HYBRIDIZATION IN THE RUFOUS-SIDED TOWHEES OF THE GREAT PLAINS

CHARLES G. SIBLEY AND DAVID A. WEST

INTRODUCTION

The Rufous-sided Towhee *(Pipilo erythrophthalmus)* is a polytypic species ranging from southern Canada to Guatemala in the west and from Maine to Florida in the east. It is absent as a breeding bird from the western deserts and from the mid-continent prairie grasslands. Wherever this species occurs it inhabits brushy undercover and its local distribution is limited by the occurrence of suitable habitat.

The populations of the western half of the continent and those of Mexico and Guatemala (the *maculatus* group, formerly called Spotted Towhees) have white spots on the scapulars, interscapulars and wing coverts. The eastern populations are unspotted or have an occasional small white spot in the positions which are heavily spotted in western birds.

The degree of sexual dimorphism also varies geographically. The males in all races breeding north of Mexico have black heads and backs. The females in the heavily spotted races are dark gray where the males are black, but in the eastern races the females are rich reddish brown on the head and back.

Differences in song have also been considered to be of value in separating the two groups as different species. The differences are real, but they are bridged by the songs of the Floridan and Mexican populations, and intermediate songs occur in the Great Plains populations.

The nomenclatural history of this species has been covered in detail in a previous paper (Sibley, 1950: 116–119), and the proposal to consider the *maculatus* and *erythrophthalmus* groups as conspecific was accepted by the Committee on Classification and Nomenclature of the American Ornithologists' Union in 1954 (Auk, **71**: 312, see A.O.U. Check-list, 5th ed.: 578–582, 1957). Dickinson (1952) has reviewed the character distribution of the populations of eastern North America.

The purpose of the present paper is to describe the secondary intergradation which occurs across the Great Plains between two races of towhees, *P. e. erythrophthalmus* of the northeastern part of the continent and *P. e. arcticus* (a member of the *maculatus* group) of the northern Rocky Mountains and eastern foothills from Alberta to Colorado and Nebraska. This study is based almost entirely upon material collected since 1950.

The term "hybridization" is used here to indicate interbreeding between populations in secondary contact regardless of their taxonomic rank. For a more extensive discussion of this term and its significance see Sibley, 1957.

ACKNOWLEDGMENTS

We are especially grateful to the other members of the field parties who assisted in the Plains: Stuart S. Peters (1954), Fred C. Sibley (1955, 1956, 1957), Lester L. Short, Jr. (1955, 1956), David B. Wingate (1956, 1957), William G. Gibson (1955), Jerome H. Smith (1955) and A. L. Nordby (1955). During field studies in North Dakota in 1953 much appreciated help was received from Dr. J. Frank Cassel, Dr. and Mrs. Robert T. Gammell and Mr. Merrill C. Hammond. In Nebraska Dr. William F. Rapp, Jr., Mr. Burt Nelson, Mr. and Mrs. George Blinco, Mr. Carl Smith and Miss Doris Gates assisted us in various ways. The late Mr. Paul Gilbert and Mr. Lloyd Vance of the Nebraska Game, Forestation and Parks Commission helped to make our work in their state a pleasant and rewarding experience. Dr. N. R. Whitney, Jr., of Rapid City, South Dakota, kindly helped us during field studies in his area. Dr. John Davis read the manuscript and has made several helpful suggestions. The field work in 1953 and 1954 was supported by a grant from The American Academy of Arts and Sciences. The National Science Foundation (NSF-G-1832) supported the work in 1955, 1956 and 1957. Certain equipment, vehicles and other assistance were provided by the New York State College of Agriculture at Cornell University. The kindness of the officials of the several museums from which loans were obtained is gratefully acknowledged.

MATERIALS AND METHODS

Between 1953 and 1957, 515 adult specimens of *Pipilo erythrophthalmus* were collected in the Plains. Additional material from the following collections has been used for comparisons: Museum of Vertebrate Zoology, U. S. National Museum, Saskatchewan Museum of Natural History, Royal Ontario Museum of Zoology, Manitoba Museum and the Cornell University collection.

Standard measurements (wing, tail, bill from nostril, and tarsus as described in Sibley, 1950: 113 and Sibley and West, 1958: 87) were taken on all specimens. Weights were obtained for most of the recently collected specimens. These data have been treated statistically.

