HYBRIDIZATION IN THE RED-EYED TOWHEES OF MEXICO: THE EASTERN PLATEAU POPULATIONS

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The occurrence and significance of hybridization is a matter of interest to investigators in many branches of biology. The role of hybridization as a factor in evolution has attracted special interest. Much of the pertinent literature concerns plant hybrids (cf. Anderson, 1949; Dobzhansky, 1951; Stebbins, 1950), but hybridization in animals is also receiving attention (cf. Mayr, 1942; Sibley, 1950, 1954, 1957; Miller, 1955). The papers just cited contain discussions of the theoretical background of the subject, especially as it relates to birds.

In the present paper we wish to present the results of a continuation of the studies reported upon in two previous papers by the senior author (1950, 1954).

ACKNOWLEDGMENTS

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MATERIALS

The present study is based primarily on a collection made in 1954 and not previously reported upon. In calculating the hybrid indexes, and other measurements of populations, the specimens described in the 1950 and 1954 papers have been included. Additional material was studied for the first time during the summer of 1954 in the collections of the British Museum (Natural History).

The 1954 collection of new material contains 338 adult specimens. These are deposited in the collection of Cornell University. The British Museum collections contain 90 specimens used in this study. Material previously reported upon from all parts of México (Sibley, 1954:254) totaled 1130 specimens. To the present time (1957) the study of Mexican towhee hybrids is based upon 1560 specimens. Approximately 1000 of these have been collected in the years 1946, 1948, 1950, and 1954 in the course of expeditions devoted to the study of this problem. The remainder are specimens contained in various collections in the United States and Europe (cf. Sibley, 1950).

THE ANALYSIS OF HYBRIDS

The "hybrid index" method was developed in the course of studies on plant hybrids (cf. Anderson, 1949) and has proved useful in the analysis of avian hybrids (Sibley, 1950; Dixon, 1955). It provides a rough quantitative evaluation of the complicated color patterns of hybrid individuals resulting from recombinations of the characters of unlike parental forms.

The two species of red-eyed towhees which hybridize in México are the Rufous-sided Towhee (= Spotted Towhee), *Pipilo erythrophthalmus*, and the Collared Towhee (*Pipilo ocai*). Detailed descriptions and a color plate are given in a previous paper (Sibley, 1950). For the convenience of those not having ready access to this paper the following synoptic descriptions are presented.

Pure populations of the two species differ in plumage color in six principal areas.

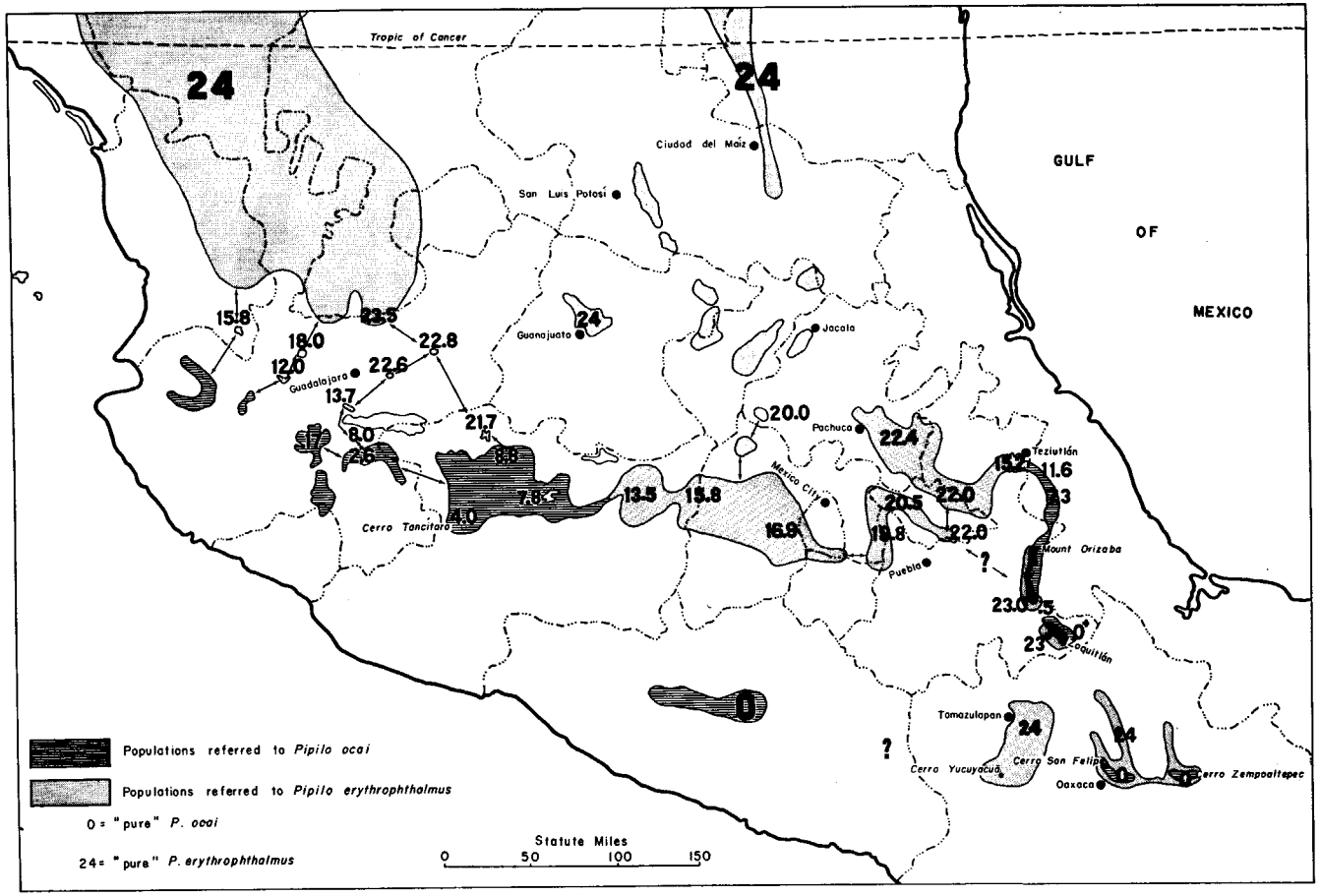

Fig. 1. Distribution of the red-eyed towhees in central México.

1. Pileum color: Chestnut in *ocai,* black in *erythrophthalmus.*

2. Back and wing spots: White spots on scapulars and wing coverts in *erythrophthalmus.* These areas are unspotted in *ocai.*

3. Back color: Green in *ocai,* black in *erythrophthalmus.*

4. Throat color: White in *ocai,* black in *erythrophthalmus.*

5. Flank color: Brownish olive in *ocai,* rufous in *erythrophthalmus.*

6. Tailspots: White spots on three outer rectrices in *erythrophthalmus,* absent in *ocai.*

For each of these six characters five gradations ranging from pure *ocai* to pure *erythrophthalmus* may be distinguished. These gradations are scored as follows:

"0" When expressed as in pure *P. ocai.*

"1" Mainly as in *ocai* but showing some influence from *erythrophthalmus.*

"2" Intermediate between *ocai* and *erythrophthalmus.*

"3" Mainly as in *erythrophthalmus* but showing some influence from *ocai.*

"4" When expressed as in pure *P. erythrophthalmus.*

A pure *ocai* specimen will thus be scored "0" for all six characters for a summated score of "0" ($6 \times 0 = 0$). A pure *erythrophthalmus* will score "4" for each of the six characters for a summated score of "24" ($6 \times 4 = 24$). Hybrid scores will fall on this "0" to "24" scale, a specimen with a score of "12" being at the midpoint, and so forth. Figure 1 indicates the average hybrid index numbers for the populations which have been sampled to date. Additions since the 1954 paper are mainly in the eastern plateau area.

