of considering additional characters to discern taxonomic relationships, (2) the need for a better understanding of the variability of those morphological characters used in the past, and (3) the need for new field observations of certain critical breeding populations.

Ridgway described *Myiarchus nuttingi* (in Nutting, 1882) on the basis of a pair of birds collected near the Gulf of Nicoya, Costa Rica, and from additional specimens representing localities from Tehuantepec south to the type locality. He recognized the close affinity of his new species to *Myiarchus cinerascens*, a well-known form of northern México and western North America (*M. c. cinerascens*; Lawrence, 1851) and Baja California (*M. c. pertinax*; Baird, 1859), but he emphasized the smaller size of the Middle American form and the differences in the dusky patterns of its rectrices. J. A. Allen (1892) reconsidered *M. nuttingi* and found the character of the rectrix pattern quite variable and of little use in "exceptional specimens." He recommended that it be considered a smaller, southern race of *M. cinerascens*. There followed a period during which most workers (American Ornithologists' Union, 1893; Bailey, 1902; Bendire, 1895; Coues, 1903; Swarth, 1904), including Ridgway (1896), accepted Allen's interpretation.

In a collection of birds from Guerrero, Salvin and Godman (1892) found several specimens which they described as *Myiarchus inquietus*. Except for the brief notes published with the original description, *inquietus* remained comparatively unknown until the spring of 1903, when Goldman and Nelson obtained specimens at the type locality and elsewhere in southwestern México. Using their material, Nelson (1904:40) recognized that *inquietus* was intermediate in size between *cinerascens* to the north and *nuttingi* to the south. He could find no evidence of intergradation between *inquietus* and *cinerascens*, but he noted that "the specimens from the Isthmus and adjacent parts of Chiapas are distinctly intergrades showing that *inquietus* is merely a northern subspecies of *Myiarchus nuttingi*." He reinstated *M. nuttingi* to species status and considered *inquietus* to be its northern representative. Accepting Nelson's treatment of the complex, Ridgway (1907) returned to his earlier convictions and maintained *M. nuttingi* and *M. cinerascens* as distinct species, an interpretation that remained unchallenged for the next twenty years (Hellmayr, 1927).

Bangs and Peters (1928), admonishing the use of the variable rectrix pattern as a good diagnostic character, considered *inquietus* to be a "poorly marked form" and rec-

commended its synonymy with *M. nuttingi*. Working with extensive new material from Central America, Griscom (1932) continued the recognition of *M. nuttingi* as a distinct species, but he agreed with Bangs and Peters in reducing *inquietus* to synonymy.

It was van Rossem (1931, 1932) who revived the movement to "lump" *nuttingi* (including *inquietus*) with *cinerascens*, the interpretation advocated by Allen and others forty years earlier. He advised upon the "extensive intergradation between *inquietus* and *cinerascens* in size, color, and tail markings," and furnished average measurements to demonstrate a cline from the large *Myiarchus c. cinerascens* in the north to the small *Myiarchus c. nuttingi* in the south. After working over new material from Guerrero (type locality of *inquietus*), Griscom (1934:388) agreed that van Rossem's treatment "is entirely permissible at the present time," but (p. 389) cautioned against precluding "hybridization of two different species." Van Rossem later commented (1936:115) on his own interpretation and Griscom's views: "Although [we] . . . are now in substantial agreement that *cinerascens*, *inquietus*, and *nuttingi* are conspecific, there remains considerable uncertainty as to the manner of intergradation." There were a number of workers during this period, however, who were reluctant to accept this polytypic species interpretation of the complex and who continued to follow Nelson, Ridgway, and Hellmayr in recognizing *M. nuttingi* as a distinct species (Carriker and de Schauensee, 1935; Sassi, 1939; and Wetmore, 1944).

A new race of this complex, *Myiarchus cinerascens flavidiol*, was described by van Rossem (1936) on the basis of material from the Pacific lowlands of Guatemala (Griscom had called attention to the peculiarities of this population in 1932) and El Salvador.

As additional material became available, van Rossem (1945:152) reversed his stand once again and recommended that the complex be divided into the two species: "two closely related but distinct species are involved and . . . the truly impressive number of intermediates are the result of hybridization on a mass scale." At this same time, he reinstated Kaup's (1851) name, *mexicanus*, to designate the southernmost breeding populations of *M. cinerascens*. Presumably this would be the race of *M. cinerascens* principally involved in the "mass hybridization" with *M. nuttingi inquietus*.

Dickerman and Phillips (1953) suggested that the number of "hybrids" could be reduced by the use of better characters to distinguish the two species. More recently, Phillips (1960) has designated the northernmost population of *M. nuttingi* (from northwestern México) as a new race, *vanrossemi*.

The treatment of *M. cinerascens* and *M. nuttingi* as distinct species received authoritative support in the Fifth Edition of the A.O.U. Check-list (1957) and the Mexican Check-list (Pacific Coast Avifauna, 1957) although the latter recognized "hybridization of considerable extent in some areas." This interpretation has not been universally accepted, however (Sutton, 1951; Blake, 1953; Rand and Traylor, 1954; Felton and Steinbacher, 1955; Brodkorb, *in litt.*, 1960). In his unpublished manuscript on the Tyrannidae for a forthcoming volume of Peters' Check-list, Zimmer, with extensive experience in the taxonomy of this family, recognized but one polytypic species, *M. cinerascens*.

MATERIALS AND METHODS

Populations in southern Arizona were studied during the summers of 1956 and 1957. An expedition from April through June, 1959, provided firsthand knowledge of critical breeding populations in Costa Rica, Nicaragua, El Salvador, Guatemala, and southern México. A second expedition, during May, 1960, concentrated on populations in western México. Emphasis in these field studies was placed on collecting a series of specimens of known sex, vocalizations, habitat preference, and mate preference. Color of mouth

linings was noted in all fresh specimens and photographed in representative individuals. Tape recordings were made of representative vocalizations of each of the breeding populations visited, using a Magnemite recorder at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. These recordings involved 68 individuals of the forms being reported on here, from Costa Rica north to Arizona. All recordings were analyzed by ear in the laboratory, and subsequently over 350 representative vocal patterns were selected for analysis with a sound spectrograph. The spectrograms presented here were chosen to demonstrate the extremes of variation evident from this analysis.

Over 1200 museum specimens of this complex were examined and analyzed for morphological variation. 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. Wing formula is expressed in terms of the length of the ninth primary relative to that of the sixth and fifth primaries. Only individuals that had completed the postjuvinal molt were included in the determination of variability of morphological characters. 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 the probability 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 particular character being analyzed.

ACKNOWLEDGMENTS

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MORPHOLOGICAL VARIATION

On the basis of evidence accumulated during this study, I recognize two species in this complex: *Myiarchus cinerascens* (Lawrence), which breeds throughout much of the western United States and the Mexican plateau (*M. c. cinerascens*) and Baja California (*M. c. pertinax*); and *Myiarchus nuttingi* Ridgway, represented in western México by

a single race (*M. n. inquietus*) and in Central America by two races (*M. n. nuttingi* and *M. n. flavidior*). I have synonymized van Rossem's *mexicanus* with *M. c. cinerascens* and Phillips' *vanrossemei* with *M. n. inquietus*.

It will be apparent from the following discussion of morphological variation that a strong case for the recognition of *M. cinerascens* and *M. nuttingi* as good species can not be based solely on the traditional analysis of museum specimens. A remarkable uniformity of coloration, considerable seasonal variation, lack of sexual dimorphism other than in size, and overlap in all mensural characters are factors contributing to the problem. Zimmer's treatment (MS) of the complex exemplifies the limitations of this approach. Field studies of these birds, on the other hand, revealed striking differences with regard to their vocalizations and to the color of their mouth linings. On a common breeding ground, as in central and southeastern Sonora, they are known to retain these distinctions and select mates accordingly. A series of 50 specimens of known vocal patterns and color of mouth lining, accumulated in this study, supplemented with a few additional specimens from other collectors who recorded this vital information, has been used better to interpret the variability within the extensive series of museum specimens brought together for comparative purposes. It is this combined field and museum approach that has been used to determine the specific limits for the characters analyzed here.

Color of mouth lining.—This is the most practical and most reliable morphological criterion for the specific identification of fresh specimens of this complex. I have found no evidence that this character varies geographically or sexually in either species. In my series of 50 specimens of known voice, there was 100 per cent agreement between the specific determinations based solely on color of mouth linings and those based on certain diagnostic vocal patterns. All fresh specimens of the three races of *M. nuttingi* (from Costa Rica to Sonora) had orange-colored mouth linings. All fresh specimens of *M. cinerascens* from Arizona and Sonora (none of *M. c. pertinax* were available) had "flesh-colored" mouth linings ("pale ochraceous-buff" of Ridgway, 1912). There is no evidence of hybridization and introgression of this character in the series at hand. With regard to color of mouth lining, *M. cinerascens* can be grouped with the Middle American populations of *M. tyrannulus* (Lanyon, 1960a) and *M. nuttingi* is placed in a group with *M. crinitus*, *M. tuberculifer*, and *M. yucatanensis* (Lanyon, MS).

Rectrix pattern.—The extent and pattern of the fuscous areas on the inner vanes of the rectrices is the most variable aspect of plumage coloration in these sibling species, as it is in Middle American *M. tyrannulus* (Lanyon, 1960a). In spite of this variability, the differences between the two species are of a greater magnitude and consistency than is that of any other morphological character save the color of mouth lining in fresh specimens. The following key, based solely on rectrix pattern, has been prepared from 485 specimens of *M. cinerascens* and 229 specimens of *M. nuttingi*, all adults in fresh plumage (September through February). Variability in rectrix pattern is identical in both races of *M. cinerascens*. The sample of *M. nuttingi* included specimens of both *M. n. inquietus* and *M. n. flavidior*, since rectrix patterns are identical in these races. Individuals of the nominate race of *M. nuttingi* have little, if any, fuscous area on the inner vanes of the rectrices. Consequently they are no problem to identify and have not been included in the calculation of percentages of the *M. nuttingi* sample. They all key out at a single point in the key, as indicated. The characteristic fuscous pattern of the adults of these species is not apparent in the juveniles and for this reason the key is applicable to adults only. Juveniles can be recognized readily by the presence of extensive rufous on the central pair of rectrices which is never retained after the postjuvinal

molt. Proper use of the key should separate fresh-plumaged specimens with nearly 100 per cent accuracy. The effect of wear at the tips of the rectrices of adult birds becomes critical in those individuals representing the extremes in the ranges of variability of the two species. Within the sample of fresh-plumaged adults used in devising the key, I estimated that one would have difficulty in correctly keying out approximately 15 per cent of the individuals of each species following normal rectrix wear. In both fresh and worn specimens, however, the determination should be double-checked with the use of other morphological characters. There is a tendency for females of *M. cinerascens* to have a lesser amount of fuscous in the rectrices than males, as was noted by Nelson

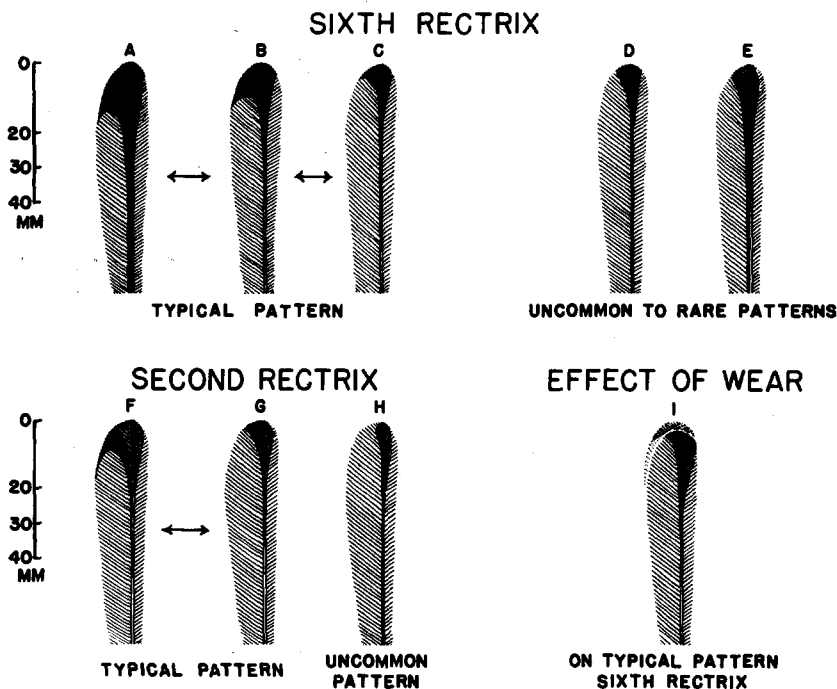


Fig. 1. Limits of individual variation in rectrix pattern of *Myiarchus cinerascens* and *M. c. pertinax*.