A hybrid index, similar to that used for the Mexican towhee hybrids

(Sibley, 1950, 1954; Sibley and West, 1958) was devised. As previously noted the males of eastern and western populations differ primarily in the degree of dorsal spotting. The females differ in spotting and in the color of the head and back. These characters were used in the hybrid index as follows:

Males and Females

"0" = unspotted coverts, scapulars and interscapulars, but with a large white patch at base of primaries as in typical *P. e. erythrophthalmus.*

"1" = trace of spotting on feathers mentioned above; white patch at base of primaries reduced.

"2" = spotting abundant; white in primary bases about half of maximum.

"3" = only slightly less spotted than typical *P. e. arcticus;* white in primary bases only a trace.

"4" = fully spotted as *P. e. arcticus;* no white at base of primaries.

In addition, the females were indexed for head and back color as follows:

"0" = rich brown head and back as in typical *P. e. erythrophthalmus.*

"1" = slightly "muddied" brown.

"2" = brownish-gray.

"3" = gray, as in typical *P. e. arcticus.*

Thus the males have a hybrid index base of from "0" to "4", the females from "0" to "7".

This index ignores the presence of small white dorsal spots in many specimens of eastern *P. e. erythrophthalmus* far from the Plains. Neither is the head color of eastern females invariably the rich brown of score "0". It seems best, however, to score the Plains specimens on the above scale rather than to attempt to include these variations in the index. The spotting in eastern birds far from the Plains may be due to "ancestral" genes or to recurrent mutations which are favored by selection in local habitats. It is highly unlikely that introgression from the western populations is the only cause, although it may be in progress.

FIELD STUDIES

When the proposal to merge the two groups was made in 1950 very little was known about the distribution of breeding towhees in the Great Plains. Judging from the few specimens available and from the meager literature records it appeared that a contact might be present "in southwestern Manitoba where the two forms have been recorded within 20 miles of one another" (Sibley, 1950: 119). To test this hypothesis the senior author visited parts of North Dakota and Manitoba in July, 1953 and collected 11 adults. Localities included the Souris River near Kenmare and near Upham, the Turtle Mountains and the Pembina River. Towhees were uncommon along the Souris River and in the Turtle Mountains but fairly numerous in the brushy cover along the Pembina River near Walhalla, North Dakota. In 1954 Stuart S. Peters collected 26 adults on the Pembina River in southern Manitoba.

When field work on avian hybrids in the Great Plains was begun in 1955 it was assumed that towhees would not be found as common breeding birds in the central Plains. A search of the literature, including such local journals as the Nebraska Bird Review, gave little indication of the presence of this species in the breeding season. It was a surprise therefore to find that towhees are one of the most abundant breeding birds in the riparian thickets of the Plains. Along the Niobrara River the population density is as high as any we have encountered in the United States or Mexico.

Between 1955 and 1957 field parties collected in Nebraska, South Dakota and Colorado. Most of the 478 adult specimens were obtained in Nebraska.

During these several field trips we made an attempt to determine the distribution of towhees in the central Plains. Most of the major river valleys were visited and a search for towhees was made in all areas of apparently suitable habitat. The map (Fig. 1) indicates the localities visited and the average back spotting index for each locality at which towhees were collected. Where no index number appears the birds were not found, or at least no towhees were obtained. Approximately 3 days were spent at each locality. Numbers of specimens and frequencies of hybrid index scores for localities in the hybrid zone are given in Table 1.

The character gradients will be described under four headings: (1) The Platte River Transect; (2) The Niobrara River; (3) South Dakota, and (4) North Dakota and Manitoba.