MEASUREMENTS OF SIZE

The weights in grams of the 338 specimens collected in 1954 were obtained. The British Museum specimens had not been weighed. Linear measurements from skins, in millimeters, were taken as follows: wing, the chord; tail, from the insertion of the two middle rectrices; tarsus, from the joint between the tarsus and the tibia (the heel) to the midpoint of the distal margin of the most distal undivided scute; bill, from the anterior margin of the nostril to the tip of the maxilla.

SUMMARY OF PREVIOUS RESULTS

The map (fig. 1) indicates the distribution of the red-eyed towhees of México as presently known. The numbers are hybrid index averages for each population sample. The Rufous-sided Towhee (*P. erythrophthalmus*) is a widespread species which ranges from Canada to Guatemala. In México it is primarily restricted to brushy undergrowth between 5500 and 9000 feet elevation. In the Mexican plateau at these altitudes oaks (*Quercus*) tend to be the dominant trees. The Collared Towhee (*P. ocai*) is restricted geographically to the higher mountains of the Mexican plateau, usually above the altitudes occupied by *P. erythrophthalmus.* The Collared Towhee inhabits the dense undergrowth associated with coniferous (pine, fir) woodland and is thus in but limited contact with the Rufous-sided Towhee.

In the state of Oaxaca, in southeastern México, the two species occur side by side (Cerro San Felipe), but no evidence of interbreeding between them has been found. In the mountains which form the eastern edge of the Mexican plateau, between Zoquitlán and the Cofre de Perote, there are populations of both species, often occurring in sympatry. Hybrids occur in this area, but they tend to be infrequent. In the Teziutlán, Puebla area, a hybrid population is found in which all individuals are intermediate between the parental forms. Extending across the central highlands, from northeast of Mexico City to the mountains of southwestern Jalisco, is a clinal series of populations which gradually bridges the geographical and morphological gaps between nearly pure *erythrophthalmus* in Hidalgo (Pachuca) to nearly pure *ocai* in Jalisco. On isolated mountain tops in western México (Cerro Viejo, Cerro Grande, Cerro Gordo, Cerro El

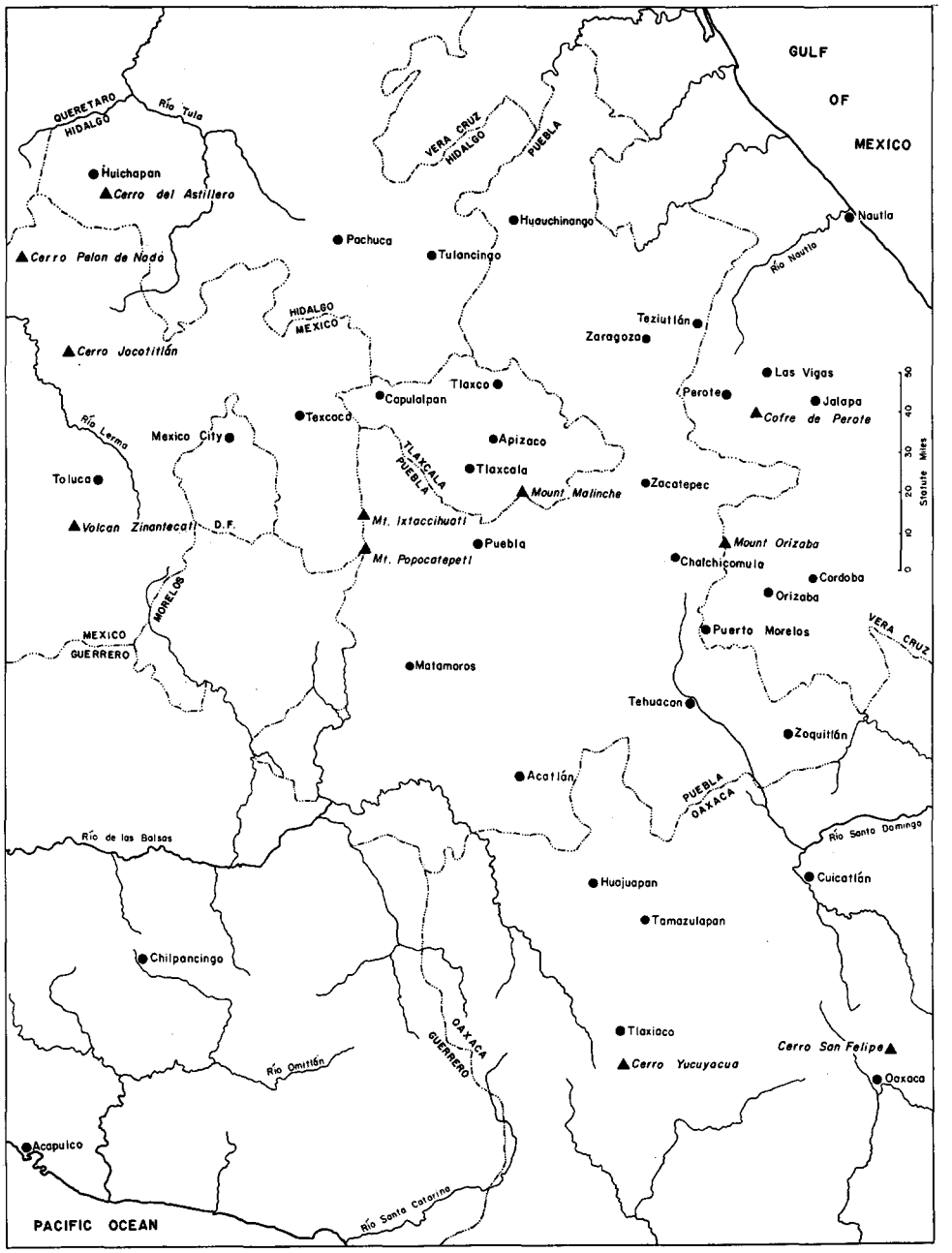

Fig. 2. Localities in eastern México mentioned in the text.

Fraile, Cerro Tequila, Cerro El Faro, Sierra de Ameca, Cerro García) occur hybrid populations which show the effects of introgression. A population of pure *ocai* is found in the Sierra Madre del Sur of Guerrero, and pure *erythrophthalmas* ranges northward in the Sierra Madre Occidental and the Sierra Madre Oriental and southward in the mountains of Chiapas and Guatemala.

The field studies in Hidalgo, Puebla, Veracruz, and Oaxaca had shown that the pattern of variation in the eastern plateau was complex and required further attention. Prior to 1954 collections had been made, or specimens collected by others had been examined, from several localities. In the following list, our localities are numbered and the years in which they were visited are noted in parentheses. Figure 2 indicates the location of localities mentioned in the text.

Hidalgo: 6 mi. N Pachuca, 9600 ft. (1946). Other specimens examined from El Chico, Real del Monte, San Agustín, Irolo, Tulancingo, and Apulco. *Puebla:* 8 mi. NE Chalchicomula, 10,350 ft. (1946, 1948); 3 mi. W Teziutlán, 7300 ft. (1950); additional material examined from Honey, Beristain, Chalchicomula, Mount Orizaba, and Tochimilco. *Veracruz:* Puerto Morelos, 8000 ft., 19 mi. WSW Orizaba (1950); additional material from Las Vigas and Cofre de Perote. *Oaxaca:* La Cumbre, 5 mi. NE Cerro San Felipe, 9000 ft. (1946, 1948); other specimens from Cerro San Felipe, Mount Zempoaltepec, and mountains near Ozolotepec. From Tlaxcala only two specimens from Mount Malinche had been examined.

THE 1954 FIELD STUDY

Two field parties collected in the eastern highlands in June, July, and August. Party number 1, consisting of Walter J. Bock, Thomas Savage, and David B. Wingate, visited the following localities on the dates indicated. The number of adult towhee specimens from each locality is given in parentheses.

