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TWO SIBLING SPECIES OF *TYRANNUS* (TYRANNIDAE)

MELVIN A. TRAYLOR, JR.
Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605 USA

ABSTRACT.—*Tyrannus couchii,* usually considered a subspecies of *T. melancholicus* ranging from southern Texas to central Veracruz, is a distinct species, with a range from southern Texas to the Yucatan Peninsula. It overlaps *melancholicus* south of southern Tamaulipas and San Luis Potosi. Where the two species are equally common, there is no sign of intergradation, but in the Isthmus of Tehuantepec, where *couchii* is rare, there is some hybridization. The characters that permit the separation of adult specimens are the form of the wing tip and the relative length of the bill. There are also average differences in color and size, and some of these vary geographically within the area of sympatry. *Received 18 September 1978, accepted 11 December 1978.*

IN the most recent checklist of the tyrant flycatchers (Hellmayr 1927), the Tropical Kingbird, *Tyrannus melancholicus,* was considered to range from southern Arizona and southern Texas south along the lowlands of both coasts of Mexico and through tropical Central and South America to northern Argentina. Three subspecies were recognized north of Panama, *occidentalis* in the western lowlands of Mexico south to Guerrero, *couchii* in southern Texas and eastern Mexico south to Veracruz and Puebla, and *chloronotus* in southern Mexico and Central America east to the northern littoral of Colombia. The same ranges were given in Miller et al. (1957: 72) in their Mexican checklist. Smith (1966: 103), however, stated that the vocalizations of *couchii* were so distinct from those of *melancholicus* that the two were almost certainly different species. He was, however, confused by the fact that in southern Veracruz birds were found that seemed to utter vocalizations of intermediate form. Mayr and Short (1970: 58) made *couchii* and *melancholicus* members of a superspecies, although admitting that they did not know what happened in southern Mexico. Finally, Davis (1972: 130) recognized three species, *couchii* from southern Texas to the Yucatan Peninsula, *occidentalis* from Sonora to Guerrero, and *melancholicus* from Veracruz and Oaxaca south through Central America. Davis' species were defined solely on differences in vocalizations. The present study, based entirely on museum specimens, shows that *couchii* is a separate species with a range as defined by Davis, but that there are no morphological distinctions between *melancholicus* and *occidentalis,* even on a subspecific level.

SEPARATION OF TWO TAXA

The recognition of sibling species on purely morphological grounds requires the discovery of one or more characters by which the available specimens may be divided

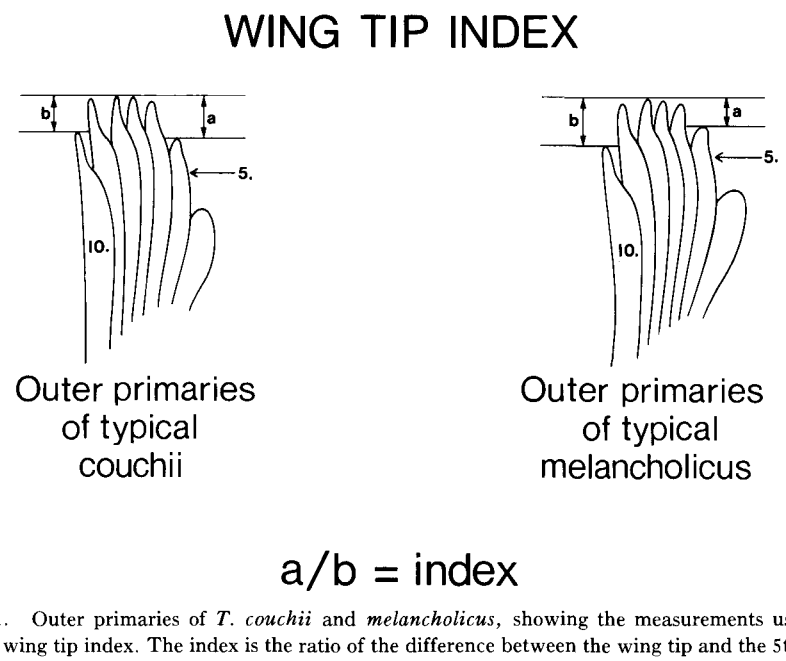

Fig. 1. Outer primaries of *T. couchii* and *melancholicus*, showing the measurements used in calculating wing tip index. The index is the ratio of the difference between the wing tip and the 5th primary (a), divided by the difference between wing tip and the 10th primary (b).

into two discrete groups and then the demonstration that various other characters correlate with them.

When all adult specimens of Tropical Kingbird from southern Texas and eastern Mexico south to Yucatan are examined, there are two characters that, taken together, permit the segregation of virtually every specimen into one of two discrete groups. These characters are the ratio bill length/wing length (bill measured from anterior edge of nostril and wing measured flat) and the wing tip index. The latter is also a ratio, that between the distance from the tip of the wing to the 5th primary and the distance from the tip to the 10th (outermost) primary (Fig. 1). Use of ratios avoids the difficulties found in absolute measurements, permitting the direct comparisons of birds of different sexes or geographic origins. The bill length as a character was suggested by Allen Phillips (pers. comm.). The wing tip index is a modification of one used by Meise (1949: 69); Meise multiplied the ratio defined above by the distance from the 10th to the 9th primary, so that he still had a dimensional parameter with the drawbacks of an absolute measurement. With absolute measurements, sexual dimorphism and geographical variation obscure the differences between taxa.

