

HYBRIDIZATION OF RUFOUS-NAPED WRENS IN CHIAPAS, MÉXICO

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TEN years ago I had an opportunity to study hybridization between two strongly differentiated subspecies of the Rufous-naped Wren (*Campylorhynchus rufinucha*) on the Pacific coastal plain of Chiapas, México, near the town of Tonalá and the Laguna de la Joya. My investigations in 1954 (Selander, *Univ. California Publ. Zoöl.*, 74: 77–116, 1964) showed that *C. r. humilis*, which occupies xeric habitats in western México, extends southeast from the Isthmus of Tehuantepec to within a few miles of Tonalá, while the form *C. r. nigricaudatus*, which is found in relatively mesic habitats on the coastal plain of southwestern Guatemala and southeastern Chiapas, ranges northwest to the southeastern edge of the Laguna de la Joya (Figure 1). Although the Laguna de la Joya forms a partial barrier between populations of these two wrens, they are in contact through the narrow Ocuilapa Valley, which lies inland from the laguna near the base of the Sierra Madre de Chiapas. Field work in the Ocuilapa Valley in 1954 revealed the existence of a linearly distributed series of partially isolated, variable, hybrid populations connecting the two parental forms (see Figure 2, below). On the basis of this finding, it is apparent that the two wrens are conspecific, notwithstanding their considerable morphological differences (Table 1).

In March, 1963, nine years after my first study, I revisited the Tonalá region while enroute to and from Nicaragua and was able to obtain additional information on the zone of hybridization. The chief purpose of my study in 1963 was to resample certain populations in the central part of the Ocuilapa Valley and, by comparing the samples with those collected at the same localities in 1954, to determine if any change in the character of the zone of hybridization had occurred. Additionally, I sought to determine the extent of introgression of genes of *C. r. humilis* into the population of *C. r. nigricaudatus* on the coastal plain southeast of the Laguna de la Joya. Finally, I was able to determine more precisely the distances between collecting stations in the Ocuilapa Valley.

For a discussion of the physiographical and ecological setting of the zone of hybridization and an analysis of characters in the hybrids, the reader should consult the detailed account in my earlier paper (Selander, *op. cit.*, pp. 80–105).

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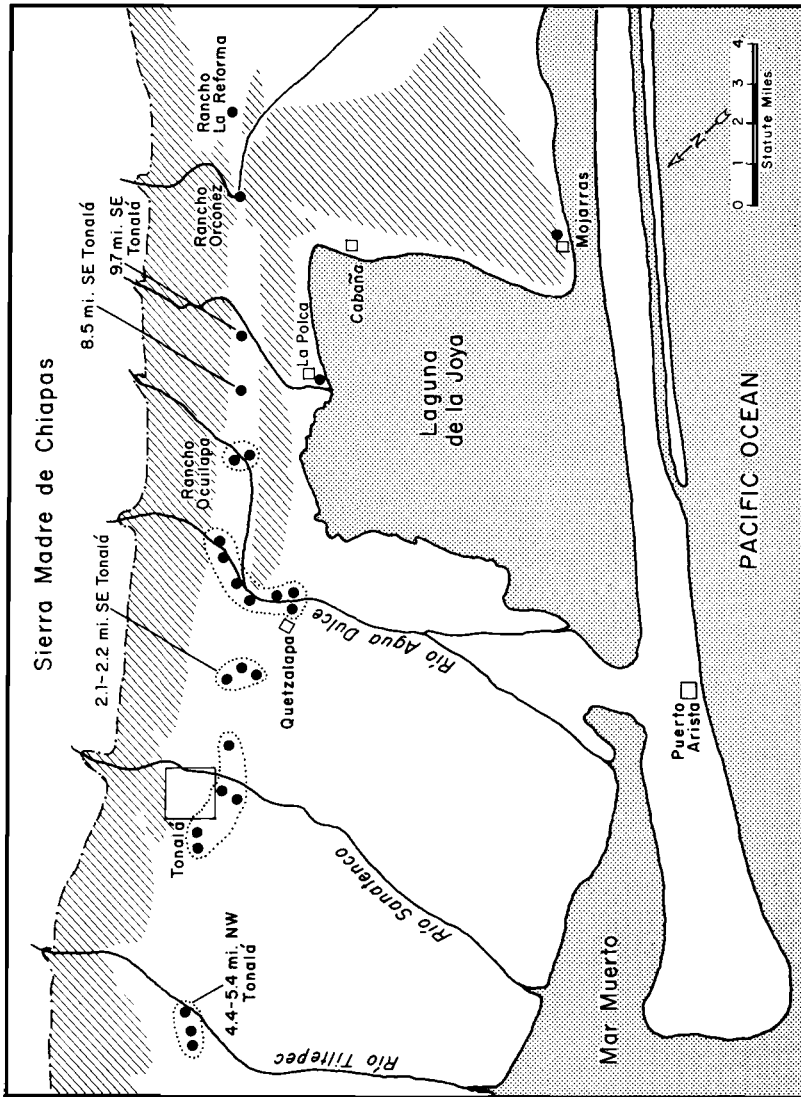