Cerro del Astillero, 9500 ft., 10 km. SSE Huichapan, Hidalgo, June 14–16, (53); Route 99, 9400 ft., at México-Tlaxcala border, 20 km. ENE Texcoco, México, June 19–23, (26); Las Mesas, 8700 ft., 13 km. WNW Apizaco, Tlaxcala, June 25–28, (17); Mount Malinche, 9400 ft., 17 km. SE Apizaco, Tlaxcala, June 29–July 1, (18); Tacopan, 13 km. W Teziutlán, 7400 ft., Puebla, July 3–6, (47); 20 km. N Perote, on Teziutlán-Perote highway, 7800 ft., Puebla, July 8–13, (23); Rancho Los Olmos, 8600 ft., 6 km. W Las Vigas, Veracruz, July 14–18, (18); Puerto Morelos, 8000 ft., 19 mi. WSW Orizaba, Veracruz, July 21–27, (73).

Party number 2, consisting of Lester L. Short, Jr., Fred C. Sibley, and Ralph H. Long, Jr., visited the following localities.

5 mi. NE Tlaxco, 9100 ft., Tlaxcala, August 1–5, (14); 10 mi. SE Mount Malinche, 8100 ft., Tlaxcala, August 9–10, (13); 4 mi. W Zoquitlán, 8400 ft., Puebla, August 11–17, (5); 2 mi. E Tlaxiaco, 5800 ft., Oaxaca, August 19–24, (10); La Cumbre, 9000 ft., 5 mi. NE Cerro San Felipe, Oaxaca, August 25–30, (21).

In the hybrid indexes and measurement tables the two localities on Mount Malinche are considered as one. The 73 specimens from Puerto Morelos are combined in this paper with 20 taken by Sibley (1954) in 1950 and the 47 from near Teziutlán with nine taken in 1950 plus two in the Chicago Natural History Museum.

THE DISTRIBUTION OF RED-EYED TOWHEES IN RELATION TO TOPOGRAPHY AND VEGETATION IN EASTERN MEXICO

The presently known distribution of red-eyed towhees in eastern México is indicated on the map, figure 1. As previously noted, *Pipilo erythrophthalmus* occurs mainly in the brushy understory associated with oak woodland, while *Pipilo ocai* occurs at higher elevations in the brush associated with pine-fir forest. In eastern México, neither species occurs below 5000 feet in the breeding season and most populations are found above 8000 feet. In addition to the direct effects of altitude on the vegetation, the "rain-shadow" effects of mountains have strongly influenced the distribution of vegetation

and hence the distribution of birds. Of principal importance is the semi-desert area to the west of Mount Orizaba resulting from the interception of moisture by the Mount Orizaba-Cofre de Perote chain. This has produced an arid region extending approximately from Tehuacán in the south to the section west of Perote in the north. Leopold (1950) includes this area in his "mesquite-grassland" formation. The northern part of this basin is a flat, open grassland extending from Zacatepec north to near the village of San Miguel, 27 miles by road north of Zacatepec. This grassland basin extends east and west for from 10 to 25 miles. South from Zacatepec to Tehuacán the rain-shadow of Mount Orizaba has produced an arid mesquite scrub area. As noted by Leopold, the principal plants include *Prosopis, Celtis, Fouquieria, Acacia,* many cacti, agave, and the pepper tree (*Schinus molle*), a non-native "escape." This arid belt, with its xerophytic habitats, is unsuitable for red-eyed towhees and constitutes an important barrier for these birds between the Mount Orizaba ranges and the uplands of Mount Malinche and other mountains west of the mesquite-grassland region.

To the south this barrier effect is continued by the arid valley in which the town of Tehuacán is situated. South of Tehuacán the valley continues to its connection with the Río Santo Domingo, a deep east-west chasm which bisects the mountains of the eastern edge of the plateau and flows eastward to enter the Río Papaloapan which drains to the Gulf of México. These valleys serve to isolate the Mount Orizaba highlands from the mountains of Oaxaca to the south and southwest. Further description of this area will be found in a previous paper (Sibley, 1954:277–279).

The rapid drop in elevation at the edge of the plateau is an effective barrier along the eastern and northern margin of the area under consideration. The highlands of the Popocatepetl-Ixtaccihuatl range communicate, via a low range of hills, with Mount Malinche (see fig. 1) and there appears to be no important discontinuity in towhee habitat between the uplands near Pachuca and the ranges running southeast toward Mount Malinche. South of Puebla the land slopes rapidly to the Río Balsas drainage system and the arid-tropical vegetation is unsuitable for towhees. More detailed information on topography, vegetation, and hybrid gradients follows.

Cerro del Astillero.—Cerro del Astillero (= C. Nopala) is located at 20° 18′N latitude and 99° 36′W longitude. It rises to 10,168 feet (World Aeronautical Chart, No. 589) from a semi-desert plateau of between 7000 and 8000 feet elevation. The xerophytic vegetation of the plateau is replaced at about 9200 feet by sparse oak woodland which continues to the summit. No pines are present. Towhees were first noted at 9000 feet and were one of the commonest bird species above 9500 feet.

The hybrid index of the 53 specimens ranges from "16" to "23" with an average of

Table 1

Measurements of Population from Cerro del Astillero

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	37	48.3±0.5	3.0	6.2
	♀	15	48.9±1.1	4.2	8.6
Wing	♂	38	88.6±0.4	2.1	2.4
	♀	15	83.4±0.6	2.4	2.9
Tail	♂	35	100.9±0.7	4.1	4.0
	♀	14	96.1±1.0	3.8	3.9
Tarsus	♂	36	29.9±0.2	0.9	2.9
	♀	15	28.7±0.3	1.0	3.4
Bill from nostril	♂	37	10.4±0.1	0.5	4.4
	♀	15	10.2±0.1	0.3	3.3

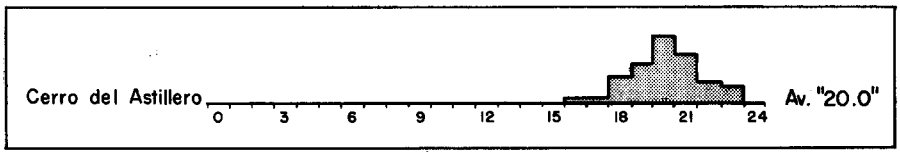

Fig. 3. Histogram of the hybrid indexes of specimens of red-eyed towhees from Cerro del Astillero, Hidalgo.

"20.0." Measurements are given in table 1 and the histogram of hybrid indexes in figure 3.

To the north and east of Cerro del Astillero the land is low and desert-like, providing a barrier to dispersal from the populations of *P. erythrophthalmus orientalis* > *maculatus* along the plateau edge north of Pachuca. To the southwest, high country extends toward eastern Michoacán. In 1950 the senior author drove north from Toluca to Querétaro. Along this route suitable towhee habitat apparently exists on Cerro Pelón de Nado, on Cerro Jocotitlan, and on all the land in this area over 9000 feet. The situation to the southeast of Cerro del Astillero is not clear, but it appears that the population of Cerro del Astillero is in closest contact with the populations to the south which form the "trans-plateau gradient" (Sibley, 1950:169–176).

20 km. ENE Texcoco.—This locality is on the highway (Route 99) which runs northeast from Texcoco, México, to Capulalpan, Tlaxcala. The actual collecting area was very near the Tlaxcala border in the state of México. The dominant trees are pines which extend to the summit at 10,500 feet. A few oaks are present and the higher slopes are covered with thick brush, including *Rhododendron.* Towhees were found in the brush above 9600 feet, but they were not abundant.

The hybrid index of the 26 specimens ranges from "16" to "24" with an average of "20.6." See table 2 for measurements and figure 4 for the histograms of hybrid indexes for this and the following localities. Figure 5 indicates the weights for the populations which were studied.