When the bill/wing ratio and the wing tip index are plotted on scatter diagrams for all adult specimens, the resulting points fall into two discrete groups. Those birds with low wing tip indices have proportionately long bills, and those with high wing tip indices have proportionately short bills. Figure 2 includes scatter diagrams for different geographic areas. In the top panel, including all specimens from Texas, Nuevo Leon, and northern and central Tamaulipas, the points fall into a single continuum, and it is evident that only the short-billed group is found here. The single female with a bill/wing ratio of 17.2% appears to belong to the long-billed

group, but it is aberrant in either group. Its bill, 20.6 mm, is the longest of any female measured and far outside the range of the short-billed group. Its wing length, 120 mm, is too long for the long-billed group, but about average for the short-billed group. I consider this bird an aberrant specimen of the latter.

In central eastern Mexico, from southern Tamaulipas and San Luis Potosi south to central Veracruz and Puebla (Fig. 2, *lower*), and on the Yucatan Peninsula in Campeche, Yucatan, and northern Quintana Roo (Fig. 3, *top panel*), the two groups occur in roughly equal numbers, without any overlap in characters. South of Mexico, in Central America, only the long-billed group occurs.

When the specimens from eastern Mexico are divided into two groups on the basis of relative bill length and wing tip index, several other characters also associate with these groups. Birds in the short-billed group a) are more yellowish, less grayish-green above; b) have paler brown wings and tail; c) have a shallower tail fork; and d) are larger than the sympatric populations of the long-billed group. On these morphological grounds, I believe there is no question that we have two sympatric species, a short-billed form ranging from southern Texas to the Yucatan Peninsula, and a long-billed form ranging from southern Tamaulipas south through Central America.

Nomenclature

There are three names in the literature based on specimens from eastern Mexico. The earliest is *Tyrannus couchii* Baird (1858), based on specimens from Nuevo Leon. This name must be given to the short-billed form, as this is the only one found in Nuevo Leon; fortunately this accords with present usage, because *couchii* has regularly been used as a subspecific epithet for the populations of Texas and northern Mexico. The next oldest name is *Laphyctes satrapa* Cabanis and Heine (1859), type locality Mexico. For many years this name was commonly used for the subspecies of the South American *melancholicus* in Mexico and Central America, but in 1907 Berlepsch (p. 474) suggested that it might be a synonym of *couchii,* and in 1921 Bangs and Penard (p. 379) formally reduced it to synonymy. Hellmayr followed the latter authors and used *Tyrannus chloronotus* Berlepsch (1907), type locality Temax, Yucatan, as the name for the Mexican and Central American populations of *melancholicus*. This was an unfortunate decision, as the type of *satrapa* proves to belong to *melancholicus,* not *couchii*. The type specimen is from Jalapa, Veracruz (Meise, *in litt.*), an area in which both species occur. Meise found the wing length of the type to be 112 mm, 5 mm smaller than any of 33 female *couchii,* but near the average of 27 female *melancholicus*. Also, the relative lengths of the 5th and 10th primaries fit the pattern typical of *melancholicus,* now called *chloronotus*. The latter name has itself been misapplied, for an examination of the original description shows that it was based on a specimen of *couchii*. Berlepsch compared *chloronotus* to "*couchii*" and gave as its characters more yellowish olive-green, less grayish-green upperparts, more shallow tail fork, and shorter and broader bill. Because these are all characters that separate *couchii* from *melancholicus, chloronotus* is a synonym of *couchii*. Both species occur in Temax.

Hybridization

There is one region in which there does seem to be hybridization, in southern Veracruz and the Atlantic slope of adjacent Oaxaca. When points representing all

