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CLINES IN THE YELLOW-THROATS OF WESTERN NORTH AMERICA

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The Yellow-throats (*Geothlypis trichas*) of western North America have long been a puzzling group of birds with respect to the variation displayed and the distribution of the various races. The species shows numerous character gradients, instances of regional differentiation, areas of intergradation and interesting mosaics of individual variants. However, attempts to express the picture of variation have led to considerable confusion. This can be judged by the following resumé of the changing concepts, influenced in some instances by the accumulation of new material.

In the early days of avifaunal exploration only one western race was known, *G. t. occidentalis*, described by Brewster (see Allen and Brewster, 1883:158), which was attributed to the whole region west of the Rocky Mountains. Oberholser (1899:257) then separated the yellow-throats of the northern Pacific Coast region as *G. t. arizela*. This was followed closely by Grinnell's description (1901:65) of the race *G. t. sinuosa* from the San Francisco Bay area and at the same time his designation of *G. t. scirpicola* from southern California. Although Ridgway (1902:670-672) recognized *sinuosa*, he synonymized *scirpicola* under *arizela*. Next Swarth (1912:71-73) denied the existence of *arizela* and placed it in synonymy under *occidentalis*. At the same time he pointed out the validity of *scirpicola*.

Grinnell a short time later (1914:202), after an independent study, reached the same conclusion as Swarth that there was no recognizable Pacific coast race *arizela*; according to his concept the name *occidentalis* applied not only to interior birds but likewise to the yellow-throats of northern California and the Pacific Northwest. Van Rossem (1930:297-300) reviewed the yellow-throats of southern California, southern Arizona and Sonora, describing the race *chryseola*. Later (1941:291-292) he described *riparia* from Sonora.

Gabrielson and Jewett (1940:511), in their studies of the birds of Oregon, considered *arizela* a recognizable race. Phillips (1947:122) made a perfunctory statement urging restoration of the name *arizela* but to further complicate things stated that he could not distinguish the type series of males of *occidentalis* from *scirpicola*. About the same time there appeared the description of the race *campicola* by Behle and Aldrich (1947:69-72) who likewise urged recognition of the coastal form *arizela*. A late publication dealing with variation in yellow-throats is a paper by Oberholser (1948) which appeared after the description of *campicola*, in which he describes twelve additional races from North America.

This nomenclatural confusion has diverted attention to some extent from the biological significance of the variation. A systematic review of these western races seems now warranted not only to clarify the taxonomic picture but also to turn attention to an analysis and interpretation of the variation displayed.

In assembling material for such a study a number of people arranged for the loan of specimens and I am indebted to the following in this connection: John W. Aldrich and Herbert Friedmann, United States Fish and Wildlife Service and United States

National Museum collections; A. M. Bailey, Colorado Museum of Natural History; Ira N. Gabrielson; George E. Hudson, Charles R. Conner Museum, State College of Washington; James L. Peters, Museum of Comparative Zoology; Alden H. Miller and Frank A. Pitelka, Museum of Vertebrate Zoology; Robert T. Orr, California Academy of Sciences; A. J. van Rossem, Dickey Collection, University of California at Los Angeles; Kenneth Stager, Los Angeles County Museum. I should like especially to acknowledge the help of John W. Aldrich who agreed to collaboration in describing the race *campicola* which we independently came to realize was another population meriting nomenclatural recognition.

TYPES OF VARIATION

Yellow-throats show variation of several types and as preliminary to the analysis of geographic variation it is desirable to comment briefly on those which are to be attributed to sex, age, individuality and plumage wear.

Sexual variation.—Females are dull and inconspicuously colored as compared with the males. Since they lack the contrasting yellow, white and black patterns of the males, they are more uniformly colored. They are inferior in size, averaging 2 to 3 millimeters smaller in wing length and about the same in tail length. The proportions of bill and tarsal length are comparable to those of the males. Females have not been well represented in the material assembled for study. Consequently the data and comparisons noted beyond apply almost exclusively to males. Females seem less geographically variable than males in color characters and, while females of some well differentiated races can be identified, those of many races are very similar in appearance and make subspecific identification exceedingly difficult.

Age considerations.—To afford an answer to the problem of whether first-year birds differ from adults, there are fortunately two series of birds taken in September containing representatives of both age groups. Of eight males collected in the vicinity of St. George, Utah, from September 9 to 11, five had adult skulls and three were immature. In a series of ten September males from Los Angeles and Orange counties, California, four are designated adults and six immatures based on skull characters. Incidentally, as indicated on the labels of certain other specimens, collectors have found the immature skull condition to persist as late as December. Comparing the examples of the two age categories in each series I can detect no differences in color tone of the dorsum, or of the yellow below, or even in the extent of yellow on the ventral surface. There are no differences either in measurable characters beyond the range of individual variation that one would expect in a series from one location. In some of the immatures the forehead and crown is unicolor, lacking the two contrasting black frontal and white post-frontal bands. This is true even at the bases of the feathers. At first this was thought to be an age difference but other examples of immature specimens have the two regions well defined. In addition some adult breeding specimens from scattered areas lack these contrasting areas. So it would appear that these differences in the series in question are due to individual variation.

Individual variation.—In a large series of the same sex and age and from a single locality, considerable individual variation is manifest in nearly every character. As to the dorsal surface, this affects not only the color tone but also the amount of contrast, if any, between head and back. The color range is from brown on the one extreme to gray on the other with most specimens in any one race favoring some shade of olive or yellowish green. With respect to head and back areas, most specimens have the crown, nape and back concolor. In occasional examples in nearly every race, the head and nape are brown and markedly different from the back color. In such specimens there may

be either a gradual blending of the one region into the other or there may be a sharp line of demarcation between the two areas. The material at hand indicates no increased occurrence of one or the other situation in different geographical regions. Neither have I detected any "linkage" of this situation with other characters. In a few specimens, and particularly noticeable in a skin from Fort Verde, Arizona, a band of lighter color extends transversely across the dorsum at the base of the neck.

The exact tone of yellow of the underparts varies slightly among individuals from the same locality. This is also true of the extent posteriorly of the yellow of the abdomen and belly. In some instances the yellow cuts off rather sharply. In others there is a gradual blending of the yellow into the white, except in those races where the entire underparts are yellow. The flank color varies individually from buff to olive.

The banding of the forehead area is subject to great individual variation, especially the distinctness and width of the postfrontal white stripe. The great majority of males have both a black and a white stripe but a few, as previously noted, lack them, in which specimens the olive green of the crown extends to the base of the bill. The line of demarcation between the black and white is nearly always sharp and clear. In most instances the white breaks off sharply where the olive or green commences. In many examples, however, the line is irregular and in a few the white blends gradually with the green of the crown. In a few specimens, especially among those from coastal southern California, the white extends so far back as to almost cover the head. To some extent this is a matter of wear exposing the underlying white but nevertheless there is great individual variation in the extent of the white. Measurements of the depth of the white made on specimens from the same area indicate that the depth varies from one to seven millimeters. Slight indications of clines appear in this measurable character, and the range of individual variability is indicated in tables 1-7.

Individual variability in the various characters seems to become accentuated in intergradational areas. Indeed this should be the case through mixing of two different racial stocks. This makes for practical problems, however, when people insist on putting racial designations on all specimens. For instance, two examples taken in the breeding season are at hand from Medora, North Dakota, which locality is in an area of intergradation between *campicola* and *occidentalis*. One is like *campicola*, the other like *occidentalis*. In southwestern Utah, most specimens are intermediate between *occidentalis* and *scirpicola* but the male in the Dickey collection from Washington is typical of *scirpicola* and was the basis for van Rossem's (1930:297) extension of the southern race's range into Utah.

Perhaps the most significant item in connection with this individual variation is that within every race extreme individual variants crop up with certain characters that are typical of or represent the average condition of those characters in a neighboring race. Thus a specimen may be taken in the center of the range of one race that resembles more closely some distant form in some character such as dorsal coloration. For instance, in the interior Great Basin population known as *occidentalis* the flanks of most specimens are buff. Yet in a few breeding examples these areas are olive, a color typical of the coastal population. The opposite is also true, for occasional buff-flanked examples crop up among breeding specimens taken along the coast. To cite some particular instances, a single specimen from Edmonton, Alberta, well within the range of *campicola*, has a dorsum like typical examples of *occidentalis*. An example from Fort Custer, Montana, also in the range of *campicola*, collected on April 27, 1885, approaches specimens of *scirpicola* from southern California in dorsal coloration. Such specimens should be recognized as the extremes they are and adequate sized series obtained to indicate the

range of individual variability. One should expect about a 25 per cent overlap in characters in yellow-throats in races that are "good." If less than 75 per cent of the individuals can be segregated a case of incipient geographic variation may be represented which is important in the evolutionary picture even though the characters are not sufficiently established to justify racial recognition.

As a generalization for yellow-throats it may be said that in any one race all the genetic characters of the species appear to be represented in individuals of the population, even those that are racial characters in other particular geographic areas. It would seem therefore, that with equal potentiality in every race, some mechanism has been operative serving to establish different frequencies of characters and to arrange them in different mosaics which have come to typify the various distinctive populations. The character combinations of the populations of the different geographic areas are presented in subsequent sections of this paper.

Molts and effects of wear.—The postjuvinal molt of yellow-throats is a complete molt as indicated by the series from St. George and southern California previously mentioned in connection with age. There appears to be no regular prenuptial molt but a few scattered individuals among the males give indication of some spring replacement of feathers especially on the chin and throat. However, due to wear of feather tips and consequent exposure of heretofore obscured contrasting areas, the breeding plumage is strikingly different from the fresh fall plumage. For instance, in most specimens in fresh fall plumage, terminal feather margins obscure the frontal black and postfrontal white areas. As wear progresses the basal portions of the feathers are exposed, resulting in the presence of the two contrasting areas. The extent posteriorly of the white band varies individually and between populations but the character is revealed only in worn specimens. Another area similarly affected is the auriculars. In the fall plumage these feathers have delicate white terminal portions and when they are worn off the underlying black is revealed as a shiny, solid patch.

Wear also produces a general brightening of the coloration, which as a rule is reaching a maximum by the time of the breeding season. The dorsum of fall birds is brownish because of the brown margins of the feathers. With wear the color tone is converted from brown to various shades of olive, green or gray-green as the case may be, depending on the race. Considerable individual variation is manifest in tone of brown in the terminal margins of fall feathers. I have gained the impression that due to wear there is seasonal variation in individual variability with respect to the dorsum. That is, as wear removes the brown tips, the underlying green is revealed which is more uniform among specimens than are the brown fall plumaged parts. In some instances where skins are present from the same area in fresh fall plumage and others in breeding dress, the latter are more uniform in the color of the dorsum. Of course this may be due to chance differences in the samples of the population; it may not hold true with a larger representation.

In any event, because of the fact that the contour feathers have margins of colors different from those of the feather vane, and because distinctive areas like the postfrontal white stripe are obscured by the margins when present, the geographic races are less distinct in fresh fall plumage than in worn breeding plumage. This is a reversal of the usual situation where birds in unworn plumage are most diagnostic and sought after for taxonomic study.

The first fall and subsequent annual molts occur relatively early. One specimen from Capistrano, California, taken on July 11 is in fresh fall plumage. In most specimens the molt is complete by mid-August.

VARIABLE CHARACTERS SHOWING CLINES

Color of dorsum.—The ground color of the dorsal surface of the species *Geothlypis trichas* is green but there are differences between populations in different geographic regions in the tone of green. The clines which run from one area to another are, however, difficult to describe or measure and so remain largely impressionistic. The dorsal coloration is not uniform enough to match Ridgway's color plates. The only tangible findings from the comparisons made with these are that populations along the Pacific Coast tend to favor Saccardo's Olive Citrine, whereas those of the interior are mostly closest to Olive or Brownish Olive. There is so much individual variation that the clines are frequently obscured unless large series are available for comparison.

