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

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THE extensive and complex patterns of variation resulting from hybridization between the Rufous-sided Towhee (*Pipilo erythrophthalmus*) and the Collared Towhee (*Pipilo ocai*) in Mexico have been described in three previous papers (Sibley, 1950, 1954; Sibley and West, 1958). The evolutionary and taxonomic significance of hybridization, with particular reference to birds, has been considered in three additional papers by the senior author (1957, 1959, 1961). Other papers, forming a related series concerned with avian hybridization, are Sibley (1958), Sibley and Short (1959a, 1959b, 1964), Sibley and West (1959), Short (in press), and West (1962).

The present paper is based upon new material collected in 1958 in an attempt to clarify the hybrid towhee situation in eastern and southeastern Mexico.

ACKNOWLEDGMENTS

We are especially grateful to Roger B. Clapp and S. Craig Smith, who assisted the junior author in the collection of the material. The support of the Faculty Research Grants Fund and the New York State College of Agriculture of Cornell University made the field work possible. Field equipment purchased with funds provided by N.S.F. Grant 1845 was utilized.

WEIGHTS AND MEASUREMENTS

All the specimens collected in 1958 were weighed to the nearest tenth of a gram. Linear measurements from the skins were taken with dial calipers to the nearest tenth of a millimeter 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 on the most distal undivided scute; bill, from the anterior margin of the nostril to the tip of the maxilla.

[1] The authors are not close relatives.

HYBRID INDEX

The hybrid index method of analyzing highly variable populations was first developed by Anderson (1949), in a series of studies on plant hybrids, and has since been used in many other studies. This method provides a quantitative evaluation of the complicated color patterns resulting from extensive backcrossing.

The two species of towhees which hybridize in Mexico have been described and illustrated in a previous paper (Sibley, 1950). The following synoptic description presents the six major plumage differences used in this hybrid index.

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 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. Tail spots: white spots on three outer rectrices in *erythrophthalmus*, white spots absent in *ocai*.

For each of these six characters five gradations 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 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. A pure *erythrophthalmus* will score 4 for each of the six characters for a summated score of 24. A more detailed description of this hybrid index is given in the original paper on hybridization between these two species (Sibley, 1950).

Weight is the one character which most closely follows the variation of the hybrid index as seen in a comparison of Figures 1 and 2. The weights of individual birds generally give a good indication of the hybrid index (Correlation coefficient = .87). None of the other four characters measured has such a high correlation with the hybrid index although the means follow much the same pattern as those for weight. The measurements are larger in *ocai* than in *erythrophthalmus*, but due to the large overlap birds cannot be separated by one of these measurements alone. There is usually no overlap in weight between the two species at a locality where they occur in sympatry.

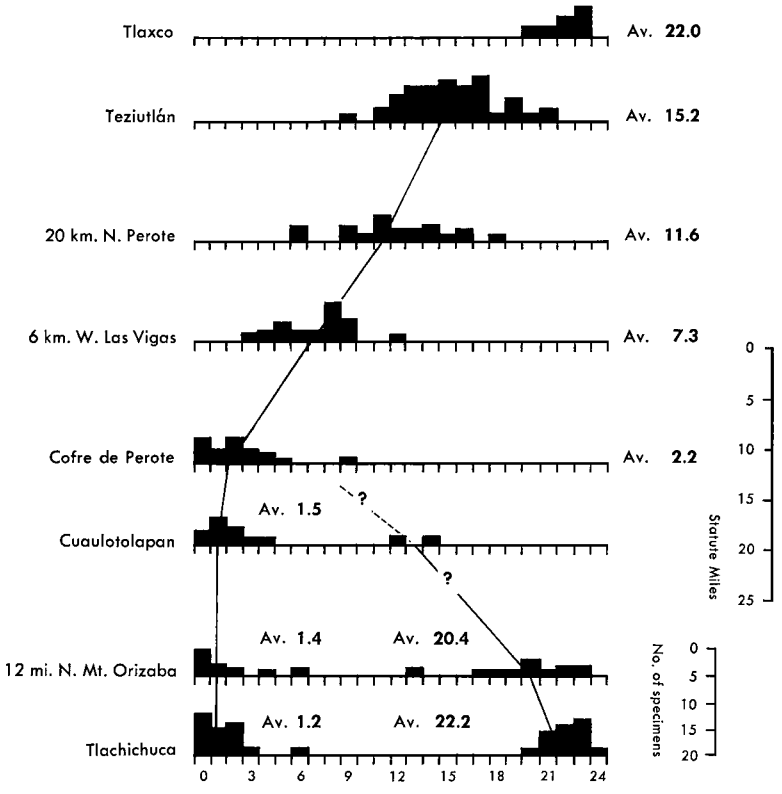

Figure 1. Histograms of some of the eastern plateau populations. Average hybrid indexes are connected by the lines between samples. Except for the top sample the distances between base lines are proportional to the actual air line distances between populations.

SUMMARY OF PREVIOUS RESULTS

In previous papers (Sibley, 1950, 1954; Sibley and West, 1958) the distributions and hybrid indexes of many of the towhee populations have been described. In Figures 3 and 4 this previous work, plus the material described in this paper, is presented. Figure 3 gives the presently known distribution of *Pipilo ocai* and *P. erythrophthalmus* with the hybrid index values of the populations which have been sampled. Figure 4 gives a more detailed view of the eastern plateau populations. Figure 5 presents a diagrammatic synopsis of the eastern plateau populations.

A series of hybrid populations at the western end of the plateau connects *P. erythrophthalmus* in the Sierra Madre Occidental to *P. ocai* in the southwest. The populations in the trans-plateau area form a clinal series

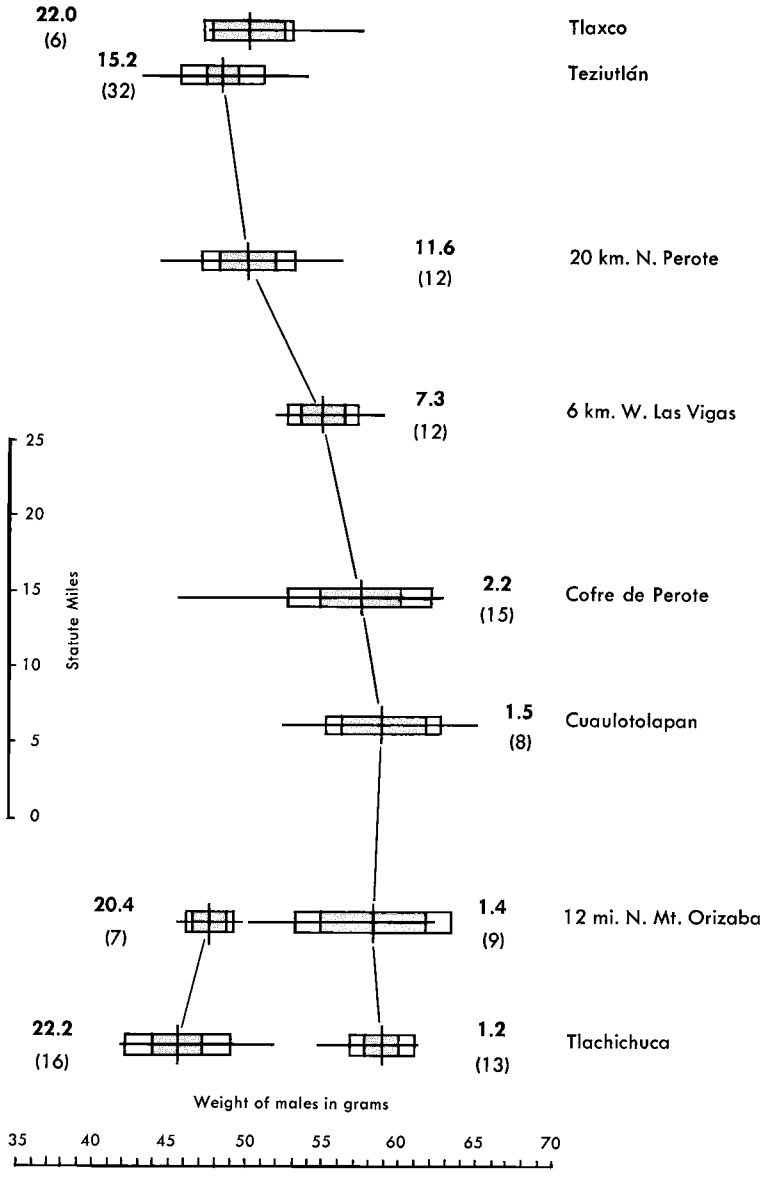

Figure 2. Statistical analysis of weights of male red-eyed towhees from the eastern plateau. See Figure 6 for explanation of symbols.