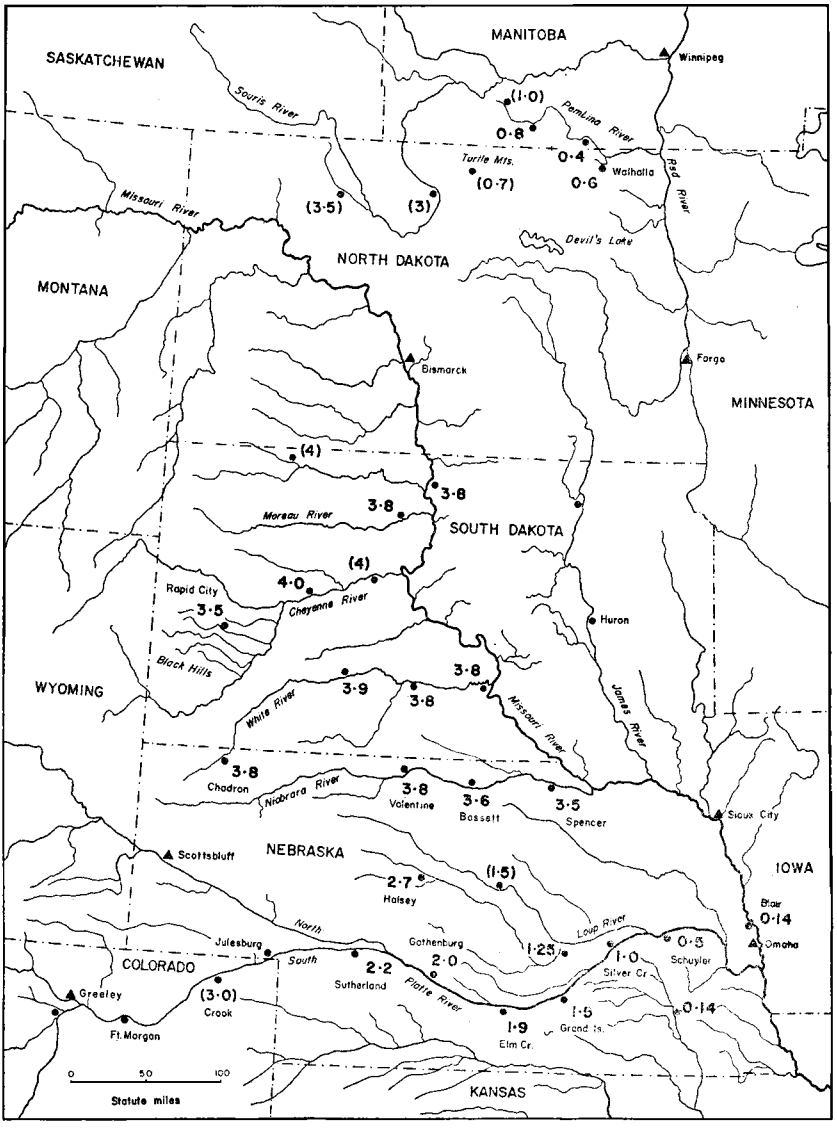

FIGURE 1. Localities mentioned in the text. Solid circles represent collecting localities; average hybrid index for back spotting is given for each locality where specimens were obtained. Where no number appears no specimens were taken. Numbers are in parentheses where fewer than five specimens were collected. Triangles indicate cities.

TABLE 1

FREQUENCIES OF HYBRID INDEX SCORES FOR LOCALITIES IN THE HYBRID ZONE

Locality	Number ♂♂	Number ♀♀	Back Spotting Index 0	1	2	3	4	Average
Crete, Nebr.	6	1	6	1	—	—	—	0.14
Platte River Transect, Nebr.								
Blair and Omaha	11	3	12	2	—	—	—	0.14
Schuyler	13	4	11	4	2	—	—	0.5
Silver Creek	13	3	8	3	3	1	1	1.0
Grand Is. and St. Paul	33	12	8	18	11	7	1	1.4
Elm Creek	23	9	3	11	7	7	4	1.9
Gothenburg	35	14	3	17	8	12	9	2.0
Sutherland	18	2	—	8	3	5	4	2.2
Nebr. National Forest								
Halsey	20	9	—	4	7	12	6	2.7
Niobrara River, Nebr.								
Spencer	8	2	—	—	1	3	6	3.5
Bassett	54	21	—	—	—	18	57	3.6
Valentine	17	7	—	—	—	4	20	3.8
Chadron, Nebr.	18	3	—	—	1	2	18	3.8
South Dakota—White River								
Chamberlain	21	7	—	—	—	5	23	3.8
Murdo	8	2	—	—	—	2	8	3.8
Kadoka	6	3	—	—	—	1	8	3.9
Cheyenne River, S. D.								
N. of Midland	—	1	—	—	—	—	1	(4)
Bridger Creek	7	1	—	—	—	—	8	4
Rapid City	11	1	—	1	—	3	8	3.5
Moreau River, S. D.	21	1	—	—	—	5	17	3.8
Mobridge, S. D.	20	5	—	—	—	5	20	3.8
N. D. and Manitoba								
Walhalla, N. D.	3	2	3	1	1	—	—	0.6
Windygates, Man.	10	3	8	5	—	—	—	0.4
Clearwater, Man.	9	1	4	5	—	1	—	0.8
Riverside, Man.	3	—	1	1	1	—	—	1.0
Turtle Mts., N. D.	2	1	1	2	—	—	—	(.7)
Bantry, N. D.	1	1	—	—	—	1	—	(3)
Kenmare, N. D.	1	1	—	—	—	1	1	(3.5)