Speaking in general terms, therefore, the yellow-throats of the northern Pacific Coast area west of the Cascades, called *arizela*, have in common with the localized *sinuosa* from the San Francisco Bay area, a dorsal coloring that is dark green, especially as compared with yellow-throats from the Great Basin of the interior (*occidentalis*) whose backs are lighter and brighter. The population of the northern Great Plains and northern Rocky Mountain area (*campicola*) is characterized by a gray aspect to the green. In southern California, the dorsum becomes brighter with a greater amount of yellow pigment. The extreme of yellow-green is reached in the yellow-throats of southern Arizona and northern Sonora (*chryseola*). Farther south and east on the Mexican Plateau the green is said to become darker, losing much of the yellow (*melanops*). Curiously, along the coastal salt marshes of western Sonora bordering the east side of the Gulf of California, the population named *riparia* possesses a dark green back like that of the restricted population of the San Francisco Bay area (*sinuosa*). The color tone of *G. beldingi* is brighter and yellower than that of the more northern races of *G. trichas* but is not as yellow as in *G. t. chryseola*.

Yellow of underparts.—The yellow of the ventral surface of birds from coastal populations is duller and more greenish than that of birds from the interior. Coastal birds conform closest to Ridgway's Strontian Yellow. Great Basin birds seem to have an orange type of yellow pigment especially on the upper breast; this is equal to Wax Yellow. The color in birds of the northern Rocky Mountains and Great Plains is somewhat intermediate. Progressing southward into southern California, Arizona, Sonora and Lower California the yellow becomes intensified, this being especially noticeable in *chryseola*.

Extent of yellow posteriorly.—Considerable individual variation exists with respect to this feature but nevertheless a character gradient extends from north to south. The least extent of yellow prevails in the population of the northern Great Plains and northern Rocky Mountains. In this section the yellow cuts off at the upper breast, thus covering only about the anterior third of the lower surface. Progressing southward the extent of the yellow increases. In the Great Basin the yellow occupies approximately two-thirds of the ventral surface, thus covering the lower breast and extending to the upper belly. In many specimens of this latter area there is a suffusion of yellow onto the lower belly but it is interspersed with light areas, the yellow being confined mostly to the center of the breast. The extent of the yellow in birds from the northern coastal areas is about the same as in the Great Basin birds but as noted in the previous section it is a different tone of yellow. It is significant that in a belt at about the same latitude running from southwestern Utah westward through southern Nevada and California both east and west of the Sierra Nevada a transition occurs whereby the yellow becomes more extensive. In populations south of this belt, as in California, both coastally and interiorly along the lower Colorado River valley, the yellow has spread to the lower belly. The

extreme in the posterior extension of the yellow is reached in birds of southern Arizona and Sonora, Mexico, where the entire underparts are brightly colored. It is in this same area that birds show yellow invading the white postfrontal stripe on a large scale. The yellow in birds of southern California, while more intense than that in the neighboring population to the north, is not as bright as in *chryseola*.

Color of flanks.—Yellow-throats of coastal races (*arizela*, *sinuosa*, *scirpicola*) have darker flanks and sides of the breast than those of the interior. The colors tend to center around Olive. The interior races, although paler, vary greatly. In the population of the Montana-Dakota region and on northward (*campicola*) the flanks are gray. This is correlated with restricted yellow on the lower ventral parts. In the Great Basin and east to Kansas and south within the range of *occidentalis* the flank color is Buff. The flank color of the specimens from southern Arizona and Sonora (*chryseola*) is intermediate between *scirpicola* and *occidentalis*, being darker than in the latter and lighter than in the coastal form. The interior portion of the race *scirpicola*, however, has flanks as dark as those of the coastal section but the gradual paling of those still farther east sets up a coast to interior cline.

Breadth of postfrontal white stripe.—In the preliminary study of several series from various geographic areas this character seemed to show geographic variation and some use has been made of it in the past by the writer and others in diagnosing races. An attempt was made actually to measure the depth of the band and get quantitative data. The character was not easily measured, however, and certainly not as exactly as other features like wing and bill. For one thing the extent of the white is affected greatly by wear. Birds in fresh fall plumage show relatively little white because the feather tip-pings of the area are brown. It is only as the brown wears off that the underlying white is exposed. However, by the time of the breeding season the true extent of the white shows and since measurements were made only on breeding birds this objection was largely eliminated. The line of demarcation between the black frontal stripe and the white postfrontal stripe is usually sharp and in most specimens the posterior margin of the white likewise cuts off abruptly. In some, however, the white blends gradually into the green of the crown. In others the border is jagged, not cutting straight across. As yet another difficulty there is often concealed white at the base of the feathers of the crown. Indeed, a few specimens have been examined where the white exposed with wear is so extensive that there is a nearly white crown. This situation crops up more frequently in the southern California population, *scirpicola*, than elsewhere. In extreme cases and where irregularities existed the measurement was not taken or at least was not used.

The results of the measurements after undesirable specimens were discarded are presented in tables 1-7. The averages are somewhat closer than expected and show little difference except for the indication that the population known as *arizela* from the coastal Pacific Northwest averages narrower in the postfrontal band whereas the area is broader in the southern Lower California group. The coefficient of variability is such as to indicate that the character is of little taxonomic value. It may be significant that the highest coefficient of variability is in the race *scirpicola* where it was noted in handling the specimens that great individual variability existed. Incidentally, this individual variability extends to other areas of white. The prominence of the white as it extends backward over the eye and posterior to the auriculars is highly variable. In some specimens the white is indistinct, in others it is conspicuous. In some there is a distinct postauricular patch of white which is lacking in others. It is my impression that there is a general conformance between large amounts of postfrontal white and extension of white along

the sides of the head. That is, those individuals characterized by an extensive postfrontal white area have a greater amount of white in the entire head area than do individuals with a narrow forehead patch of white.

No attempt was made to measure the frontal stripe of black but the observation was made that the breadth varied greatly between specimens, being in some nearly twice as wide as in others. Doubtless this character is as unstable as is the white postfrontal stripe.

Purity of the postfrontal white stripe.—In all the northern races the postfrontal band is white in nearly every individual, that is, after the wearing off of the brown feather tippings. In the race *scirpicola* there is a sprinkling of individuals that possess a few narrow, indistinct streaks of yellow in the white stripe. The frequency of occurrence of birds so characterized seemingly increases in the lower Colorado River valley. In southern Arizona and southward in Sonora, where the race *chryseola* ranges, the postfrontal stripe is decidedly yellow. The yellow most often occurs as a fairly uniform wash on all feathers but in some there may be individual feathers that are brightly yellow. This contamination of the white seems to be correlated with a greater development of yellow pigment generally as manifested in the brighter breast color and more extensive distribution on the entire underparts. When yellow pervades the postfrontal stripe, it also occurs above the eye and extends back to the postauricular area. The yellow postfrontal stripe occurs sporadically in southern Lower California birds.

This behavior of the yellow pigment in the otherwise white areas suggests it has become established as a racial character only in the form *chryseola* and that the gene or genes for it may be penetrating into the neighboring form *scirpicola*. The character is not universally present in specimens of *chryseola* and seems to be generally lacking in specimens from areas of intergradation with *occidentalis*. The yellow occasionally appears, however, even in *occidentalis* but specimens showing yellow in the postfrontal stripe are widely scattered. For instance, one is from Pyramid Lake, Nevada, another from Clear Creek, Colorado.

Length of wing.—Unlike the characters previously discussed, this is readily measurable and has yielded quantitative data of significance which are summarized in tables 1–7. The differences between the populations are relatively slight. The interior and coastal forms are all comparable with the exception of that from the San Francisco Bay region which averages slightly smaller. This is said to be a sedentary race although some individuals wander widely in the postbreeding season. Thus the small wing may be of significance in connection with the nonmigratory behavior pattern. The small sample of birds from the coastal strip of Sonora also averages smaller, thus being similar to the restricted population of the San Francisco Bay in wing length. The population (*G. beldingi*) of southern Lower California is characterized by greater wing length.

Length of tail.—The variability of this character is greater than is wing length and shows little correlation with the latter. There is also greater difference between adjacent populations than in wing length. The measurements are summarized in tables 1–7. The northern Great Plains birds strangely average smaller than the neighboring group to the south called *occidentalis*. *Scirpicola* still further south, has an even longer tail. Thus there is a cline in which tail length increases as one progresses southward. This is continued in the southern Lower California population, *G. beldingi*. Again the San Francisco Bay birds are small.

Ratio of wing to tail length.—The independent clines in wing and tail length are indicated by the ratio of wing to tail length. The two parts more nearly approach each other in length the farther south one goes. Results of wing-tail comparisons are sum-

marized in tables 1-7. In the northernmost population, *campicola*, the greatest difference exists, whereas the San Francisco Bay race, *sinuosa*, has a similar ratio even though the actual lengths are smaller. The race *chryseola* is not greatly different from *occidentalis* and *arizela* in the ratio, while *scirpicola* has a proportionately longer tail than *arizela* and *occidentalis*. The small samples of *modesta* and *riparia* make it difficult to judge the true situation but indications are that the tail is essentially as long as the wing in them. In *G. beldingi* the two extremities are nearly equal.

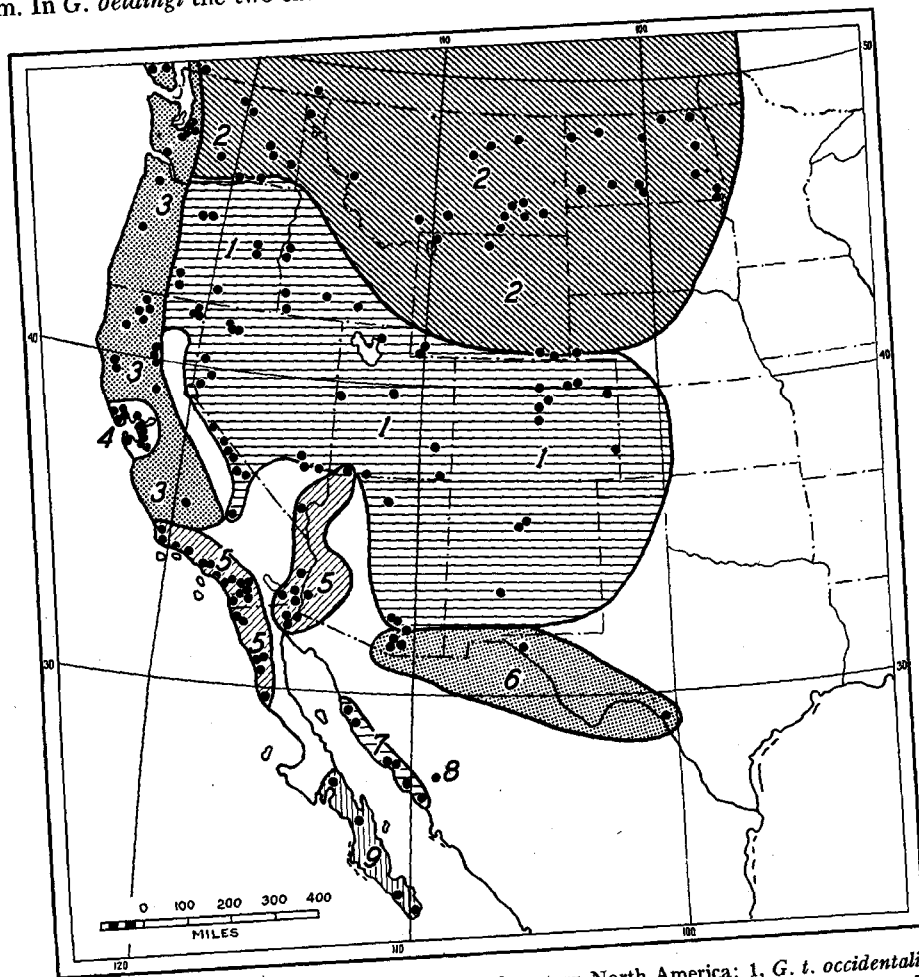


Fig. 32. Breeding ranges of the yellow-throats of western North America: 1, *G. t. occidentalis*; 2, *G. t. campicola*; 3, *G. t. arizela*; 4, *G. t. sinuosa*; 5, *G. t. scirpicola*; 6, *G. t. chryseola*; 7, *G. t. modesta*; 8, *G. t. riparia*; 9, *G. beldingi*.