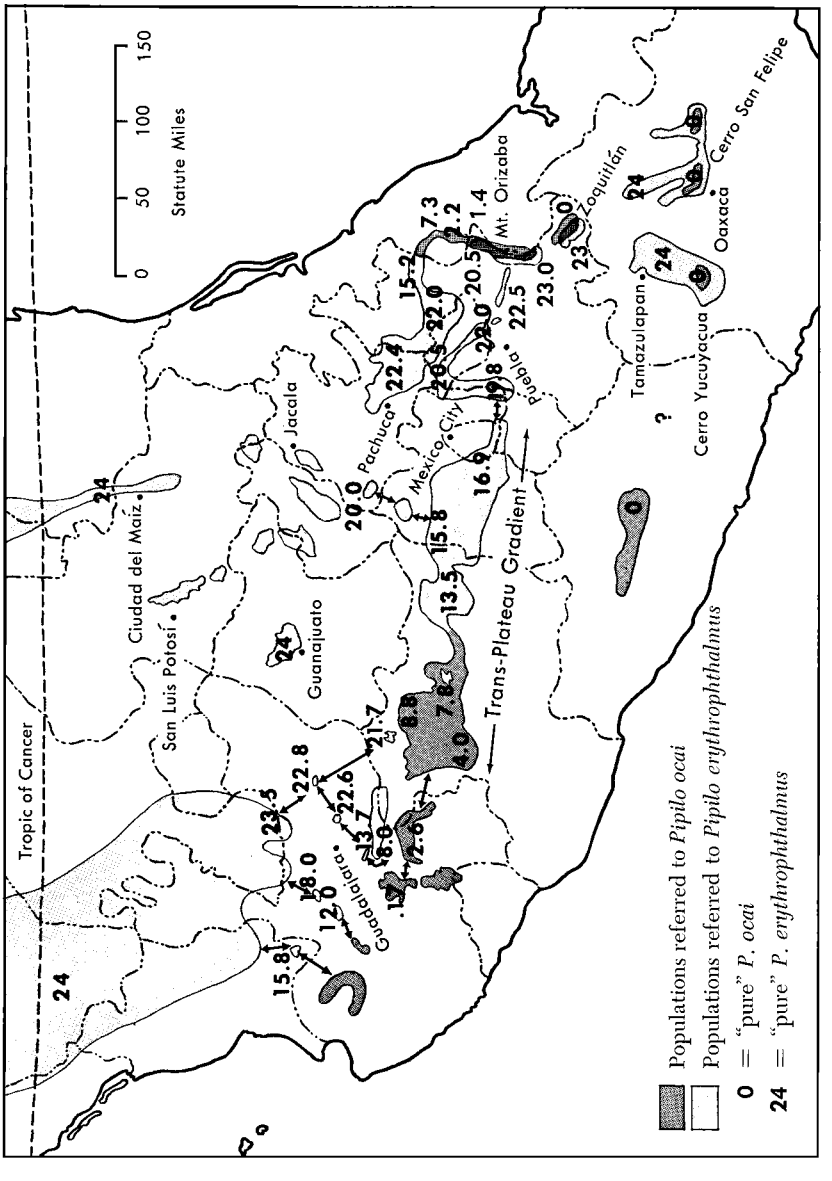

Figure 3. Distribution of the red-eyed towhees in central Mexico.

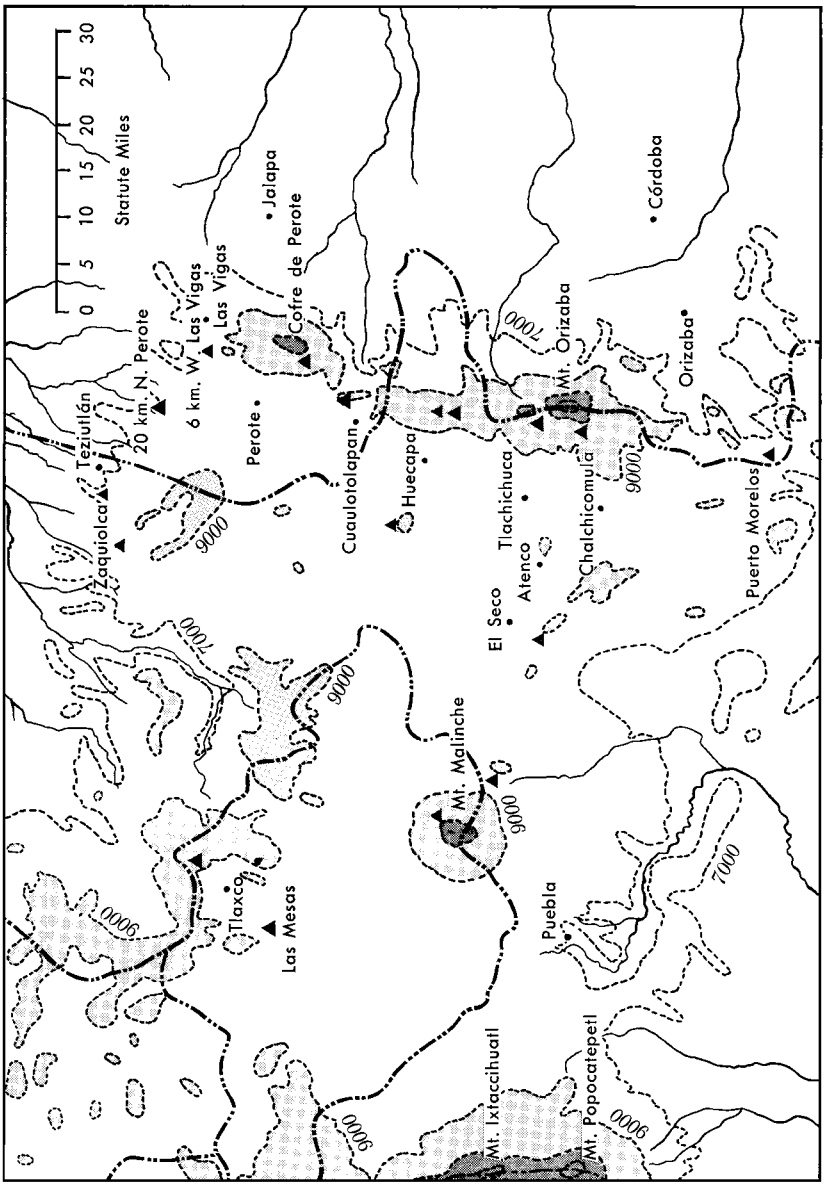

Figure 4. Localities and topographic features in the eastern plateau region.