Table 2

Measurements of Population from 20 km. ENE of Texcoco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	20	50.9±0.6	2.7	5.3
	♀	6	46.7±1.3	3.3	7.0
Wing	♂	20	89.2±0.4	1.8	2.0
	♀	6	85.5±1.5	3.8	4.4
Tail	♂	19	105.9±0.8	3.6	3.4
	♀	6	101.2±2.8	6.9	6.9
Tarsus	♂	20	30.6±0.2	1.0	3.1
	♀	6	28.6±0.6	1.4	4.7
Bill from nostril	♂	20	10.4±0.1	0.1	1.0
	♀	6	10.0±0.2	0.4	4.5

This locality is situated at the northern end of the Popocatepetl-Ixtaccihuatl highlands. To the north and west the country is low and unsuitable for towhees. To the east low ridges extend to Mount Malinche providing suitable towhee habitat. The next locality lies in this area.

Las Mesas.—This locality is 32 miles east of the one described above. It too is on Route 99, at 8700 feet, in a pine-oak woodland where the conifers are dominant. The

land is badly eroded and there is little brush. Towhees, although not common, were found throughout the area. The 17 specimens have an average hybrid index of "20.5," ranging from "18" to "23."

Table 3

Measurements of Population from Las Mesas

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	47.9±0.9	3.2	6.6
	♀	5	46.3±1.0	2.3	5.0
Wing	♂	12	86.9±0.7	2.4	2.7
	♀	5	81.2±0.4	1.5	1.8
Tail	♂	12	100.0±1.2	4.1	4.1
	♀	5	94.7±0.8	2.9	3.0
Tarsus	♂	12	30.2±0.1	1.2	4.0
	♀	5	29.3±0.1	0.8	2.5
Bill from nostril	♂	11	10.2±0.2	0.6	5.5
	♀	4	10.3±0.1	0.1	1.4

Las Mesas is at the northern edge of suitable towhee habitat in this area. To the southeast, patches of suitable habitat provide a dispersal pathway to Mount Malinche.

Mount Malinche.—Both field parties worked on the slopes of Mount Malinche. Party number 1 collected on the northwest side of the peak from a camp at 9400 feet. Below 9700 feet, the land is cultivated and open, with brush restricted to the ravines and hedgerows. Pines are dominant from 10,000 to 13,300 feet, and above that point to the summit at 14,636 feet the peak is treeless. Towhees were found mainly in the hedgerows between cornfields from approximately 9000 to 10,000 feet. Very few were found in the pine forest, and the population was considered sparse by the collectors. Northward from Mount Malinche hedgerows, suitable for dispersal but probably not for breeding, extend across the lower country toward the Tlaxco region, approximately 25 miles north of Malinche. From the highlands near Tlaxco, there seems to be uninterrupted towhee habitat extending northwest to near Pachuca and, probably, around to the east to Teziutlán.

Party number 2 investigated the eastern and southeastern slopes of Mount Malinche. The eastern slope is similar to the northwestern side, as described previously. To the southeast, between the main mass of Malinche and a large parasitic cone near its base, the slope is gentler and scrub oaks, madrones, and brushy cover are more abundant. In this habitat towhees were fairly common.

Table 4

Measurements of Population from Mount Malinche

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	24	46.2±0.6	3.0	6.4
	♀	7	46.6±0.9	2.3	4.9
Wing	♂	24	87.8±0.8	3.8	4.3
	♀	7	80.4±0.7	1.8	2.2
Tail	♂	24	100.8±0.8	3.7	3.6
	♀	3	94.2		
Tarsus	♂	24	29.3±0.6	0.9	3.1
	♀	7	28.6±0.2	0.6	2.0
Bill from nostril	♂	24	10.1±0.1	0.5	4.8
	♀	7	10.0±0.2	0.5	5.4

The two parties collected a total of 31 specimens on Mount Malinche. These are considered together in all calculations. The hybrid index ranges from "20" to "24" with an average of "22.0."

Tlaxco.—The Tlaxco area, 25 miles north of Mount Malinche, is in the highlands which connect directly with the Pachuca region. At 9100 feet, 5 miles northeast of Tlaxco, pine forest, with thick undergrowth, is the dominant vegetation. Towhees were abundant and the 14 specimens have an average hybrid index of "22.0," ranging from "20" to "23." Specimens from Pachuca approximate this figure ("22.4"), and it is the same as for the Mount Malinche population. These figures indicate that gene flow from Pachuca to Malinche is relatively unimpeded. Measurements are given in table 5.

Table 5

Measurements of Population from Tlaxco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	6	48.9±1.1	2.7	5.5
	♀	5	49.8±1.7	3.7	7.4
Wing	♂	9	87.9±0.1	0.4	0.4
	♀	5	82.3±1.6	2.5	3.1
Tail	♂	9	101.4±0.2	2.2	2.1
	♀	5	97.6±2.2	4.8	4.9
Tarsus	♂	9	30.1±0.2	0.5	1.7
	♀	5	28.5±0.2	0.4	1.4
Bill from nostril	♂	9	10.2±0.2	0.5	4.6
	♀	5	9.9±0.2	0.5	4.8

Teziutlán.—This area was visited briefly in 1950 (Sibley, 1954:277) and 11 specimens were taken of which nine were adults. Two specimens from the collection of the Chicago Natural History Museum were also studied.

Party number 1 collected at Tacopan, 13 kilometers west of Teziutlán at 7400 feet. Towhees were common in the brushy undergrowth of pine-oak woodland, and 47 specimens were taken. Including the 11 adults reported on in 1954, a total of 58 specimens is now available. Of these 55 could be indexed and these range from "9" to "21" with an average hybrid index of "15.2." Measurements are given in table 6.

Table 6

Measurements of Population from Teziutlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	32	47.3±0.4	2.6	5.5
	♀	15	45.2±1.1	4.2	9.3
Wing	♂	34	82.6±0.4	2.4	2.9
	♀	20	78.8±1.4	2.0	2.5
Tail	♂	24	95.2±0.7	3.4	3.6
	♀	16	92.7±1.0	3.8	4.1
Tarsus	♂	35	29.9±0.2	1.1	3.7
	♀	20	28.6±0.2	0.9	3.1
Bill from nostril	♂	35	10.3±0.1	0.4	4.4
	♀	20	9.9±0.1	0.4	4.2

The Teziutlán hybrid population occupies a small basin of pine-oak woodland lying between the edge of the plateau to the east and a low range of hills to the west, beyond which the arid grasslands previously described constitute a barrier. Towhees extend at least to Zaragoza, 12 airline miles west of Teziutlán, and to Rancho San Miguel (Vera-

cruz), eight airline miles northeast of Teziutlán (= Km. 347, on the road to Nautla). To the southeast, toward Las Vigas, a narrow band of suitable habitat extends along the edge of the plateau between 6000 and 8000 feet elevation. This provides a slender, but seemingly unbroken, connection between the Teziutlán basin and the Cofre de Perote-Mount Orizaba region.

20 km. N Perote.—This locality is near the edge of the plateau at 7800 feet, approximately 13 miles southeast of Teziutlán and 12 miles north of Perote. The land is cultivated, but dense brush occurs in ravines. Pines are present, but with little undergrowth, and towhees are not common.

Table 7

Measurements of Population from 20 km. N of Perote

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	49.1±0.8	2.9	5.9
	♀	12	46.8±0.6	2.0	4.3
Wing	♂	12	83.3±0.5	1.7	2.0
	♀	12	78.2±0.8	2.6	3.3
Tail	♂	12	96.6±1.0	3.4	3.5
	♀	5	90.5±1.1	2.5	2.7
Tarsus	♂	12	29.7±0.2	0.2	0.7
	♀	12	28.8±0.2	0.6	2.1
Bill from nostril	♂	12	10.3±0.2	0.5	5.1
	♀	11	10.1±0.1	0.5	4.7

The 23 specimens range from "6" to "18" with an average hybrid index of "11.6." Table 7 contains data on measurements.