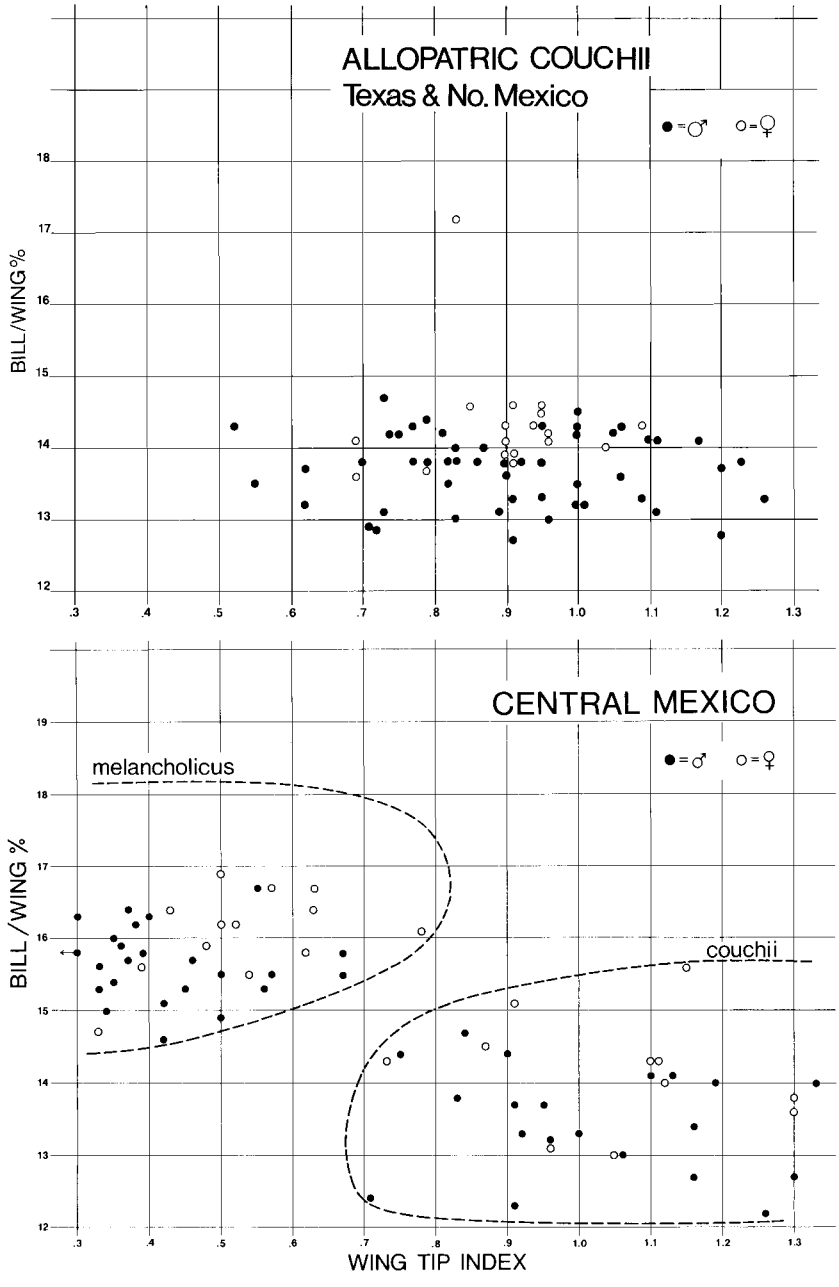

Fig. 2. The ratio bill length/wing length (in percent) plotted as a function of wing tip index for all adult specimens from several geographic areas. **Upper**, specimens of *couchii* from areas of northern Mexico and Texas where *melancholicus* does not occur. **Lower**, specimens of *melancholicus* and *couchii* from central Mexico, from southern Tamaulipas and San Luis Potosi to central Veracruz and Puebla. The dashed lines show the range of variation in each taxon for the combined populations of central Mexico and the Yucatan Peninsula.