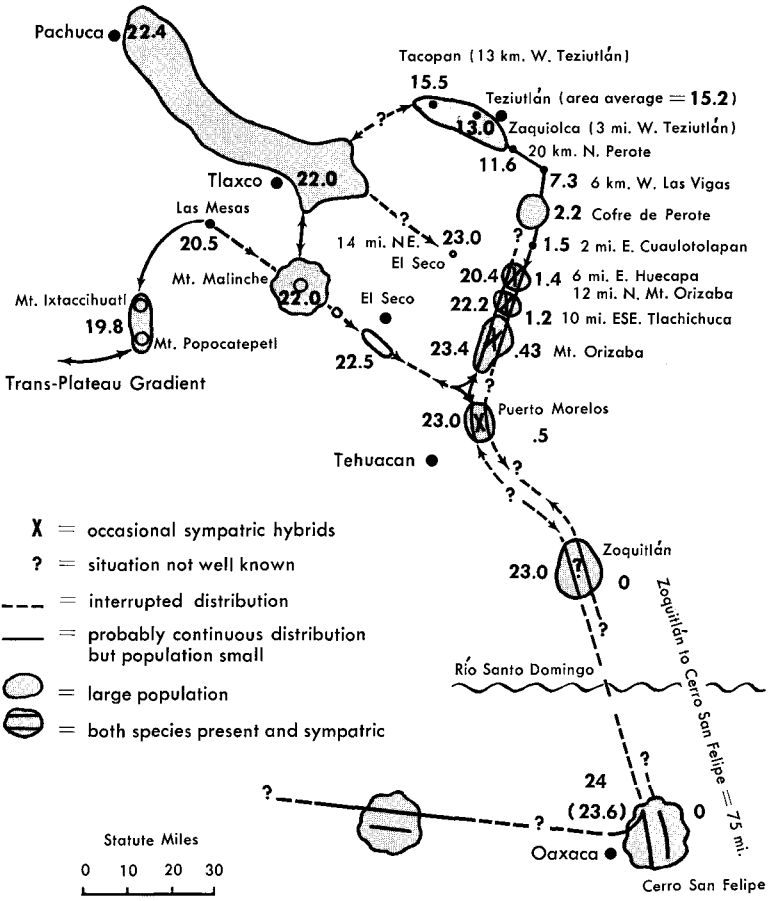

Figure 5. The pattern of hybridization and gene migration in the red-eyed towhees in eastern Mexico.

of populations connecting *erythrophthalmus* in the east (Hidalgo; Puebla) to *ocai* in the west (Jalisco; Colima).

Another hybrid cline connects *Pipilo erythrophthalmus* in the Tlaxco area with *P. ocai* on the Cofre de Perote and Mount Orizaba. On Mount Orizaba the two species exist in sympatry although there is evidence of some hybridization between them.

Since 1946 the two species have been known to exist sympatrically, apparently without interbreeding, on Cerro San Felipe in Oaxaca. However, it was not known how far west *Pipilo erythrophthalmus* extended toward Guerrero, whether *Pipilo ocai* occurred on Cerro Yucuyacua, or if any hybridization occurred there. A previous attempt to reach this area in

1954 failed because of poor roads. In the eastern plateau area there was no known connection of suitable habitat between Mount Malinche and Mount Orizaba, although such a connection was indicated by the previous data. The extent of the range of *Pipilo erythrophthalmus* between Mount Orizaba and the Cofre de Perote was known from only a few specimens. The field work in 1958 was therefore planned to collect in the area between Mount Orizaba and the Cofre de Perote, the area between Mount Malinche and Mount Orizaba, and on Cerro Yucuyacua in Oaxaca.

FIELD STUDY IN 1958

The field party, composed of Roger B. Clapp, S. Craig Smith, and Fred C. Sibley, collected during June and July at the following localities (the number of adult towhee specimens collected at each locality is given in parentheses): 12 miles N Mt. Orizaba, 10,000 feet, Puebla, 14–18 June (12); 14 miles NE El Seco, 8,500 ft., Puebla, 18–19 June (4); 2 miles E Cuaulotolapan, 9,500 ft., Veracruz, 20–22 June (14); Cofre de Perote, 10,000 ft., 5 miles E Tenextepec, Veracruz, 23–25 June (20); 6 miles E Huecapa, 10,500 ft., Puebla, 26–27 June (10); Route 140, 3 miles SW El Seco, 8,000 ft., Puebla, 28–29 June (52); 10 miles ESE Tlachichuca, 10,000 ft., Puebla, 30 June–2 July (40); Cerro Yucuyacua, 10,800 ft., 8 miles S Tlaxiaco, Oaxaca, 5–10 July (63).

The populations from 12 miles north of Mount Orizaba and 6 miles east of Huecapa are only three miles apart and are treated as one population in this paper. The specimens of *Pipilo erythrophthalmus* from Cerro Yucuyacua are combined with the 10 collected near Tlaxiaco in 1954.

ECOLOGICAL DISTRIBUTION

Pipilo erythrophthalmus inhabits a drier, warmer, and more open habitat than does *P. ocai*. In the eastern plateau area this means that *erythrophthalmus* will occur where there is a mixture of brush and pine or oak. Such habitat occurs mainly between approximately 9,000 and 10,000 feet in this area but there is considerable local variation and under suitable conditions *erythrophthalmus* occurs as low as 7,000 feet and up to 11,000 feet. *P. ocai* is mainly restricted to the cooler, moister fir and pine forests of the higher elevations above the usual range of *erythrophthalmus*. Although mainly found between 9,500 and 12,000 feet *ocai* occurs at lower elevations if cool, moist conditions prevail, as at Puerto Morelos. Thus, to some extent, the two species replace one another both ecologically and altitudinally but they overlap in many places.

MOUNT MALINCHE–MOUNT ORIZABA CONTACT

Mount Malinche rises to 14,636 feet and is covered with an open pine forest from approximately 9,500 to 13,300 feet. Collecting in 1954 revealed the presence of *Pipilo erythrophthalmus* in limited numbers and the presence of suitable pathways of dispersal to the Tlaxco area approximately 25 miles to the north (see Figure 4). Towhees were also found on

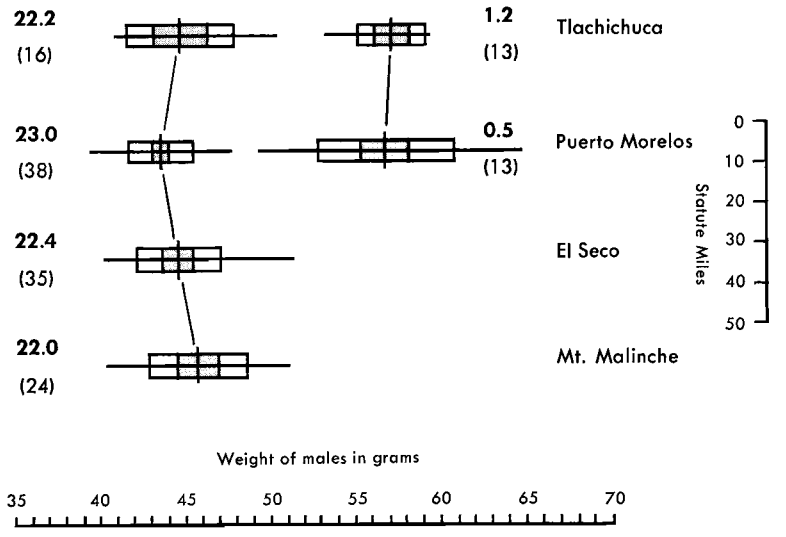

Figure 6. Statistical analysis of the weights of male red-eyed towhees from the area between Mount Orizaba and Mount Malinche. Numbers in boldface type are average hybrid indexes based on color; numbers in parentheses indicate the number of specimens in the sample. Horizontal lines represent range; open rectangles indicate one standard deviation; solid black rectangles indicate twice the standard error of the mean; the mean is indicated by a vertical line. The distances between samples are proportional to the actual air line distance between populations.

a small volcanic cone about 10 miles SE of Mount Malinche, but it was not known if there was a contact between Mount Malinche and Mount Orizaba. Such a contact appeared unlikely from the nature of the vegetation in the intervening area.