6 km. W Las Vigas.—This locality is approximately 10 miles southeast of the one previously described. The pine-oak woodland is dense and the undergrowth is thick. Towhees were found near 8600 feet but were not common. The 18 specimens collected in 1954, plus two in the British Museum (N.H.) from Las Vigas taken in 1888, range from "3" to "12" with an average index of "7.3." See table 8 for measurements.

Table 8

Measurements of Population from 6 km. W of Las Vigas

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	54.0±0.6	2.2	4.1
	♀	6	49.9±1.5	3.8	7.5
Wing	♂	12	84.1±0.8	2.7	3.2
	♀	6	79.2±0.8	2.0	2.6
Tail	♂	11	97.0±1.0	3.2	3.3
	♀	6	92.0±1.6	4.0	4.3
Tarsus	♂	12	31.1±0.2	0.7	2.2
	♀	6	29.4±0.5	1.1	3.8
Bill from nostril	♂	12	10.4±0.2	0.5	4.9
	♀	6	10.3±0.2	0.4	3.6

The shift in average hybrid index from the Teziutlán area ("15.2") to Las Vigas ("7.3") is extremely rapid. Over this distance of 23 airline miles the shift is 7.9 hybrid index units or .34 units per mile. This change is not as rapid as that between Cerro El Fraile and Las Joyas, Michoacán (.614/mile) but it compares closely with the shift between Cerro Grande and Cerro Viejo (.32/mile) and between Cerro Viejo and Cerro García, Jalisco (.33/mile) as previously reported (Sibley, 1954:264–273).

The El Fraile-Las Joyas shift is apparently the result of the vastly different ecological situations prevailing at these two localities which are 21 miles apart. The Cerro

Grande-Cerro Viejo and Cerro Viejo-Cerro García shifts reflect the influence of large gene pools at each end of the gradient on the small intervening mountain-top populations. The rapid shift in the Teziutlán-Las Vigas area is due, seemingly, to this same effect. Introgression from the large *erythrophthalmus* populations between Pachuca ("22.4") and the Malinche area ("22.0") impinges upon the Teziutlán-Las Vigas gradient from one side while the Cofre de Perote *ocai* population exerts its influence from the other. The intervening populations, especially those between Teziutlán and Las Vigas, are small. Two specimens in the British Museum (N.H.), collected on the Cofre de Perote in 1889, have hybrid indexes of "2" and "3."

Cofre de Perote-Mount Orizaba.—The Cofre de Perote rises to more than 14,000 feet approximately 10 miles south of Las Vigas. The elevation drops to approximately 8000 feet at the south base of the Cofre, 20 miles south of Las Vigas, then rises rapidly southward to the summit of Mount Orizaba, 18,696 feet. The summit of Mount Orizaba is 43 miles south-southwest of Las Vigas and 13 miles north-northeast of Chalchicomula (= Ciudád Serdán). Twenty-four miles south of the summit, at Puerto Morelos, the altitude is 8000 feet.

The forest has been cleared on the western slope of Mount Orizaba up to approximately 10,000 feet. Originally these levels were covered with pines and oaks. Brush and small trees now occur in the ravines and on uncultivated areas. Between 10,000 and 10,500 feet, firs and alders are mixed with pine-oak woodland. A shrubby undergrowth of *Baccharis, Lupinus,* and other shrubs provides towhee habitat.

The occurrence of towhees in this region is complex. Both species are present, *erythrophthalmus* from approximately 8000 to 10,500 feet, *ocai* from 10,000 to at least 11,000 feet. Both are common in the overlap zone and occasional hybrids have been collected. Of 117 specimens, representing both species, 19 show evidence of hybridization (Sibley, 1950:162). As indicated in figure 4, a similar low incidence of hybridization is also present at Puerto Morelos and, so far as is known, at Zoquitlán. The *ocai* population of the Mount Orizaba area is in genetic contact with the Cofre de Perote population and on through the Teziutlán region to the *erythrophthalmus* populations of the Tlaxco-Pachuca area. The *erythrophthalmus* population of the Mount Orizaba-Puerto Morelos section apparently does not extend north much beyond Chalchicomula but just where it stops is not known. No specimens of *erythrophthalmus* are known from the Cofre de Perote. Another unknown factor is the amount of contact between the Mount Orizaba populations and that of Mount Malinche. Between Malinche and Orizaba there is a range of low hills, sparsely vegetated with oaks, junipers, and various xerophytes. This does not appear to be highly favorable for towhees but may permit some dispersal between Malinche and Orizaba. On the map (fig. 1) this connection is indicated by a "?" and arrows. Further work in this area is required to assess its influence.

Puerto Morelos.—Twenty-four miles south of the summit of Mount Orizaba, at 8000 feet, the road from Tehuacán, Puebla, to Orizaba, Veracruz, passes through this small village which is located at the highest point of the pass. The steep drop down the Cumbres de Acultzingo begins just east of Puerto Morelos. Oak woodland with *Baccharis* brush on the hillsides is the principal native vegetation. Pines occur in part of the area.

This locality was first visited in 1949 by R. J. Newman (Lowery and Dalquest, 1951:642–643) who collected one specimen each of *ocai* and *erythrophthalmus*. Neither showed evidence of hybridization but were found only 100 feet apart. In 1950, 13 specimens of *erythrophthalmus* and seven of *ocai* were obtained. Complete sympatry was established and evidence of hybridization was found (Sibley, 1954:277–278).

In 1954, party number 1 collected 53 *erythrophthalmus* and 20 *ocai,* providing a total from this locality of 67 *erythrophthalmus* and 28 *ocai.*