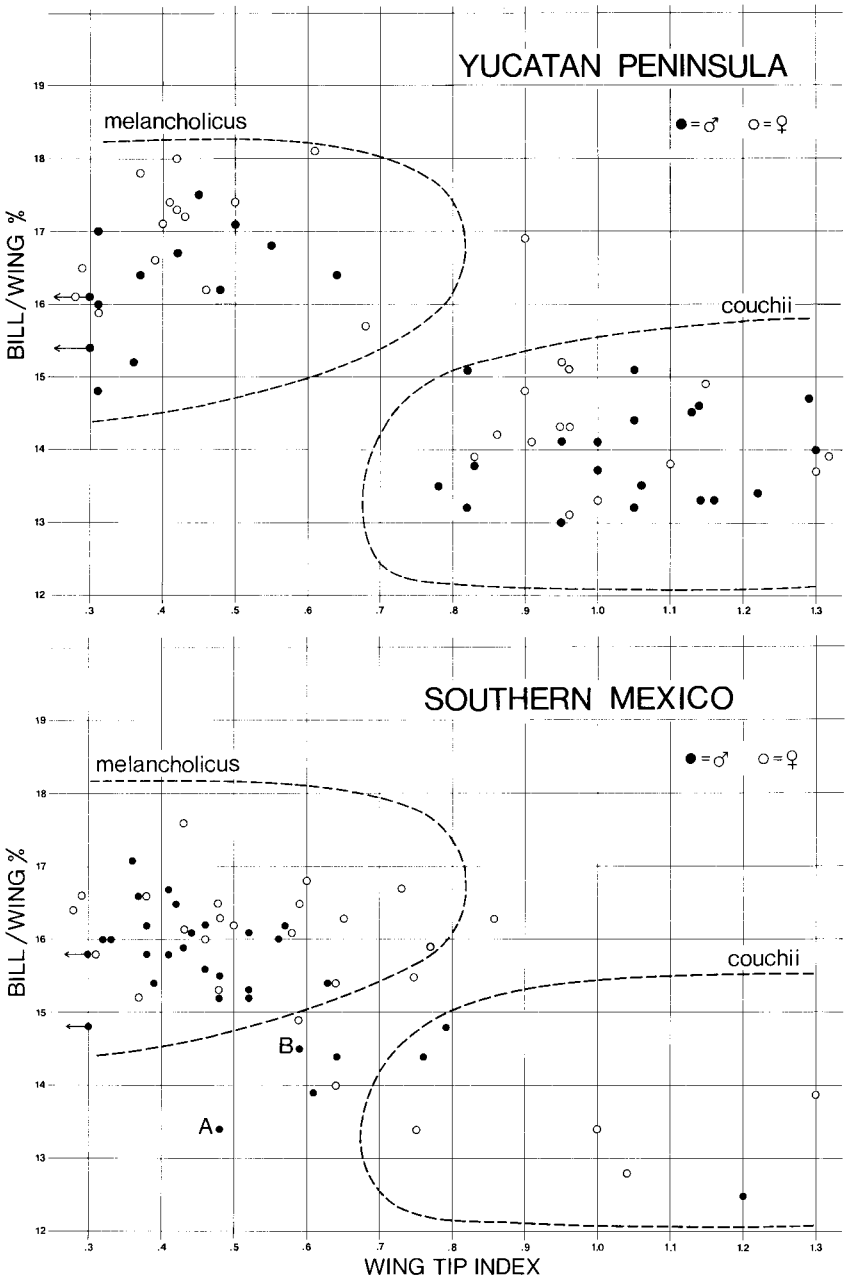

Fig. 3. The ratio bill length/wing length (in percent) plotted as a function of wing tip index. **Upper**, all adult specimens from the Yucatan Peninsula. **Lower**, all adult specimens from southern Veracruz and adjacent Oaxaca. The dashed lines as in Fig. 2. The specimens falling between the two taxa are presumed hybrids, particularly males A and B, which also have mixed absolute measurements.

adult specimens are plotted (Fig. 3, *lower panel*), there is a significant proportion that falls between the limits of the taxa as determined by the populations from central Mexico and the Yucatan Peninsula. This does not appear to be a case in which the characters of one or both taxa have shifted so that there is overlap between them. The normal range of variation is represented by specimens of both *melancholicus* and *couchii*. The specimens that appear as intergrades when plotted by wing tip index and bill/wing ratio frequently have intermediate absolute measurements as well. The two males, A and B, are the best examples of this, having wing lengths well within the range of *melancholicus* but bill lengths characteristic of *couchii*. The one aspect in which Veracruz differs from central Mexico and the Yucatan Peninsula is that typical *couchii* are much less common there than typical *melancholicus*. The significance of these hybrids will be discussed in more detail below.

VOCALIZATION

With morphological evidence showing the presence of two species of kingbird in eastern Mexico, an attempt can be made to reinterpret Smith's (1966: 103) data on the different vocalizations of *couchii* and *melancholicus*. He recorded the vocalizations of *couchii* in southern Texas, and these were completely different from the calls of *melancholicus* that he had recorded in Panama and heard in Sonora, western Mexico. He heard the same *couchii* calls in Antiguo Morelos, southern Tamaulipas, and on a tape made by Irby Davis just north of Valles, San Luis Potosi. Even though Smith took no specimens, he must be correct in identifying these calls with *couchii,* since that is the only form in Texas. Similarly, the vocalizations from Panama and Sonora are properly assigned to *melancholicus,* as that is the only form occurring in those localities, and based on a tape from Irby Davis, the same *melancholicus* call is used in Veracruz.

However, when Smith observed the kingbirds about 48 km southwest of Veracruz, he found a peculiar mixture of calls. Although this was the region from which Davis had recorded pure *melancholicus,* Smith heard both *couchii* and *melancholicus* calls, although he could not be sure whether they came from the same individual, but one bird definitely used intermediate type vocalizations. Since he was in an area near where the intermediate specimens were found, it is probable that this was a hybrid. However, until intensive fieldwork is done in southern Veracruz, and voucher specimens of known song type collected, the relationship of *couchii* and *melancholicus* in this region must remain speculative.

IMMATURES

The above discussions are based on the study of adult specimens, which can be allocated to species. The form of the wing tip in immature birds appears to be much more variable, and when immatures from the area of sympatry are plotted using wing tip index and bill/wing ratio, the points hardly segregate at all (Fig. 4). The birds plotted here are in their first winter and can be easily separated from fully adult specimens by their unnotched primaries. In *couchii* and in the populations of *melancholicus* from eastern Mexico, post-juvenal molt is incomplete, and the juvenal primaries are retained through the first year. Although some of the immatures from the area of sympatry can be identified on the basis of absolute measurements,