Length of tarsus.—This appears to be a very stable character, averaging essentially the same in every race of *Geothlypis trichas* that was considered. There is a significant difference between *G. trichas* and *G. beldingi*, the latter average longer (see tables 1-7).

Length of bill from nostril.—This character was capable of exact measurement and the results indicate little if any geographic variation except for a slight tendency for longer length and a more stable condition in the race *chryseola*. *G. beldingi* has a longer and larger bill than *G. trichas* (see tables 1-7).

Summary of clines.—The existence of clines or character gradients in western populations of yellow-throats is demonstrable in a number of instances. In some cases they appear to be correlated, but most seem to progress independently. An example of two characters with parallel clines is intensity of yellow and distribution of yellow. Northern birds have pale yellow of limited extent whereas southern birds are brightly yellow, with the yellow suffusing over the entire lower surface and even appearing in the dorsal green. Two clines of independent nature are wing and tail lengths. In northern birds there is a considerable differential but in southern birds the tail becomes proportionately longer, thus actually equalling wing length in many instances. The lack of correlation of the several characters shows up in areas of intergradation. In such areas of blending of two racial stocks some characters may be intermediate between the averages of the two races whereas others adhere to one pattern or the other. For instance the yellow-throats in a belt through central eastern Oregon and central western Idaho are intermediate between *occidentalis* and *campicola* in dorsal coloration. They have the flank color of *campicola* but the orange yellow of *occidentalis*.

One might expect the migratory forms to have longer wings than resident populations. This is the case with some but not with others. The sedentary form *sinuosa* has a small wing but *scirpicola* of southern California, also resident, has dimensions of wing equal to those of migratory races like *occidentalis* and *campicola*. The race *chryseola*, still another resident form, likewise has a wing length equal to that of the more northern representatives.

There is similar lack of uniformity of ratio of tail length to wing length in resident and nonresident races. In the resident form *sinuosa* there is a differential between the two extremities but in *scirpicola*, *riparia* and *modesta*, also resident, the wing and tail are nearly equal. In the resident race *chryseola*, there is again a difference between the two measurements. In *G. beldingi*, which is resident, the wing and tail are essentially equal. In all the northern migratory races of *G. trichas* the wing is longer than the tail.

Geothlypis trichas occidentalis Brewster

Western Yellow-throat

Geothlypis trichas occidentalis Brewster, Bull. Nuttall Ornith. Club, 8, 1883:159.

Type.—Adult male, no. 205550, Mus. Comp. Zool.; Truckee River, Nevada; May 4, 1881.

Distribution.—Breeds in Great Basin region, including Nevada, southeastern Oregon, southern Idaho, and Utah; thence east through southwestern Wyoming and Colorado to western portion of Great Plains, including southwestern Nebraska, western Kansas, and Texas; also northern New Mexico and northeastern Arizona. Winters through Lower California and western Mexico.

Racial characters.—In general distinguished by yellow of breast having an orange tint, the yellow extending posteriorly about two-thirds length of underparts; light buffy flanks. As compared with *campicola*, dorsum more yellow olive green, less grayish color; yellow of underparts more extensive posteriorly, belly and flanks less gray, more buffy. Differs from *arizela* in more orange, less green, tone of yellow on underparts and brighter, yellower green of dorsum. Distinguished from *scirpicola* by less extensive yellow posteriorly and by lighter, more buffy flanks and belly. Differs from *chryseola* in being duller throughout, with yellow less extensive on underparts, and in purer white postfrontal stripe.

Variation.—The fairly large sample of adult males available for the race indicates (table 1) a fairly stable condition of the measurable characters. The color characters are uniform over most of the range, no intra-racial clines being apparent in the material examined. In other words I have been unable to detect any one area in the extensive range from which specimens come that can be cited as the most typical. Examples from both Nevada and Utah in the Great Basin are the same and those from eastern Colorado are identical with those from the Great Basin. This latter is contrary to what one might expect, for it indicates that the Rocky Mountains do not serve as a barrier. The type

specimen from the extreme western margin of the range up against the east flank of the Sierra Nevada is identical with a breeding male from four miles east of Bushnell, Kimball County, Nebraska, as well as with examples from the Denver area in Colorado and from several sites in Utah.

Table 1
Measurements of Breeding Adult Males of *G. t. occidentalis*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 70 | 52.5-60.0 | 56.5±0.14 | 1.73 | 3.07 |
| Tail | 67 | 46.0-58.0 | 52.9±0.20 | 2.49 | 4.71 |
| Culmen | 70 | 9.7-12.4 | 11.1±0.04 | 0.55 | 4.96 |
| Bill from nostril | 70 | 7.0-8.7 | 7.8±0.02 | 0.35 | 4.46 |
| Tarsus | 70 | 17.8-22.1 | 20.3±0.06 | 0.75 | 3.69 |
| Depth of white postfrontal stripe | 69 | 1.0-7.0 | 3.6±0.08 | 1.01 | 27.85 |
| Weight | 14 | 9.5-10.7 | 10.1 | | |
| Ratio of wing to tail based on means | | | 1.067 | | |

This viewpoint about the stability of the race does not find corroboration in the statements of other systematists. For instance, Twomey (1942:446) in reporting upon a series from the Uinta Basin in northeastern Utah comments upon supposed local variation displayed by his birds involving brighter yellow on throat and upper belly, light creamy tan lower belly and flanks, yellow under tail coverts tinged with cream buff, and extensive, white, postfrontal band. These are just the traits that characterize *occidentalis* and while I have not seen his specimens, since they were not available for loan, from Twomey's description I should say they are typical *occidentalis* and probably similar to series I have examined from the Denver area to the east and from Midway, Wasatch County, Utah, to the west. Since he was making comparisons with material from Oregon, British Columbia and Saskatchewan, he probably had representatives of *campicola* and his Texas specimens probably incline toward *chryseola* or some other form. Oberholser (1948) has recognized five races in the range I ascribe to *occidentalis*. Critical comment on this will be made later.

Relationships with adjacent forms.—In marginal areas a blending occurs between *occidentalis* and *campicola*, *arizela*, *scirpicola*, *chryseola* and doubtless with more eastern populations, although I have had no material to work out details for the last mentioned. The intergradation with *campicola* occurs in a region extending from eastern Oregon, eastward through northern Idaho, and parts of Wyoming. Character gradients between the two races are confined to color characters, for there are no significant size differences between the races. There is a graying of the dorsum and flank color and a gradual diminution in the extent of the yellow posteriorly on the underparts as one progresses northward. The result is that the specimens in this belt show varying degrees of intermediacy between the two races in typical form.

The beginning of the intergradation may occur even as far south and west as the northeastern corner of California, although the situation there is obscure owing to the probable influence of intergradation there likewise with the coastal form *arizela*. In any event, breeding males from Alturus, Eagle Lake, Goose Lake near Davis Creek, and Eagleville in Modoc and Lassen counties, California, although closest to *occidentalis*, have the yellow slightly greener or less orange. There is a slight graying of the flanks. The series from Quinn River Crossing, Big Creek Ranch and Virgin Valley of the Pine Forest Mountains of northwestern Nevada that Swarth relied upon as being typical of *occidentalis* show the beginnings of the cline toward *campicola*. The gradient then continues northward into Oregon as indicated by specimens from Plush, Haycreek and Bear Creek. Yellow-throats of this whole area in northeastern California, northwestern Nevada and north to central southern Oregon show what I consider on the basis of my materials to be intergradation; they comprise what Oberholser (1948:4) has designated *oregonicola*. Specimens from this area are so very slightly different from typical *occidentalis* that even should additional material demonstrate constancy of characters throughout the region assigned to *oregonicola*, the differentiation is so slight that I doubt the utility of recognizing the birds as a separate race.

The next group of atypical *occidentalis* tending toward *campicola* is represented in my materials from southwestern Idaho and adjacent Oregon. Localities involved are Beulah, Oregon, and several Idaho localities as follows: South Fork Owyhee River, 4500 feet, 2 miles north Nevada line, Owyhee County, Idaho; 2½ miles east of Jordan Valley (Oregon), 4500 feet, but in Owyhee County, Idaho; American Falls; 2 miles south Payette, and Weiser. In northern Idaho (Coolin) the yellow-throats are typical *campicola*; in Utah (mouth of Bear River) they are typical *occidentalis*. The portion of this intergradational area in eastern Oregon and in Idaho, Oberholser (1948:3) considers to be a new form *idahonicola* but he includes central northern Utah also in the range of *idahonicola*. Another treatment with which I can not agree is his splitting off of the Utah population (except the north-central portion) and the western Wyoming birds from *occidentalis* and calling them *utahicola*.

In Wyoming a specimen from Fort Bridger seems to me typical *occidentalis* but specimens farther east from Muddy Creek and Laramie Peak show gray flanks and restricted yellow, suggesting the influence again of *campicola*. Two birds from nearby northern Colorado taken at Jackson Reservoir, Morgan County, also have grayer flanks and less yellow on the belly. One has a grayer back. These latter two may have been late migrants on May 6. Specimens from the Montana-Dakota region, possibly further indicative of intergradation between *occidentalis* and *campicola*, are discussed under the latter race since their affinities are closest to *campicola*. Part of this intergradational area as well as the region of central Colorado and on south into northern New Mexico and northeastern Arizona, Oberholser (*loc. cit.*) includes in the range of his race *coloradonicola*. I can not distinguish, however, between my specimens of *occidentalis* from central Colorado east of the Rocky Mountains and those from the Great Basin.

Intergradation of *occidentalis* with *scirpicola* is nearly as extensive as with *campicola*. The center of differentiation of *scirpicola* is seemingly in coastal southern California but according to my concept the race extends inland to include interior southern California and the lower Colorado River valley. Thus a wide area of contact with *occidentalis* is established and a blending of characters occurs over a long gradient throughout the Owens Valley east of the Sierra Nevada and thence eastward in adjacent California and southern Nevada to southwestern Utah. The intergradation between these two races starts as far southwest as Caliente, California, near Walker Basin at the southern end of the Sierra Nevada and extends thence east to Olancho and Death Valley. Other breeding specimens from east of the Sierra Nevada representing this intergrading population are from or close to the following locations. California: Mono Lake P. O.; Big Pine; Walter's Ranch, 2 miles north Independence; Laws. Nevada: Fish Lake, Esmeralda County; 10½ miles south of Yerington.

Phillips (1947:122) states he cannot distinguish the males in the type series of *occidentalis* from examples of *scirpicola*. As the foregoing discussion indicates, in my comparisons I could see little similarity between these same specimens and typical examples available of *scirpicola*. Van Rossem (1930:297) extended the range of *scirpicola* north to include Washington, southwestern Utah, on the basis of a single specimen from there. This skin happens to be an extreme variant typical of *scirpicola* in practically all its characters. A series obtained in recent years by the writer (Behle, 1943:66) in the vicinity of St. George contains specimens more intermediate, and some individuals are indistinguishable from *occidentalis*. A similar intermediate situation exists in the Pahrnagat Valley of southeastern Nevada. Farther east, however, the intergradation ceases, for a series of yellow-throats from Kanab, Utah, is definitely *occidentalis*.

The race *occidentalis* seems to extend south and eastward through northeastern Arizona and New Mexico. In southern Arizona there are indications of intergradation with *chryseola* and perhaps this blending extends eastward into New Mexico. Two breeding males from Espanola and Rinconado, New Mexico, seem referable to *occidentalis* as is one from Palomas Spring in the Rio Grande Valley.