Three miles SW El Seco.—This locality is located at 8,000 feet just off Route 140. The vegetation is composed of low oaks and thick brush with taller pines and madrones, and is restricted mainly to the northern side of the low ridge between Mount Malinche and Mount Orizaba. Suitable towhee habitat is about a mile wide at the widest point and extends at least five miles west along the ridge toward Mount Malinche. It continues eastward along the road between El Seco and Atenco for a short distance and then extends eastward along a series of low hills to the north of this road. Towhees were unusually abundant and the 52 specimens collected here have hybrid indexes between 20 and 24 with an average of 22.5 for the series. This value is intermediate between the average hybrid index of the Mount Malinche birds (22.0) and the Mount Orizaba birds (23.4). The average weight (Figure 6) also falls between those of Mount Malinche and Puerto Morelos. Measurements are given in Table 1.

TABLE 1

MEASUREMENTS OF THE SAMPLE OF *P. ERYTHROPHTHALMUS* FROM THREE MILES SW OF EL SECO

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	35	45.1 ± 0.4	2.5	5.5
	♀	17	44.0 ± 1.0	4.0	9.1
Wing	♂	35	86.0 ± 0.4	2.3	2.7
	♀	17	81.4 ± 0.6	2.3	2.8
Tail	♂	31	101.7 ± 0.7	4.0	3.9
	♀	13	96.2 ± 1.0	3.7	3.8
Tarsus	♂	32	28.7 ± 0.2	0.9	3.1
	♀	16	27.8 ± 0.2	0.7	2.5
Bill from nostril	♂	35	9.9 ± 0.1	0.4	4.0
	♀	15	9.9 ± 0.3	1.2	12.2

This contact, then, is apparently providing a pathway for gene flow from the trans-plateau gradient, via Mount Malinche, to the birds on Mount Orizaba and is partly responsible for the *ocai* genes which are present in the *erythrophthalmus* population on Mount Orizaba. The birds of Mount Orizaba exhibit less evidence of *ocai* genes than birds from El Seco.

The original dispersal of *P. erythrophthalmus* to the south may have been along this contact, which still exists between Mount Orizaba and Mount Malinche. Present knowledge of the distribution of *P. erythrophthalmus* rules out dispersal in the past from the Cofre de Perote area or from the west through Guerrero. Dispersal along either of these routes would probably have resulted in present-day populations existing there. Instead, at present we find *P. erythrophthalmus* extending into these areas from the south and east respectively.

MOUNT ORIZABA–COFRE DE PEROTE CONTACT

Previous work showed a hybrid cline to the north (Teziutlán) of the Cofre de Perote and both species occurring, with little hybridization, on Mount Orizaba (Sibley, 1950; Sibley and West, 1958). Previous collections had been made on the SW slope of Mount Orizaba and two specimens from the Cofre de Perote were indexed at 2 and 3. No specimens were available from the 35 miles between these two peaks. In the summer of 1958, 95 specimens were collected at five localities between these peaks to determine the northern limit of *P. erythrophthalmus* on the ridge and to determine the pattern of hybridization and introgression in the intervening populations.

Ten miles ESE of Tlachichuca, 10,500 feet.—This locality is on the NW side of Mount Orizaba some 600 feet below a saddle between it and a

TABLE 2

MEASUREMENTS OF THE SAMPLE OF *P. OCAI* FROM 10 MILES ESE OF TLACHICHUCA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	13	58.2 ± 0.5	2.0	3.4
	♀	8	56.2 ± 0.7	1.9	3.4
Wing	♂	13	86.1 ± 0.8	2.9	3.4
	♀	8	81.8 ± 0.8	2.3	3.8
Tail	♂	8	102.5 ± 0.9	2.5	2.4
	♀	7	95.1 ± 2.2	5.9	6.2
Tarsus	♂	12	31.0 ± 0.2	0.7	2.2
	♀	7	30.0 ± 0.8	2.0	6.7
Bill from nostril	♂	13	10.6 ± 0.2	0.6	5.7
	♀	8	10.6 ± 0.1	0.4	3.7

small peak to the north. Pines start to occur at 9,000 feet, are joined by firs at about 9,500 feet, and disappear entirely around 10,000 feet. The fir forest continues to about 10,800 feet on the ridge and higher on Mount Orizaba. The top part of the ridge is covered with sparse pines and bunch grass. This series of vegetational zones is found along the entire ridge between Mount Orizaba and the Cofre de Perote.

Almost all of the area is planted to potatoes although there are still numerous patches of brush and fir around the edges of the fields or on the steeper parts of the fields. Also the ravines and the forest above 10,500 feet are relatively undisturbed. *P. ocai* and *P. erythrophthalmus* were about equally abundant and both were frequently found in the same isolated patches of vegetation, although no mixed pairs were observed. *P. ocai* occurred in a wider range of habitats, being common in the thick, wet, fir forest, while *P. erythrophthalmus* occurred only on the edge of this area and in the scattered patches of vegetation in the fields.

TABLE 3

MEASUREMENTS OF THE SAMPLE OF *P. ERYTHROPHTHALMUS* FROM 10 MILES ESE OF TLACHICHUCA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	16	45.1 ± 0.8	3.3	7.3
	♀	2	47.1		
Wing	♂	16	84.3 ± 0.6	2.4	2.8
	♀	3	79.4		
Tail	♂	15	98.6 ± 0.6	2.4	2.4
	♀	3	92.3		
Tarsus	♂	15	28.7 ± 0.2	0.7	2.4
	♀	1	27.2		
Bill from nostril	♂	15	10.0 ± 0.1	0.6	6.0
	♀	2	9.8		

TABLE 4

MEASUREMENTS OF SAMPLES OF *P. OCAI* FROM 12 MILES N OF MOUNT ORIZABA AND FROM 6 MILES E OF HUECAPA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	9	57.6 ± 1.6	4.8	8.3
	♀	1	57.1		
Wing	♂	9	86.0 ± 1.0	3.0	3.5
	♀	1	79.8		
Tail	♂	9	100.2 ± 1.8	5.4	5.4
	♀	1	92.9		
Tarsus	♂	9	31.3 ± 0.5	1.4	4.5
	♀	1	30.1		
Bill from nostril	♂	9	10.5 ± 0.2	0.6	5.7
	♀	1	10.2		

Of the 40 specimens collected here 21 were *ocai* with hybrid indexes ranging from 0 to 6 (average, 1.3). The 19 *erythrophthalmus* range from 21 to 24 (average, 22.5). These scores suggest that occasional mixed pairs may occur but none was seen and no specimens ranked between 6 and 21 were collected. Measurements are given in Tables 2 and 3. This situation is rather similar to that on the SW face of Mount Orizaba (Sibley, 1950), although a larger percentage of the specimens show evidence of hybridization on the NW slope (78 per cent as opposed to 16 per cent on the SW slope).

Twelve miles N of Mount Orizaba, 10,000 feet; and 6 miles E of Huecapa, 10,500 feet.—These two localities are only three miles apart and are considered together. The first is approximately eight miles north of the locality discussed just above. Cultivated fields extend up to 10,300 feet and from here open fir forest reaches to 10,800 feet, with the final 200 to 300 feet to the top of the ridge being open pine and grass. The east side of the ridge did not seem to have any suitable habitat, even along the stream beds, when examined through a binocular. No towhees were found in the open fir woods and they were not common in any of the surrounding area. The 12 birds collected were taken from hedgerows or abandoned fields which had become covered with brush 5 to 10 feet high. In one such area 7 birds were collected and several others seen. The *ocai*-like birds occurred around the edge of this area and the *erythrophthalmus*-like birds occurred both here and in the center of the area.