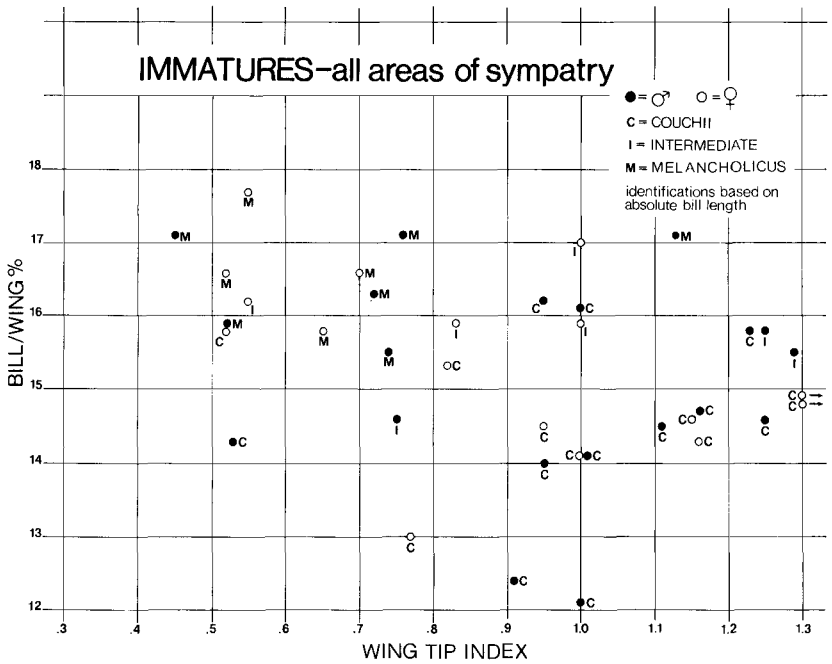

Fig. 4. The ratio bill length/wing length (in percent) plotted as a function of wing tip index for all immatures from the area of sympatry between *melancholicus* and *couchii*. The points do not segregate into two groups as do those of the adults, and identifications were made on absolute bill lengths; C = *couchii*; I = intermediate, M = *melancholicus*.

particularly bill length, identification is impossible when the latter falls in the region of overlap.

Geographic Variation

The geographical range of *couchii* (Fig. 5) has been determined from specimens examined for this report, except for Texas where it is taken from Oberholser (1974: 535). *Tyrannus couchii* is found in southern Texas and throughout the eastern lowlands of Mexico, occurring up to about 610 m in Puebla and Veracruz, and at the base of the Yucatan Peninsula in British Honduras (now Belize) and northern Guatemala south to Alta Vera Paz. Of particular interest is that *couchii* at no point crosses over to the Pacific drainage, even in the Isthmus of Tehuantepec where the lowest pass in the divide is only 230 m. Possibly the presence of the congeneric *T. crassirostris* on the western slopes inhibits its spread. The northern limit of the range of *melancholicus* in eastern Mexico proves to be extreme southern Tamaulipas at Tampico and along the Tamesi River, and southeastern San Luis Potosi. Its range south through Veracruz and northern Puebla is almost identical with that of *couchii,* but in eastern Oaxaca it crosses to the Pacific slope where it is found north to Arizona and south through Central America. Although both species are found throughout the Yucatan Peninsula, only *melancholicus* is found on Cozumel Island and other coastal islands. There is no evidence that either species is regularly migratory. The 62 adult specimens of *couchii* from Texas are distributed evenly throughout the

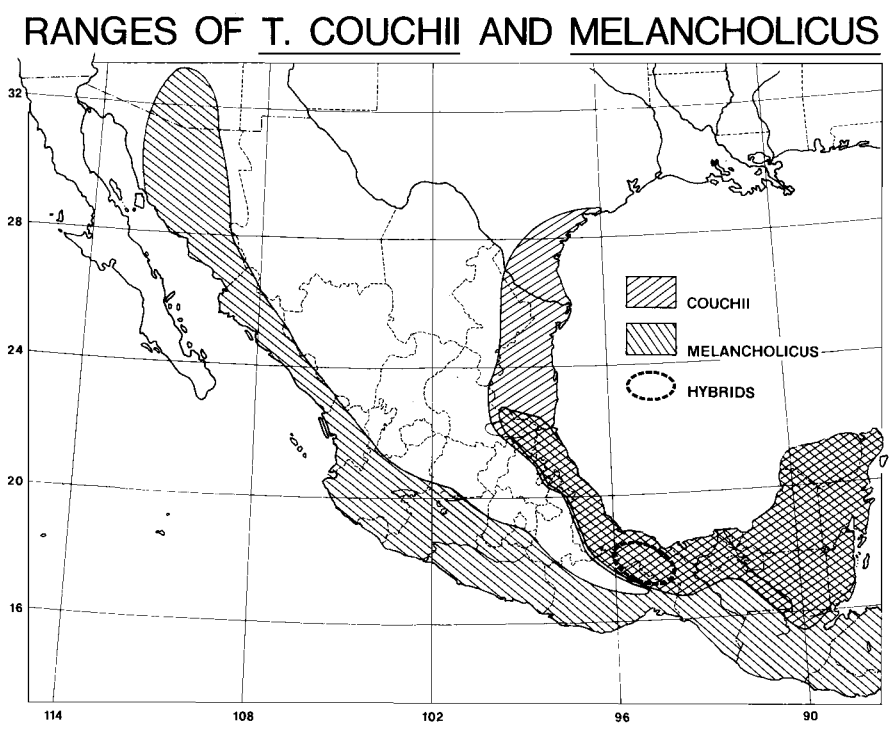

Fig. 5. The distribution of *melancholicus* and *couchii* in northern Central America, Mexico and the United States. Hybrids occur in the area surrounded by the heavy dashed line.