(1904), although there is virtually complete overlap in this regard. No sexual dimorphism in this character could be detected in the sample of *M. nuttingi*. Presence of a character or condition on either the left or right rectrix is acceptable in the use of the key. It is important to ascertain that a specimen has the full complement of twelve rectrices, since there is a definite gradient of markings within the rectrices and this is reflected in the key's organization. Rectrices are numbered from the central pair outward. The phrase "35 mm. point" designates that point along the shaft of the feather that is located 35 mm. from the tip of the feather. Figures 1 and 2 should be consulted with the use of the key.

- I. Sixth rectrix with fuscous area on inner vane expanding abruptly near the tip of the feather and often, but not always, extending forward again along the outer edge of the vane; fuscous area variable in size, but within the limits illustrated by figure 1 A-C; fuscous area not as in figure

1 D-E and figure 2 A-C; fuscous area may extend as a stripe of variable width and length along the shaft ("shaft stripe"):

- A. Sixth rectrix with shaft stripe less than 1 mm. wide at the 35 mm. point.....typical *M. cinerascens* pattern; 74 per cent of sample.
- B. Sixth rectrix with shaft stripe 1 mm. wide or greater at 35 mm. point:
 - 1. Sixth rectrix with shaft stripe less than 2 mm. wide at 40 mm. point:
 - a. Second and/or fifth rectrix with fuscous area on inner vane as described for sixth rectrix in (I) above; usually with shaft stripe absent or less than 0.5 mm. wide at 30 mm. point of rectrices two through five.....not uncommon *M. cinerascens* pattern; 12 per cent of sample.
 - b. Neither second nor fifth rectrix with fuscous area as designated for sixth rectrix in (I) above; usually with shaft stripe 0.5 mm. or wider at 30 mm. point on at least one of rectrices two through five.....rare *M. nuttingi* pattern; 4 per cent of sample.
 - 2. Sixth rectrix with shaft stripe 2 mm. wide or greater at 40 mm. point (see fig. 2 E).....rare *M. nuttingi* pattern; 3 per cent of sample.
- II. Sixth rectrix without fuscous area on inner vane as described in (I) above; but rather reduced or present as a shaft stripe of variable width and length, as in figure 1 D-E and figure 2 A-C:
 - A. Sixth rectrix with shaft stripe less than 0.5 mm. wide at 20 mm. point (see figure 1 D) uncommon *M. cinerascens* pattern (mostly females); 9 per cent of sample. (*Myiarchus n. nuttingi*, of inland Central America, also keys out here; differs from this group of *M. cinerascens* in usually having no fuscous in inner vane of sixth rectrix, or, a trace only on that rectrix and none in the inner vanes of rectrices two through five; properly sexed individuals of *M. n. nuttingi* are readily separable from *M. cinerascens* on the basis of mensural characters alone).
 - B. Sixth rectrix with shaft stripe 0.5 mm. wide or greater at 20 mm. point:
 - 1. Shaft stripe absent or less than 0.5 mm. wide at 30 mm. point on all rectrices two through five:
 - a. One or more of rectrices two through five with fuscous area on inner vane expanded within the limits shown in figure 1 F-H, but not as in figure 2 G-H.....rare *M. cinerascens* pattern (mostly females); 5 per cent of sample.
 - b. No fuscous area in inner vanes of rectrices two through five, or if present, as in figure 2 G-H but not within the limits shown in figure 1 F-H.....not uncommon *M. nuttingi* pattern; 19 per cent of sample.
 - 2. Shaft stripe 0.5 mm. wide or greater at 30 mm. point on at least one of rectrices two through five.....typical *M. nuttingi* pattern; 75 per cent of sample.

I am aware of the reports of others (J. A. Allen, 1892; Nelson, 1904; Bangs and Peters, 1928) discounting the value of rectrix pattern as a diagnostic character in this complex. But I am convinced that it has been an unawareness of three factors that has led to this confusion and uncertainty: (1) the true limits of specific variability of the pattern on any given rectrix, (2) the necessity of considering the patterns of two or more rectrices in the determination of certain specimens, and (3) the effect of feather wear in altering typical patterns. Some examples will serve to illustrate these points. The abruptly-expanded fuscous pattern is characteristic of *M. cinerascens* (fig. 1 A-C). Few workers appreciate that a small percentage of *M. n. inquietus* and *M. n. flavidior* (7 per cent of my sample) also exhibit this pattern (for example, AMNH 104799 from Nayarit—"inside mouth dark orange," size and wing formula typically *M. nuttingi*; see fig. 2 D-E). The shaft stripe is characteristic of *M. n. inquietus* and *M. n. flavidior* (fig. 2 A,F), but a well developed stripe occasionally appears on the sixth rectrix of *M. cinerascens* (12 per cent of my sample; see fig. 1 A). Identification of specimens that

appear to share these species-characteristic patterns of the outer rectrix rests upon a consideration of the inner rectrices as well. Those *M. nuttingi* having an abruptly expanded fuscous pattern will also exhibit a well developed shaft stripe on the inner rectrices (fig. 2 I)—a combination not yet observed in *M. cinerascens* (fig. 1 F-H).

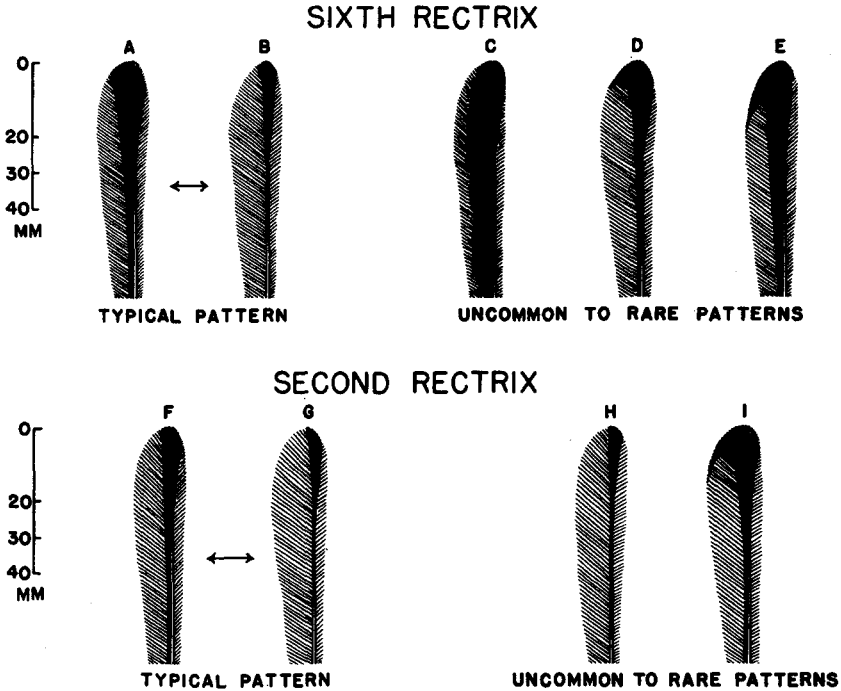


Fig. 2. Limits of individual variation in rectrix pattern of *Myiarchus nuttingi inquietus* and *M. n. flavidior*.

Another group that has puzzled workers are those *M. cinerascens* in which the sixth rectrix is without the characteristically expanded fuscous area but does have a shaft stripe (14 per cent of my sample; see fig. 1 E). The inner rectrices of these specimens may or may not have the expanded fuscous area but will *not* have a well-developed shaft stripe. Frequently in such cases, the fuscous area on the second rectrix will be reduced to a bulbous-shaped terminal pattern (fig. 1 H), thus making a distinction possible from those *M. nuttingi* having the shaft stripe reduced to a short, linear pattern terminally located (fig. 2 G-H). A typical rectrix pattern of *M. cinerascens* is sometimes transformed into something suggestive of *M. nuttingi* by the loss of a few millimeters from the tip of the rectrix, due to wear (fig. 1 I). Some badly worn specimens are thus difficult if not impossible to identify to species on the basis of rectrix pattern alone.

Except in the nominate race of *M. nuttingi*, as just noted, the considerable variability of rectrix pattern has no geographical basis. Specimens of *M. nuttingi* with characteristic vocalizations, mensural characters, and color of mouth lining, but having rectrix patterns with tendencies toward the condition in *M. cinerascens* have been taken well outside the latter's breeding range, for example, in Nayarit, Colima, and Guerrero. Similarly, specimens of *M. cinerascens* having rectrix patterns with tendencies toward the condition in *M. nuttingi* have been taken in California, Coahuila, and Nuevo León.

These instances might be interpreted by some as evidence of introgression. The specimens taken in areas of sympatry, however, show no indication of the extensive hybridization of this character that would presumably be required for such introgression. The simpler explanation would seem to be that rectrix pattern is controlled by a highly variable gene complex in both species. Admittedly, occasional hybridization would be difficult if not impossible to establish or deny on the basis of a character in which there is such a close approach in the ranges of variation within the two forms.

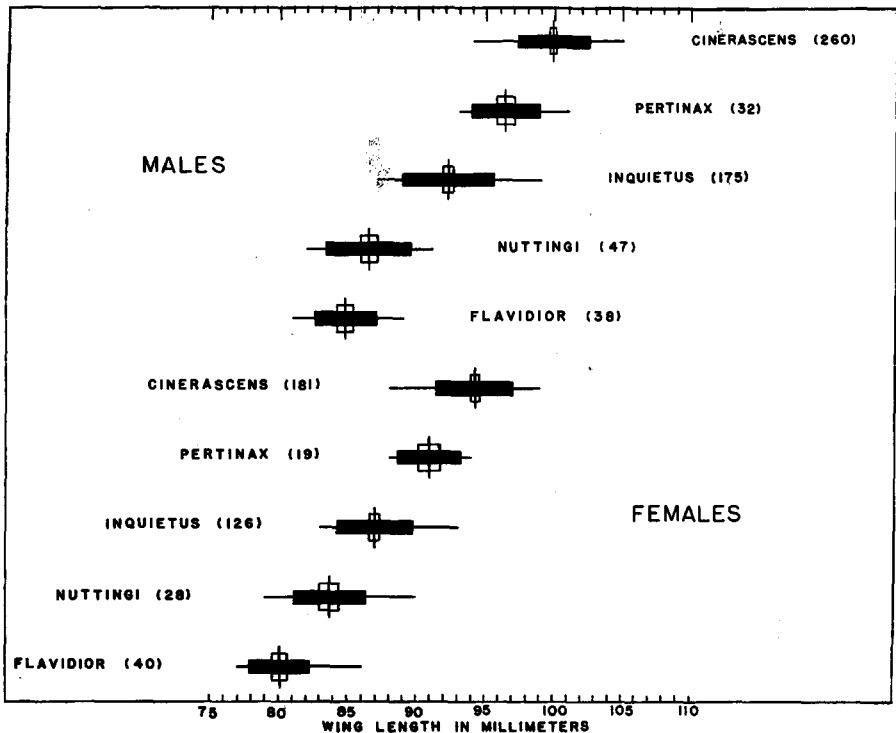


Fig. 3. Population-range diagram of wing length. Numbers in parentheses indicate sample size. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

Plumage coloration.—Seasonal variation due to feather wear makes the use of plumage coloration extremely hazardous except when comparing fresh-plumaged birds. Neither species shows sexual dimorphism with regard to this character, nor is there any pronounced intraspecific variation in coloration other than rectrix pattern.