The second locality of these two was only a few hundred feet below the top of the ridge. Again towhees were uncommon, apparently due to the lack of suitable habitat. *P. ocai* occurred in the firs along the edges of fields and streams and in the thicker areas of fir near the top of the ridge. *P. erythrophthalmus* occurred both along the borders and in the centers

TABLE 5

MEASUREMENTS OF SAMPLES OF *P. ERYTHROPHTHALMUS* FROM 12 MILES N OF MOUNT ORIZABA AND FROM 6 MILES E OF HUECAPA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	7	47.1 ± 0.5	1.4	3.0
	♀	4	45.3		
	♂	1 (index 13)	50.2		
Wing	♂	7	85.4 ± 0.9	2.4	2.8
	♀	4	80.5		
	♂	1 (index 13)	86.9		
Tail	♂	7	100.6 ± 1.3	3.5	3.5
	♀	4	89.7		
	♂	1 (index 13)	101.6		
Tarsus	♂	7	28.9 ± 0.5	1.3	4.5
	♀	4	28.4		
	♂	1 (index 13)	28.7		
Bill from nostril	♂	7	10.1 ± 0.1	0.3	3.0
	♀	4	10.1		
	♂	1 (index 13)	10.0		

of abandoned fields although it was rare above 10,000 feet due to the lack of suitable habitat. To the north the ridge is lower and flatter on top and as a result is extensively cultivated. All of the trees and brush have been removed and there is very little towhee habitat.

Of 22 birds taken, the 10 *ocai*-type specimens range from 0 to 6 (average, 1.4) and the 11 *erythrophthalmus*-type specimens range from 17 to 23 (average, 20.5). In addition there is a single intermediate specimen with an index of 13. These specimens indicate that hybridization does occur in this area although the frequency is not high. The measurements for these specimens are presented in Tables 4 and 5.

Two miles E of Cuaulotolapan, 9,500 feet.—This locality lies atop a low ridge which is situated between the Cofre de Perote and the northern extension of the ridge from Mount Orizaba, and is approximately 10 miles north of the previous localities. Suitable habitat is limited to the brush and trees lining the streams and this occurs mostly above 9,300 feet. There is a gap of about three miles between the last suitable habitat here and the nearest suitable habitat on the Cofre de Perote. The three days collecting produced only 14 birds and the sighting of 3 others. This probably represents a large percentage of the population along about three miles of the ridge.

Of the 14 specimens 12 are of the *ocai* type and have an average hybrid index of 1.5 and a range of 0 to 4. One bird has a hybrid index of 14 and one of 12. These last two specimens are treated separately in the analysis of measurements in Table 6.

TABLE 6

MEASUREMENTS OF THE SAMPLE OF *P. OCAI* AND HYBRIDS FROM 2 MILES E OF CUAULOTOLAPAN

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	8	58.1 ± 1.3	3.6	6.2
	♀	4	59.1		
	♀	2 index 12 and 14	47.8		
Wing	♂	8	84.8 ± 0.6	1.7	2.0
	♀	4	80.8		
	♀	2 index 12 and 14	79.7		
Tail	♂	6	101.3 ± 1.0	2.8	2.8
	♀	4	92.6		
	♀	2 index 12 and 14	91.6		
Tarsus	♂	8	30.4 ± 0.4	1.2	3.9
	♀	4	29.6		
	♀	2 index 12 and 14	29.3		
Bill from nostril	♂	8	10.5 ± 0.1	0.3	2.8
	♀	4	10.4		
	♀	2 index 12 and 14	10.4		

Cofre de Perote.—This locality is on the southwest side of the peak of the Cofre de Perote and only eight miles north of the previous locality. Pines appear at about 9,500 feet and continue to 9,800 feet. Here they begin to be replaced by fir which continues to approximately 11,000 feet, where it gives way to open pine forest. Between 9,800 and 10,000 feet there are many patches of brush and fir and thick hedgerows which are inhabited by towhees. Above 10,000 feet the vegetation is composed of broad belts of forest separated by equally broad expanses of grass and lupine. These belts run parallel to the slope, following the drainage pattern. Towhees were very abundant in this habitat especially along the edges between the forest and the more open areas. The 20 specimens have an average hybrid index of 2.2 with a range of 0 to 9. However, Figure 1 shows that this large spread is due mainly to one bird with a hybrid index of 9. Measurements are given in Table 7.

Previous work (Sibley and West, 1958) had revealed the series of hybrid populations between the Cofre de Perote and Teziutlán to the north (Figures 3 and 4) and it was proposed that the reason for the sharp change in hybrid index in the intervening populations was the large size of the terminal populations. The present series of birds, indicating a large, slightly hybrid population on the Cofre de Perote, further supports this hypothesis. The Teziutlán population is also large and has an average hybrid index of 15.2.

Fourteen miles NE of El Seco.—At this locality there are two volcanic cones which rise to a height of some 9,500 feet. These were the only small peaks near the Mount Orizaba–Cofre de Perote ridge which seemed to

TABLE 7

MEASUREMENTS OF THE SAMPLE OF *P. OCAI* FROM THE COFRE DE PEROTE

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	15	56.4 ± 1.2	4.6	8.2
	♀	5	53.1 ± 2.1	4.8	9.0
Wing	♂	15	85.3 ± 1.0	4.0	4.7
	♀	5	77.6 ± 1.7	3.7	4.8
Tail	♂	15	101.1 ± 1.2	4.5	4.5
	♀	5	90.6 ± 2.6	5.7	6.3
Tarsus	♂	15	30.6 ± 0.3	1.1	3.6
	♀	5	29.3 ± 0.4	0.9	3.1
Bill from nostril	♂	14	10.6 ± 0.1	0.4	3.8
	♀	5	10.1 ± 0.2	0.5	4.9

have suitable towhee habitat. Pines start at about 9,000 feet and continue to the top where firs can be found in the wetter and cooler areas. Only four adults and one immature were collected although several other adults were seen. This population is interesting in being separated from the nearest population to the northwest by 17 miles and from suitable habitat on the Mount Orizaba–Cofre de Perote ridge by about 12 miles. The birds all have a hybrid index value of 23 and all show the same evidence of *ocai* influence, a small white throat patch. It would appear most likely that the population had originally invaded this peak from the northwest and not from the Mount Orizaba–Cofre de Perote ridge. It would be of interest to determine if this is actually a stable isolated population as it now appears from the limited number collected. It would appear that this area was invaded by a small number of birds and that there has been very little gene flow into the population. Measurements are given in Table 8.

Commentary.—The past history of the Mount Orizaba–Cofre de Perote contact seems fairly clear from the knowledge of present distribution (Figure 4). *Pipilo erythrophthalmus* from the north spread toward Teziutlán and south toward Mount Malinche. The birds which reached the Teziutlán–Cofre de Perote region hybridized with *P. ocai* and estab-

TABLE 8

MEASUREMENTS OF THE SAMPLE OF *P. ERYTHROPHTHALMUS* FROM 14 MILES NE OF EL SECO

Item	*Sex*	*Number of specimens*	*Mean*	*Extremes*
Weight	♂	4	43.0	42.0– 43.9
Wing	♂	4	84.3	81.7– 85.6
Tail	♂	4	99.0	94.0–102.1
Tarsus	♂	4	27.9	27.3– 29.1
Bill from nostril	♂	4	10.1	9.9– 10.4

TABLE 9

MEASUREMENTS OF THE SAMPLE OF *P. OCAI* FROM CERRO YUCUYACUA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	37	61.0 ± 0.6	3.4	5.6
	♀	15	58.2 ± 1.1	4.1	7.1
Wing	♂	36	88.9 ± 0.4	2.5	2.8
	♀	16	84.6 ± 0.6	2.6	3.1
Tail	♂	31	105.8 ± 0.8	4.3	4.1
	♀	8	100.1 ± 1.4	4.0	4.0
Tarsus	♂	36	31.3 ± 0.1	0.7	2.2
	♀	14	30.7 ± 0.2	0.9	2.9
Bill from nostril	♂	38	10.8 ± 0.1	0.5	4.6
	♀	13	10.9 ± 0.1	0.4	3.7

lished a series of hybrid populations from the Teziutlán region to the Cofre de Perote. These populations then prevented further advance along this route. Gene flow would be limited by the small amounts of habitat present on each side of the Teziutlán area. Since it is unlikely that an individual bird would cross even half the width of the hybrid zone in its dispersal from its point of origin (the fact that the hybrid zone exists would support this), the only way *P. erythrophthalmus* could spread into this new area would be the genetic swamping out of *P. ocai.* But as mentioned above the series of hybrid populations and their small size would make this a very slow process. Also, because of the large population on the Cofre de Perote, this effect would not spread to any great extent beyond this point.