1. THE PLATTE RIVER TRANSECT

Suitable towhee habitat in the Plains is found chiefly along the major streams. The Platte River, which flows from west to east across Nebraska, was selected for intensive study because it provides a natural "bridge" of vegetation from the Rockies to the Missouri River.

Our easternmost locality was at Blair, Nebraska on the Missouri River, 25 miles north of Omaha. From this point camps were established at 50 mile intervals along the Platte to Greeley, Colorado on

the South Platte River. This transect covers approximately 500 miles along the river and from 1000 feet elevation at Blair to 4800 feet at Greeley.

The habitat preferred by towhees along the Platte consists chiefly of cottonwoods (*Populus*) with a thick undergrowth of dogwood (*Cornus sp.*), False Indigo (*Amorpha fruticosa*), Prickly Ash (*Xanthoxylum americanum*), Snowberry (*Symphoricarpos sp.*) and other shrubs. The actual understory species vary from locality to locality, but the form of the vegetation is similar. Willow thickets also harbor towhees which were among the common species at each locality to the forks of the Platte. West of this point, on the South Platte River, the strip of riparian woodland is narrower and drier and the cottonwoods are smaller and more scattered. The understory becomes thinner and towhees are uncommon or absent. Four camps were made in Colorado west of the forks of the Platte: Julesburg, Crook, Fort Morgan and Greeley. At Julesburg three towhees were seen, none taken; 50 miles west, near Crook, two males were taken, indexing "2" and "4" respectively in back spotting. West of Crook no towhees were found and the nearest populations are apparently those in the Rocky Mountains above Fort Collins and Loveland, Colorado (*P. e. montanus*).

Figure 2 shows the frequency distribution of hybrid index scores for the specimens taken at the Platte River camps. The shift per mile in average hybrid index is also indicated. It will be seen that even as far west as Sutherland, Nebraska, just west of the forks of the Platte, the sample averages only "2.2" in back spotting. This westward influence of eastern birds is in marked contrast to the situation along the Niobrara River (see below) where nearly pure western towhees are found far down the river to northeastern Nebraska. The factors which seem to permit these contrasting situations will be discussed in the Niobrara River section.

Although few females were collected along the Platte River, histograms of hybrid index scores for color and back spotting have been constructed. They show a cline similar to that for back spotting alone and have not been included for that reason. The samples of females from Sutherland averages "4.5" in hybrid index on a scale of from "0" to "7".

There is no significant difference between birds from the Missouri River at Blair and those of the forks of the Platte in any of the measurements taken. Samples from Montana (*P. e. arcticus*) likewise are not significantly different from those of eastern Nebraska in mensural characters.