Series of yellow-throats definitely known to have been breeding are not available from critical areas in central interior California which part of the state has in the past been assigned to the range of *occidentalis*. Admittedly much of the California material examined by Swarth and Grinnell shows close resemblance to examples of the interior race *occidentalis*. An explanation may be afforded by either of two possibilities. There may be a broad area of intergradation between *scirpicola* and *arizela* where the intergrades resemble *occidentalis*. The other possibility is that the specimens were actually migrant examples of *occidentalis*. The latter hypothesis is probably the more tenable, for examples of *occidentalis* occur throughout the range of *scirpicola* as migrants.

Breeding localities.—NEVADA. Washoe County: Pyramid Lake; Truckee River. Ormsby County: Carson. Humboldt County: Quinn River Crossing; Virgin Valley; Big Creek Ranch, Base of Pine Forest Mountains. Esmeralda County: Fish Lake, 4800 ft. Lyon County: 10½ miles south Yerington, 4500 ft., West Walker River. CALIFORNIA. Modoc County: Goose Lake near Davis Creek; Alturas; Eagleville. Lassen County: Eagle Lake. Mono County: Mono Lake P. O., 6500 feet. Inyo County: Farrington Ranch, 4115 feet, Laws; Big Pine and 1½ miles southwest Big Pine, 4500 feet; Walter's Ranch, 2 miles north Independence; Olancha, 3700 feet, Owens Lake; Furnace Creek, Death Valley. OREGON. Lake County: Plush. Malheur County: Beulah. Jefferson County: Haycreek; Bear Creek. Sherman County: Miller. IDAHO. Owyhee County: American Falls; South Fork Owyhee River, 2 miles north Nevada line; 2½ miles east Jordan Valley (Oregon). Gooding County: 2 miles east Hagerman. UTAH. Tooele County: Sheridan Ranch, 2 miles north Irapah. Boxelder County: Mouth of Bear River. Wasatch County: Midway. Kane County: Kanab and vicinity. Grand County: Moab. San Juan County: Bluff; Colorado River. WYOMING. Uinta County: Fort Bridger. COLORADO. Adams County: Barr. Douglas County: Littleton. Prowers County: Holly. Jefferson County: Wheat Ridge; Clear Creek. Weld County: Empire Reservoir; Windsor. Riverside County: Denver. Morgan County: Jackson Reservoir. NEBRASKA. Kimball County: 4 miles east Bushnell. NEW MEXICO. Rio Arriba County: Espanola; Riconada; Palomas Spring, Rio Grande Valley. ARIZONA. Coconino County: Pasture Canyon near Tuba City.

Geothlypis trichas campicola Behle and Aldrich

Northern Plains Yellow-throat

Geothlypis trichas campicola Behle and Aldrich, Proc. Biol. Soc. Wash., 60, 1947:69.

Type.—Adult male, no. 79842, Mus. Vert. Zool.; Yellowstone River, 5 miles west Forsyth, 2750 feet, Rosebud County, Montana; June 8, 1940; collected by W. C. Russell, original number 7262; weight, 10.0 grams; testis, 8 mm.

Distribution.—Breeds east of Cascade Mountains in northern Oregon, Washington, and British Columbia, thence east through northern Idaho, Alberta, Saskatchewan, Montana, northern and eastern Wyoming, and extreme northern Colorado, to North Dakota. In migration occurs southward in Utah, Colorado, Arizona and California. Winter range undetermined.

Racial characters.—Distinguished in general by grayness of dorsum, gray flanks and restricted yellow on ventral surface. Distinguished from *occidentalis* by grayer, less yellowish olive-green upper parts; yellow of underparts less extensive posteriorly; belly and flanks grayer, averaging more whitish, less buffy. Appears closer to *arizela* but also grayer on upper parts; yellow of underparts slightly paler and less extensive; posterior underparts whiter, less buffy. Differs from *brachydactyla* in grayness of dorsum, and in restriction of yellow of flanks and belly to anterior third.

In addition to these morphological characters, *campicola* appears to be differentiated ecologically and behavioristically from southern neighbors. In most races in the writer's experience, yellow-throats are found during the breeding season in fairly close proximity to water and occupy dense vegetation such as streamside thickets or forest understory. They are rather seclusive in their habits. I was told by Ward Russell that at the type locality of *campicola*, he found yellow-throats occurring considerable distances from water and that they tended to occupy low shrubby vegetation along hillsides and in open country where they were conspicuous in their activities.

Variation.—The data available for measurable characters is summarized in table 2. For color characters about the usual amount of individual variation exists, with extreme individual variants occasionally occurring that have combinations of characters such that they resemble the averages of other races. For example, a specimen taken on June 18, 1923, at Edmonton, Alberta, well within the range of *campicola*, is scarcely distinguishable from *occidentalis*, whereas another from the same location taken June 14, 1924, is good *campicola*. The flank color character seems to be the most variable. Most representatives have the flanks pale gray but some are as brown as the average found in *arizela* or *scirpicola* or are as yellow as in *chryseola*. Often these extremes are found in breeding birds from the same locality.

There are no clear indications of geographic variation within the race. In its distribution, this race is similar to *occidentalis* in that the Rocky Mountains cut through the middle of the range;

Table 2
Measurements of Adult Males of *G. t. campicola*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 72 | 51.0-59.5 | 55.0±0.14 | 1.88 | 3.42 |
| Tail | 68 | 45.0-57.5 | 50.3±0.20 | 2.55 | 5.06 |
| Culmen | 70 | 9.2-12.2 | 10.8±0.05 | 0.64 | 6.00 |
| Bill from nostril | 71 | 6.6-8.6 | 7.8±0.03 | 0.37 | 4.84 |
| Tarsus | 72 | 18.7-22.4 | 20.1±0.05 | 0.62 | 3.12 |
| Depth of white postfrontal stripe | 70 | 1.0-7.0 | 3.1±0.08 | 1.04 | 34.24 |
| Weight | 7 | 9.8-11.5 | 10.4 | | |
| Ratio of wing to tail based on means | | | 1.093 | | |

seemingly the mountains do not constitute an effective isolating mechanism. The yellow-throats of eastern Washington have closest affinities with the population of the northern Great Plains region, yet they exhibit a slight approach to the race *arizela*. Because of the Cascade Mountains there is probably little impinging of the ranges of the two races, however. Maximum grayness and the extreme in restriction of yellow occurs east of the Rocky Mountain axis in an area extending north into Saskatchewan. Oberholser (1948:2) has characterized these birds as *alberticola* but whether they represent a race different from *campicola* or merely mark the end of a cline I cannot say.

Relationships with adjacent forms.—The race *campicola* doubtless blends with eastern populations but the picture of variation is confused owing to the recent vague descriptions by Oberholser (1948) of *novascoticola*, *quebecicola*, *ontarionicola*, *ohionicola*, *alberticola* and *minnesoticola* with the attendant reduction in range of *brachydactyla*. These problems are outside the scope of the present study. As noted in the account of *occidentalis* an extensive belt of intergradation occurs between that race and *campicola* from eastern Oregon and southern Idaho, east to Wyoming. The eastern limits of this intergradation are obscure and it may extend north to include southeastern Montana and even southwestern North Dakota. In the last named area particularly, a mixed population occurs. Several specimens from Genullin, Fairmount, Walhalla, and Fish Lake seem to approach *occidentalis* by reason of browner flank color and less gray dorsum. At other localities like Medora and Valley City some individuals in small series favor *campicola*, others are intermediate between the two races. Perhaps this indicates the presence of some one of the races Oberholser described. This does not fit in, however, with the circumstance that the range of *campicola* extends south into extreme northern Colorado. Specimens taken in June from near Avalo and Wray are gray like *campicola*. Two from Jackson Reservoir, Morgan County, seem to be intergrades. The transition between *campicola* and *occidentalis* is seemingly more abrupt in northern Colorado than elsewhere in this belt because specimens from Denver and vicinity are typical *occidentalis*.

In the northwestern portion of its range in southeastern Alaska the race *campicola* is apparently extending its area of occurrence. Swarth (1911:101) discovered yellow-throats at two points on the coast of southeastern Alaska and obtained a small series of breeding birds from along the Chickamin River. He decided their affinities were with the birds of the interior rather than with the more southern coastal form *arizela* and pointed out that the two places where yellow-throats were found were along the margins of large rivers which pierce the mountains paralleling the coast and which, therefore, form direct and favorable passes from the interior. Swarth believed that the birds reached the coast by following down these streams. His specimens were not examined in this study but I did have an opportunity to see two breeding birds lately acquired by J. Dan Webster near the mouth of the Stikine River. As Swarth stated they are of the interior race (now *campicola* rather than *occidentalis*) instead of *arizela* as indicated by the orange shade of yellow, the restricted distribution of the yellow, the gray flanks, and gray dorsal surface. Webster (1950:35) on the basis of his field work in the region agrees with Swarth that the yellow-throat is a very recent arrival in southeastern Alaska from the interior and is not yet well established. Swarth comments: "We find here an extraordinary instance of a bird race from the arid interior which has invaded a region of extreme humidity through narrow passes, and which has undergone no modification in its coloration in the direction of melanism."

Breeding localities.—SOUTHEASTERN ALASKA. Mouth of Aaron Creek [Stikine River]; 1 mile N. Stikine River at Popof Creek. BRITISH COLUMBIA. Clearwater Post Office; Indianpoint Lake; Creston, Kootenay Valley. WASHINGTON. Okanagan County: Omak Lake. Douglas County: Grand Coulee. Whitman County: Pullman; Rock Creek. Yakima County: Yakima. Lincoln County: 6 miles south Sprague. Walla Walla County: College Place, Walla Walla. Chelan County: Wenatchee Lake. Benton County: Kiona (toward *occidentalis*). OREGON. Malheur County: Juntura. ALBERTA. Camrose; Edmonton. IDAHO. Bonner County: Sinyakwateen Depot; Coolin. Washington County: Weiser. Payette County (toward *occidentalis*): 2 miles south Payette, between Payette and Snake Rivers. MONTANA. Rosebud County: Lolo Creek, 3470 feet, 6½ miles west Lolo; Yellowstone River, 2750 feet, 5 miles west Forsyth; Lame Deer. Sweet Grass County: Big Timber; 4 miles east of Big Timber. Yellowstone County: Fort Custer. Big Horn County: Crow Agency; Spring Creek, 6500 feet, Big Horn Mountains. Powder River County: Powderville. Gallatin County: Bozeman. Valley County: Glasgow. Fergus County: Hilger. Phillips County: Zortman; Darnall's; Lismas. In addition, Sioux River 5 miles northwest Fairmount; Boxelder Creek, 15 miles southwest Sykes. NORTH DAKOTA. Billings County: Medora. Williams County: Buford. McHenry County: Towner. Pembina County: Walhalla. Grand Forks County: Larimore. Buleigh County: Bismark. Morton County: Glenullin; Fort Rice. Richland County: Wahpeton; Fairmount. Barnes County: Valley City. In addition, Tokio; Fish Lake; Fort Clark. COLORADO. Yuma County: Wray; Chimney Canyon, 10 miles east Avalo. WYOMING. Big Horn County: Greybull. Uinta County: Head of Muddy Creek, 6500 feet. Albany County: Laramie Peak. In addition, Two Ocean Lake; Black Mountain, Head of Pat O'Hara Creek.

Geothlypis trichas arizela Oberholser

Pacific Northwestern Yellow-throat

Geothlypis trichas arizela Oberholser, Auk, 16, 1899:257.

Type.—Adult male, no. 7918, U. S. Nat. Mus.; Fort Steilacoom, Pierce County, Washington; May 13, 1856, collected by Dr. George Suckley.

Distribution.—Breeds along coastal strip west of Cascade-Sierra Nevada cordillera from extreme southern British Columbia south through Washington and Oregon to central California. Winters in central and southern California.