The *erythrophthalmus* which spread south to Mount Malinche probably crossed to the west side of Mount Orizaba and the Puerto Morelos area. These birds evidently were able to invade in large enough numbers to avoid frequent hybridization with *ocai* and the formation of hybrid populations. *P. erythrophthalmus* then spread north toward the Cofre de Perote. However, the restricted amount of suitable habitat, which permits only very small populations of either species, has produced a situation which permits detection of the results of occasional hybridization, although there has not been a complete breakdown anywhere along the ridge. This situation is unusual in that this is the only area known in which both pure parental types and intermediate hybrids occur at the same locality. A similar situation is known in the genus *Passerina* in the Great Plains of the United States (Sibley and Short, 1959b).

OAXACA POPULATIONS

Cerro Yucuyacua.—This peak is located about 60 miles west of the sympatric populations on Cerro San Felipe. Previous attempts to reach

TABLE 10

MEASUREMENTS OF THE SAMPLE OF *P. ERYTHROPHTHALMUS* FROM CERRO YUCUYACUA

Item	*Sex*	*Number of specimens*	*Mean with standard error*	*Standard deviation*	*Coefficient of variation*
Weight	♂	15	44.0 ± 0.6	2.3	5.2
	♀	4	43.1		
Wing	♂	15	84.8 ± 0.6	2.4	2.8
	♀	4	80.6		
Tail	♂	13	97.3 ± 0.9	3.3	3.4
	♀	4	94.4		
Tarsus	♂	15	28.3 ± 0.2	0.9	3.2
	♀	4	28.0		
Bill from nostril	♂	15	10.0 ± 0.2	0.7	7.0
	♀	4	10.0		

this mountain, in 1954, were not successful, although it was established that *P. erythrophthalmus* was very common in most of the surrounding country. In 1958, pack animals were hired and it was possible to establish a camp at 10,800 feet, about 300 feet below the summit.

P. erythrophthalmus occurs along all the streams, around the corn fields, and in any patches of pine or brush from 7,000 feet up. However, as the streams become narrower the amount of habitat decreases greatly until at 9,000 feet the habitat occurs only in small patches. At 9,300 feet two pairs were seen and three of these birds were collected. One of these pairs was in the same large patch of brush occupied by a pair of *P. ocai* with young out of the nest. From here to 10,000 feet habitat is limited for both species. Above 10,000 feet only one place was found where *P. erythrophthalmus* occurred. This was in the brushy edges around a series of fields at 10,500 feet. Six adults were collected at this locality, which was surrounded on all sides by suitable *P. ocai* habitat.

P. ocai was found in only one place below approximately 10,000 feet. Above this altitude the slope became more gradual and the amount of brush increased greatly. The forest cover on this part of the mountain has been heavily cut over and dense brush has grown up almost everywhere. The cool, wet climate has produced a much more luxuriant growth than that found at lower elevations. As a result *P. ocai* occurred almost everywhere in great abundance and the 54 specimens collected represented only a fraction of the birds in the small area covered by our hunting.

The 54 *P. ocai* have an average hybrid index of 0 and the 19 *P. erythrophthalmus* have an average hybrid index of 23.6 with a range of 22–24. These are the same values found on Cerro San Felipe, which presents a situation similar to the present one. Measurements are given in Tables 9 and 10.

Commentary.—It seems likely that the *ocai* characters which are found in the *P. erythrophthalmus* populations in Oaxaca are the result of introgression from the north and not from local hybridization. The Río Santo Domingo has been proposed as a barrier between the towhees in the Mount Orizaba–Zoquitlán area and those on Cerro San Felipe (Sibley, 1954). This barrier probably is highly effective in relation to *P. ocai* but does not prevent the dispersal of *P. erythrophthalmus* because of its tolerance of warmer and drier areas. As a result there would be introgression of *ocai* genes from the north into the *erythrophthalmus* populations in Oaxaca but no traces of *erythrophthalmus* genes in the Oaxaca *ocai* populations. It has previously been suggested that these traces of *ocai* genes might be similar to those found in towhee populations in the United States and are merely "ancestral" genes. However, the higher percentage of *ocai* characters and the geographic location of the Oaxaca populations would seem to favor the introgression hypothesis.

It thus appears that the populations of *P. ocai* in Oaxaca, and probably also in Guerrero, have been able to maintain reproductive isolation from *P. erythrophthalmus* even in areas in which the two occur in sympatry. In the more than 120 specimens of *P. ocai* from Oaxaca which have been examined there is no evidence of hybridization. If there had been any previous hybridization, or any recent exchange of genes with the populations of *ocai* to the north of the Río Santo Domingo, one would expect to find traces of it in the Oaxaca *ocai* populations today.

At present *P. erythrophthalmus* may be spreading toward Guerrero, although its western limit is still not known. It appears likely that there are other peaks near Cerro Yucuyacua where the two species must come into contact. It also appears unlikely that collecting in these areas will reveal any hybridization or that future collecting on Cerro Yucuyacua will reveal hybridization.

MAN'S INFLUENCE

The effects of agriculture, deforestation, afforestation, irrigation, and other human activities upon native animals are often profound. Because speciation can proceed only when extrinsic barriers prevent gene flow between two diverging conspecific populations it is not surprising to find evidence that human activities sometimes destroy such barriers before speciation is complete and permit secondary contacts between divergent, but still interfertile populations. In Colombia, for example, the destruction of virgin rain forest and the establishment of extensive coffee and banana plantations has permitted a secondary contact between two brush-dwelling forms of the tanager genus *Ramphocelus*. The resulting hybridization has produced a cline in color between two strikingly different-

looking populations (Sibley, 1958). Similarly, across the Great Plains of North America the planting of trees has provided an avenue for increased gene exchange between eastern and western populations of several woodland birds. Hybridization between the eastern and western forms of the buntings, *Passerina* (Sibley and Short, 1959b); the orioles, *Icterus* (Sibley and Short, 1964); the flickers, *Colaptes* (Short, in press); and the grosbeaks, *Pheucticus* (West, 1962) has resulted. Additional examples have been noted by Sibley (1961).

In most of these cases the human activities responsible for the breakdown of the barrier have been quite recent, usually within the last century. In Mexico, however, it is highly probable that human activities modified the ecological barriers between *Pipilo ocai* and *Pipilo erythrophthalmus* at least 300 and possibly as much as 3,000 years ago. There is evidence of continuous occupancy of the Valley of Mexico dating back to ancient times. De Terra *et al.* (1949) believe the Tenexpan Man belonged to a hunting culture which existed about 10,000 to 9000 B.C. After this there was a series of hunting and fruit-gathering cultures which they call the Chalco-Culture Complex. The archaic culture which followed this, sometimes called the Middle Culture, was a well developed agricultural culture (Vaillant, 1941). This is generally placed by most Mexican archeologists from 2000 or 1500 B.C. to 500 or 400 B.C. (Sears, 1952). Therefore, by 1500 B.C. there was a culture which probably cleared land by burning, as in most primitive societies, and provided the disturbed habitat which would increase the likelihood of hybridization.