One camp was made in the Nebraska National Forest (Bessey

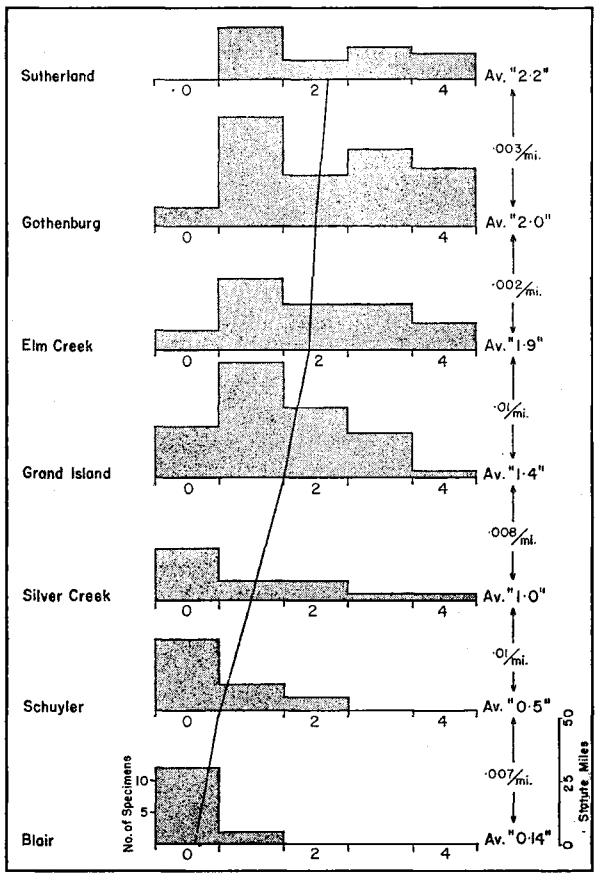

FIGURE 2. Histograms of hybrid index for back spotting for localities in the Platte River Transect. (The Grand Island sample includes eight specimens from St. Paul, 25 miles to the north.) The shift in hybrid index units per mile of river is indicated.

Division) on the Middle Loup River near Halsey in the Sandhills. This forest was planted in the Sandhills grassland starting in 1902, and at the present time a considerable area of native grassland is covered by yellow pine *(Pinus ponderosa),* red cedar *(Juniperus virginiana)* and other evergreen species. Parts of this forest have sufficient undergrowth to harbor towhees. In 1955, 20 males and nine females were collected here. The average back spotting index of these birds is "2.7". This population is almost totally isolated from the towhee populations of the Platte and lower Loup Rivers, although a small contact must exist with the latter river system. To the north

lies a large part of the Sandhills, with very little suitable habitat. The colonization of this area by towhees was probably accomplished by birds from the rivers to the southeast and by migrants on their way to the north.

2. NIOBRARA RIVER

In 1955 four localities were visited on the Niobrara River and in northwestern Nebraska: Spencer, Holt County; near Bassett, Keya Paha County; Valentine, Cherry County; and near Chadron, Dawes County. Through much of its course the Niobrara River runs in a gorge the sides of which are cut by tributary gullies. These small side valleys are usually wooded with oaks *(Quercus macrocarpa),* elms and other trees with dense undergrowth (e.g. *Symphoricarpos sp.*). Pines are common on the higher slopes and towhees are extremely abundant in many areas. These large populations are apparently connected through the pine forests of the upper Niobrara with those of northwestern Nebraska. The pines occur at least as far east as Holt County, about 60 miles from the junction of the Niobrara with the Missouri in northeastern Nebraska. As can be seen on the map (Fig. 1) spotted towhee influence is strong far east along the Niobrara. The sample of ten adults from Holt County averages "3.5" in dorsal spotting (1 specimen = "2", 3 = "3", and 6 = "4"). The explanation of this stituation is found in the character of the vegetation along the Niobrara and its connections to the west. The Platte River (see above) occupies a broad sandy valley with an essentially eastern riparian woodland, at least as far west as the forks of the Platte. West from there the habitat is largely unsuitable for towhees, as has been pointed out. The woodland connection to the east, however, is solid. The Niobrara, on the other hand, is wooded with a more western type of vegetation and the habitat has an apparently good contact with the west. There is also a good woodland connection to the east via the Missouri River but the large population of towhees in the western areas apparently exerts a strong influence through the pine forest contact and tends to swamp out eastern towhee genes which might otherwise predominate in north-central Nebraska. The western influence is further strengthened by the fact that eastern towhees are rare north of the Missouri in eastern South Dakota. Thus all eastern towhee influence must come up the Missouri. In southern Nebraska the greater number of wooded streams from the east, which flow parallel to the Platte, certainly helps to permit gene flow from populations of eastern towhees into central and western Nebraska. In northern Nebraska the midpoint in the cline of intergradation will surely be