Figure 1. Map of the Tonalá region, Chiapas, showing collecting stations in the zone of hybridization between subspecies of *Campylorhynchus rufinucha*. Dots represent localities where specimens were collected. Low foothills adjacent to the Sierra Madre de Chiapas are indicated by the pattern of oblique lines.

TABLE 1

SUMMARY OF DIFFERENCES BETWEEN SUBSPECIES OF *CAMPYLORHYNCHUS RUFINUCHA*

<i>Character</i>	<i>C. r. humilis</i>	<i>C. r. nigricaudatus</i>
Size	Small	Large
Nape color	Light, more yellow	Dark, more red
Back	Highly patterned	Unpatterned
Pileum and post-ocular stripe	Mostly brown	Black
Tail	All rectrices conspicuously barred	Barring of rectrices reduced; central pair with barring absent basally and medially
Under parts	Under tail-coverts barred; flanks often barred or spotted	Unpatterned
Submalar stripe	Present	Absent
Song	Higher pitched; tempo more rapid	Lower pitched; tempo less rapid
Habitat	More xeric types	More mesic types

MATERIALS AND METHODS

My study in 1954 was based on 125 specimens (115 skins) collected in March and April in the zone of hybridization, nearly all of which show evidence of mixed ancestry. This material, together with that obtained in 1963, is in the Museum of Vertebrate Zoology.

Morphological characters analyzed quantitatively in the parental forms and in the hybrids were body weight, eight linear dimensions taken from skins, and six characters of color and pattern. Scores assigned to each of five characters of color and pattern (back, pileum, tail, under parts, and submalar stripe) were summed for each individual to permit analysis of variation by means of a hybrid index (Figure 2). The "pure" sample of *C. r. nigricaudatus* from southeastern Chiapas has an average index score of 0.9 and a range of variation from 0 to 3; and the "pure" sample of *C. r. humilis* from the Isthmus of Tehuantepec, Oaxaca, has an average index score of 18.9 and a range of variation from 17 to 21. Hence, specimens having index scores from 4 through 16 are intermediate between the two parental populations in one or more of the five characters on which the hybrid index is based.

In March, 1963, the following additional material was collected: Rancho La Reforma, 15 miles southeast of Tonalá, 9 March, 12 specimens; Rancho Orconez, 13.0 miles "E" [= southeast] of Tonalá, 8 March, 1; Rancho Ocuilapa, 7.1 miles southeast of Tonalá, 10 March, 14; Río Aqua Dulce, 4.3 miles southeast of Tonalá, 30 March, 14; 8.2 miles northwest of Tonalá, 11 March, 1.

The characters of specimens collected in 1963 were scored by direct comparison with specimens taken in 1954.

RESULTS

DISTANCES BETWEEN COLLECTING STATIONS

Since there was no road through the Ocuilapa Valley in 1954, collecting stations were reached by driving along ox-cart trails; and it seemed probable that a considerable error was involved in estimating air-line distances between the stations. In 1963 the distances were measured by driving

TABLE 2
MEASURED DISTANCES (IN MILES) OF COLLECTING STATIONS FROM TONALÁ, CHIAPAS

Collecting station	Miles southeast of Tonalá	
	1954	1963
"2.6-2.7" miles southeast of Tonalá	2.6-2.7	2.1-2.2
Río Agua Dulce	5.6	4.3
Rancho Ocuilapa	8.6	7.1
"10.6" miles southeast of Tonalá	10.6	8.5
"12.1" miles southeast of Tonalá	12.1	9.7
Rancho Orconez	16.1	13.0
Rancho La Reforma	—	15.0

along a new, paved road, the recently completed Arriaga-Tapachula highway, which runs straight through the valley. As shown in Table 2, my earlier estimates were too great by about 20 per cent. In both years, distances southeast of Tonalá were measured from the Río Sanatenco at the eastern edge of the town.