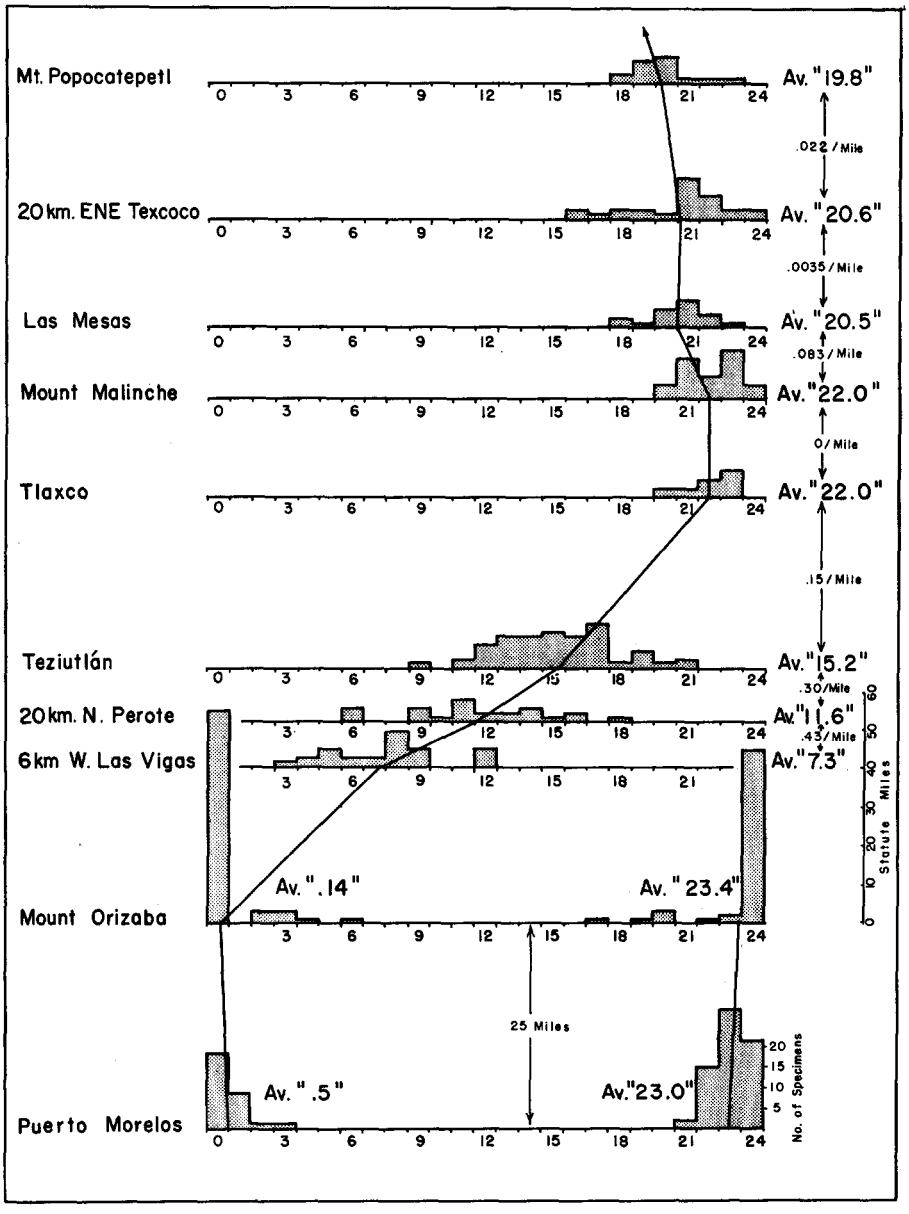

Fig. 4. Histograms of some hybrid populations in eastern México. Average hybrid indexes are connected by the line between samples. The shift in hybrid index units per air line mile is indicated. Except for the bottom sample the distances between base lines are proportional to actual air line distances between populations.

The *erythrophthalmus* range from "21" to "24" with an average hybrid index of "23.0." The *ocai* range from "0" to "3," averaging "0.5." The situation at Puerto Morelos is thus virtually identical to that on the west slope of Mount Orizaba. See tables 9 and 10 for measurements.

Zoquitlán.—In 1950 three specimens from "Zoquitlán, Puebla" in the collection of

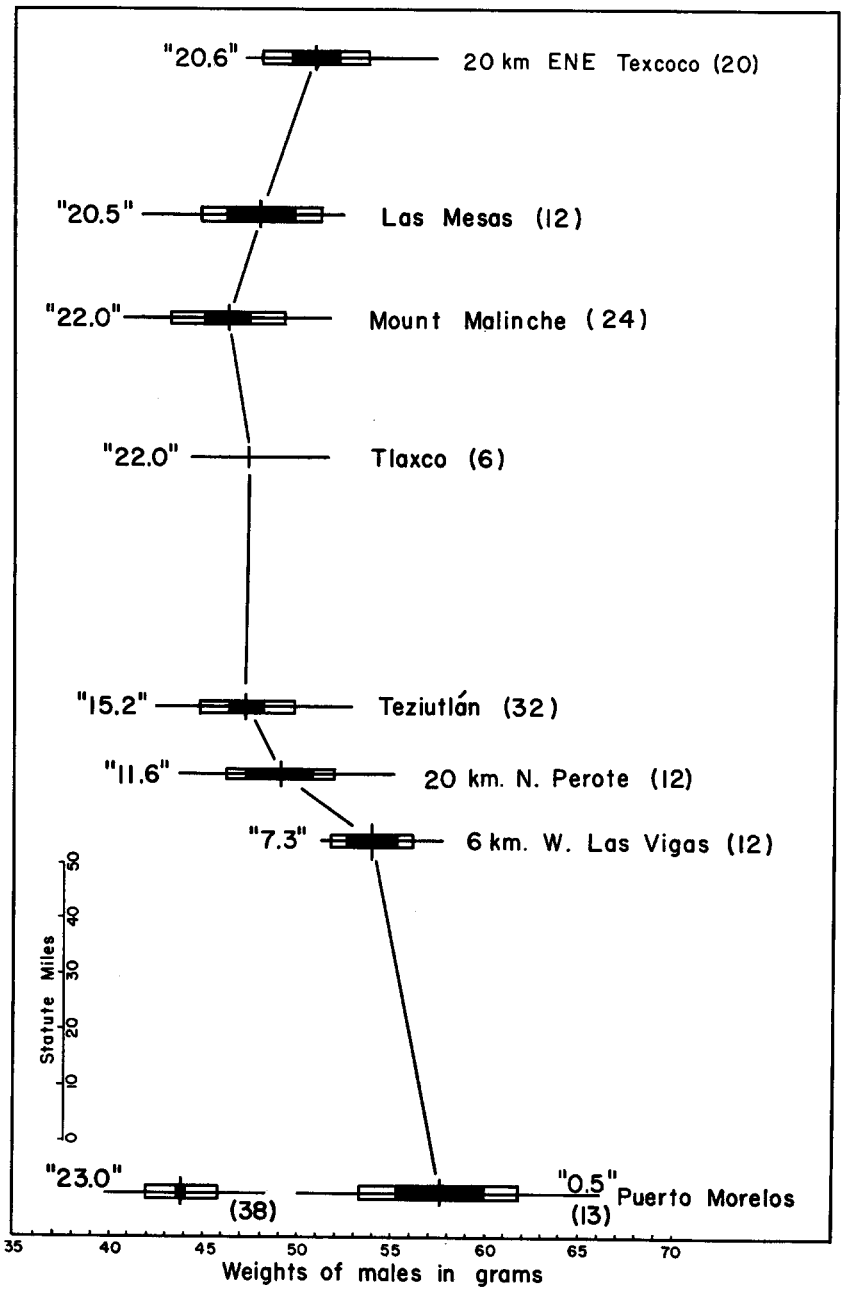

Fig. 5. Statistical analysis of weights of hybrid male red-eyed towhees from eastern México. Numbers in quotes are average hybrid indexes based on color; numbers in parentheses indicate number of specimens in the sample. Horizontal lines represent range; open rectangles indicate one standard deviation; solid black rectangles indicate twice the standard error of the mean; means are indicated by a vertical line; distance between samples is proportional to actual air line distance between populations; the angles formed by the lines connecting the means are proportional to the shift in weight between populations.

Table 9
Measurements of Population of *Pipilo erythrophthalmus* from Puerto Morelos

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	38	43.9±0.1	1.9	4.4
	♀	15	43.1±1.0	3.7	8.6
Wing	♂	44	83.3±0.3	2.0	2.1
	♀	20	78.9±0.4	1.6	2.0
Tail	♂	33	97.2±0.4	2.4	2.5
	♀	15	92.2±0.7	2.7	2.9
Tarsus	♂	43	28.4±0.2	1.0	3.5
	♀	20	27.6±0.4	1.8	6.5
Bill from nostril	♂	42	10.0±0.1	0.4	4.5
	♀	20	10.1±0.1	0.2	2.2

Table 10
Measurements of Population of *Pipilo ocai* from Puerto Morelos

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	13	57.7±1.1	4.1	7.1
	♀	7	56.1±1.9	5.0	8.9
Wing	♂	14	85.2±0.5	1.9	2.2
	♀	10	80.6±0.8	2.4	2.9
Tail	♂	13	98.9±1.1	3.9	4.0
	♀	4	92.3		
Tarsus	♂	14	30.8±0.2	0.9	3.0
	♀	10	30.8±0.5	1.5	4.9
Bill from nostril	♂	14	10.7±0.1	0.2	1.4
	♀	10	10.8±0.1	0.3	3.0

the Museo Nacional de la Historia Natural in Mexico City were examined (Sibley, 1954:278–279). One was a pure *ocai*, one a pure *erythrophthalmus*, and the third a hybrid with a summated index of "15."