Racial characters.—Marked in general by dark green dorsum, and greenish yellow tone of underparts. Distinguished from *campicola* by greener, less gray, dorsum and more extensive yellow on ventral surface. As compared with *occidentalis*, has darker green dorsum, yellow of underparts greener, less orange, flanks darker, less buffy. Longer winged than *sinuosa* and slightly lighter in coloration, especially on flanks and sides. Can be told from *scirpicola* by its less extensive yellow on posterior underparts and by duller, more greenish upperparts.

Table 3

Measurements of Adult Males of *G. t. arizela*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 54 | 51.0-60.5 | 55.1±0.15 | 1.66 | 3.02 |
| Tail | 52 | 47.0-57.5 | 52.0±0.18 | 1.99 | 3.83 |
| Culmen | 53 | 9.5-11.9 | 10.9±0.05 | 0.56 | 5.16 |
| Bill from nostril | 53 | 7.0-8.5 | 7.6±0.02 | 0.31 | 4.11 |
| Tarsus | 55 | 17.8-21.4 | 20.0±0.05 | 0.63 | 3.18 |
| Depth of white postfrontal stripe | 55 | 0-5.0 | 2.4±0.07 | 0.87 | 36.18 |
| Weight | 5 | 9.0-10.8 | 9.9 | | |
| Ratio of wing to tail based on means | | | 1.057 | | |

Variation and relationships with surrounding races.—The variability of the measurable characters is summarized in table 3. These data do not indicate that this race is much different in variability than are other races. The tail length seems a little less variable. Considerable individual variation exists in the color characters, especially the dorsal coloration and the depth of the white post-

frontal stripe. The material studied indicates little geographic variation within the race, especially in the northern segment of its range. The northernmost specimens are from 23 miles north of Hazelton. Coastal specimens from still farther north near the mouth of the Stikine River are *campicola* (see p. 205).

From the southern part of British Columbia southward, *arizela* seems confined by the Cascade Range to the humid coastal belt. Possibly it touches the race *campicola* to the east along the Columbia River but no specimens are at hand to confirm this. Because of the Cascade-Sierra Nevada cordillera, *arizela* is likewise essentially isolated from *occidentalis*. Any contact between these two races would be most likely to occur in central northern California and central southern Oregon, where the physical barrier is less formidable and might consequently allow intermingling of the two groups. As previously noted the yellow-throats of extreme northeastern California, while closest to *occidentalis* are not typical of that race. From the fact that similar specimens occur north along the east side of the Cascade Range to the Columbia River, it would seem that an influence of *campicola* is manifest. Yet *arizela* may intergrade here too. If so, the situation would give rise to a mixed population where three genetic stocks are intermingling. As indicative of the mixing of characters, one of two males from Eagleville, California, has characters typical of *occidentalis*, whereas the other is grayer in the flank area. A specimen from Alturas nearby is gray all over and so is either intermediate between *occidentalis* and *campicola* or it stands between *occidentalis* and *arizela*, or possibly all three. Examples from the west side of the mountain ridge as at Mayten, Edgewood, Shasta Valley, and Hornbrook in California are closest to *arizela*, although not as typical as those from the Puget Sound area.

The breeding range of this race seemingly extends south to northern Sonoma County, California, where it presumably meets the highly localized form *sinuosa* which is resident in the San Francisco Bay area. Little material is at hand to indicate the relationships of these two races but *arizela* appears to skirt the bay area to the east and then seemingly continues south through Solano and eastern Contra Costa counties (*vide* Grinnell and Miller, 1944:411) to the Monterey Bay area and Salinas Valley where contact with *scirpicola* is made north of Santa Barbara along the coast. In the interior it also seemingly extends south into the central San Joaquin Valley where it intergrades with *scirpicola*. Specimens from Buena Vista Lake are, as Van Rossem (1930:297) has noted, predominately of the *scirpicola* type. The intergradation between *arizela* and *scirpicola* in the southern San Joaquin Valley is in the form of a long, gradual cline whereby the yellow of posterior underparts becomes more extensive.

In his recent paper, Oberholser (1948:4) describes a race that he calls *californicola* and gives it a range extending "north to central northern California; west to middle California; south to central and southeastern California; and east to eastern California." This would include my intergradational areas between *arizela* and *scirpicola*, *arizela* and *sinuosa*, and in part between *scirpicola* and *occidentalis*. The birds from many of these areas are divergent from typical representations of these races mentioned, but this is in my opinion because of intergradation. There is no constancy of characters in the material that I have examined from the range Oberholser has outlined.

Remarks.—This race has had a history characterized by numerous rejections and acceptances. Soon after its proposal, its validity was questioned when Palmer (1900:225) commented that "Mr. Oberholser's *arizela* is based on extremely slight characters, but chiefly on 'geographic-reasoning'." He stated also that the type of *arizela* is unfortunately an old and badly made skin. Ridgway (1902: 670) recognized *arizela* but made no distinction between the Pacific Northwest form and *scirpicola* of California. Swarth (1912:71-73) would not accept *arizela*. He based his judgment largely on his comparison between a series from Vancouver Island and another from the Pine Forest Mountain area, Humboldt County, Nevada, in which he failed to find significant differences. Grinnell (1914: 202) reached the same conclusion as Swarth after an independent study, but he was working largely with the same specimens.

Reexamination of the Vancouver Island and Nevada series indicates that both lots of specimens are worn, especially the desert representatives. With wear and fading *occidentalis* loses its brighter green color of the dorsum and becomes darker and thus in this character at such times is more nearly like *arizela*. Furthermore, the Vancouver Island series is variable as to the color of the dorsum. As yet a further consideration, the Nevada series is, as we have seen, not entirely typical of *occidentalis* and according to my concept, at least, as opposed to Oberholser's (1948:3), marks the beginning of a

transition between *occidentalis* and *campicola*. The gray flanks of the Nevada series are intermediate in color but the orange tint of the yellow on the underparts and the greater posterior extent of the yellow distinguishes the Nevada series from the Vancouver Island one. Much additional material has accumulated of recent years which demonstrates the distinctness of the two populations.

When Phillips (1947:122) stated that the name *arizela* should "be restored to the small, dull, coastal and Canadian race now improperly called *occidentalis*," he evidently failed to note the differences between the coastal and interior form which later was designated as *campicola* (Behle and Aldrich, 1947:69) but he presumably found no difficulty in distinguishing *arizela* from *occidentalis* farther south. Gabrielson and Jewett (1940:511) in speaking of the yellow-throats east and west of the Cascade Mountain Range in Oregon comment as follows: "We feel that the two forms are subspecifically distinguishable and are therefore proposing the revival of Oberholser's *G. t. arizela* for the race in Oregon and Washington west of the Cascades."

Breeding localities.—BRITISH COLUMBIA. Kispiox Valley, 23 miles north Hazelton; Chilliwack Depot. Vancouver Island: Alberni Valley; Errington; Little Qualine River; Comox. WASHINGTON. Pierce County: Tacoma; South Tacoma; Fort Steilacoom. King County: Seattle; Redmond; Sammamish River. Grays Harbor County: Copalis. Wahkiakum County: Cathlamet. OREGON. Washington County: Forest Grove. Benton County: Corvallis. Coos County: Arago. Klamath County: Upper Klamath Lake; Fort Klamath. CALIFORNIA. Siskiyou County: Klamath River, 2100 feet, 2 miles south Hornbrook; Hornbrook; Edgewood; Big Spring, 2700 feet, Shasta Valley; Mayten; Scott River, 6 miles northwest Callahan. Mendocino County: Willits. Tehama County: Mill Creek, 260 feet, 2 miles northeast Tehama; Dale's, 600 feet, on Paine's Creek. Butte County: Chico. Yolo County: Grafton; Grand Island, 25 feet, 2 miles north Knight's Landing.

Geothlypis trichas sinuosa Grinnell

San Francisco Bay Yellow-throat

Geothlypis trichas sinuosa Grinnell, Condor, 3, 1901:65.

Type.—Adult male, no. 37786, Mus. Vert., Zool., willow patch where San Francisquito Creek enters the San Francisco Bay marshes, near Palo Alto, Santa Clara County, California; May 31, 1900; collected by J. Grinnell, original number 4270.

Distribution.—Breeds in San Francisco Bay area, from Tomales Bay, Marin County, and Napa sloughs, southern Sonoma County, on the north, east to Carquinez Strait and thence south to vicinity of San Jose, Santa Clara County (*vide* Grinnell and Miller, 1944:413). For most part resident in breeding range but some individuals scatter in postbreeding and winter seasons, occurring south to San Diego. For such records of occurrence outside of breeding range, see Grinnell and Miller (*op. cit.*: 414).

Table 4

Measurements of Adult Males of *G. t. sinuosa*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 21 | 52.0-56.5 | 53.6±0.20 | 1.41 | 2.63 |
| Tail | 20 | 45.0-54.0 | 49.3±0.32 | 2.13 | 4.33 |
| Culmen | 20 | 9.6-11.9 | 10.7±0.10 | 0.67 | 6.30 |
| Bill from nostril | 20 | 6.7-8.4 | 7.5±0.06 | 0.46 | 6.10 |
| Tarsus | 21 | 18.9-21.2 | 20.0±0.09 | 0.63 | 3.16 |
| Depth of white postfrontal stripe | 21 | 2.0-5.0 | 3.1±0.13 | 0.92 | 29.09 |
| Weight | 2 | 9.2-9.3 | 9.2 | | |
| Ratio of wing to tail based on means | | | 1.087 | | |

Racial characters.—Dark, brownish-green coloration and short wing; the tail length equals that of wing. Similar to *arizela* in coloration, being a little darker on flanks but distinguished principally on basis of shorter wing. Likewise smaller than *scirpicola*, duller, and lacking extensive yellow suffusion on the posterior underparts.

Variation.—Despite the restricted range of this race it is not a uniformly characterized population. The range of individual variation in color of dorsum, flanks, and yellow below is as great among breeding examples of *sinuosa* as in any other race. The data for measurable characters are presented in table 4. The material examined shows no apparent geographic variation within the range. Likewise obscure is the relationship of *sinuosa* with the surrounding form *arizela*. In every character there is morphological intergradation between the two populations and were more critical specimens available from actual areas of contact the details of intergradation would doubtless be revealed. As it now stands about all this reviewer can do is to point out that the transition between *sinuosa* and *arizela* is rather abrupt, for birds closest to *arizela* breed at Santa Rosa, Sonoma County, and at the Suisun Marshes, Solano County.

Breeding localities.—CALIFORNIA. Marin County: Olema; Point Reyes; Black Point; Saint Vincent. Sonoma County: Petaluma; Second Napa Slough. Solano County: Vallejo. Contra Costa County: Richmond; San Pablo. Alameda County: Cerrito Creek; Bay Farm Island; Hayward; San Leandro; Mowry; Alvarado; Melrose. San Francisco County: Lake Merced. San Mateo County: Baden. Santa Clara County: Palo Alto; Santa Clara; Alviso; San Jose.

***Geothlypis trichas scirpicola* Grinnell**
Tule Yellow-throat

Geothlypis trichas scirpicola Grinnell, Condor, 3, 1901:65.

Type.—Adult male, no. 37811, Mus. Vert. Zool.; San Gabriel River bottom, three miles south of El Monte, Los Angeles County, California; March 20, 1897; collected by J. Grinnell, original number 2217.

Distribution.—Breeds in southern California from vicinity of Santa Barbara along coast and southern end of the San Joaquin Valley (Buena Vista Lake, intergrades) of the interior south to latitude 30° along west side of Lower California. Intergrades with *occidentalis* through Owens Valley, southern Nevada, and southwestern Utah, but in typical form breeds locally southward throughout Lower Colorado River and Imperial valleys to Colorado Delta. Also occurs during breeding season east into Arizona along the Gila River, intergrading with *chryseola* as far east as Tucson area.