In Figure 2, hybrid index scores for the various samples of wrens are plotted, with the distances between the base lines of the histograms proportional to air-line distances between collecting stations, as determined in 1963. Note that the zone of hybridization is only 20 miles wide, and that the population at the Río Agua Dulce, a station midway in the zone, is in its average character almost precisely intermediate morphologically between the two parental types.

EXTENT OF INTROGRESSION

In 1954 I was unable to drive beyond the Rancho Orconez at the southeastern edge of the Ocuilapa Valley, and therefore I failed to sample the population of *C. r. nigricaudatus* on the coastal plain immediately southeast of the valley. However, two pieces of evidence suggested that introgression of genes of *C. r. humilis* would be evident for only a short distance beyond the valley. (1) A single specimen collected in 1939 by P. Brodorb at Mojarras, a fishing village at the southeastern edge of the Laguna de la Joya, was a "pure" example of *C. r. nigricaudatus*, having a hybrid index score of 0. (2) A sample of 11 males and 16 females taken at the Rancho Orconez showed comparatively slight morphological deviation from the "pure" population of *C. r. nigricaudatus* of southeastern Chiapas beyond Pijijiapan. The mean hybrid index score for the sample from the Rancho Orconez was 2.2 (Figure 2), and the scores of only 4 of the 27 specimens fell beyond the range of variation in "pure" *C. r. nigricaudatus*.

On 9 March 1963, I collected 12 specimens at the Rancho La Reforma, a station two miles southeast of the Rancho Orconez or 15 miles southeast