Party number 2 collected at this locality, 35 miles southeast of Puerto Morelos, in August, 1954. The ridge forming the edge of the plateau reaches 9000 feet in altitude a short distance west of the town of Zoquitlán. To the east the slope drops rapidly through cloud forest to the lowlands of Veracruz. The western slope is drier and drops away to the arid valley south of Tehuacán. Near the summit of the ridge, pine-oak woodland, interspersed with cornfields, is the dominant vegetation. In this area, between 8000 and 9000 feet, the two species of towhees occur in sympatry, but neither seemed abundant. One specimen of *ocai* ("0") and four of *erythrophthalmus* were collected. The latter average "23.0," one being "22," two "23," and one "24." See tables 11 and 12 for measurements.

These specimens suggest that the situation at Zoquitlán is similar to that at Puerto Morelos and on Mount Orizaba, but additional material is needed from this area. In twenty-five miles, south of Zoquitlán, the land descends to 4000 feet in the valley of the Río Santo Domingo. As previously noted this valley, with its tributaries, isolates the Mount Orizaba-Zoquitlán highlands from the mountains to the south and west in Oaxaca.

Cerro San Felipe.—Collections have been made near the village of La Cumbre at 9000 feet, five miles northeast of the summit of Cerro San Felipe, in 1946, 1948 (Sibley, 1950:151–155), and 1954 when party number 2 obtained four *erythrophthalmus* and 17 *ocai*. To date a total of 31 adult *P. e. oaxacae* and 65 adult *P. o. brunnescens* have

Table 11

Measurements of Population of *Pipilo erythrophthalmus* from Zoquitlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	3	43.6		
	♀	1	(40.0)		
Wing	♂	3	80.9		
	♀	1	(79.0)		
Tail	♂	2	97.8		
	♀	1	(92.6)		
Tarsus	♂	3	28.2		
	♀	1	(28.1)		
Bill from nostril	♂	3	9.6		
	♀	1	(10.0)		

Table 12

Measurements of Population of *Pipilo ocai* from Zoquitlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	1	(62.8)		
	♀				
Wing	♂	1	(87.2)		
	♀				
Tail	♂	1	(102.5)		
	♀				
Tarsus	♂	1	(30.7)		
	♀				
Bill from nostril	♂	1	(11.4)		
	♀				

been examined from the highlands of Oaxaca; most of them have come from the Cerro San Felipe region. No convincing evidence of hybridization has, as yet, been detected.

At La Cumbre the two species are sympatric and abundant. As noted in the 1950 paper (Sibley, *op. cit.*:155), "these two forms react as good species in Oaxaca."

Although the absence of evidence of hybridization in this sample of 96 specimens does not prove that occasional hybrids are not produced, it does indicate that the incidence is less than at Puerto Morelos or on the west slope of Mount Orizaba. From Puerto Morelos the sample size (95) is the same, but of these at least 44 show some indication of introgression. Measurements are given in tables 13 and 14.

Table 13

Measurements of Population of *Pipilo erythrophthalmus* from Cerro San Felipe

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	14	42.9±0.2	2.7	6.2
	♀	10	40.5±0.6	1.8	4.4
Wing	♂	16	84.4±0.5	1.9	2.2
	♀	12	80.6±0.7	2.4	2.9
Tail	♂	15	95.4±0.6	2.4	2.5
	♀	12	92.0±0.9	3.0	3.3
Tarsus	♂	16	28.4±0.2	0.8	2.8
	♀	12	28.0±0.2	0.7	2.4
Bill from nostril	♂	16	10.1±0.3	0.1	1.1
	♀	12	9.9±0.1	0.4	3.8

Table 14

Measurements of Population of *Pipilo ocai* from Cerro San Felipe

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	31	61.3±0.6	3.4	5.5
	♀	22	58.5±0.8	3.8	6.5
Wing	♂	33	88.0±0.4	2.1	2.4
	♀	23	83.9±0.4	1.8	2.1
Tail	♂	32	105.1±0.7	3.8	3.6
	♀	20	98.8±0.8	3.4	3.4
Tarsus	♂	33	31.5±0.2	1.1	3.5
	♀	24	30.1±0.2	1.1	3.6
Bill from nostril	♂	33	11.5±0.1	0.6	5.4
	♀	23	11.2±0.1	0.5	4.6

Tlaxiaco.—Sixty-five miles west of Cerro San Felipe is the peak of Cerro Yucuyacua, rising to 11,074 feet. Party number 2 collected at 5800 feet near the town of Tlaxiaco which is on the north slope of Cerro Yucuyacua. The 10 specimens obtained may all be scored as "24" but, in some, there are suggestions of *ocai* influence which, if other specimens showing strong evidence of hybridization were also present, would logically be attributed to local introgressive effects. These include small amounts of white in the throats of four specimens, chestnut shaft streaks in the crown feathers of one, and some clouding of the tail spots of one. Similar variations occur in populations of *erythrophthalmus* in the United States, many hundreds of miles from the nearest *ocai* population.

Table 15

Measurements of Population from Tlaxiaco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	9	43.5±0.7	2.3	5.2
	♀	1	(42.6)		
Wing	♂	9	85.0±0.8	2.5	2.9
	♀	1	(80.3)		
Tail	♂	8	98.9±1.0	2.8	2.8
	♀	1	(93.9)		
Tarsus	♂	9	28.6±0.3	1.0	3.4
	♀	1	(29.3)		
Bill from nostril	♂	9	10.2±0.1	0.3	2.7
	♀	1	(11.0)		

For the present, therefore, it seems best to consider that these individuals represent "pure" examples of *erythrophthalmus,* but the area near Tlaxiaco, and west toward the Sierra Madre del Sur of Guerrero, should be more thoroughly explored. It is possible that a population of *ocai* occurs on the higher parts of Cerro Yucuyacua. Measurements are given in table 15.

The area near Tlaxiaco is covered with pine-oak woodland where it is not under cultivation. A similar forest seems to be present to the summit of Cerro Yucuyacua.

DISCUSSION

The information in this paper functions mainly to fill in detail and to add substance to speculations made in previous publications. Inevitably some new questions have been raised by this study. Since the beginning of this investigation in 1946, the situation in the Mount Orizaba-Puerto Morelos area has been recognized as of special interest. The

picture, as outlined in the present paper, is now much clearer than it was 11 years ago, but we are now even more convinced that this area deserves further detailed study. The principal question to be answered is this: Why should there be a seemingly unimpeded introgressive gradient from *erythrophthalmus* in the Pachuca area through the Teziutlán hybrids to the *ocai* on Mount Orizaba while these latter birds can exist in sympatry with another *erythrophthalmus* population with but little hybridization? In other words, why have the two species on Mount Orizaba and at Puerto Morelos not formed a hybrid population similar to the one at Teziutlán?

A second question relates to the situation in the mountains of western Oaxaca (for example, Cerro Yucuyacua) and eastern Guerrero. So little is known of this area that the present question must be restricted to a recognition of the need for exploration of the region between Cerro San Felipe, Oaxaca, and the mountains east of Chilpancingo, Guerrero.

The sympatric situation on Cerro San Felipe, Oaxaca, remains unchanged by the material collected in 1954. There is still no evidence of hybridization and no indication that appreciable dispersal occurs across the Río Santo Domingo barrier (see Sibley, 1954:287). We remain convinced that the patterns of variation observed in the Mexican red-eyed towhees are the result of hybridization and introgression.