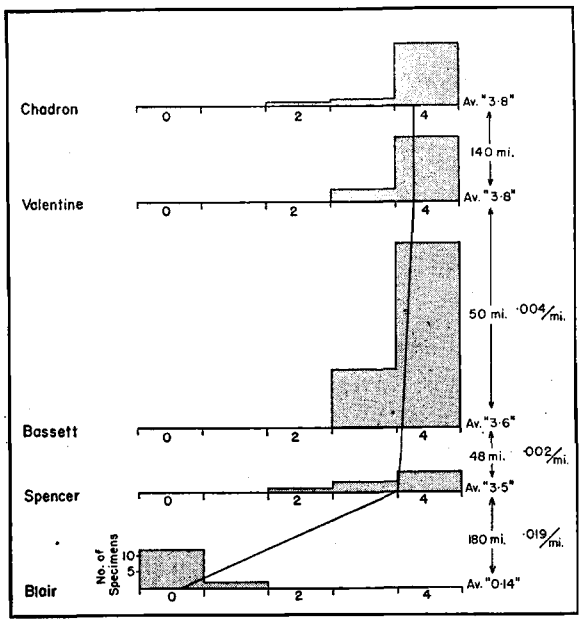

FIGURE 3. Histograms of hybrid index for back spotting for Blair and the Niobrara River localities. See Figure 2 for explanation.

found to lie on the Missouri between Blair and the mouth of the Niobrara River and probably well east of this latter point.

Histograms of hybrid index for Niobrara River localities are shown in Figure 3. The sample from Blair is included also, and the shift per mile of average hybrid index along the Missouri and Niobrara Rivers is shown. Comparison with the similar chart of hybrid index for Platte River specimens (Fig. 2) shows that the shift per mile between Blair and Spencer is more rapid than any along the Platte. Female head color was also indexed and shows a situation similar to that of back spotting alone.

3. SOUTH DAKOTA

In 1955, 11 localities were visited in South Dakota. Two of these were on the James River in eastern South Dakota. The others were west of the Missouri River. The James River was found to be unsuitable for most woodland birds, at least north of Mitchell about 70 miles north of the Missouri River. It seems apparent that there is an important gap between eastern and western towhees between the Missouri River and the woodlands of extreme eastern South Dakota. The existence of a gap is further indicated by the pattern of back

spotting of the towhees taken west of the Missouri (Fig. 1). The absence of streams flowing east-west across this strip of land seems important in this regard. Towhees from west of the Missouri are nearly all pure western birds. The relatively low index average for Rapid City ("3.5") is due to one bird indexing "1" in a sample of 12, the rest of which index "3" and "4".

4. NORTH DAKOTA AND MANITOBA

Towhees were obtained at four localities on the Pembina and South Pembina Rivers in North Dakota and Manitoba in 1953 and 1954. In addition three other areas of North Dakota were visited, the Turtle Mountains and the Souris River system in two places. Much of the country between Devil's Lake, the Pembina River and the Turtle Mountains was investigated but no towhees were found. The Turtle Mountains themselves proved to have very few of these birds. Although many areas of apparently suitable habitat were searched for towhees only 3 adults were taken. One was taken on the Souris near Upham, McHenry County and two were obtained near Kenmare on the same river system. It is apparent that towhees occur sparsely across northern North Dakota west of the Pembina River. However, the Pembina itself proved to have many towhees and 31 adults were taken at 4 localities. The map (Fig. 1) indicates the spotting index average for all localities. Although strongly eastern in character the Pembina samples show considerable back spotting, especially in the more western localities. Female head color shows a similar pattern.

DISCUSSION

The geological history of the Great Plains, the present pattern of vegetation and the nature of the character gradients in the towhees of the Plains indicate that the present situation is the result of a secondary contact. During the Pleistocene glaciation the eastern and western populations were presumably isolated by unsuitable environmental conditions in the Plains. After the retreat of the glaciers suitable habitat developed along the streams and birds from both sides spread out along these slender riparian connections and re-established a "filter bridge" type of secondary contact along some of the trans-Plains streams. The post-Pleistocene contact has never been on a broad front and thus the amount of gene exchange has been greatly restricted. The large populations on the two sides of the Plains, each adapted to its own environment, easily swamp alien genes entering from the other side. Presumably selection is also removing alien genes

for there is some indirect evidence that the back spotting pattern is indirectly correlated with climatic differences (see below).

Man has been an important factor in the increase of suitable habitat for some species of woodland birds in the Plains. The planting of trees for various purposes in areas which originally were grassland has enabled the eastern and western populations of such species as the Baltimore Oriole *(Icterus g. galbula* and *I. g. bullockii)* to come into broad, freely interbreeding, secondary contacts. Such plantings have probably had but limited influence on the towhees because of the absence of the required dense undercover in most man-made woodlands. In a few areas, for example the Nebraska National Forest at Halsey, a planted woodland has been permitted to develop understory vegetation and towhees are present. If this type of planting should be greatly increased the extent of introgression would presumably also increase.