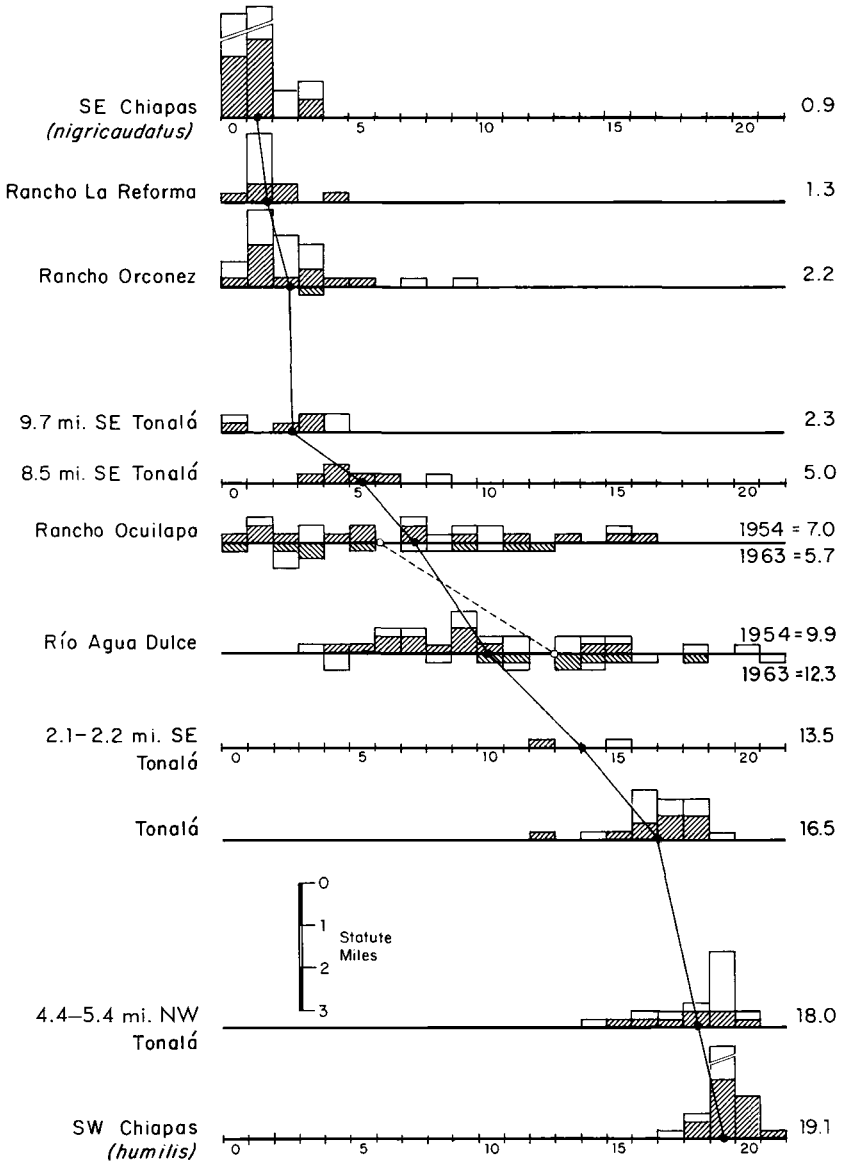


Figure 2. Hybrid index scores of samples of the "pure" parental forms and of populations in the zone of hybridization between subspecies of *Campylorhynchus rufinucha*. Males are represented by hatched rectangles, females by open rectangles. Scores of samples taken in 1963 at Rancho Orconez, Rancho Ocuilapa, and Río Agua Dulce are plotted below the base lines for comparison with samples collected at these stations in 1954. Mean scores of samples are connected by a solid (1954) or a dashed (1963) line. From Rancho La Reforma through the zone to the station 4.4 to 5.4 miles northwest of Tonalá, the distances between base lines are proportional to actual air-line distances between collecting stations.

TABLE 3
MEAN MEASUREMENTS (MM) OF MALES OF *CAMPYLORHYNCHUS RUFINUCHA*

<i>Locality</i>	<i>Number of specimens</i>	<i>Wing</i>	<i>Tail</i>	<i>Bill from nostril</i>	<i>Tarsus</i>	<i>Weight (g)</i>
Southeastern Chiapas						
<i>(C. r. nigricaudatus)</i>						
1954	14	77.14	70.96	15.91	23.96	33.50
Rancho La Reforma						
1963	6	76.98	68.22	16.07	25.22	32.78
Rancho Orconez						
1954	10	75.38	67.12	16.17	24.12	30.33
1963	1	74.3	68.6	15.1	26.3	31.6
Rancho Ocuilapa						
1954	13	72.43	64.32	15.21	23.14	29.69
1963	8	73.49	65.69	15.44	23.75	31.41
Río Agua Dulce						
1954	12	72.58	64.47	14.95	23.10	28.91
1963	7	73.04	64.73	14.80	23.26	27.81
Southwestern Chiapas						
<i>(C. r. humilis)</i>						
1954	14	67.66	60.34	13.78	21.43	27.02

of Tonalá. As predicted, the sample is closely similar morphologically to that of the "pure" population of *C. r. nigricaudatus* from farther southeast on the coastal plain. The mean hybrid index score is 1.3, which is only 0.4 units greater than that of the sample from southeastern Chiapas. Only one specimen, a male with a hybrid index score of 4, falls beyond the range of variation in *C. r. nigricaudatus*. In size, birds from the Rancho La Reforma are larger than those from the Rancho Orconez and are closely similar to those from southeastern Chiapas (Table 3).

It is evident that genes of *C. r. humilis* reaching the coastal plain southeast of the Laguna de la Joya through the hybrid populations in the narrow Ocuilapa Valley are being swamped or counter-selected, or both, in the large population of *C. r. nigricaudatus* beyond the southeastern edge of the valley. Similarly, my analysis of the hybridization of these wrens in 1954 showed that introgression of genes of *C. r. nigricaudatus* into the large population of *C. r. humilis* at the other end of the zone was evident for no greater distance than 4.4 to 5.4 miles northwest of Tonalá, where a sample of 20 specimens showed only slight deviation (average hybrid index score, 18.0) from phenotypically "pure" *C. r. humilis*, as exemplified by large series of specimens from southwestern Chiapas (nine miles northwest of Tonalá to Arriaga) and southeastern Oaxaca (Figure 2).

REDUCED POPULATION DENSITY IN 1963

In working at collecting stations in the Ocuilapa Valley and at the *C. r. humilis* end of the zone of hybridization in 1963, I found wrens decidedly less numerous than they were in 1954.

In 1954 wrens were common at the Rancho Ocuilapa, where two collectors took 28 specimens, which, according to my estimate, represented approximately one-half the population in the area. But wrens were decidedly less common in 1963, and, hunting over the same area, my assistant and I could collect only 14 specimens, which seemed to represent at least two-thirds of all wrens in the area.

Hunting along the Río Agua Dulce from the foothills to the railroad track near Quetzalapa in 1954, my assistant and I collected 28 specimens, and I estimated that there was a total population of 45 wrens in this area. On 30 March 1963, my assistant and I hunted over the same area but saw only about 20 wrens, 14 of which we collected. Whereas in 1954 wrens were common in the riparian growth and also in dry, thorn-scrub vegetation back from the river, in 1963 I found most of the wrens in the latter habitat.