No significant divergence in plumage coloration could be detected between the two races of *M. cinerascens*. Of the three races of *M. nuttingi*, *inquietus* and *nuttingi* are indistinguishable on the basis of general coloration, whereas *flavidior* has a somewhat richer and brighter yellow abdomen. Phillips (1960) gave racial status (*vanrossemi*) to the populations of *M. nuttingi* breeding in extreme northwestern México, on the basis of their being slightly paler below and grayer above than *inquietus*. I have examined and compared 14 fresh-plumaged specimens from Sonora, including one topotypic

female, with a series of 39 fresh-plumaged specimens from Sinaloa south through Guerrero, and I am unable to recognize any consistent differences of this nature.

The following four color characters were found to be useful in differentiating *M. cinerascens* from all races of *M. nuttingi* and are given in order of decreasing effectiveness. The second character is the most transitory and is of no use in specimens taken after November. The remaining three characters are of limited value in specimens taken from December through February and are useless thereafter.

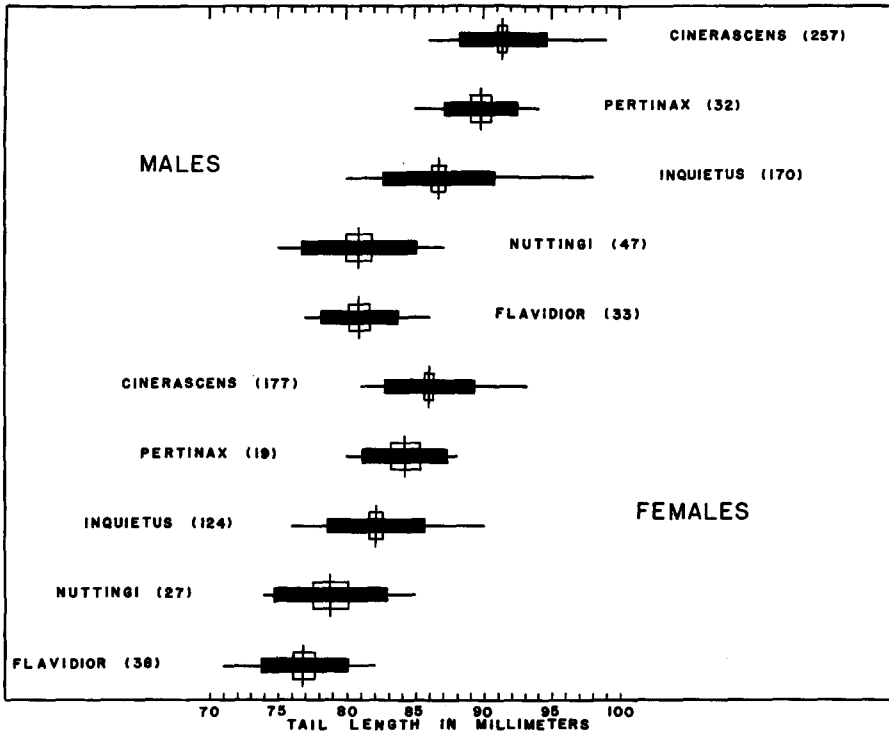


Fig. 4. Population-range diagram of tail length.

(1) *M. cinerascens* is noticeably paler below. This is most evident at the junction of the gray chest and yellow abdomen, at which point *M. cinerascens* has an extremely pale, frequently white area separating the gray from the yellow. In *M. nuttingi*, the yellow borders directly on the gray chest, rendering a more contrasty sequence of colors.

(2) *M. cinerascens* has the fringed leading edges of the secondaries whiter than those of *M. nuttingi*. In *M. cinerascens*, the deep rufous edging characteristic of the primaries is never present on the secondaries (the first secondary may be edged with a very pale rufous) and the remaining secondaries and tertials are edged with white or grayish white. In *M. nuttingi* the deep rufous edging of the primaries is always present on at least the first secondary and then fades to a pale rufous or brownish white on the remaining secondaries—only the tertials are white or grayish white. In using this character one must be careful to recognize those specimens of *M. cinerascens* that are still in the process of postjuvinal molt, for the secondaries of the juvenal plumage of that species are edged with pale rufous and would be confusingly similar to the condition found in adult *M. nuttingi*. It is not uncommon to find specimens collected as late as November and December that still retain one or two of the juvenal secondaries; for example, a specimen taken on December 18 from Guerrero (MVZ 111059)

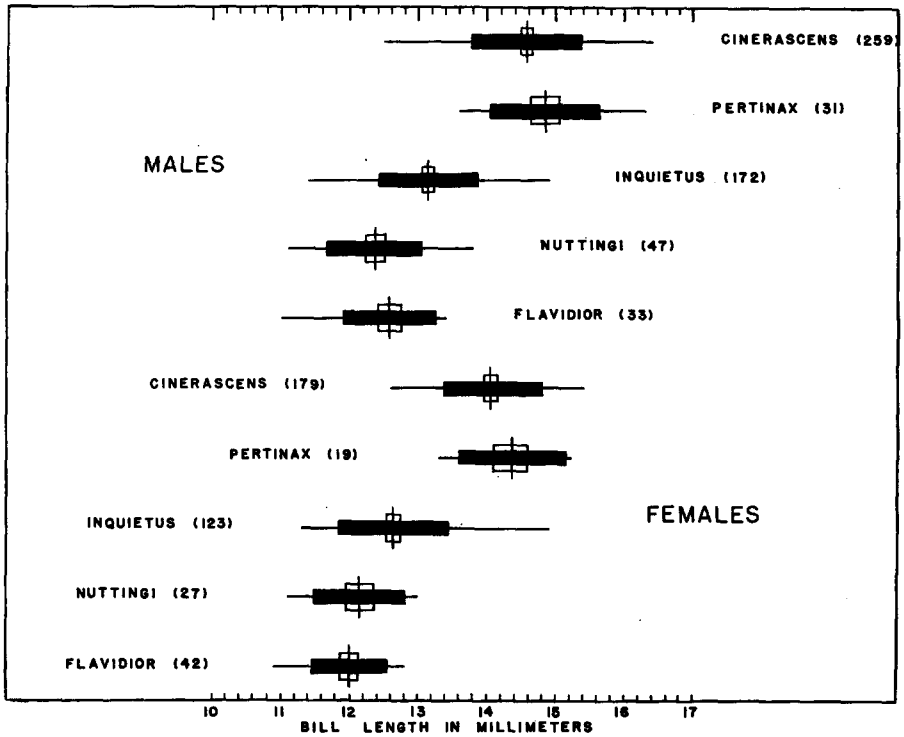


Fig. 5. Population-range diagram of bill length.

has 3 inner juvenal secondaries, and a bird from Guatemala (AMNH 395049) taken on December 5 has 2 inner juvenal secondaries. The character can be used even in these specimens, however, for the last secondaries to be replaced are the inner ones (next to the tertials). Consequently, in molting *M. cinerascens* those secondaries located adjacent to the primaries will have the white edges typical of adults.

(3) The gray of the throat in *M. cinerascens* extends dorsally as a prominent nuchal band, thus creating an area of contrast between the browner crown and back. There is no prominent nuchal band in *M. nuttingi*.

(4) The auriculars, forehead, and lores are conspicuously gray in *M. cinerascens* and brown in *M. nuttingi*.

Here again, as with the use of rectrix pattern, detection of the occasional hybrid on the basis of plumage coloration alone would be difficult if not impossible.

Wing formula.—*Myiarchus cinerascens*, the more northerly distributed and more migratory of the two species, has the more pointed wing. This correlation between migratory habit and wing shape is also reflected in a racial character that helps to differentiate *M. c. cinerascens* from *M. c. pertinax*: *pertinax*, the sedentary form in lower Baja California, has the more rounded wing. The females of both species have a more rounded wing than that of the males. To document these differences, wing formula is expressed in terms of the length of the ninth primary relative to that of the sixth and fifth primaries. Only those specimens were used in which wear had not obliterated the true relationship of these flight feathers. Table 1 summarizes the results.

TABLE 1
WING FORMULAE IN *Myiarchus cinerascens* AND *Myiarchus nuttingi*

Population	Sample size	Percentage distribution for each formula			
		9 = 6 or 9 > 6	9 closer to 6 than to 5	9 closer to 5 than to 6	9 = 5 or 9 < 5
<i>M. c. cinerascens</i>	(429)	(67)	(32)	(1)	(0)
Males	253	79	21	0	0
Females	176	50	47	3	0
<i>M. c. pertinax</i>					
Males	32	34	54	9	3
Females	16	6	69	19	6
<i>M. n. inquietus</i>	(254)	(0)	(6)	(34)	(60)
Males	145	0	9	42	49
Females	109	0	3	22	75
<i>M. n. nuttingi</i>					
Males	33	0	6	36	58
Females	18	0	11	17	72
<i>M. n. flavidior</i>					
Males	21	0	10	42	48
Females	27	0	7	19	74

Note: Vertical lines separate the majority of *M. c. cinerascens* from *M. n. inquietus*.

Wing formula is a useful character for the specific identification of unworn specimens of this complex. It has the distinct advantage over the use of wing length (the most reliable of the mensural characters) of not being as dependent upon sex. When one compares the data in table 1 for *M. c. cinerascens* and *M. n. inquietus* (the two forms involved in sympatry), it is possible to evaluate the effectiveness of wing formula as a diagnostic character. They may be conveniently differentiated by the vertical lines shown in this table. In the samples available, 99 per cent of all *M. c. cinerascens* (regardless of sex) were thus separable from 94 per cent of all *M. n. inquietus* on the basis of wing formula alone. When the sex of a specimen is known, my samples suggest that the use of this character will separate 91 per cent of the males of *M. n. inquietus* from 100 per cent of the males of *M. c. cinerascens*, and 97 per cent of the females of *M. n. inquietus* from 97 per cent of the females of *M. c. cinerascens*.

Wing formula *per se* would be of no value in the detection of the occasional hybrid in this complex. But if, as some workers maintain, extensive hybridization occurs between *M. n. inquietus* and *M. c. cinerascens*, this condition is not reflected in wing formula according to the data in table 1. There was no significant difference in the wing formulae of the samples of the three races of *M. nuttingi*, and presumably all are about equally sedentary in habit.

Size.—The data taken on mensural characters is summarized in tables 2 and 3 and diagrammed in figures 3 to 5. Wing length had the lowest coefficient of variability of these characters. The data in figure 3 suggest the probability that at least 90 per cent of the males of *M. c. cinerascens* are separable from 90 per cent of the males of *M. n. inquietus* on the basis of wing length alone. The wing length of males averages 5 mm. longer than that of females in both species, as is the case in *Myiarchus tyrannulus* in Middle America (Lanyon, 1960a). Consequently, the range of variation in wing length of males of *M. n. inquietus* broadly overlaps that of females of *M. c. cinerascens*. Wing length thus constitutes a useful supplemental character in the specific determination of

individuals of this complex, providing the sex of the specimens has been accurately determined.

Although larger than *M. nuttingi* in all respects, *M. cinerascens* has a disproportionately longer wing than tail. This character, expressed here as "wing minus tail" (table 2), has the advantage of showing little, if any, sexual dimorphism. Its use, however, is of value only as a supplemental character below the population level. This wing-to-tail

TABLE 2
Measurements of *Myiarchus cinerascens* and *Myiarchus nuttingi*

Population	Range	Wing length (mm.)			Range	Tail length (mm.)			Wing minus tail (mm.)	
		Mean, S.E.	S.D.	C.V.		Mean, S.E.	S.D.	C.V.	Range	Mean
<i>M. c. cinerascens</i>										
Males	94-105	99.9±.13(260) ¹	2.04	2.04	86-99	91.4±.16(257) ¹	2.50	2.74	3-13	8.5
Females	88-99	94.2±.16(181)	2.21	2.35	81-93	86.0±.19(177)	2.55	2.97	3-13	8.2
<i>M. c. pertinax</i>										
Males	93-101	96.4±.35(32)	1.98	2.05	85-94	89.8±.37(32)	2.11	2.35	4-10	6.6
Females	88-94	90.9±.41(19)	1.79	1.97	80-88	84.2±.56(19)	2.43	2.88	4-9	6.7
<i>M. n. inquietus</i>										
Males	87-99	92.2±.19(175)	2.59	2.81	80-98	86.7±.24(170)	3.20	3.69	1-10	5.5
Females	83-93	87.0±.19(126)	2.14	2.46	76-90	82.1±.25(124)	2.75	3.35	0-8	4.9
<i>M. n. nuttingi</i>										
Males	82-91	86.5±.35(47)	2.38	2.75	75-87	80.9±.48(47)	3.26	4.03	2-10	5.6
Females	79-90	83.7±.39(28)	2.05	2.45	74-85	78.8±.61(27)	3.17	4.02	2-8	4.9
<i>M. n. flavidior</i>										
Males	81-89	84.8±.30(38)	1.83	2.16	77-86	80.9±.38(33)	2.18	2.69	0-8	3.9
Females	77-86	80.1±.29(40)	1.84	2.30	71-82	76.9±.39(38)	2.42	3.15	0-8	3.2

¹ Sample size.