Table 5
Measurements of Adult Males of *G. t. scirpicola*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 50 | 51.0-60.0 | 55.9±0.20 | 2.10 | 3.76 |
| Tail | 49 | 48.0-57.5 | 54.2±0.27 | 2.80 | 5.16 |
| Culmen | 48 | 10.0-12.4 | 11.3±0.05 | 0.60 | 5.33 |
| Bill from nostril | 50 | 7.1-8.3 | 7.5±0.04 | 0.43 | 5.83 |
| Tarsus | 47 | 19.4-21.8 | 20.6±0.05 | 0.59 | 2.88 |
| Depth of white postfrontal stripe | 47 | 2.0-7.0 | 3.0±0.13 | 1.37 | 44.6 |
| Weight | 11 | 8.2-10.0 | 9.2 | | |
| Ratio of wing to tail based on means | | | 1.031 | | |

Racial characters.—Marked by intensification of yellow and extension of the yellow posteriorly to cover entire lower surface. Differs from *sinuosa* and *arizela* in larger size, its brighter coloration throughout, and more extensive yellow posteriorly. As compared with *occidentalis*, yellow tone greener, less orange, and yellow more extensive on posterior underparts; flanks darker brown or clay colored, less buffy. Not as brightly yellow as *chryseola* and with less yellow in white, postfrontal stripe.

Variation and relationships with surrounding races.—Extremes of individual variation in color characters show up in this race seemingly more than in other races. This is especially noticeable in the amount of white on the forehead. In other races the white takes the form of a distinct transverse line back of the black of the forehead. In many examples of *scirpicola* there is no clear line of demarcation posteriorly so that the white continues backward blending with the brown or green of the crown. Indeed, the white is so extensive in some individuals that they actually appear to have a white crown. Another variable character pertains to the purity of the white of the postfrontal stripe. Representa-

tives from scattered localities have small amounts of yellow in the otherwise white postfrontal stripe. This character is accentuated in *chryseola* to the southeast where the incidence of occurrence is even greater; in most specimens the yellow suffuses the whole postfrontal area with bright yellow. Considerable individual variation exists in the color of the dorsum. The yellow on the underparts is fairly constant. The data for measurable characters are summarized in table 5.

It would appear that the race *scirpicola* has an eastern desert population somewhat separated from the western population by a hiatus of inhospitable country along the fringe of the mountains. Grinnell (1914:202) found the breeding yellow-throats of the lower Colorado River valley to be of the race *scirpicola*, as did van Rossem (1930:297; 1941:291). I too find the characters of the two groups exceedingly similar, yet Oberholser (1948:4) includes southeastern California, northeastern Lower California, south-central and central Arizona and southwestern Utah in the range of a form which he calls *arizonicola*.

Along the coastal plain, yellow-throats of the *scirpicola* type occur as far north as Santa Barbara. Although breeding specimens are not available to demonstrate it, there is presumably an area of intergradation to the north between *scirpicola* and *arizela* as also in the San Joaquin Valley (see p. 207). A similar type of intergradation occurs east of the Sierra Nevada in the Owens Valley area in Inyo and Mono counties. Specimens closest to *scirpicola* occur as far north as the Walker Basin, Kern County; beyond this they are closest to *occidentalis*.

Specimens are not available to follow the intergradation southward from Utah into typical *scirpicola* but in northwestern Arizona the yellow-throats are probably much the same as in the St. George area. A male from Hackberry, Arizona, taken September 24, corresponds to September birds from St. George. A May 7 specimen from Fort Verde, Arizona, is intermediate but closer to *scirpicola* than to *occidentalis*. Fort Verde incidentally is the type locality of Oberholser's *arizonicola*. The situation here is similar to that in northeastern California, southeastern Oregon and adjacent country, where a name may have been applied to an intergrading population.

Grinnell (1928:204) has shown that yellow-throats of this species and race occur south to include the northern fourth of Lower California. Latitude 30° apparently marks the southernmost occurrence of the species. Farther south the species *Geothlypis trichas* is replaced by *Geothlypis beldingi*.

Remarks.—In the past considerable difference of opinion has existed among systematists as to the validity of this southern California race, but it now seems to have gained general acceptance. The difficulty has centered around two features. One is the abundant presence of vagrant wintering and transient representatives of more northern races in the breeding range when the local race is nesting. Both Grinnell (1901:65; 1914:203) and van Rossem (1930:297) noted this. The other item concerns the relatively great individual variation of *scirpicola* as compared with that of other races.

Breeding localities.—CALIFORNIA. Santa Barbara County: Point Concepcion; Guadalupe Lake; Santa Barbara. Kern County (intergrades): Buena Vista Lake; Walker Basin; 12 miles north Caliente. Ventura County: Ventura; Santa Clara River. Kings County: Tulare Lake, 9 miles south Lemoore. Los Angeles County: Nigger Slough; Bixby; Long Beach; Compton; Greening; Los Angeles; El Monte and 3 miles south El Monte; Pasadena. Orange County: Hog Island; Anaheim Landing; Newport. Riverside County: San Jacinto Lake; Riverside; Coachella Valley; Palm Springs; Mecca. San Diego County: Escondido; Vallecito; San Diego. Imperial County: 8 miles northwest Calipatria; Bard; Riverside Mountain; 4 miles south Potholes; 5 miles northeast Yuma; near Pilot Knob opposite Cibola. LOWER CALIFORNIA. San Ramon; San Telmo, San Jose, 2500 feet; El Valle de la Trinidad; San Felipe; Colorado River, 20 miles south of Pilot Knob at latitude 32° 15'; Alamo River, 20 miles southwest of Pilot Knob; 7-9 miles east of Cerro Prieto; Tecate. ARIZONA. Yuma County: Colorado River, 5 miles south Laguna; Ehrenberg. UTAH (toward *occidentalis*). Washington County: Washington; St. George and 3 miles south St. George. NEVADA (toward *occidentalis*). Lincoln County: Hiko; Crystal Spring and 5 miles south Crystal Spring, Pahranaagat Valley, 4000 feet. Clark County: Colorado River, opposite Fort Mohave, 500 feet.

***Geothlypis trichas chryseola* van Rossem**
Golden Yellow-throat

Geothlypis trichas chryseola van Rossem, Condor, 32, 1930:298.

Type.—Adult male, no. 28584, Donald R. Dickey Coll., Univ. Calif. Los Angeles; Saric, north-central Sonora, Mexico; June 12, 1929; collected by J. T. Wright; original number 3557.

Distribution.—Breeds in north-central Sonora, northeast to Altar, San Pedro, and Santa Cruz River valleys in southern Arizona; Bavispe River valley, northeastern Sonora; east through northern Chihuahua and northern Coahuila to Rio Grande Valley of southern New Mexico and El Paso region of Texas and south at least to Del Rio.

Racial characters.—Yellow coloration bright and extensive. As compared with *scirpicola*, more yellow in dorsum and yellow of underparts brighter and more extensive; flanks of males only slightly tinged with brown or gray; postfrontal band in most specimens suffused with yellow. Distinguished from *occidentalis* by brighter and more extensive yellow throughout and by yellow in postfrontal stripe. Compared with *G. t. melanops*, size smaller, brighter with more yellowish in dorsum and on ventral surface.

Table 6
Measurements of Adult Males of *G. t. chryseola*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 33 | 53.0-60.5 | 56.5±0.20 | 1.72 | 3.05 |
| Tail | 31 | 49.5-57.0 | 53.6±0.21 | 1.80 | 3.37 |
| Culmen | 30 | 10.8-12.4 | 11.7±0.04 | 0.37 | 3.22 |
| Bill from nostril | 30 | 7.6-8.5 | 8.1±0.02 | 0.22 | 2.71 |
| Tarsus | 32 | 19.5-21.7 | 20.5±0.79 | 0.66 | 3.25 |
| Depth of white postfrontal stripe | 33 | 1.0-7.0 | 3.9±0.15 | 1.34 | 34.08 |
| Ratio of wing to tail based on means | | | 1.055 | | |

Variation and relationships with surrounding races.—There is less difficulty identifying examples of this race than is encountered for the other races of western North America because of the bright yellow appearance, the light flanks and yellow postfrontal stripe. The tinge of yellow in the forehead is not a universal character, however, in *chryseola* and as previously noted occasionally appears in *scirpicola*. Indeed, some evidence of relationship between *chryseola* and *scirpicola* may be afforded by the circumstance that both races have an intensification of yellow and in both forms yellow invades the otherwise white postfrontal stripe. *Occidentalis* and *chryseola* also have something in common in that the tint of the yellow tends toward orange rather than the greenish yellow found in coastal populations. Also the flanks are light in color in *chryseola* and *occidentalis* in contrast to the brown flanks of coastal races.

Although I have not had opportunity of examining the form *melanops* from farther south in Mexico (see Ridgway, 1902:673), from the remarks of van Rossem who has examined the type and two other males from the Valley of Mexico, I judge *chryseola* is closer in its characters to *scirpicola* and *occidentalis* than to *melanops* of south-central Mexico. Van Rossem states (1930:298): "These three specimens are all very much larger than any of the more northerly subspecies . . . They bear, in color, close resemblance to *scirpicola* save that the posterior underparts are continuously yellow and there is more concealed yellow in the crown."

I have detected no clines within the range of *chryseola* nor areas of local variation. The non-geographic type of variation is summarized in table 6.

The geographic range for *chryseola* has not been fully determined. There are indications of intergradation with the two races to the west and north. The southern distribution is the most obscure. When originally described, the race was known to breed from north-central Sonora northeast to the San Pedro River in Cochise County, Arizona, and east to northwestern Chihuahua. Van Rossem later (1941:292) extended the range to include the Altar and Santa Cruz River valleys in southern Arizona and the upper Bavispe River valley in northeastern Sonora. Several skins in the collections of the United States National Museum indicate that the range should now be extended still farther north and east to include the Rio Grande Valley of southern New Mexico and the adjacent El Paso region of Texas.

Intergradation with *scirpicola* is revealed by the four specimens from the San Pedro River, Cochise County, Arizona, commented on many years ago by Swarth (1912:73 and 1929:339) and

called *scirpicola* by him before the existence of the race *chryseola* was known. They are a heterogeneous lot aptly described by van Rossem (1930:298) as follows: "They are so variable that, as a lot, they could go into one race just as unsatisfactorily as into the other. One (no. 2913, Swarth coll.) is close to typical *chryseola*, another (19,116, Mus. Vert. Zool.) is nearest *chryseola*, a third (19,118) is just about intermediate, while the fourth (19,117) is, except for the very wide post-frontal band, closer to *scirpicola*. The preponderance in the small series is certainly closer to *chryseola* and accordingly I have so called them."

Seemingly there is a gradual fusing of *chryseola* and *occidentalis* farther north through central-eastern and southeastern Arizona and adjacent New Mexico. This is indicated by specimens from Safford and Pima, Arizona, which are intermediate between the two races. Some of these intergrades are like *scirpicola* which may indicate a blending with characters of that race too. If so, it is reminiscent of the area in southeastern Oregon where *occidentalis*, *arizela* and *campicola* may come together. However, as there, it may prove that Oberholser's race *arizonicola* (1948:4) is valid and that this intermediate condition is constant and associated with a geographical range.

A worn specimen taken in mid-August at Socorro, New Mexico, is an unusual example. It appears to be intermediate toward *occidentalis* in that there is a suffusion of orange to the yellow of the throat, but the yellow is more extensive below as in *chryseola*, the dorsum is yellow, and yellow appears in the postfrontal area. A peculiarity is that the head is grayish-white and a collar-like band separates the head from the back, a situation found elsewhere only in some coastal members of *scirpicola* and a May specimen from Fort Verde, Arizona. A June example from Palomas Spring in the Rio Grande Valley, New Mexico, also approaches *occidentalis*.