year (Fig. 6). The early records of migrant *couchii* from southern Mexico and northern Guatemala were based on extra large specimens of the resident *couchii* populations. Birds of the year, however, must wander more than the adults, because I have examined an immature *couchii* from Cameron Parish, Louisiana, and two immature *melancholicus* from Marin and Alameda counties, California.

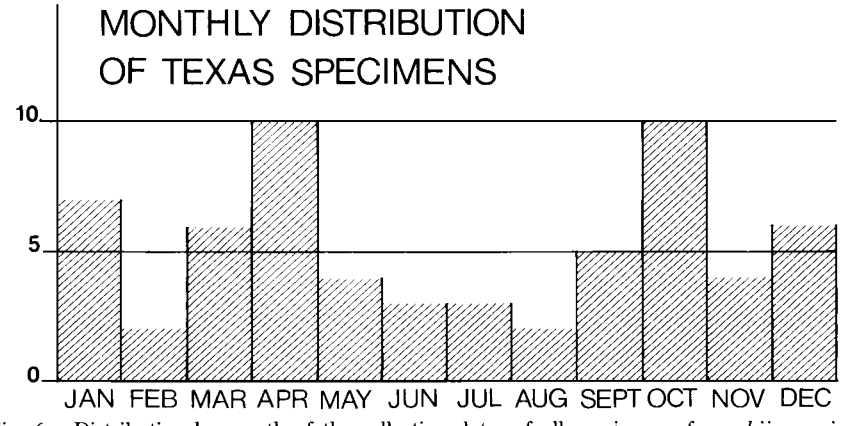

Fig. 6. Distribution by month of the collecting dates of all specimens of *couchii* examined from Texas. There is no suggestion of regular migration.

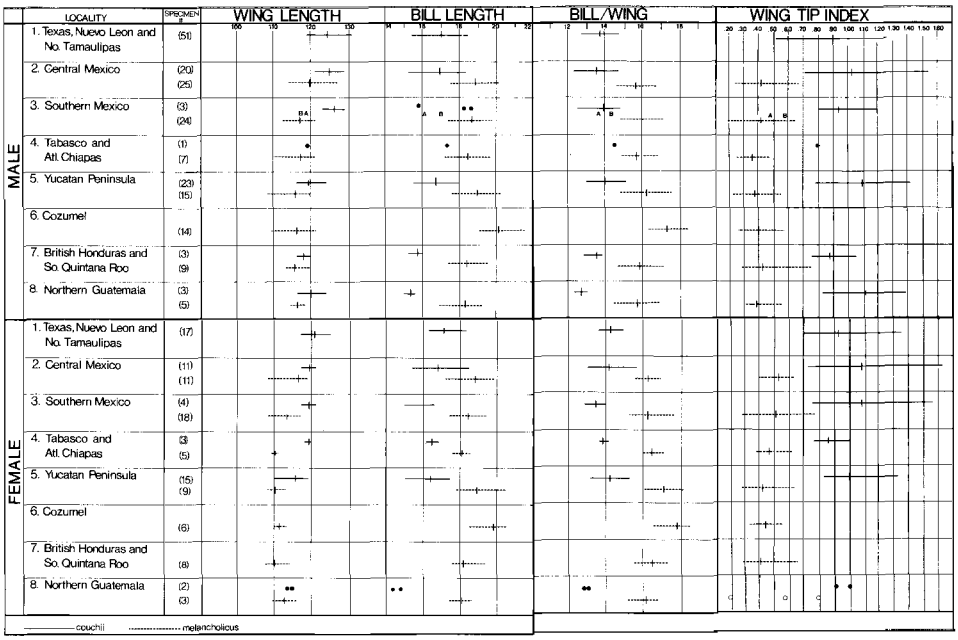

Fig. 7. Variation in wing length, bill length (from anterior edge of nostril), the ratio bill length/wing length, and wing tip index of various populations of *couchii* (solid line) and *melancholicus* (dashed line) from within the range of *couchii*. Males plotted above, females below. The lines show the observed ranges of measurements, and the vertical dashes the means. The letters A and B refer to the presumed hybrids on Fig. 3.