The geographic distribution of the dorsal color pattern suggests that it has adaptive significance in some way correlated with climate. The races which are spotted dorsally (*maculatus* group) tend to live in areas which are more arid than those occupied by the unspotted *erythrophthalmus* group. The vegetation occupied by the spotted races is usually a "chaparral" formation of woody shrubs without an arboreal cover. The unspotted races tend to occupy the understory shrubbery of eastern deciduous woodlands, a formation of more humid climates. Common observation indicates that the amount of sunlight reaching the ground and producing a sun-dappled pattern will be greater in a chaparral habitat than in a woodland habitat where the canopy will intercept more of the light. Hence we suggest that the dorsal spotting is a cryptic pattern induced by selection through predation and correlated indirectly with climate through the effects described. This explanation is supported by the fact that the least spotted race of the *maculatus* group is *P. e. oregonus* which occurs in the understory vegetation of the coastal forests of the Pacific Northwest. This is a habitat in which a minimum amount of sun-dappling of the ground would be present. In this connection it should not be forgotten that individuals of the eastern populations are also frequently spotted with white on the back and wing coverts (Sibley, 1950: 116–118). The comparison with *P. e. oregonus* is emphasized by the statement by Miller (1897: 276) who wrote as follows concerning a spotted eastern towhee taken at North Truro, Massachusetts, on August 2, 1889. This bird was ". . . normal in all respects except that the scapulars on each side are conspicuously edged with white. The marking is only slightly less extensive than in a specimen of

Pipilo maculatus oregonus taken at Victoria, B. C., on August 1, 1888. Eastern towhees with spotted scapulars have been recorded before but such specimens are always of interest."

SUMMARY

A collection of 515 adult specimens of the Rufous-sided Towhee *(Pipilo erythrophthalmus)* taken in the Great Plains between 1953 and 1957 is described. A secondary post-Pleistocene contact between the eastern (unspotted) and western (spotted) populations has occurred along the streams crossing the Plains. A gradient in the amount of spotting and in female color character is present. Size differences are not significant.

The present situation is one of normal geographic variation in which the area of contact between the eastern and western groups of races is restricted to the narrow riparian strips of habitat. Selection against alien genes helps to prevent marked introgression in both directions. The differences in degree of white dorsal spotting appear to be adaptive.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION, COMMITTEE ON CLASSIFICATION AND NOMENCLATURE. 1954. Twenty-ninth supplement to the American Ornithologists' Union Check-List of North American Birds. Auk, **71**: 310–312.

AMERICAN ORNITHOLOGISTS' UNION, COMMITTEE ON CLASSIFICATION AND NOMENCLATURE. 1957. Check-list of North American Birds, Fifth Ed. 691 pp. American Ornithologists' Union.

DICKINSON, J. C., JR. 1952. Geographic variation in the red-eyed towhee of the eastern United States. Bull. Mus. Comp. Zool., **107**: 271–352.

MILLER, G. S., JR. 1897. Some abnormal color markings. Auk, **14**: 276–277.

SIBLEY, C. G. 1950. Species formation in the red-eyed towhees of Mexico. Univ. Calif. Publ. Zool., **50**: 109–194.

SIBLEY, C. G. 1954. Hybridization in the red-eyed towhees of Mexico. Evolution, **8**: 252–290.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor, **59**: 166–191.

SIBLEY, C. G., and D. A. WEST. 1958. Hybridization in the red-eyed towhees of Mexico: The eastern plateau populations. Condor, **60**: 85–104.

Department of Conservation, Cornell University, Ithaca, New York.

CORRESPONDENCE WITH THE TREASURER

Dr. Charles G. Sibley, Treasurer of the American Ornithologists' Union and Professor of Ornithology at Cornell University, will spend the year from July 1959 to August 1960 in England as a Guggenheim Fellow. Nevertheless, correspondence relating to A.O.U. membership, dues, etc. should continue to be addressed to him to Fernow Hall, Cornell University, Ithaca, New York. Dr. Sibley's personal address in England will be c/o The Edward Grey Institute, Botanic Garden, Oxford.