TABLE 3
Measurements of *Myiarchus cinerascens* and *Myiarchus nuttingi*

Population	Weight (gm.)		Range	Bill length (mm.)		S.D.	C.V.
	Range	Mean		Mean, S.E.			
<i>M. c. cinerascens</i>							
Males	24.0-31.0	27.8(22) ¹	12.5-16.4	14.57±.04(259) ¹	.612	4.20	
Females	24.5-27.8	25.8(10)	12.6-15.4	14.05±.04(179)	.580	4.13	
		(34.0) ²					
<i>M. c. pertinax</i>							
Males			13.6-16.3	14.83±.11(31)	.619	4.17	
Females			13.3-15.2	14.37±.14(19)	.593	4.13	
<i>M. n. inquietus</i>							
Males	23.8-28.2	25.8(13)	11.4-14.9	13.14±.04(172)	.562	4.28	
Females	22.9-29.5	26.0(11)	11.3-14.9	12.64±.06(123)	.623	4.93	
<i>M. n. nuttingi</i>							
Males	20.4-22.5	21.6(3)	11.1-13.8	12.36±.08(47)	.530	4.29	
Females	21.7-25.7	23.9(4)	11.1-13.0	12.15±.10(27)	.505	4.16	
<i>M. n. flavidior</i>							
Males	23.6-24.9	24.1(3)	11.0-13.4	12.58±.09(33)	.524	4.16	
Females	21.5-25.2	23.2(3)	10.9-12.8	12.00±.07(42)	.430	3.58	

¹ Sample size.

² "Laying."

ratio appears to be correlated with migratory habit, as is wing shape, for the sedentary *M. c. pertinax* has a significantly lower ratio than the nominate race. The significance of a possible similar racial difference in the case of *M. n. flavidior* is uncertain. In spite of its overall decrease in body size, *M. c. pertinax* has a slightly longer average bill length than the northern race.

Van Rossem (1945:151) recognized *M. c. mexicanus*, essentially the Mexican populations of the species, on the basis of its "slightly smaller size, proportionately slightly longer tail, and more rounded wing." When I compared a sample (61) of breeding birds from the alleged range of *mexicanus* with a sample (166) representing the northern populations of the species I found a difference of 1.5 mm. in the mean wing length of the two samples of males and a difference of only 0.8 mm. in the mean wing length of the two samples of females. These differences are less than those found between any of

TABLE 4
SUMMARY OF MORPHOLOGICAL CHARACTERS

Character	Value in specific identification	Condition in <i>M. cinerascens</i>	Condition in <i>M. nuttingi</i>	Sexual dimorphism
Color of mouth lining	Excellent, in fresh specimens only	"Fleshy"	Orange	None
Rectrix pattern	Excellent in unworn specimens; good to fair in worn birds	See fig. 1	See fig. 2	Slight, in <i>cinerascens</i>
Plumage coloration	Good in fresh plumage; no value in worn birds	a. Pale to white area between gray chest and yellow abdomen b. Secondaries edged with white or grayish white c. Gray nuchal band d. Auriculars, forehead, lores gray	a. Gray chest borders upon yellow abdomen b. Secondaries edged with rufous or brownish white c. No nuchal band d. Auriculars, forehead, lores brown	None
Wing formula (primaries)	Good in unworn birds; no value in worn birds	9th usually >6th or =6th, rarely closer to 5th than to 6th	9th usually <5th or =5th, rarely closer to 6th than to 5th	Males average more pointed wing
Wing length	Good supplemental character in properly sexed birds	Longer; see fig. 3	Shorter; see fig. 3	Males average 5 mm. longer
Wing minus tail	Fair supplemental character	Larger wing to tail ratio; see table 2	Smaller wing to tail ratio; see table 2	None
Tail length	Fair supplemental character in properly sexed birds	Longer; see fig. 4	Shorter; see fig. 4	Males average 5 mm. longer
Bill length	Fair supplemental character in properly sexed birds	Longer; see fig. 5	Shorter; see fig. 5	Males average 0.5 mm. longer
Weight	Poor (possible specific, racial, and sexual differences masked by daily and seasonal variability)			

the other taxa in the complex. Likewise, the differences between these samples with regard to tail length, wing minus tail, and wing formula were not significant. Although, as van Rossem has correctly stated (1945), the Mexican populations do tend to be slightly smaller and exhibit the morphological adaptation of a more resident form, I believe the degree of differentiation along these lines is below the justifiable criteria for subspecific recognition in this complex.

In *M. nuttingi*, *inquietus* is the best differentiated of the three races on the basis of mensural characters. In Oaxaca and Chiapas, there is a rather sudden decrease in size, giving rise to the two Central American races. Of the latter, the interior *nuttingi* averages very slightly larger than the coastal *flavidior* (not *vice versa*, as reported by van Rossem, 1936).

VARIATION IN VOCALIZATIONS

Myiarchus cinerascens.—Recordings of representative vocalizations were made from breeding populations in southern Arizona (Sonoita, Santa Cruz County; Portal, Cochise County), central Sonora (about 25 miles northeast of Hermosillo), and southeastern Sonora (Rancho Guirocoba, about 30 miles east of Alamos). The two Sonoran populations were breeding sympatrically with *M. nuttingi*. Geographical variation between these populations of *M. cinerascens* was found to be no greater than the individual variation recorded within each population. The sound spectrograms shown in figures 6 and 7 were selected to demonstrate this point.

The vocal repertoire of the species consists of four basic patterns. Various combinations of these basic patterns are rendered, thus enlarging the apparent variety of the

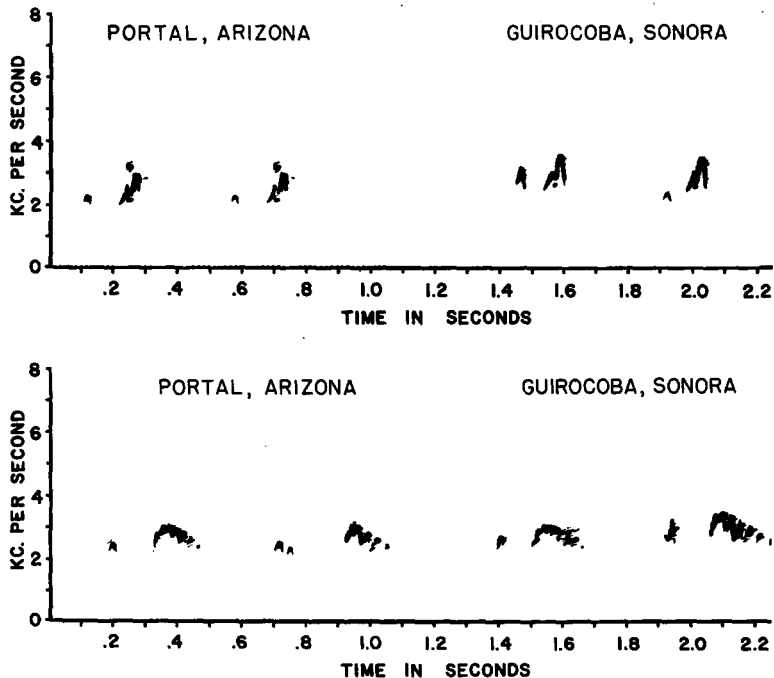


Fig. 6. Sound spectrograms of two diagnostic vocalizations of *Myiarchus cinerascens*. Neither of these calls has a counterpart in the vocal repertoire of *M. nuttingi*. Three basic patterns are represented here and a fourth one is shown in the bottom row of figure 7.

repertoire to at least six recognizably different "calls." The two most diagnostic calls, that is, those having no counterpart in the repertoire of *M. nuttingi*, are shown in figure 6. They are almost certainly the calls phonetically described in Bent (1942) as *ha-whip* and *ha-wheer*, respectively. In my field notes I have referred to the first as *ka-brick*. Each of these disyllabic calls is derived from a combination of two of the four basic vocal patterns, with three of the basic patterns all together represented in the figure. The fourth basic pattern is shown in various combinations in the bottom row of figure 7. The latter is not dissimilar to a basic pattern in the repertoire of *M. nuttingi* (see fig. 11, next to top row).

The basic pattern shown in the middle row of figure 7 is subject to some variability depending upon the level of excitement of the bird during rendition. The selection from

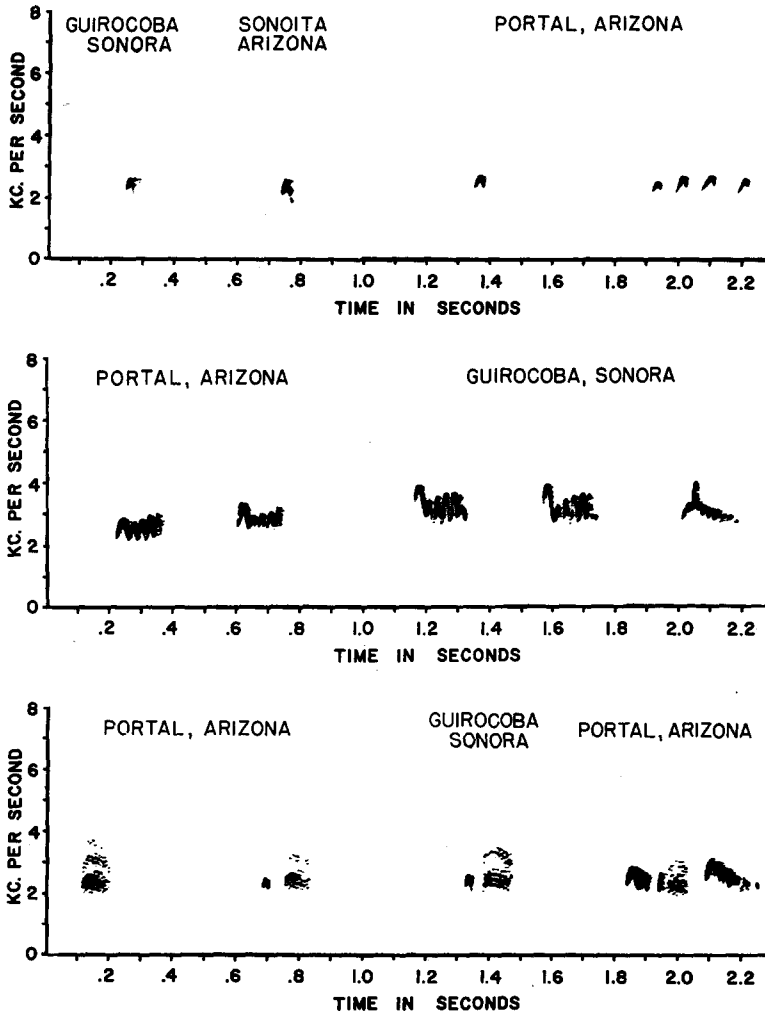


Fig. 7. Sound spectrograms of some vocalizations of *Myiarchus cinerascens*. Two of four basic vocal patterns are shown in the upper two rows. A third basic pattern appears in various combinations in the bottom row. The fourth basic pattern is shown in the top row of figure 6.