In a recent paper (Sibley, 1957) the results of hybridization in birds have been considered in some detail. There is considerable evidence that hybridization is occasionally an important evolutionary factor and that the ultimate effects depend largely upon the direction of natural selection upon the hybrid genotypes. If the hybrids are not at a selective disadvantage, in comparison with the pure parental populations, the result will be introgression leading to swamping of the differences between the parental forms. Following a period of increased variability a new adaptive peak will become established, the variability will decrease to a "normal" amount, and a single, freely interbreeding population will have been re-established.

On the other hand, if the hybrids are selected against, they function as a source of selection against the individuals of both parental species which enter into mixed pairs. Any mechanism which reduces the incidence of mixed pairs is thus selected for with the result that, as long as the interaction continues, the isolating mechanisms of the parental species are reinforced relative to one another. Actual hybridization is not required to achieve "reinforcement" of isolating mechanisms or of characters which respond to interspecific competition. Any interaction between species which results in deleterious competition or the wastage of gametes will act as a source of selection tending to reduce that competition. It is apparently this source of selection which has brought about the diversity in species specific characters in sympatric species.

In the Mexican towhees, we may be observing several levels of these processes. So far as we can determine there is no evidence that selection is operating against the hybrids in the Teziutlán population or in the hybrid populations in Jalisco and Michoacán (Sibley, 1954). In these areas swamping may be in progress. The situation in the Mount Orizaba-Puerto Morelos section, where there is a low incidence of hybridization although both species are abundant and sympatric, suggests that selection in this area may be against the hybrids and that reinforcement is in progress. We do not necessarily favor this explanation and present it only as a possibility. It is difficult to believe that selection against hybrids could be reinforcing the isolating mechanisms of the Mount Orizaba birds faster than introgression from the Teziutlán population is breaking them down. We prefer to await further study of this situation before proposing an explanation of this problem.

The above remarks also serve to introduce our comments concerning the suggestion

by Brown and Wilson (1956:61–62) that "character displacement" may account for the characteristics of the hybrid populations of Mexican towhees. By "character displacement" these authors mean the same thing we have called "reinforcement." We might reconcile these two terms by the statement that the process of reinforcement results in character displacement (see Brown and Wilson, *op. cit.*:59). In other words, interspecific responses, when selected against, result in the reinforcement of characters which will act to reduce competition, gamete wastage, and the like. Brown and Wilson agree with this but favor the term "character displacement" when taxonomic characters are involved.

Although we agree (Sibley, 1957) with the interpretation of Brown and Wilson concerning the situation in the rock nuthatches (*Sitta neumayer* and *S. tephronota*) of Iran, we do not find evidence that the variational patterns in the Mexican towhees may readily be interpreted as due to the same causal factors. In the rock nuthatches selection against interspecific responses has resulted in the reinforcement of characters (facial mask) which apparently function in species recognition, and in changes of feeding structures (bill) which act to reduce competition for food. It seems quite appropriate to call this "character displacement" in the sense intended by Brown and Wilson. In the towhees the situation is more complex. In some areas such as at Teziutlán and Pátzcuaro, introgression is, apparently, resulting in swamping of the differences between *ocai* and *erythrophthalmus* while in Oaxaca there is no evidence of hybridization. To complicate the picture further there is the low incidence of hybridization on Mount Orizaba and at Puerto Morelos. As previously noted, it does not seem possible to decide definitely whether introgression in these areas has not yet become extensive or whether selection is against the hybrids and reinforcement of isolating mechanisms is in progress. If such reinforcement should be occurring, it would be appropriate to call it "character displacement" due to selection against hybrids. This, as noted by Brown and Wilson (*op. cit.*: 49), is not a new concept. Because one of us (Sibley, 1957) has recently reviewed the problem in some detail, we prefer to refer interested persons to that review rather than to repeat the discussion here. We may say that we find no serious disagreement with the idea of "character displacement" when equated with the concept of "reinforcement." This concept was first proposed by Fisher (1930), discussed by Sturtevant (1938), and it has been developed in detail by Dobzhansky (1940, 1951).

Brown and Wilson (*op. cit.*:62) call attention to the danger of using the greater variability of a population as an indication that it is of hybrid origin. We acknowledge this danger and agree further with the comments by Miller (1955:11) on the subject. To support their belief that high variability is not always a reliable criterion for the identification of a hybrid population, Brown and Wilson cite data on the size of the tail spot in the populations of *Pipilo erythrophthalmus* studied by Dickinson (1952). Brown and Wilson note that the coefficient of variation in this character is 12 in the northeastern United States and 22 in the Florida population. Since these are areas far removed from the influence of *ocai* these high coefficients of variation cannot, say these authors, be ascribed to hybridization. We agree that hybridization is not involved in this instance, but neither is the variability of the tail spot in the Florida race significantly greater than in the other populations of *erythrophthalmus*. Brown and Wilson have here fallen into a common error in the application of the coefficient of variation. It is simply this.

The coefficient of variation is a measure of variability relative to the mean. This statistic has several faults and limited usefulness. For example, if the standard deviation remains constant and the mean increases, then the coefficient of variation simply decreases as the mean increases. If the mean is a constant and the standard deviation

changes, then a comparison of the coefficients of variation is identical with a comparison of the standard deviations except for division by a constant. In some situations, there is a linear relationship between the mean and the standard deviation and, although both decrease, they may decrease at the same rate resulting in the same value for the coefficient of variation. In these instances the coefficient of variation is of some usefulness. However, if one wishes to consider the variability of a character in several subspecies the mean and standard deviation should be examined separately. The mean gives information on the mean value of the population while the standard deviation gives information on the variability in the population.

Using Dickinson's (1952) data on the size of the tail spot, Bartlett's chi-square test for the homogeneity of variances (Snedecor, 1946:251) was computed for the four variances obtained for males and for the four variances obtained for the females. In neither case was the chi-square value large enough to be declared significant at the 5 per cent level. In fact, the probability of obtaining chi-square values as large or larger than those obtained was between .15 and .20 for both sexes. These facts simply mean that the variability in the tail-spot size of Florida towhees is not greater than that in other populations of eastern North America. The example chosen by Brown and Wilson is thus without foundation as a basis for criticism.

The tail-spot size in the Mexican towhee hybrids has been used and measured in a somewhat different fashion from that employed by Dickinson. The latter actually measured the size of the spot in millimeters. In the Mexican hybrids, we have merely assigned specimens to one of five categories on the basis of the "clarity" or "clouding" of the spots. In pure *P. erythrophthalmus* the tail spots are clear white. The influence of *ocai* is indicated in hybrids by progressive clouding with dusky or greenish coloration. Pure *P. ocai* has an unspotted solid green tail. It may be noted that Davis (1957) has shown that the width of the white spot on the fourth rectrix of *P. erythrophthalmus* is smaller in first-year birds than in adults. This should be considered if actual measurements of tail-spot size are used. The method used in scoring *erythrophthalmus* x *ocai* hybrids seems not to be seriously affected by this discovery.

The comments of Brown and Wilson (*op. cit.*:62) concerning the occurrence of chestnut in the pileum of *P. erythrophthalmus* in areas far removed from the Mexican hybrid zones were apparently based upon Dickinson's (1952:332) data. On this point we have nothing to add beyond the discussion in a previous paper (Sibley, 1954:288).

SUMMARY

A collection of 338 specimens representing the Rufous-sided Towhee (*Pipilo erythrophthalmus*), the Collared Towhee (*P. ocai*), and hybrids between them was made in eastern México in 1954. Hybrid populations were analyzed using the "hybrid index" system and measurements of size and weight were made.

Reference to the map, figure 1, will provide a summary of the distribution of populations and their average hybrid indexes. Of particular interest is the situation on Mount Orizaba where the two species are sympatric with a low incidence of hybridization although the Orizaba *ocai* population is in genetic contact with the hybrid population at Teziutlán only 65 miles to the north. In Oaxaca, the two species occur in sympatry with no evidence of hybridization yet found in 96 specimens.

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