At the time of his description of *chryseola*, van Rossem (1930:298) commented that "Three of the four localities from which the new race is known (Satic, Tecoripa, and San Diego) indicate an upland habitat, and when finally worked out the range will probably be found to center on the northern part of the Mexican plateau." He stated in addition that this form occurs south to Tecoripa in east-central Sonora at least in spring but this may only indicate a southward seasonal movement by at least part of the population. Van Rossem later pointed out (1945:229) that the southernmost breeding station is Pilares in the Bavispe River valley.

Breeding localities.—ARIZONA. Graham County (toward *occidentalis*): Pima; Safford. Cochise County: San Pedro River, midway between Fairbanks and Charleston; Fairbanks; San Simon Valley. Santa Cruz County: Tubac; Santa Cruz River west of Patagonia Mountains; Santa Cruz River, 2 miles south Tumacacori Mission, 3300 feet. Pima County: Continental; Altar Valley, 15 miles north International Boundary. NEW MEXICO. Socorro County: Socorro. TEXAS. El Paso County: El Paso; Frijole. Valverde County: Del Rio. SONORA. Satic; Tecoripa.

Geothlypis trichas modesta Nelson

San Blas Yellow-throat

Geothlypis trichas modestus Nelson, Auk, 17, 1900:269.

Type.—Adult male, no. 157204, U. S. Nat. Mus., Biol. Surv. Coll.; San Blas, Tepic (= Nayarit), Mexico; June 12, 1897; collected by E. W. Nelson and E. A. Goldman.

Distribution.—Resident in coastal marshes of western Mexico from Kino and Tepopa bays, Sonora, south through Sinaloa, Nayarit, and Jalisco at least to Colima. Apparently individuals occasionally wander across the Gulf of California to Lower California.

Racial characters.—Differs from *scirpicola* and *chryseola* in darker coloration throughout and by tendency toward smaller bill and tail. Differs from *riparia* in being smaller, especially the bill measurements.

Measurements.—Six breeding males: wing, average 53.5 (52.5-54.8); tail, 52.0 (50.4-53.4); wing/tail ratio, 1.027; bill from nostril, 7.6 (7.4-8.0); tarsus, 20.2 (19.2-21.0); width of white postfrontal stripe, 3.3 (2.0-5.0).

Remarks.—As van Rossem (1930:298) noted, this race is exceedingly close in its characters to *sinuosa* of the San Francisco Bay region even though separated from the northern form by several hundred miles. The general coloration is similar and both are small in wing, tail and bill lengths. The dorsum is slightly grayer in *modesta*. There is a greater amount of concealed white in the head area

of *modesta* in some specimens so that wear produces a much whiter head. The flanks of *modesta* are darker and browner than in *sinuosa*.

These two races have other features in common too. They both occupy a salt marsh habitat. Van Rossem raises the question (1941:292) whether they may both be remnant colonies of a former more generally distributed salt marsh stock or whether similar environments have produced similar color characters. Possibly bearing on this matter of relationships is the circumstance that although they are both essentially resident races, postbreeding season wandering carries some individuals well out of the breeding range. There are several records of *sinuosa* from southern California. Van Rossem collected two examples of *modesta* on southern Lower California, one at Magdalena Bay (North Estero) on March 3, 1930, and one on San Jose Island, in the Gulf, on March 14, 1930. Both occurred in a mangrove-salicornia association which constitutes their typical habitat in their breeding range (see van Rossem, 1930:298-299).

With its restricted habitat and range fronting on the gulf, it would appear that *modesta* has no immediate neighbors except in the race *riparia* from which it is separated ecologically as well as morphologically.

Breeding localities.—SONORA. Kino Bay; Tobarí Bay; Empalme.

Geothlypis trichas riparia van Rossem

Mayo Yellow-throat

Geothlypis trichas riparia van Rossem, Condor, 43, 1941:292.

Type.—Adult male, no. 31945, Donald R. Dickey Coll., Univ. Calif. Los Angeles; Tesia, Mayo River, 200 feet, Sonora, Mexico; June 22, 1937; collected by A. J. van Rossem and Robert Hannum.

Distribution.—Breeds along Mayo River valley of Sonora, Mexico. Limits of range undetermined but known to occur at least in winter in the Yaqui River valley in southern Sonora.

Racial characters.—Distinguished from *G. t. modesta* of adjacent tidal marshes by larger bill and longer tail, lighter flanks, and more extensive yellow posteriorly. From *G. t. chryseola* it differs in duller yellow, longer tail, and larger bill. Similar in bill size and proportions of tail and wing length to *G. t. melanops* so that tail is equal to wing, but differs from that race in being lighter.

Measurements.—Two breeding males: wing, average 54.7 (54.4-55.0*); tail, 53.8 (53.1*-54.6); wing/tail ratio, 1.016; bill from nostril, 8.4 (8.1-8.7*); tarsus, 20.4 (20.0-20.8*); width of white postfrontal stripe, 3.0 (2.0-4.0). The measurements marked with an asterisk are those of the type.

Remarks.—When Nelson described the race *modesta* he attributed to it a range along the west coast of Mexico from southern Sinaloa south at least to Colima. Van Rossem (1930:298) noted the variability among the breeding yellow-throats from the Mayo River area and interpreted it as being indicative of intergradation with *chryseola*. Later (1941:292) in describing *G. t. riparia* he noted that the two races were separated ecologically. *G. t. modesta* he found, at least in Sonora, to be strictly an inhabitant of the coastal marshes, frequenting scrubby mangrove and other salt water associations; the larger billed race, *riparia*, in contrast, selects the riparian habitat found along fresh-water streams extending inland from the coast along the Mayo River. Thus a situation exists supposedly comparable to the relation between *sinuosa* and *arizela* in the San Francisco Bay area of California. Whether the two races actually intergrade through interbreeding is not known. Neither are data available to indicate the extent of the range of the race *riparia* or whether it impinges upon other races. Indeed, only two specimens representing the race have been available in the present study, both loaned through the courtesy of A. J. van Rossem, one being the type specimen and both from Tesia. The series he had at the time of his description is now scattered. These two examples show the differences from *modesta* in larger bill and longer tail. In these characters, this population shows an approach to *G. t. melanops* and *G. beldingi*.

Geothlypis beldingi Ridgway

Belding Yellow-throat

Geothlypis beldingi Ridgway, Proc. U. S. Nat. Mus., 5, 1882:344.

Type.—Adult male, no. 87685, U. S. Nat. Mus.; San Jose del Cabo; taken by Lyman Belding; no date given.

Distribution.—Resident in the central and southern part of Lower California from about latitude 28° south to Cape San Lucas.

Specific characters.—Distinguished from *G. trichas* by larger size throughout. As compared with *G. t. scirpicola*, also brighter and yellow more extensive, especially in the postfrontal area, crown and postocular region.

Variation and distribution.—According to Grinnell (1928:204) a hiatus exists between the southernmost breeding station of *Geothlypis trichas scirpicola* at about latitude 30 degrees and the northernmost locality of record of *G. beldingi* at San Ignacio. This would seem to be a factor in the differentiation of the two populations at the species level. From the fact that two geographic races of *G. beldingi* have been described with intermediates or intergrades from Comondú located between them, it would appear that clines exist in several characters. However, I am not convinced either that clines do exist within the species or that there are two subspecies present.

Table 7

Measurements of Adult Males of *G. beldingi*

| Measurement | Number of specimens | Range | Mean with probable error | Standard deviation | Coefficient of variability |
|--------------------------------------|---------------------|-----------|--------------------------|--------------------|----------------------------|
| Wing | 40 | 59.0-68.5 | 64.7±0.27 | 2.54 | 3.9 |
| Tail | 40 | 57.5-69.0 | 63.4±0.26 | 2.52 | 3.9 |
| Culmen | 37 | 12.0-14.7 | 13.1±0.07 | 0.64 | 4.7 |
| Bill from nostril | 37 | 8.6-10.0 | 9.1±0.03 | 0.31 | 3.46 |
| Tarsus | 41 | 21.3-25.4 | 23.1±0.08 | 0.83 | 3.61 |
| Depth of white postfrontal stripe | 10 | 3.0-7.0 | 4.8±0.28 | 1.31 | 27.41 |
| Weight | 28 | 13.8-17.7 | 15.7 | | |
| Ratio of wing to tail based on means | | | 1.020 | | |

Although Oberholser (1917:183) stated that since *G. beldingi* occurs only in the southern portion of the peninsula of Lower California, its development into two subspecies would seem hardly probable, he found "very conspicuous differences between individuals of this species from the Cape San Lucas region and those from the central portion of the Lower California peninsula," and described the latter as *Geothlypis beldingi goldmani* with type locality at San Ignacio. The males of the northern subspecies were said to differ from those of *G. b. beldingi* of the Cape region in having a whitish crown band instead of yellow, less yellowish upper parts, and whitish abdomen. Birds from San Ignacio representing the northern limit of distribution of the species were said to be most extreme in *goldmani* characters. Examples from Comondú appeared to be intermediate but referable to the race *goldmani*. Oberholser noted some individual variation in *G. b. goldmani* in the extent of the yellow on the lower parts and in the amount of yellow in the postfrontal stripe but his material representing the new race consisted of only 7 males and 3 females from these two localities.

When I examined the material in the Museum of Vertebrate Zoology reported on by Grinnell (*op. cit.*: 204-205), these specimens showed the differences noted by Oberholser as did those specimens in the Dickey collection. However, it puzzled me that many of the lighter examples supposedly typical of *goldmani* seemed to be in process of molt with the conspicuous feature being that the new feathers coming in were intensively yellow. Upon receipt of the series of ten breeding males in the California Academy of Sciences from San Ignacio it was found that most of the specimens were as intensively yellow as examples of *G. b. beldingi* from extreme southern Lower California. The specimens were labelled *G. b. beldingi* possibly because of this yellow color. Yet the San Ignacio birds were from the type locality of *G. b. goldmani*! The few that are lighter and so conform to the description of *G. b. goldmani* through having a white postfrontal area and being generally paler also seem to have been undergoing a molt when taken and the new feathers are intensely yellow. The indications are, then, that birds of this species in first-winter plumage, as compared with adults, have a lighter, more grayish, less greenish, dorsal coloration. Their underparts are lighter or whiter with less yellow showing. The postfrontal stripe also tends to be more whitish, rather than yellow. The

intense yellow all through seems to develop with the first prenuptial molt. In *G. trichas*, as previously noted, first-year birds are indistinguishable from adults.

The possible difference between *G. trichas* and *G. beldingi* in molt sequence is fraught with considerable significance, for not only does it strengthen the idea that the southern Lower California population is specifically distinct, but it also might account for *G. b. goldmani* having been described in the first place. The describer may have chanced to get a series of pale first-year birds.

Apart from differences seemingly due to molt and age, there is still not enough constancy of characters in the material available to me from the northern portion of the range of *G. beldingi* to justify subspecific separation from the population of the Cape region proper. In addition to the pale and yellow types noted, other specimens are present of a decided orange caste. Furthermore, no constant measurable differences between specimens from the two areas seem to exist. It would seem, then, that very little reason exists for dividing *G. beldingi* into two geographic races.

Certain clines manifest in northern populations of *G. trichas* seem to continue on into *G. beldingi*. And in certain color characters there is overlap between the two species. For instance, the color of the dorsum and flanks of *G. beldingi* can be matched in *G. t. sinuosa*. The cline of postfrontal stripe changing from white to yellow in *G. t. chryseola* continues on into *G. beldingi* where not only is the stripe yellow but the yellow extends extensively back on the top and sides of the head. The general intensity of yellow is of a deeper orange than in races of *G. trichas*. An approach to this was indicated in *G. t. chryseola* which, however, has a brighter yellow.