Guirocoba at the far right shows the transition to the format assumed by this pattern when used in combination with another basic pattern, as shown in the bottom row of figure 6. In this combination it becomes characteristic of only *M. cinerascens*, although

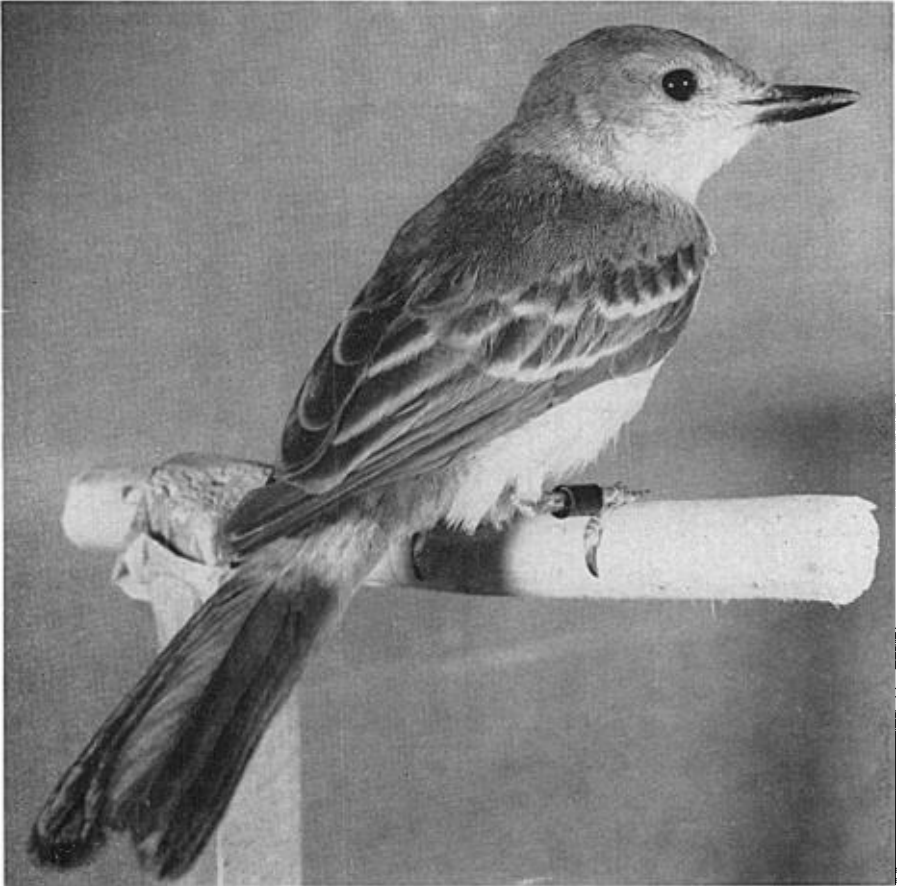


Fig. 8. Hand-reared *Myiarchus cinerascens*, photographed at 22 days of age; this bird had its species-characteristic calls as early as 16 days of age. Photograph by Willis Peterson of Phoenix, Arizona.

when rendered singly it has its counterpart in the basic repertoire of *M. nuttingi* (see fig. 11, top row).

All four of the basic vocal patterns of the species are developed in young *M. cinerascens* by the time of fledging (approximately 16 days of age). Species-characteristic calls were recorded from individuals that had been removed from a nest near Portal, Arizona, as early as six days of age and hand-reared in isolation from adults of their own species (fig. 8). This rapid development of adult vocal patterns in these hole-nesting, sub-oscine birds is suggestive of the development of the "call notes" but not of the "primary song" of those oscine species that have been studied thus far (Lanyon, 1960*b*). It may also have some bearing on the constancy of certain diagnostic calls and their reliability as species indicators throughout extensive geographical areas.

Myiarchus nuttingi.—Recordings of representative vocalizations were made from breeding populations near the following localities: Santa Cruz, Costa Rica; Jinotega, Nicaragua; La Unión and El Carmen, El Salvador; San José and Progreso, Guatemala; in México from El Camaron, Oaxaca; Acatlán, Puebla; Chilpancingo, Guerrero; Uruapan, Michoacán; Guirocoba, Sonora, and 25 miles northeast of Hermosillo, Sonora. The two Sonoran populations were breeding sympatrically with *M. cinerascens*.

The vocal repertoire of the species consists of four basic patterns. Various combinations and modifications of these basic patterns are rendered, thus enlarging the apparent

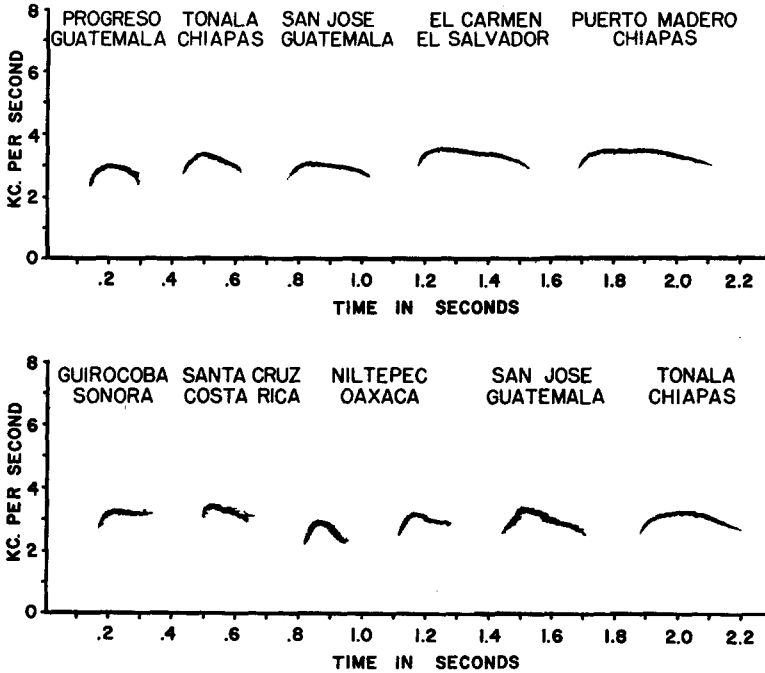


Fig. 9. Sound spectrograms of one of the basic vocal patterns of *Myiarchus nuttingi*. This diagnostic vocalization has no counterpart in the vocal repertoire of *M. cinerascens* and is an excellent character for the field identification of *M. nuttingi*.

variety of the repertoire to at least six recognizably different "calls." The most diagnostic call, that is, the one having no counterpart in the repertoire of *M. cinerascens*, is shown in figure 9. This is a clear, penetrating whistle which I have phonetically described as *peer* in my field notes. Spectrographic analysis demonstrates that it is subject to considerable variation in duration and configuration, much of which is individual in nature as illustrated in the three selections from Tonalá, Chiapas, in figure 10. When the *peer* note lasts for as long as 0.5 second, it is somewhat suggestive of the diagnostic notes of the other two "whistling species" of the genus in North and Middle America, *M. tuberculifer* and *M. yucatanensis*. It is usually at a higher frequency, however, and is more "piercing," less "sad" or plaintive to the ear. This characteristic note was recorded from all populations of *M. nuttingi* that were studied. Geographical variation between these populations was no greater than the individual variation recorded within each of the populations, as indicated by the sound spectrograms in figures 9 and 10.

Occasionally a second basic vocal pattern, somewhat similar to that of *M. cinerascens* shown in the top row of figure 7, is added as an introductory syllable to the *peer* note,

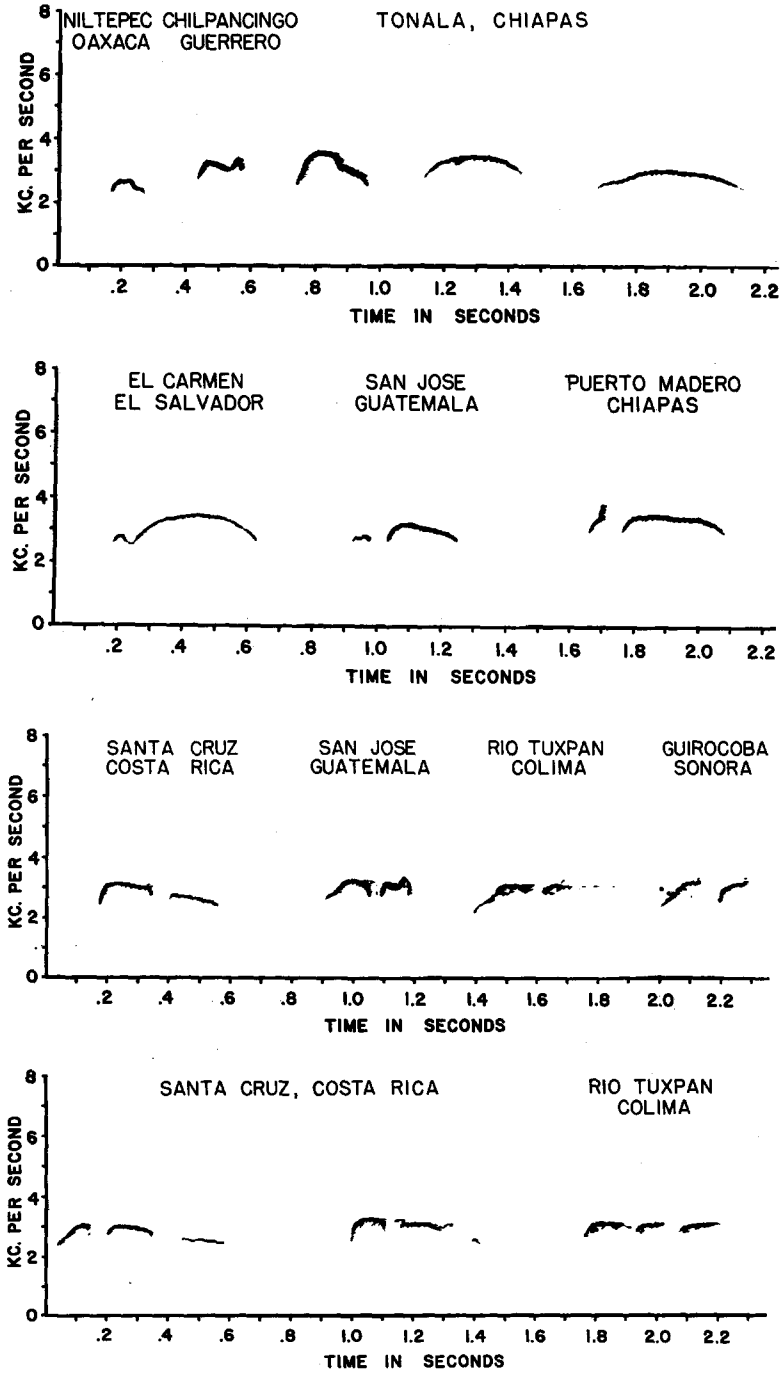


Fig. 10. Sound spectrograms of one of the basic vocal patterns of *Myiarchus nuttingi* (top row) and combinations and modifications of this basic pattern to form a variety of calls (remaining rows).

forming the *pit-peer* combination graphed in the second row of figure 10. In these calls, the "accent" or greater sound energy is consistently on the second syllable. Further variety is achieved by a repetition of the basic *peer* note, either in disyllabic or trisyllabic combinations as shown in the two lower rows of figure 10. In these calls, the "accent" is consistently on the first syllable.

The remaining two basic vocal patterns of the species are graphed in the top two rows of figure 11. Both have their counterparts in the vocal repertoire of *M. cinerascens* (see bottom two rows of fig. 7). The pattern in the top row is characteristically rendered by *M. nuttingi* in a rather nervous and repetitious manner. I have not heard it modified and combined with another basic note as is characteristically done by *M. cinerascens* (fig. 6, bottom row). The rolling call graphed in the bottom two rows of figure 11 is apparently the result of a rapid repetition of the basic pattern shown as the introductory note in the next to the top row of figure 10. Both of the other "whistling" species of *Myiarchus* in North and Middle America, *M. tuberculifer* and *M. yucatanensis*, also have a rolling call similar to this (Lanyon, MS). There is no counterpart in the repertoire of *M. cinerascens*, however.

These basic vocal patterns are apparently well developed by the time of fledging, as already noted for *M. cinerascens*. Near Progreso, Guatemala, I was photographing and recording a pair of *M. nuttingi* as they made repeated trips to their nest. By aiming the parabolic reflector toward the nest cavity, I was able to record the species-characteristic calls of the young birds within. Further examination disclosed that they were fully feathered and ready to fledge.

GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION

The breeding ranges of the forms under consideration here are indicated in a general way in figure 12. Only the localities for those breeding specimens actually examined during this study have been included.