By 900 A.D., Vaillant (1941) believes, the Teotihuacan Culture which was by then inhabiting the area was forced to move because of crop failure and drying up of the streams due to deforestation. The tremendous quantities of lime cement used in building their temples and cities and the wasteful methods of obtaining charcoal to reduce the limestone were the major reasons for this deforestation. Cook (1949a) reported evidence of heavy erosion dating back to this time. The same author (Cook, 1949b) estimated the population of the Teotlalpan (roughly the northern part of the State of Mexico north of the latitude of Pachuca, an area of 2,300 square km) in 1000 A.D. as being 200,000 compared with a 1940 population of 110,000. Thus in the period around 1000 A.D. there is evidence of extensive alteration of the forest cover and, in some areas, of a higher population than at present. Cook estimates that by 1520 the population of Teotlalpan was 500,000 after a period of reduced population. Cook and Simpson (1948) estimated that the population of Central Mexico was 11,000,000 in 1520 dropping to 6,400,000 in 1540 and to 2,500,000 in 1600. According to an official census in 1793 the population was approximately 3,700,000. From these figures it becomes evident that there must

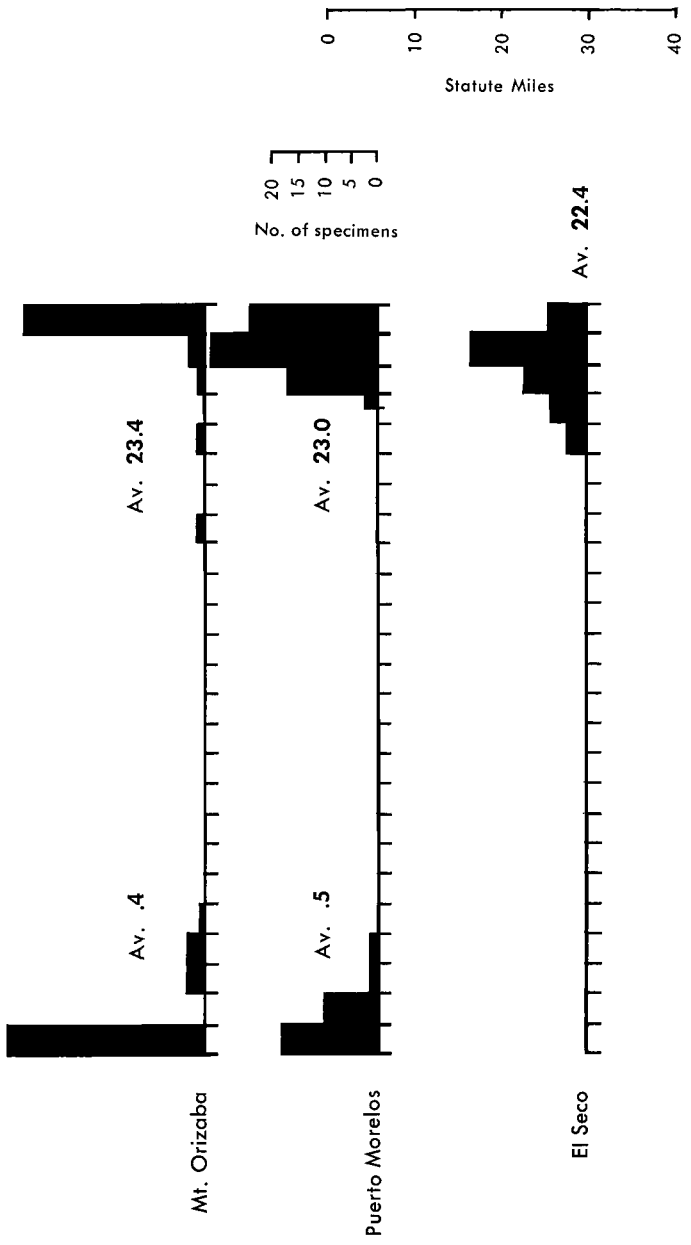

Figure 7. Histograms of populations between Mount Orizaba and Mount Malinche.

have been tremendous changes, in the period from 1000 to 1500 A.D., in the forest cover. These changes were probably as extensive as those produced by the Spanish in their introduction of livestock (Simpson, 1952) and in their mining activities (West, 1949). Cook (1949a) says: "The important cycle of erosion and deposition therefore accompanied intensive land use by huge primitive populations in central Mexico, and had gone far toward the devastation of the country before the white man arrived. Spanish agriculture, deforestation, and livestock grazing merely finished what the red man had already nearly carried to completion." In connection with the erosional evidence he states: "If we wish to give credence to the testimony of the land itself we must concede the passage of 3,000 to 5,000 years since the first establishment of the corn-cultivating, pottery-making cultures on the plateau."

From this evidence it may be assumed that the extensive areas of second-growth brush and resulting interdigitation of *ocai* and *erythrophthalmus* habitats that seem important in increasing the probability of hybridization have existed for at least a thousand years and possibly longer.

DISCUSSION

This study has clarified several aspects of the distribution and variation of the red-eyed towhees in eastern and southeastern Mexico. Of particular interest is the remarkable situation existing in the region that includes Mount Malinche, Mount Orizaba, the Cofre de Perote, and Teziutlán. The new material collected in 1958 now makes it possible to present a fairly clear picture of the effects of hybridization and the pathways of gene migration in this area which was so puzzling in the past (Sibley and West, 1958: 101).

Reference to Figure 5, as well as to Figures 1, 3, 4, and 7 should make the following discussion clear.

The large populations of *Pipilo erythrophthalmus* in the Sierra Madre Oriental (hybrid index 24.0) are in contact with the Pachuca population (22.4) which shows the effects of introgression via the Tlaxco (22.0) area. There seems to be little or no direct contact between the Pachuca area and the population on mounts Popocatepetl and Ixtaccihuatl (19.8) except via the Mount Malinche area. Thus the Mount Malinche–Tlaxco area (22.0) receives a strong *erythrophthalmus* influx from the north and also some *ocai* genes from the west via the long trans-plateau gradient (Sibley, 1950: 169–176). In addition, *erythrophthalmus* genes enter the Malinche population via El Seco (22.5) and *ocai* genes via the Teziutlán (15.2) population. Thus the Malinche–Tlaxco population stands at a crossroads in the network of gene migration pathways, receiving and extending effects in four directions.

Before examining the Orizaba–Perote area in detail it is important to consider the fact that *erythrophthalmus* genes also come into this region from the south. The essentially "pure" population on Cerro San Felipe is apparently in limited contact, via dispersing juveniles, with the Zoquitlán area. As noted previously, both the character evidence and the topography indicate that juvenile *erythrophthalmus* can and do occasionally cross the barrier of the Río Santo Domingo lowlands. It is apparently this exchange route that accounts for the occurrence of chestnut crown streaks in a percentage of the *erythrophthalmus* in Oaxaca. This gives them an average hybrid index value of 23.6 although the sympatric *ocai* show no evidence of hybridization. This population has been considered "pure" (24.0) because the *ocai* characters did not result from sympatric hybridization.

The introgression of *erythrophthalmus* genes from Oaxaca into the Zoquitlán–Puerto Morelos (23.0) area is apparently effective in shifting the *erythrophthalmus* of the west side of Mount Orizaba to 23.4 in spite of the 22.5 influx from El Seco and the still lower values (20.4 and 22.2) produced by the limited hybridization and introgression with *ocai* in the area from Mount Orizaba to the Cofre de Perote.