In pointing out the necessity of a generic revision before the relationships of the several groups of yellow-throats can be clarified, van Rossem (1941:292) comments as follows on the situation between *G. trichas* and *G. beldingi*, "The ranges of all members of the *trichas* complex are complementary and it is a perfectly simple matter to 'prove' intergradation throughout the series by playing leap-frog without regard for intervening forms. For instance, it is not in the least a difficult task to prove *beldingi* a race of *trichas* by picking out almost any character and following it through *goldmani*, *melanops*, *riparia*, *chryseola*, *scirpicola*, etc. It is, indeed, rather surprising that such a course has not been advocated." There seems little doubt, however, that the yellow-throats of southern Lower California constitute a separate and full species. In addition to the hiatus in range and consequent lack of interbreeding between *G. trichas* and *G. beldingi* the data in tables 6 and 7 for length of extremities and weight indicate that *G. beldingi* is actually a larger form. A summary of the measurements of adult males of *G. beldingi* is given in table 7.

Breeding localities.—LOWER CALIFORNIA. San Ignacio; Comondú; San José del Cabo; Todos Santos.

SUMMARY OF VARIATION

As our knowledge of the variability of yellow-throats increases, it becomes evident that the species is more plastic than previously supposed. It also appears that we have represented in the yellow-throats of western North America, as in many other species of geographically variable birds in the same general area, several levels of differentiation. Starting with localized groups of individual variants one can progress through intergradational areas which, perhaps, represent "preracial" stages, to races of various degrees of distinctness and up to full species.

Numerous cases of individual variants have been pointed out in the subspecies accounts. Likewise numerous areas of intergradation have been discussed. In some instances these areas of blending are widespread but elsewhere they are seemingly narrow. Some of these cases of local variants and areas of intergradation have been handled differently by systematists in their attempt to express the nature of the variation. The writer, for instance, with his concept of broad areas of intergradation between two and sometimes three races (southeastern Oregon and northwestern Arizona) differs in his handling of the problem from Oberholser (1948) who has described many additional races. Actually there is not at the present time enough breeding material available from the critical areas to work out perfectly the validity of either concept and it may very well be that the characters of the populations of the intermediate areas in question

will be shown to be stable and associated with a range rather than behaving as long gradients. However, it is my feeling that even should the former situation prove to be the case, the degree of difference between these populations and the now generally recognized races is too slight to justify nomenclatural recognition. Nevertheless this imperfect or incipient geographic variation is exceedingly important, as indicating, perhaps, races in process of formation.

To illustrate the other levels of differentiation, the race *G. t. chryseola* is rather distinctive and fairly stable as compared with either *scirpicola* or *campicola* which seem more variable in color characters. This is borne out by measurable data also. *G. trichas* and *G. beldingi* are the distinct species in the area that has been considered. Continuing up the scale, but going outside the area studied, there are according to some writers, indications of "complexes" or groups among the species of the genus. For instance, *G. beldingi* is apparently closest to the western races of *G. trichas* and thus may be considered a part of the "*trichas* complex" as opposed to certain darker forms of the Mexican area or the isolated species of the Bahamas.

Pursuing this idea of representation of different stages in speciation, the genus seems to serve as a good example of the effects of isolation. According to Ridgway (1902) warblers of the genus *Geothlypis* occupy the whole of temperate North America and tropical America, the Bahama Islands and in winter, Cuba, Puerto Rico, Haiti, and Jamaica. There are seventeen species in the genus. Two (*G. velata* and *G. aequinoctialis*) are exclusively South American species. Another form (*G. semiflava*) has one race in Ecuador but has a strange distribution whereby a second race occurs in Central America and ranges from southern Honduras and eastern Nicaragua to Costa Rica. Seven more species are insular forms in the Bahamas. Three of these species (*G. rostrata*, *G. maynardi* and *G. flavida*) inhabit a single small island, while two others (*G. incompta* and *G. tanneri*) inhabit another island. The other two insular species are each confined to an island apiece which islands are not occupied by other members of the genus. Five species are distributed through various sections of southern Mexico (*G. flavovelata*, *G. flaviceps*, *G. chiriquensis*, *G. speciosa*, *G. nelsoni*), one of the five having two subspecies. In southern Lower California there occurs the distinctive form (*G. beldingi*). The last species (*G. trichas*) has a very extensive range covering most of North America and extending south into northern Mexico. Thus it would seem that historic factors making for isolation may have been operative in speciation.

Just as significant as the seeming effect of isolation in speciation is the circumstance that the species *G. trichas* is the truly wide-ranging species and it has become differentiated into a great many geographic races or subspecies. Thus environmental differences seem to have made their impress generally on *G. trichas* in various parts of its range, resulting in much subspecific differentiation. The process of riation seems to have been accentuated in western North America with its great climatical and topographical diversity. It is here that character gradients or clines best show up.

The pattern of distribution and differentiation of the western races of yellow-throats corresponds only in part to the general picture of faunal relationships among other species of birds in the area studied. On the one hand, it seems rather surprising that the Rocky Mountains do not serve as a barrier of some sort separating populations on either side. This lack of influence is seen in both the races *occidentalis* and *campicola*. On the other hand the Cascade-Sierra Nevada axis does seem to serve as a barrier save possibly in northern California where the mountain mass is less formidable. The lack of differentiation in *scirpicola* between the coastal areas in southern California and those of the Colorado River valley is likewise surprising. The presence of the small, dark, *sinuosa* confined as a breeding bird to the San Francisco Bay area is yet another puzzling feature.

The picture of distribution revealed is such that it is difficult to detect centers of differentiation for the various races which could be cited as evidence that the populations had originated locally. Indeed, many of these races may have moved in from points of origin elsewhere. In support of this, one might cite the lack of correlation in behavior of characters in intergrading zones as in southern Idaho between *occidentalis* and *campicola* where the blending of the various racial characters does not exactly coincide in the broad area where they intergrade. Such characters may serve as an indication of a type of intergradation which has arisen through interbreeding in a transverse strip intervening between the ranges of forms once separated and distinctly differentiated that have since moved into an area of contact. This would be an alternative to the idea of an origin of this intergradation through incomplete differentiation under the influence of some intermediate environmental condition. This latter situation may, however, prevail in other areas, for there are vast areas of intergradation between some races where the transition in all the characters is gradual and synchronized. In some cases the races blend over so long a distance that the two populations are definitely recognizable only at the extremes of the clines. This is seemingly what occurs between *arizela* and *scirpicola* all through the Great Valley of California. Another such cline occurs between *scirpicola* and *occidentalis* in eastern California, southern Nevada and southwestern Utah. In contrast to this, interbreeding between *sinuosa* and *arizela* is seemingly confined to a narrow band fringing the San Francisco Bay. Yet one other type of intermingling of races is indicated in the southern deserts where the distribution of yellowthroats is especially discontinuous and intergradation seems to show up in small, scattered populations in isolated areas.

Even though the whole picture of relationships is obscure, it may be worthwhile pointing out that three separate stocks may be represented among the yellowthroats of western North America. One is clearly *G. beldingi* of southern Lower California, isolated and of large size. This may be a relict population. *G. t. sinuosa* and *G. t. modesta* as previously discussed and as originally pointed out by van Rossem (1941:292) seem to have some features in common suggesting close affinities even though they are widely separated geographically. Each is characterized by small size and dark coloration and each has a range confined to a restricted area, the former to the San Francisco Bay region and the latter to a narrow fringe of coastal marshes along the Sonoran coast. So little material is available for *modesta* that conclusions must be tentative. Van Rossem (*loc. cit.*) mentions the possibility that the similar characters in these two races may have evolved in relation to similar environmental conditions. In this connection it should be pointed out that *sinuosa* is seemingly not confined to the salt marsh habitat. According to Schussler (1918:62) "not only is it found much more commonly in the neighborhood of fresh water throughout most of this region, but even in areas directly adjacent to the lower bay where salty flats largely predominate it shows marked preference for the reaches of non-saline streams." The possibility exists that these two restricted populations represent vestiges of a single antecedent population. A third stock appears to be represented by *campicola*, *occidentalis*, *scirpicola*, *chryseola*, and *riparia*.

Through natural selection the influence of the environment is doubtless making itself felt on the various populations in the various geographic regions. In this connection it is noteworthy that the potentiality for all the characters seems to be present in greater or lesser degree in all races. Individuals appear in one race that possess characters of an adjacent or distant race. For instance, occasional specimens of *scirpicola* show the yellow postfrontal stripe that is typical of *chryseola*. Whether this is due to recurrent mutations or gene spread from *chryseola* stock is problematical.

The data for the measurable characters are summarized in figure 33, where a comparison is given of average wing, tail, tarsal and bill lengths of breeding males. Tarsal length shows the least variation between races with bill length being similar. Tail and wing are most variable between races. In every character there is a sharp increase in size in *G. beldingi* as compared with the races of *G. trichas*. The increase in length of extremities in *G. beldingi* seems to accompany increase in body size. Average weights

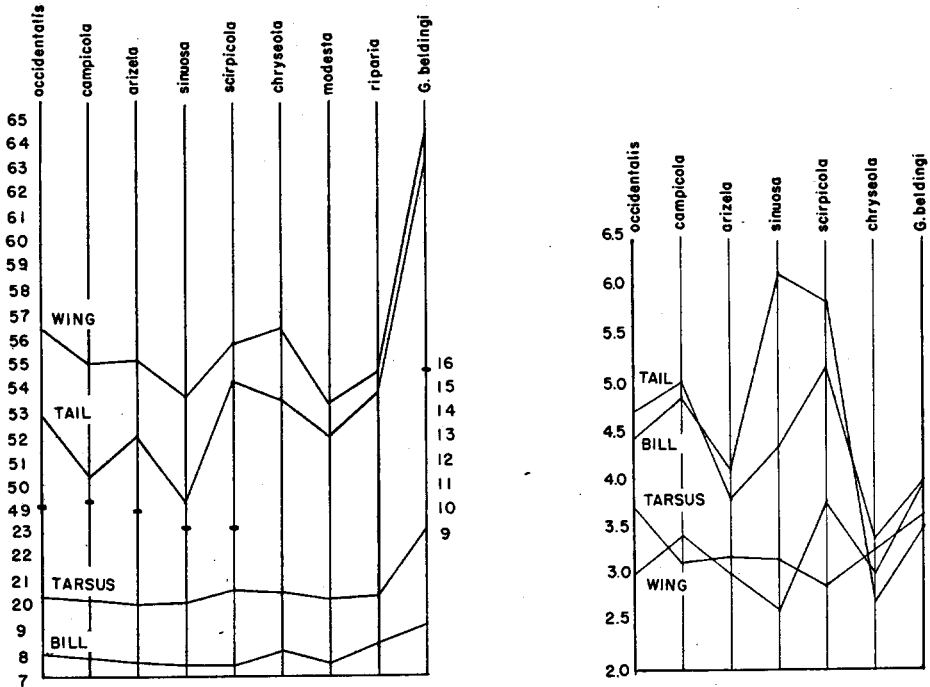


Fig. 33. Left. Comparison of average length of wing, tail, tarsus, and bill of breeding males, with scale in millimeters on left margin; scale in grams on right margin applies to spots which indicate average weights for six of the forms.
 Right. Comparison of coefficients of variability for length of wing, tail, tarsus, and bill.

range around 9 or 10 grams for the various races of *G. trichas* whereas *G. beldingi* has an average body weight of about 15 grams.

The coefficients of variability for various characters are compared in figure 33. They are more nearly alike in *chryseola* than in any of the other races of *G. trichas* whereas in *G. t. sinuosa* there is the greatest divergence. Perhaps having such a restricted range and interbreeding with the surrounding populations of *arizela*, the San Francisco race is becoming more heterogeneous genetically. Yet *scirpicola* shows a similar pattern of variability. The species *G. beldingi* shows less fluctuation than any of the other populations considered, which is in accord with its isolated position.

As to correlations, the coefficients of variability of wing and tail lengths show a certain parallelism in most races. Tarsal length is essentially the same in each race but wing and tail are not comparably uniform in the graph. Bill length shows little correlation with wing or tail.

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