Myiarchus cinerascens.—The Ash-throated Flycatcher is essentially a desert species and its distribution is roughly coincident with that of such well-known vegetation communities as mesquite scrub, cactus and acacia desert, creosote and sagebrush desert, and chaparral. It is also successful in riparian communities of cottonwoods, sycamores, and oaks to which it is apparently attracted by the availability of nesting cavities of suitable size rather than the accessibility of water *per se*.

The southern limits of the breeding range of *M. c. cinerascens* have never been accurately reported in the literature. The confusion arises in part from the fact that some individuals of the species are migrating (or straggling?) northward until the end of May and that many, perhaps all, juveniles and adults begin moving southward prior to the postjuvinal and postnuptial molts (Phillips, 1960). In other instances, southern breeding localities have been reported in the literature on the basis of what I consider to be misidentified specimens of *M. nuttingi inquietus*.

That at least some individuals of *M. c. cinerascens* do lag behind the main northward movement in late spring is well documented: for example, a male taken at Pijijiapan, Chiapas, on May 1, 1939 (Univ. Mich. 102602) and a "fat" female taken at Arriaga, Chiapas, as late as May 30, 1939 (Univ. Mich. 102601); a male taken on Isabel Island, Nayarit, on May 24, 1925 (Cal. Acad. Sci. 27860); a female taken at Guadalajara, Jalisco, on May 27, 1950 (Univ. Kansas 29689); and two silent males that I took at Guirocoba, Sonora, as late as May 19, 1960 (AMNH 766804 and 766805) that had fat deposits and undeveloped testes in marked contrast to the lean, breeding males collected at the same place and on the same date.

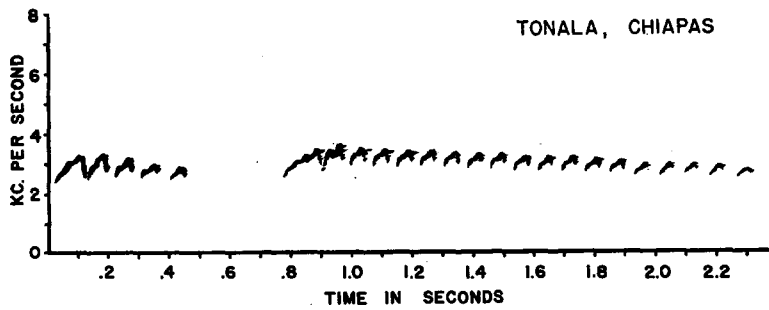
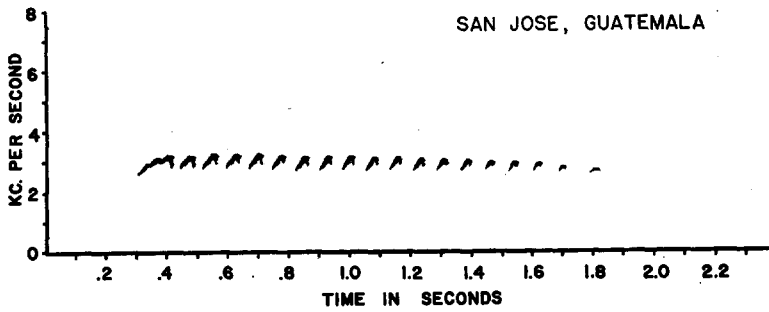
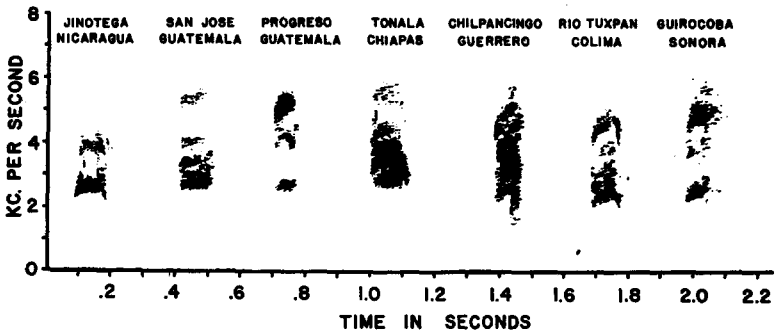
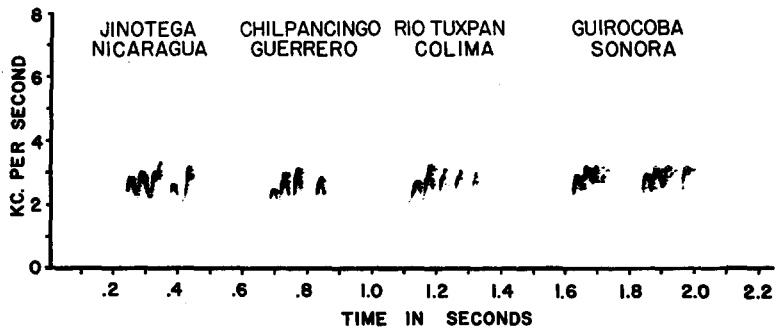


Fig. 11. Sound spectrograms of two of the basic vocal patterns of *Myiarchus nuttingi* (top two rows); a combination of a third basic pattern forms the rolling note graphed in the bottom two rows.

The contention that *M. c. cinerascens* breeds in Guerrero (Griscom, 1934; Pacific Coast Avifauna, 1957) rests mainly on a series taken by W. W. Brown near Chilpancingo, which I have re-examined. There are six *M. c. cinerascens* in this series that were taken during the latter half of May, and none of them has data on fat or gonad condition: May 15, 1943 (MVZ 110996); May 19, 1943 (MVZ 110997); May 23, 1931 (MCZ 163566, 163568, 163569) and May 27, 1941 (MVZ 111001). I worked the vicin-

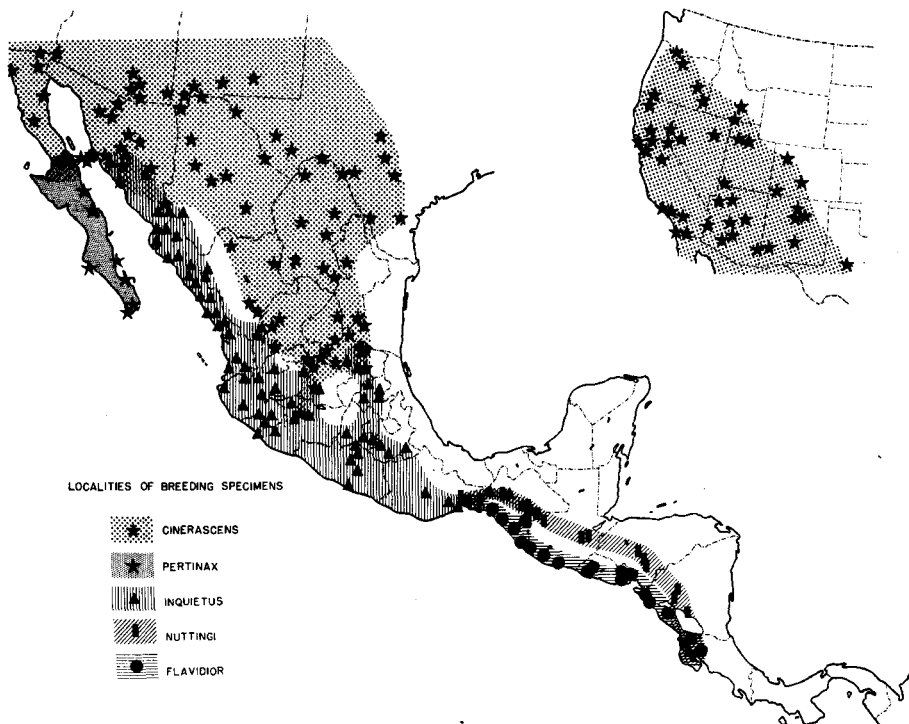


Fig. 12. Breeding ranges of *Myiarchus cinerascens* (*cinerascens* and *pertinax*) and *M. nuttingi* (*inquietus*, *nuttingi*, and *flavidior*) as indicated by localities of breeding specimens examined.

ity of Chilpancingo from May 10 to 14, 1960, and found no *M. c. cinerascens*, although *M. nuttingi inquietus* was a common breeding bird. Furthermore, the absence of a single specimen of *M. c. cinerascens* in the collections of W. W. Brown made near Chilpancingo during June and July (he took at least 21 *M. n. inquietus* from there in those months) is also significant. In view of this evidence, I think the simpler explanation is that the specimens from Chilpancingo listed previously were not breeding birds but rather late migrants or stragglers, a possibility suspected by van Rossem (1936) and considered by Griscom himself (1934:390).

The Mexican Check-list records *M. c. cinerascens* as breeding in Puebla and Hidalgo (Pacific Coast Avifauna, 1957). The evidence for Puebla rests upon two specimens in the Moore collection (57245, 57280) taken at Matamoros on May 9, 1954, and a specimen in the Sutton collection taken near Matamoros on August 14, 1952 (EPE 1545). The two specimens taken on May 9 were correctly identified as *M. c. cinerascens*: one is a female ("ovary small") and the other is a male (testes "full size"). I have examined

the specimen taken on August 14 and find it to be a male *M. nuttingi inquietus* that has nearly completed the molt. The fresh plumage permits a positive identification on the basis of rectrix pattern and plumage coloration. A specimen (Moore coll. 5353) taken by Lamb at Portezuelo, Hidalgo, on April 16, 1942, was recorded as having the testes "full size." The presence in Puebla and Hidalgo of migrating males with enlarged gonads is not unexpected at these dates which are early in view of the evidence of late stragglers already cited.

The evidence that *M. c. cinerascens* breeds at Puerto Vallarta, Jalisco (Pacific Coast Avifauna, 1957) rests on a juvenile dated June 24, and two adult males dated June 10, 1950 (Moore coll. 51149, 51150). The juvenile is too brightly colored on the abdomen to be *M. cinerascens*. The adults are correctly identified but their labels indicate that the testes were " $\frac{1}{4}$ full size"; they are almost certainly late migrants or nonbreeding birds. The Mexican Check-list also states that *M. c. cinerascens* "breeds" in Sinaloa, but no specific evidence is cited. I have seen one specimen taken at Ahome, Sinaloa, on September 2, 1933 (Moore coll. 11171). It is in juvenal plumage, has been correctly identified and is, I believe, an example of the southward movement of juveniles of this species prior to the molt. I would place the same interpretation on the two specimens (AMNH 92872, 92873) taken at Escuinapa, Sinaloa, by Batty on August 6 and 16, 1904 (W. DeW. Miller, 1905) which are in postjuvenal molt. The other specimens of *M. c. cinerascens* in this collection of Batty's, which were considered by Miller as evidence that *M. cinerascens* breeds in southern Sinaloa, are clearly migrants. I have seen no specimen of this species from the Pacific lowlands of Sinaloa or Jalisco that I feel establishes its presence there as a breeding bird.

The two specimens taken by Sartorius (USNM 35126, 35127) near Mirador, Veracruz, are difficult to interpret. Although dated June, 1864, the labels read "pine forest W. of Mirador" (not an expected breeding habitat for *M. cinerascens*) and the plumage is not especially worn. Since the locality is so clearly extralimital to the known breeding range of the species, I prefer to consider these specimens as migrants, with the distinct possibility of a labeling error.

In the Pacific lowlands of México, the southern limit of the breeding range of *M. c. cinerascens* apparently coincides roughly with the juncture of mesquite desert (from the north) and tropical deciduous and thorn forest (from the south) in central and southeastern Sonora. Elsewhere in México the species is essentially confined to the plateau region. Breeding specimens from Tamaulipas have been taken from only two localities, both on the eastern edge of the plateau: for example, Miquihuana, June 7, 1898 (USNM 158785), and Jaumave, July 20, 1922 (AMNH 756584).