When the specimens are separated by wing tip index and relative bill length, the mensural characters and geographic variation for both species can be determined. In absolute size, as exemplified by wing length, *couchii* is larger than *melancholicus* throughout the area of sympatry (Fig. 7). This has been masked in the past, because they vary geographically in parallel, with the larger populations in the north and the smallest in the Yucatan Peninsula, and *melancholicus* in northern Mexico is almost identical in wing length with *couchii* in Yucatan. Females are slightly smaller than males (wing length 95–97% of males). Tail length varies as the wing but is proportionately shorter in the female, about 80% compared to 85% of wing. Variation in bill length is roughly parallel to that in wing length in both species, with two notable exceptions (Fig. 7). In *couchii* from British Honduras (now Belize) and Guatemala, the bill is markedly smaller than in populations from the northern part of the peninsula. Although there are only eight specimens altogether, the differences are so marked in both sexes that they are certainly significant. Populations of *melancholicus* from the same region have slightly smaller bills than those from further north, but not nearly to the same degree. On the other hand, the population of *melancholicus* on Cozumel Island has remarkably large bills compared to populations on the adjacent mainland, only 19 km away. In both species, bills of females are almost equal to those of males, hence proportionately longer. Tarsal length is essentially the same for both species and both sexes, so that *melancholicus* has a relatively longer tarsus than *couchii,* and females longer tarsi than males.

The depth of the tail fork, the difference between the lengths of the inner and

outer pairs of rectrices, is greater in *melancholicus* than in *couchii,* as noted by Phillips (*in litt.*). However, there is considerable overlap between them, and only extreme specimens can be identified by this character alone. The difference is greater in males than females, because female *melancholicus* have relatively shallower forks than males and are more nearly like *couchii*; there is no sexual dimorphism in the latter.

The two critical indices, bill/wing and wing tip index (Fig. 7), show surprisingly little variation geographically. Cozumel Island birds have a markedly high bill/wing ratio, as would be expected from the long bill lengths, and this high ratio is adumbrated in the Yucatan populations. Guatemalan *couchii* have low bill/wing ratios, but the difference is not as great as in the absolute bill measurements. The wing tip index is extremely variable by its very nature. The measurements on which it is based are small differences between long feathers, and a 1% difference in the length of the 5th primary can make a 20% difference in the distance from the tip of the wing to the tip of the 5th primary, the numerator of the fraction. When the effects of differential wear are added in, I find it remarkable that the index is as consistent as it is. The one variation of significance is the low average value in the allopatric populations of *couchii* in Texas and northern Mexico; this is discussed in more detail below.

Populations of *melancholicus* from western Mexico, from Sonora to Guerrero, generally called *occidentalis,* do not differ in any significant way from those in Oaxaca, Chiapas, or eastern Mexico, formerly called *chloronotus* and now to be known as *satrapa.* There are minor variations in relative bill length within this population, but none that set them off from *satrapa* or that are of the same magnitude as the large bills of Cozumel birds. The alleged pale coloration of *occidentalis* is not evident when fresh, fall specimens are compared. The only way in which the western populations differ from *satrapa* is in the timing of post-juvenal molt. In *satrapa* of eastern Mexico and in the sympatric *couchii,* post-juvenal molt is normally incomplete, and the juvenal remiges are retained through the first winter. Of 206 birds in adult contour plumage, 54 have juvenal remiges, including some in their second calendar year marked as breeding. Only three juveniles are molting their primaries during the post-juvenal molt, and these were taken within four days of each other at Tezonapa, Veracruz, and probably came from the same nest. On the other hand, in western Mexico, only 8 of 246 specimens in adult contour plumage retain any juvenal remiges, and 3 of them have a mixture of adult and juvenal primaries. In addition, there are nine juveniles in complete post-juvenal molt, wings as well as body. The normal mode in western Mexico is evidently to have a complete post-juvenal molt. The reason for this difference in molt pattern may be a response to the harsher and more arid conditions prevailing in western Mexico, but the difference is hardly worth considering as a subspecific character. Despite the fact that Davis (1972: 131) considered the song of the western birds sufficiently distinct to treat them as a separate species, Smith (1966: 104) considered their vocalizations just like those of any *melancholicus.* I believe that *occidentalis* should be considered a synonym of *satrapa.* Only careful field studies in Oaxaca, where "*occidentalis*" would meet *satrapa,* can show whether there actually are two taxa.

DISCUSSION

Since *couchii* and *melancholicus* occur commonly together in roughly equal numbers in central Mexico and the Yucatan Peninsula without any suggestion of inter-

breeding, the presence of apparent hybrids in southern Mexico is difficult to interpret. I believe that the explanation is to be found in the ecological differences of the two species and the habitat changes that have occurred since Spanish settlement. Smith (1966: 211–213) gives an excellent summary of these factors. He found that in Texas and northern Mexico *couchii* is basically a bird of thorn-scrub; in fact he suggests the name Thorn-scrub Kingbird for the species. He points out that, since the arrival of the Spaniards with their cattle, overgrazing has caused the spread of scrub into areas that were previously grassland, and *couchii* has extended its range into these newly created habitats. On the other hand, *melancholicus* will tolerate a much broader range of habitats, and occurs along any forest edge, in partially wooded pastures and second growth, or around cultivation. It will also breed in thorn-scrub, in habitat similar to that of *couchii*.