The series of populations from Tacopán (15.5) and Zaquiolca (13.0) and on south (11.6, 7.3) to the Cofre de Perote is of special interest because these populations form the bridge between the strongly *erythrophthalmus* Tlaxco (22.0) area and the nearly pure *ocai* populations from the Cofre de Perote (2.2) on south along the ridge (1.5, 1.4, 1.2) to Mount Orizaba (.43), Puerto Morelos, and Zoquitlán. In addition, along the ridge between Mount Orizaba and the Cofre de Perote, *erythrophthalmus* and *ocai* populations, both contaminated by introgression, are sympatric and occasionally hybridize.

These facts lead to the most puzzling question: why do not the sympatric populations along the Orizaba–Perote ridge hybridize much more freely and form a single hybrid population, as in the Teziutlán area? This is the question that stimulated the 1958 field work (Sibley and West, 1958: 101).

The 1958 field study showed that the populations of both species along the Perote–Orizaba ridge were sparse and that suitable habitat, for both species, has been severely reduced by human activities. There is little or no habitat intermediate between the types optimal for the two species, thus there is no "hybrid habitat," in Anderson's (1948) sense, that would provide a favorable environment for a hybrid population as, for example, the Teziutlán area affords. The lack of an intermediate habitat will, theoretically, select against hybrids and could be an important factor in reducing the incidence of sympatric hybridization because such selection will act to reinforce interspecific isolating mechanisms (Sibley, 1957,

1961). This explanation is attractive but only speculative. To determine whether or not it is correct will require even more detailed field studies.

The large terminal gene pools at each end of the Cofre de Perote–Mount Orizaba ridge must also have profound effects on the small intervening populations. The large *erythrophthalmus* (23.4) population on Mount Orizaba easily swamps any *ocai* genes received by introgression via the Perote–Orizaba ridge. Similarly the *ocai* populations on the ridge and the Cofre de Perote absorb the trickle of *erythrophthalmus* genes from the south. The tenuous contact between the north end of the *erythrophthalmus* series and the *ocai* on the Confre de Perote is a partial barrier, erected by human agriculture, that further reduces the opportunity for introgression. Nevertheless, there is some gene exchange between the Cofre de Perote population and the *erythrophthalmus* populations of the Orizaba ridge as shown by the fact that the hybrid indexes of these populations form a gradient pattern from 20.4 at 12 miles north of Mount Orizaba to 22.2 at Tlachichuca and 23.4 on the west slope of Mount Orizaba. Some *ocai* genes are also contributed by sympatric hybridization but the gradient clearly indicates introgression between the Cofre de Perote *ocai* (2.2) and the *erythrophthalmus* of the Orizaba area. Because the populations of *erythrophthalmus* along the Perote–Orizaba ridge are so sparse the *ocai* effect is quickly swamped in the large *erythrophthalmus* gene pool of the Mount Orizaba–Puerto Morelos area. Figure 5 summarizes this situation.

The gradient in hybrid indexes of the series of *ocai* populations between the Cofre de Perote and Mount Orizaba also testifies to the fact that introgression in this area is more effective than sympatric hybridization in determining the characteristics of the populations. In spite of the occasional sympatric hybrids the gradient progresses smoothly from 2.2 on the Cofre de Perote to 1.5 eight miles to the south near Cuaulotolapan. Twelve miles farther south the index is 1.4 and it drops to 1.2 in another eight or nine miles (at 10 miles ESE of Tlachichuca). On Mount Orizaba the average index is .43. Thus, in a distance of about 32 miles, the average index changes 1.77 hybrid index units or .05 units per mile. The slope of this gradient (see Figure 1) is characteristic for the section of an introgressive cline near one of the terminal species. Several examples are known in Jalisco and Michoacán (Sibley, 1954).

The introgressive gradient from the Mount Malinche–Tlaxco area through the Teziutlán region to the Cofre de Perote, Mount Orizaba, Puerto Morelos, and Zoquitlán is also of interest for taxonomic reasons. This series of populations gradually bridges the morphological gap between the pure *erythrophthalmus* populations of the Sierra Madre Oriental and the virtually pure *ocai* at Puerto Morelos and Zoquitlán. In this respect it presents exactly the same problem as found in the trans-plateau

gradient (Sibley, 1950) and in the several *erythrophthalmus–ocai* gradients in Jalisco and Michoacán (Sibley, 1954). The similarity to the cline from Mesa de los Puercos (23.5) to Cerro Gordo (22.8), Cerro Grande (22.6), Cerro Viejo (13.7), Cerro García (8.0), Mazamitla (2.6), and the mountains of southwestern Jalisco (.17) is striking. The Teziutlán populations (average 15.2) provide an interesting parallel to the Cerro Viejo (13.7) population. Both are at the center of the gradient and both show the expanded variability expected from the recombination of genes resulting from a fertile interspecific cross. The Cerro Viejo sample of 76 specimens ranges from 6 to 20, covering 15 index units. The Teziutlán sample of 55 specimens ranges from 9 to 21, covering 13 index units.

The populations in the center of the trans-plateau gradient (Pátzcuaro, 7.8, and Mil Cumbres, 13.5) exhibit the same variational pattern (Sibley, 1950).

The taxonomic difficulty presented by this type of situation was first encountered during the study of the trans-plateau series. Because of the sympatric populations on Cerro San Felipe and Mount Orizaba it was decided to maintain *ocai* and *erythrophthalmus* as separate species and to view the long introgressive gradients as elongate hybrid zones. For purely nomenclatural purposes the division between *ocai* and *erythrophthalmus* in the trans-plateau gradient was placed at 10 miles east of Morelia, Michoacán. In the present situation this division point would fall between the area 12 mi. north of the town of Perote and Teziutlán, judging from the average hybrid indexes for the samples from 12 mi. north of Perote and from Zaquiolca (= 3 mi. W Teziutlán). South of this point the populations should be referred to *ocai*, north of it to *erythrophthalmus*. However: "This must be recognized as a practical solution to the incompatibility of Linnaean nomenclature in this special situation and should not be regarded as a synopsis of the biological situation" (Sibley, 1950: 176).

The 1958 field work has provided answers to several of the questions posed by Sibley and West (1958) but, as always, additional questions are exposed. It would be instructive to know more about the actual numbers of birds in each of the populations in the eastern plateau area and to determine, in considerable detail, their exact limits of distribution. Thus censuses, transect studies, and a detailed ecological survey of the entire area would be appropriate as a next step. Collecting should be continued to fill in the gaps in the known gradients and to locate additional avenues of gene migration. The situation at Zoquitlán and the precise nature of the Río Santo Domingo lowlands need to be explored. In addition it would be useful to know more about the interspecific interactions that must occur where the two species are sympatric. Observations of their behavior,

especially with regard to the nature of interspecific isolating mechanisms, competition, etc., should be instructive.

SUMMARY

Study of a collection of 215 adult specimens of *Pipilo erythrophthalmus* and *Pipilo ocai* obtained in 1958 in the southern plateau region of Mexico shows the following:

1. The Mount Malinche population is in contact with the populations on the west slope of Mount Orizaba via the El Seco area.

2. The complex situation between Mount Orizaba and the Cofre de Perote (Sibley and West, 1958) is clarified. It seems to involve: (a) sparse, sympatric populations of the two species, each nearly pure but both tainted by introgression; (b) occasional sympatric hybrids, which (c) may be selected against because of the lack of intermediate habitat; (d) large terminal gene pools that quickly swamp the effects of introgression.

3. The population of *P. ocai* on Cerro Yucuyacua in Oaxaca is sympatric with *P. erythrophthalmus* but no evidence of hybridization is evident.

Man's role in providing the ecological conditions favorable for hybridization between the two species of towhees is reviewed. Evidence that such conditions may have been produced more than a thousand years ago is discussed.

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