The southernmost breeding locality for *M. c. cinerascens*, in the material available at present, appears to be Uruapan, Michoacán. Lamb obtained a female, correctly identified to this species, on June 6, 1939 (Moore coll. 24098), and indicated that it was "nesting" (basis not given) at this locality. I visited the same area on May 14-15, 1960, and found the vegetation in the immediate environs of Uruapan to be dominantly pine. Some 20 miles southward there is a sharp drop in elevation and a narrow ecotone of pine-oak and eventually tropical deciduous forest. *Myiarchus nuttingi inquietus* was a common breeding bird in the latter community. I found no *M. c. cinerascens*. I am inclined to accept Lamb's breeding record but believe it to be extralimital to the main breeding range of the species to the north. There is a good series of specimens of *M. c. cinerascens* taken in June and July in the Moore collection that definitely establishes breeding in the vicinity of Irapuato, Guanajuato, some 90 air miles northeast of Uruapan. The main breeding populations of the plateau extend southward as far as north-

ern Jalisco (Ojuelos and Lagos de Moreno) and northern Guanajuato (Ibarra) as established by good series in the Moore collection, and extreme southern San Luis Potosí (Bledos, Villa de Reyes, and Santa María del Río) as established by good series in the Moore collection and at Louisiana State University.

Breeding specimens from Baja California indicate that *M. c. cinerascens* intergrades with *M. c. pertinax* at about latitude 29° N. *Myiarchus c. pertinax* is a resident race of the desert communities south of that latitude. After the breeding season, *M. c. cinerascens* moves southward and both races have been taken at Cabo San Lucas during the winter.

Myiarchus c. cinerascens is migratory throughout most, if not all, of its range. Wintering specimens have been taken throughout most of southern México and southward through Central America to Nicaragua and Costa Rica. The southernmost wintering specimens of this species that I have examined are a female taken at Juigalpa (Chontales), Nicaragua (T. Howell 1122) and a male taken by A. P. Smith at San Carlos, in the foothills of the Caribbean lowlands of northeastern Costa Rica (Moore coll. 13686). The specimens of "*M. c. cinerascens*" reported by Chapman (1896) as wintering in Yucatán are a male and female of *Myiarchus tyrannulus cooperi* (AMNH 66866, 66867).

Simon (1958) and Williams (1959) have summarized the records of vagrant *M. c. cinerascens* that have been taken in the United States east of the Mississippi River. Some of these specimens have been birds in juvenal plumage, additional evidence supporting movement of the species prior to the molt (as suggested previously).

Myiarchus nuttingi.—This species is essentially a resident throughout its range from central Sonora to northwestern Costa Rica. Its distribution is roughly coincident with the tropical deciduous and thorn woodlands and arid scrub of the Pacific lowlands of México and Central America and of the arid interior valleys and slopes from Chiapas southward through Nicaragua.

The range of *M. n. inquietus* extends from central Sonora to Chiapas. At the northern edge of the range a vagrant individual was taken in southern Arizona on January 8, 1952 (Dickerman and Phillips, 1953) and Phillips (1960) has interpreted Batty's specimens (AMNH 56460, 56461) from Oputo and Bacadehuachi in northeastern Sonora to be vagrants. A breeding pair (the female "ready to lay") was taken by Phillips (UCLA 33950, 33951) just west of Hermosillo on April 28, 1947. I collected both breeding adults and fledged juveniles in May, 1960, 25 miles northeast of Hermosillo, where the tropical deciduous woodland from the south penetrates into the northern mesquite desert along the Río Sonora. These are the northernmost breeding localities for the species in so far as I know.

An apparent extension of the Balsas Basin population in Guerrero and Puebla is an extensive breeding population of *M. n. inquietus* in Hidalgo and southern San Luis Potosí. Sutton and Burleigh (1941) were the first to call attention to this population, reporting on a single specimen taken at Jacala, Hidalgo, on April 12, 1939. Subsequently a good breeding series (specimens examined from the Moore collection, Louisiana State University, and University of Kansas) has been taken that confirms its presence and throws additional light on the size of the area involved (Atotonilco, Portezuelo, and Metztlán, Hidalgo; Santa Catarina, Río Verde, Pinihuan, Canoas, Labor del Río, and other localities in southern San Luis Potosí). The northernmost specimens from this particular population that have come to my attention are a molting bird taken at Ciudad del Maíz, San Luis Potosí, on July 30, 1950 (Univ. Kansas 30036) and a male taken at Pendencia, San Luis Potosí, on November 30, 1946 (LSUMZ 11501). Attention should be called here to a series of seven specimens in the Moore collection taken during the

fall at Santo Domingo, in northwestern San Luis Potosí. I have examined them and there is no question that they are *M. n. inquietus*. There is a possibility, however, that these birds were vagrants and the status of the species at this extralimital locality remains to be determined.

The puzzling specimen (AMNH 81964) taken on May 4, 1888, near Cañon Cabeleros (just north of Ciudad Victoria), Tamaulipas, has been re-examined and is definitely a male *M. n. inquietus*. There is some indication that this may be a case of a "switch" in labels. If correctly labeled, the specimen would have to be regarded as a vagrant at best.

In the Isthmus region of Oaxaca, *M. n. inquietus* intergrades with both *M. n. flavidior* and *M. n. nuttingi*. The intergradation with *M. n. flavidior* is detectable only on the basis of size and is completed in a relatively narrow zone in eastern Oaxaca. All of the specimens that I have examined from Tonalá, Chiapas, and southward through the Pacific lowlands have been referable to *flavidior*. The intergradation of *inquietus* with *M. n. nuttingi*, recognizable by both size and rectrix pattern, is apparently accomplished over a much larger zone. The westernmost specimens of *M. n. nuttingi* examined were taken at Chivela, Oaxaca (MCZ 238286) and Tapanatepec, Oaxaca (MCZ 135543, 135552), and there is a good series of this race from the Chiapa Valley of interior Chiapas (USNM and Univ. Mich.). *Myiarchus n. inquietus* extends into the Chiapa Valley as well and has been taken as far south as Comitán (Univ. Mich. 109237) and San Vicente (USNM 193969, 193972).

Myiarchus n. flavidior breeds throughout the tropical deciduous woodland of the Pacific lowlands of Chiapas southward to northwestern Costa Rica. Its presence in Guanacaste Province, Costa Rica, is confirmed by two breeding specimens taken by A. P. Smith at Miravalles (Univ. Mich. 87583) and Las Canas (AMNH 391058) which are closer to this race than to *M. n. nuttingi*.

The range of *M. n. nuttingi* is comparatively less well known, but populations south of those in the Chiapa Valley are known from the Río Motagua in Guatemala, the Choluteca and Comayagua valleys in Honduras, the arid slopes in the vicinity of Matagalpa, Nicaragua, and the tropical deciduous woodland of Guanacaste Province, Costa Rica. In addition to the contact with *M. n. flavidior* in Oaxaca, then, there is a second zone of intergradation with that race in southern Nicaragua (?) and Guanacaste Province, Costa Rica. The majority of the specimens that I have examined from Guanacaste are referable to *nuttingi* (Ridgway's type locality was Lea Palma, Guanacaste). The material at hand is presently insufficient to determine the extent of contact, if any, between *flavidior* and *nuttingi* elsewhere in Central America other than at the northern and southern points of their ranges in Oaxaca and Costa Rica. Griscom (1932) implied that his series from the Pacific lowlands of Guatemala included two specimens of *M. n. nuttingi*. I have examined this entire series (AMNH, MCZ) and find them all to be referable to the race *M. n. flavidior*, in concurrence with the distribution suggested in figure 12.

Areas of sympatry of breeding populations.—When viewed in terms of the entire breeding ranges of the two species, the areas of sympatry during the breeding season are extremely limited in size. The rather sharp distinctions in the climate and vegetation of the respective breeding ranges suggest that the two forms have evolved differences in their ecology which now operate, in areas of contact, as partial isolating mechanisms.

Information on the overlap of the breeding ranges in central and southeastern Sonora was summarized by van Rossem (1945). The best documented Sonoran areas now known to be common breeding grounds for these species are located as follows: between Kino Bay and Hermosillo, and between Hermosillo and Ures in west-central

Sonora; immediately southeast of Guaymas and in the vicinity of San Javier in south-central Sonora; and at Guirocoba in extreme southeastern Sonora. No doubt additional localities will be found elsewhere among the poorly worked foothills of the Sierra Madre in eastern Sonora, as in the upper valleys of the Río Yaqui and Río Mayo.

Next to these areas in Sonora, the most extensive zone of sympatry during the breeding season is apparently at the southern limit of the range of *M. c. cinerascens*, in southern San Luis Potosí, northwestern Guanajuato, and northern Jalisco. Specific references have already been made to these populations. Elsewhere, as along the western edge of the central plateau, the two species seem to be ecologically isolated from one another, with *M. c. cinerascens* seldom breeding below the pine-oak or oak-juniper zones and *M. nuttingi inquietus* rarely breeding above the tropical deciduous or thorn woodlands of the lowlands. Joe T. Marshall, Jr., came to this conclusion (*in litt.*, 1959) with regard to the areas that he has worked in southern Sonora, suggesting that even in that state the degree of overlap of breeding ground may not be as extensive as implied by the observations at Guirocoba and El Gavilán. It is quite likely that where the preferred habitats merge, as for example along the upper reaches of the major rivers that drain the Sierra Madre and the plateau, the two species may breed side by side to a limited extent. J. Dan Webster (*in litt.*, 1959) has suggested such a possibility in the valley of the Río Juchipila in extreme southern Zacatecas; there he has found *M. c. cinerascens* among the cottonwoods and willows at the northern end of the valley, between Villanueva and Zacatecas City, and *M. n. inquietus* some 75 miles farther south in the tropical deciduous woodland near Moyahua.

THE QUESTION OF HYBRIDIZATION

One basic principle that I adopted early in my monographic study of the genus *Myiarchus* was that the proof for interbreeding between various populations of this complex of sibling forms must necessarily be based upon a knowledge of (1) the interactions of the respective forms on a common breeding ground, in combination with (2) the conventional morphological analysis of a museum series, rather than upon the latter alone. In other words, apparent "intergradation" between two forms in terms of one or more morphological characters does not, *ipso facto*, constitute evidence of interbreeding of those forms. From a strictly pragmatic viewpoint it would certainly be desirable if such were the case, but unfortunately these flycatchers do not lend themselves readily to this sort of treatment.

The principal "evidence" in the literature for hybridization of Ash-throated and Nutting flycatchers consists of the inferences made by Griscom (1934) in his review of W. W. Brown's material from Guerrero, and the material from Sonora that has been worked over and reviewed by van Rossem (1931, 1932, and 1945). I have already presented my case against the concept that the two species are sympatric in Guerrero. Griscom, of course, had no field experience in that region to support his morphological analysis. That his data indicate "intergradation" is not surprising in view of the availability of large samples of both species in Guerrero during the nonbreeding months and in view of the overlap or close proximity of the extremes in their variability as demonstrated in this study. One might reach the same conclusion of "intergradation" by looking at figures 3, 4, and 5, providing other criteria are ignored.

A review of van Rossem's treatment of this complex suggests the increasing significance that that veteran field worker attached to his observations of the two forms on a common breeding ground. Initially, working with a rather meager series and with the emphasis upon an intermediacy of morphological characters, van Rossem subscribed to the view that "in Sonora *cinerascens* intergrades gradually and in perfectly conven-

tional manner with *inquietus*" (1936:115). Subsequent observations made on a common breeding ground, especially at Guirocoba in 1937, gave him cause to question the simplicity of his earlier statement, yet he insisted that "the truly impressive number of intermediates are the result of hybridization on a mass scale" (1945:152).

I decided that it would be informative to re-examine, as a group, those Sonoran specimens which van Rossem had considered to be "hybrids," the "intermediate" specimens from Guerrero that puzzled Griscom, and a number of other specimens labeled "intermediate," "hybrid," or otherwise misidentified by various workers, in order to determine the morphological basis for this alleged hybridization. Many of these specimens fell within the zone of overlap between the two species with respect to wing and tail length and no doubt this was a factor contributing to the confusion. It is altogether clear now that these mensural characters cannot be used as evidence of hybridization. For example, a male specimen from Michoacán (Sutton coll., EPE 215) has a wing length of 99 mm. One worker identified it as *M. cinerascens*, presumably because of the large size and possibly because he was unfamiliar with the outer rectrix pattern, which approached the diffuse condition shown in figure 2C. However, the specimen is quite typically *M. nuttingi inquietus*, with the exception of the extreme size. Fortunately the collector had indicated on the label that the mouth lining was "dull orange." But even in the absence of that revealing information, the 9th primary is shorter than the 5th (I have yet to see a specimen of *M. cinerascens* with the wing this rounded), and the rectrix patterns and general coloration are typically those of *M. n. inquietus*. As it turned out, this was the largest specimen of *M. nuttingi* encountered in my study, but there is no reason to suspect that the explanation is anything other than individual variation.