Along the Río Tiltepec, 4.4 to 5.4 miles northwest of Tonalá, I found strongly *C. r. humilis*-like wrens common in 1954 and collected 20 specimens in a few hours of hunting. However, in 1963, I could find no wrens of this species in the same area, despite the fact that I hunted for five hours through habitat that seemed to be well-suited for this wren. In 1963, I found wrens of this species no closer to Tonalá than a dry river bed 8.2 miles northwest of Tonalá. Four birds were seen there and the one bird, a female, that I collected is a "pure" example of *C. r. humilis* (hybrid index score, 20; weight, 23.1 g).

A single specimen, a male, taken at the Rancho Orconez on 8 March 1963, has a hybrid index score of 3, which is near the mean value for the large sample collected there in 1954 (Figure 2). It was my impression that wrens were less numerous at the Rancho Orconez in 1963 than in 1954, but, unfortunately, I did not work long enough in this area in 1963 to make a reliable estimate of the population size.

I am unable to suggest a cause for the lower population densities observed in 1963 as compared with 1954. According to residents of the Rancho Ocuilapa, the region has received normal amounts of rainfall, at least in the past few years, and I could detect no changes in the structure or general condition of the habitat in which the wrens occurred. Possibly the wren populations in the zone of hybridization had failed to recover from the effects of my extensive collecting in 1954, although this seems to me unlikely.

STABILITY OF THE HYBRID ZONE

As shown in Figure 2, samples taken in 1954 at the Rancho Ocuilapa and along the Río Agua Dulce, in the central part of the zone of hybridization, are highly variable, showing together the complete range of index scores from one parental type to the other. These two populations were sampled a second time in March, 1963, and, for comparative purposes, the hybrid index scores of the 1954 and 1963 samples are plotted together in Figure 2. The mean morphological character of the 1963 sample from the Rancho Ocuilapa is slightly more like *C. r. nigricaudatus* than is that of the sample taken there in 1954; the data show a shift in average hybrid index score from 7.0 in 1954 to 5.7 in 1963. In the case of the two samples from the Río Agua Dulce, the 1963 sample is more like *C. r. humilis* than is that taken in 1954; the shift is from an average hybrid index score of 9.9 in 1954 to one of 12.3 in 1963.

Although the data suggest the possibility of a slight steepening of the gradient of change in morphological characters from 1954 to 1963, Chi-square tests for homogeneity of the samples show that the observed differences are not statistically significant (e.g., $P > .1$ for the comparison of the two samples from the Río Agua Dulce). Moreover, the close similarity in mean measurements of linear dimensions and of body weight of the 1954 and 1963 samples (Table 3) strongly supports the thesis that there was no significant change in the genetic character of the populations at the Rancho Ocuilapa and the Río Agua Dulce. The observed differences in mean hybrid index scores may be attributed to sampling error and to error inherent in the subjective procedure of assigning specimens to character categories.

In conclusion, it was apparent from my study in 1963 that, except for a reduction in population densities of wrens in the Ocuilapa Valley and in the region northwest of Tonalá, the zone of hybridization between *C. r. humilis* and *C. r. nigricaudatus* had remained essentially unchanged in the nine years since its discovery in 1954.

SUMMARY

Reinvestigation in 1963 of a zone of hybridization between *Campylorhynchus rufinucha humilis* and *C. r. nigricaudatus* in the Tonalá region and the Ocuilapa Valley on the Pacific coastal plain of Chiapas, México, indicated that the zone had remained essentially unchanged in the nine years since its discovery and initial study in 1954.

Population densities of wrens at several collecting stations in the zone were reduced in 1963 as compared with 1954.

Samples taken in 1954 and 1963 at two collecting stations in the central

part of the zone did not differ significantly in linear dimensions and weight or in hybrid index scores based on five characters of color and pattern.

A sample of wrens taken in 1963 at the *C. r. nigricaudatus* end of the zone of hybridization confirmed an earlier prediction that introgression of genes of *C. r. humilis* is scarcely apparent beyond the southeastern limit of the Ocuilapa Valley. Complete morphological transition between *C. r. humilis* of southwestern Chiapas and *C. r. nigricaudatus* of southeastern Chiapas occurs over a distance of 20 miles.

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