Tyrannus couchii is presumably a derivative of a *melancholicus* stock that was isolated in the dry Yucatan Peninsula during some pluvial period and speciated there. During a subsequent arid period, scrub conditions were continuous in the eastern lowlands of Mexico, and *couchii* extended its range west and north to Texas. Finally, during a more recent wet period, forest became continuous through southern Mexico, dividing the range of *couchii* into two isolated areas, Texas to central Veracruz, and the Yucatan Peninsula. At the same time, the more tolerant *melancholicus* moved back into the area, extending north to Yucatan and to southern Tamaulipas, where it widely overlapped the range of *couchii* without hybridization. A previous complete separation of the two populations of *couchii* is supported by the abrupt change in wing length between birds from the Yucatan Peninsula and those from Texas to Veracruz. The change in *melancholicus* is more clinal, suggesting that the range has been continuous.

This was presumably the status of the two species at the time of the arrival of the Spaniards, when more sustained agriculture and cattle grazing began to create artificial clearings in the forest. From the first, these edge situations would be attractive to *melancholicus,* and it would only be later, as further degradation of the habitat produced scrub conditions, that *couchii* would move into southern Veracruz and eastern Oaxaca, probably from the north. It is easy to understand why *melancholicus* would be much more common in this area, and it is probably this disparity in numbers that encourages the occasional *couchii* to mate with *melancholicus.* It is possible that as the number of *couchii* increases, this hybridization will prove to be transitory. However, until intensive fieldwork is carried out in the area of apparent hybridization, we can only speculate.

While relative bill length and the shape of the wing tip are of prime importance to the ornithologist as species recognition marks, it is not clear what their roles are in the economy of the birds. Considering the modest differences in absolute size that produce the distinctive ratios, and the fact that there is some overlap between the two species, it is difficult to believe that they are of major importance as species recognition marks to the birds themselves. If they should prove to have such a role, then we would expect that the differences between the ratios would be more accentuated in the area of sympatry than in the area of allopatry, and that the ratios would show more variability in areas where only one species occurs.

The relative bill length in *couchii* is remarkably constant throughout the range of the species. The only place where a significant difference is found in both sexes is Guatemala, where bill lengths are very short. There is no difference between the allopatric populations of Texas and northern Mexico and the sympatric populations

of central and southern Mexico. The variability within all populations is roughly the same. On the other hand, the relative bill length of *melancholicus* is quite variable geographically, although the changes bear no relation to the presence or absence of *couchii*. If this character were important in recognition, one would expect the highest values to be found in areas of sympatry with short-billed *couchii*. However, the longest bills, relatively and absolutely, are found on Cozumel Island, where *couchii* does not occur, and the next relatively largest occur in Sinaloa and Sonora, also an area of allopatry. On the other hand, the relatively smallest bills are also found in an area of allopatry, in Panama. There is no suggestion that bill length is associated with species recognition in either species. However, the constancy of relative bill length in *couchii* and its variability in *melancholicus* are probably related to their ecology; *couchii* is fairly rigidly restricted to arid thorn-scrub, while *melancholicus* is much more catholic in its choice of habitat.

The significance of the differing wing-tip forms is more difficult to analyze. It is not a problem that can properly be attacked through a study of *couchii* and *melancholicus* alone. Almost every species within *Tyrannus* has a unique form of wing tip, as determined by the relative lengths of the primaries and the extent of notching on the inner web. The differences between *couchii* and *melancholicus* are much less than between the sympatric pairs *verticalis* and *vociferans,* or *crassirostris* and *melancholicus;* even the subspecies of *savana* (olim *Muscivora tyrannus*) show much greater differences than those between *couchii* and *melancholicus*. The means by which the form of the wing tip could function in interactions between these two species are not clear, but there is some evidence that in areas of sympatry the forms of the wing tip are displaced to accentuate the differences. The average wing tip index of male *couchii* is 0.90 in Texas and northern Mexico, where this species occurs alone, and 1.03 in central Mexico, where it is found with *melancholicus*; the corresponding female figures are 0.93 and 1.08. These differences are significant at the 0.01 and 0.05 level respectively and are in the direction of increasing the difference between the two forms in areas of sympatry. In *melancholicus,* the index is remarkably constant throughout the region where it overlaps *couchii,* but in western Mexico north of Guerrero, where *couchii* does not occur, the index is much higher, 0.52 versus 0.42 in males and 0.65 versus 0.51 in females, differences that are significant at any level. However, south of Guatemala, the indices are the lowest of all, 0.36 in males and 0.46 in females, so we may be dealing with a geographical trend coincidentally superimposed on areas of sympatry and allopatry. Another confusing factor is the sexual dimorphism that is obvious in the above measurements of *melancholicus* but not found in *couchii*. Whatever the significance of the differing wing tip indices, the taxonomist may be thankful they serve our purposes so well.

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