The most obvious source of confusion over the identity of these particular specimens was an unawareness of the ranges of variability in rectrix pattern of the two species. Those individuals of *M. cinerascens* that key out at II, B, 1a in the rectrix key (only 5 per cent of my sample) are frequently misidentified or regarded as "intermediate" because that particular pattern of the sixth rectrix (fig. 1E) *does* fall within the range of variability exhibited by the pattern of the sixth rectrix of *M. nuttingi inquietus* (fig. 2A-B). But if the inner rectrices of these specimens are examined, as well as their wing formulae, the problem of identification is greatly simplified. A specimen (UCLA 31976) collected by van Rossem at Guirocoba on May 27, 1937, is a case in point. The label identifies it as a "hybrid," probably because it exhibits this particular rectrix pattern on the outer rectrix. It agrees favorably, however, with a specimen (AMNH 766806) that I took at the same locality on May 20, 1960, which had a "fleshy" mouth lining and a vocal repertoire (recorded on tape) typically that of *M. cinerascens* in all respects. Both of these specimens have the 9th primary longer than the 6th, a condition not yet observed in any specimen of *M. nuttingi*. Furthermore, a consideration of the inner rectrices (as well as the outer ones) would identify both specimens as *M. cinerascens* on the basis of rectrix pattern alone. Likewise, many workers have been unaware that the fuscous pattern on the rectrices of *M. n. inquietus* ever approaches the abruptly-expanded condition illustrated in figure 2 D,E,I (only 7 per cent of my sample) and understandably have mistaken it in some cases for the typical pattern of *cinerascens*. Again, consideration of the width of the stripe on the inner rectrices of these specimens gives the essential additional information needed for proper identification.

I spent from May 18 to May 21, 1960, at Guirocoba, Sonora, and May 22-23, 1960, at El Gavilán, 25 miles northeast of Hermosillo, Sonora. I found both species present at each of these localities, with no indication of mixed pairing and no intermediacy in the diagnostic vocal patterns or color of mouth lining. The worn plumage of the speci-

mens taken from these breeding populations precludes a discriminating analysis of intermediacy in the other morphological characters discussed previously. Nevertheless, I had no difficulty in identifying each of the specimens to species on the basis of these other characters, without recourse to the data on vocalizations or mouth lining.

I have no data on the interspecific aspects of territorialism in these areas of sympatry. Four species of *Myiarchus* breed at Guirocoba (*cinerascens*, *nuttingi*, *tyrannulus*, and *tuberculifer*) and individuals of all four can be seen and heard from any one of a number of observation points on the ranch. Marshall (1957) has commented on the lack of noticeable competition between members of this genus, in spite of "frequent occurrence together, even in the same trees," and this has been my experience in all of the areas where I have found three or four of the forms breeding sympatrically. There is some evidence that the breeding cycles of *M. cinerascens* and *M. nuttingi* are not synchronized in areas of sympatry, at least initially in the breeding season. In late May I found recently fledged young of *M. nuttingi* at both Sonoran localities, whereas the pairs of *M. cinerascens* had no fledged young but rather appeared to be still in the process of establishing territory or possibly incubating.

As I have pointed out in the discussion of morphological variation, the identification of a hybrid specimen on the basis of any one of the various characters (rectrix pattern, plumage coloration, wing formula, or body size) would be difficult if not impossible. The overlap or close proximity of the extremes of variability precludes this test. The effect of hybridization, if it occurs, upon the color of mouth lining and the characteristic vocal patterns is unknown. I can only state that to date I have not seen a specimen of this complex that could not be logically identified to species on the basis of a consideration of all the available characters. Nor have I found any correlation of intermediacy of characters or other evidence of hybridization in those specimens taken from areas of sympatry. The non-overlap in color of mouth lining and certain diagnostic vocal patterns, and the virtual non-overlap in rectrix pattern, coloration of fresh plumage, and wing formula militate against the view that there is "mass hybridization" between these forms.

SUMMARY

A combined field and museum approach has been used to determine the specific limits of various morphological and vocal characters for discriminating between Ash-throated and Nutting flycatchers. Certain diagnostic vocal patterns, color of mouth lining, rectrix pattern, and wing formula were found to be the most reliable criteria. Two species are recognized in this complex: *Myiarchus cinerascens*, which breeds throughout the western United States and the Mexican plateau (*M. c. cinerascens*), and Baja California (*M. c. pertinax*); and *Myiarchus nuttingi*, represented in western México by a single race (*M. n. inquietus*), and in Central America by two races (*M. n. nuttingi*, and *M. n. flavidior*).

The Ash-throated Flycatcher is largely a migratory species of the temperate desert and scrub communities. The southern limits of its breeding range are established for the first time, and erroneous breeding records are corrected. The Nutting Flycatcher is a resident species of the tropical deciduous and thorn woodlands. The zone of sympatry of these sibling species during the breeding season, extremely limited in area, is best documented for Sonora, southern San Luis Potosí, and northern Guanajuato and Jalisco.

The evidence for the alleged "mass hybridization" of these species is re-examined and discounted. Overlap or close proximity of the extremes of variability and an unawareness of the true specific limits of variability have caused much of the confusion in studies of this complex. Field work on two common breeding grounds in Sonora

revealed no indication of mixed pairing and no intergradation in the more diagnostic specific criteria.

LITERATURE CITED

- Allen, J. A.
1892. On a collection of birds from Chapada, Matto Grosso, Brazil, made by Mr. H. H. Smith. Part II.—Tyrannidae. *Bull. Amer. Mus. Nat. Hist.*, 4:331-350.
- American Ornithologists' Union
1893. Fifth supplement to the American Ornithologists' Union Check-list of North American Birds. *Auk*, 10:59-63.
1957. Check-list of North American birds. Fifth ed. (published by the Union, Baltimore, Md.).
- Bailey, F. M.
1902. Handbook of birds of the western United States (Houghton, Mifflin Co., Boston and New York).
- Baird, S. F.
1859. Notes on a collection of birds made by Mr. John Xantus, at Cape St. Lucas, Lower California, and now in the Museum of the Smithsonian Institution. *Proc. Acad. Nat. Sci. Phila.*, 11:299-306.
- Bangs, O., and Peters, J. L.
1928. A collection of birds from Oaxaca. *Bull. Mus. Comp. Zool.*, 68:385-404.
- Bendire, C. E.
1895. Life histories of North American birds. Vol. II. U.S. Nat. Mus. Special Bull. No. 3:ix+1-518.
- Bent, A. C.
1942. Life histories of North American flycatchers, larks, swallows, and their allies. U. S. Nat. Mus. Bull. 179.
- Blake, E. R.
1953. Birds of Mexico (Univ. Chicago Press).
- Carriker, M. A., Jr., and de Schauensee, R. M.
1935. An annotated list of two collections of Guatemalan birds in the Academy of Natural Sciences of Philadelphia. *Proc. Acad. Nat. Sci. Phila.*, 87:411-455.
- Chapman, F. M.
1896. Notes on birds observed in Yucatan. *Bull. Amer. Mus. Nat. Hist.*, 8:271-290.
- Coues, E.
1903. Key to North American birds. Fifth edition. Vol. I (Dana Estes and Co., Boston).
- Dickerman, R. W., and Phillips, A. R.
1953. First United States record of *Myiarchus nuttingi*. *Condor*, 55:101-102.
- Felten, H., and Steinbacher, J.
1955. Zur Vogelfauna von El Salvador. *Senckenbergiana Biol.*, 36:9-20.
- Griscom, L.
1932. The distribution of bird-life in Guatemala. *Bull. Amer. Mus. Nat. Hist.*, 64:ix+1-439.
1934. The ornithology of Guerrero, Mexico. *Bull. Mus. Comp. Zool.*, 75:367-422.
- Hellmayr, C. E.
1927. Catalogue of birds of the Americas. *Field Mus. Nat. Hist., Zool. Ser.*, 13, pt. 5.
- Kaup, D.
1851. Descriptions of some new birds in the museum of the Earl of Derby. *Proc. Zool. Soc. London*, 1851:39-53.
- Lanyon, W. E.
1960a. The Middle American populations of the crested flycatcher *Myiarchus tyrannulus*. *Condor*, 62:341-350.
1960b. The ontogeny of vocalizations in birds. *In Animal Sounds and Communication*, ed. W. E. Lanyon and W. N. Tavolga. Amer. Inst. Biol. Sci. Publ. No. 7:321-347.
- Lawrence, G. N.
1851. Descriptions of new species of birds of the genera *Toxostoma* Wagler, *Tyrannula* Swainson, and *Plectrophanes* Meyer. *Ann. Lyc. Nat. Hist. N.Y.*, 5:121-123.

- Marshall, J. T., Jr.
1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. *Pac. Coast Avif.* No. 32:1-125.
- Miller, W. DeW.
1905. List of birds collected in southern Sinaloa, Mexico, by F. H. Batty, during 1903-1904. *Bull. Amer. Mus. Nat. Hist.*, 21:339-369.
- Nelson, E. W.
1904. A revision of the North American mainland species of *Myiarchus*. *Proc. Biol. Soc. Wash.*, 17:21-50.
- Nutting, C. C.
1882. On a collection of birds from the Hacienda "La Palma," Gulf of Nicoya, Costa Rica. *Proc. U. S. Nat. Mus.*, 5:382-409.
- Pacific Coast Avifauna
1957. Distributional check-list of the birds of Mexico. Part 2. *Pac. Coast Avif.* No. 33:1-436.
- Phillips, A. R.
1960. La acrecencia de errores acerca de la ornitología de Mexico, con notas sobre *Myiarchus*. *Anales del Inst. de Biol.*, 30:355-357.
- Rand, A. L., and Traylor, M. A.
1954. *Manual de las aves de El Salvador* (Univ. El Salvador).
- Ridgway, R.
1896. A manual of North American birds. Second ed. (Philadelphia).
1907. The birds of North and Middle America. *Bull. U. S. Nat. Mus.* No. 50, pt. IV.
1912. Color standards and nomenclature (published by the author, Washington, D.C.).
- Salvin, O., and Godman, F. D.
1892. *Biología Centrali-Americana. Aves. Vol. II* (London).
- Sassi, M.
1939. Die Vögel der österreichischen Costa-Rica-Expedition (Sweiter Teil). *Temminckia*, 4:135-222.
- Simon, S. W.
1958. An ash-throated flycatcher (*Myiarchus cinerascens cinerascens*) in Maryland. *Auk*, 75:469.
- Sutton, G. M.
1951. Mexican birds: first impressions based upon an ornithological expedition to Tamaulipas, Nuevo León, and Coahuila (Univ. Oklahoma Press, Norman).
- Sutton, G. M., and Burleigh, T. D.
1941. Birds recorded in the state of Hidalgo, Mexico, by the Semple Expedition of 1939. *Ann. Carnegie Mus.*, 28:169-186.
- Swarth, H. S.
1904. Birds of the Huachuca Mountains, Arizona. *Pac. Coast Avif.* No. 4:1-70.
- van Rossem, A. J.
1931. Report on a collection of land birds from Sonora, Mexico. *Trans. San Diego Soc. Nat. Hist.*, 6:237-304.
1932. The avifauna of Tiburon Island, Sonora, Mexico, with descriptions of four new races. *Trans. San Diego Soc. Nat. Hist.*, 7:119-150.
1936. Description of a race of *Myiarchus cinerascens* from El Salvador. *Trans. San Diego Soc. Nat. Hist.*, 8:115-118.
1945. A distributional survey of the birds of Sonora, Mexico. *Occas. Papers Mus. Zool., Louisiana State Univ.*, No. 21:1-379.
- Wetmore, A.
1944. A collection of birds from northern Guanacaste, Costa Rica. *Proc. U. S. Nat. Mus.*, 95:25-80.
- Williams, L. E., Jr.
1959. Ash-throated flycatcher in Alabama. *Auk*, 76:528.

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