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CENTURUS (AVES)

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INTRODUCTION

THE PRINCIPAL OBJECTIVE of the present study was to ascertain the systematic relationships among populations of woodpeckers of the genus *Centurus* occurring in the United States, México, and northern Central America. Because the distributional pattern of species of this complex is strongly allopatric and the morphologic criterion of relationship is notably unreliable, considerable controversy as to species limits has developed among taxonomists working with museum specimens alone. But recent field investigations in zones of contact between allopatric or narrowly sympatric forms, together with analyses of morphologic variation in specimens, have yielded important information that contributes to our understanding of systematic relationships within the genus.

The present report is primarily concerned with species of *Centurus* occurring in the United States and in northern and central México, namely, *C. carolinus*, *C. aurifrons*, *C. uropygialis*, *C. hypopolius*, and *C. chryso-genys*; but, in addition, we have treated *C. hoffmanni* of Costa Rica and Nicaragua and have included systematic comments on several other forms referred to the genus. The geographic distribution of species considered in detail in this report is indicated in figure 1, and specimens of several species are shown in plates 53 to 55.

Research on *Centurus* was supported by the National Science Foundation (Grant 3448) and the Research Institute of the University of Texas (Grant URI-871). The study was completed in 1960, while the senior author was a Research Fellow in the Department of Ornithology of the American Museum of Natural History.

FIELD WORK AND MATERIALS

Field work was undertaken in México in June and July, 1958, for the primary purpose of studying the relationship of *Centurus aurifrons* and *C. uropygialis* in Aguascalientes and Jalisco; but some time was devoted to *C. chryso-genys* in Colima and Nayarit, *C. hypopolius* in Puebla, and *C. aurifrons* in Coahuila, San Luis Potosí, and Tamaulipas. Our investigations are based on 231 specimens collected in México in 1958, all of which have been deposited in the American Museum of Natural History, and on material obtained on loan from the following institutions:

The American Museum of Natural History (A.M.N.H.), through the courtesy of Dr. Dean Amadon and Mr. C. E. O'Brien; British Museum (Natural History) (B.M.N.H.), through Dr. R. W. Sims; Chicago Natural History Museum (C.N.H.M.), through Dr. M. E. Traylor; Donald Dickey Collection (University of California, Los Angeles) (D. C.), through Dr. T. R. Howell; Museum of Zoology, Louisiana State University (M.Z.L.S.U.), through Dr. R. J. Newman; Museum of Zoology, University of Michigan (M.Z.U.M.), through Dr. R. W. Storer; Museum of Vertebrate Zoology, University of California, Berkeley (M.V.Z.), through Dr. A. S. Leopold and Dr. F. A. Pitelka; and United States National Museum (U.S.N.M.), through Dr. H. Friedmann.

In addition, specimens in the Museum of Comparative Zoölogy, Harvard University, and the Peabody Museum, Yale University, were examined in October, 1960, through the courtesy of Mr. J. C. Greenway, Jr., and Dr. S. D. Ripley, respectively.

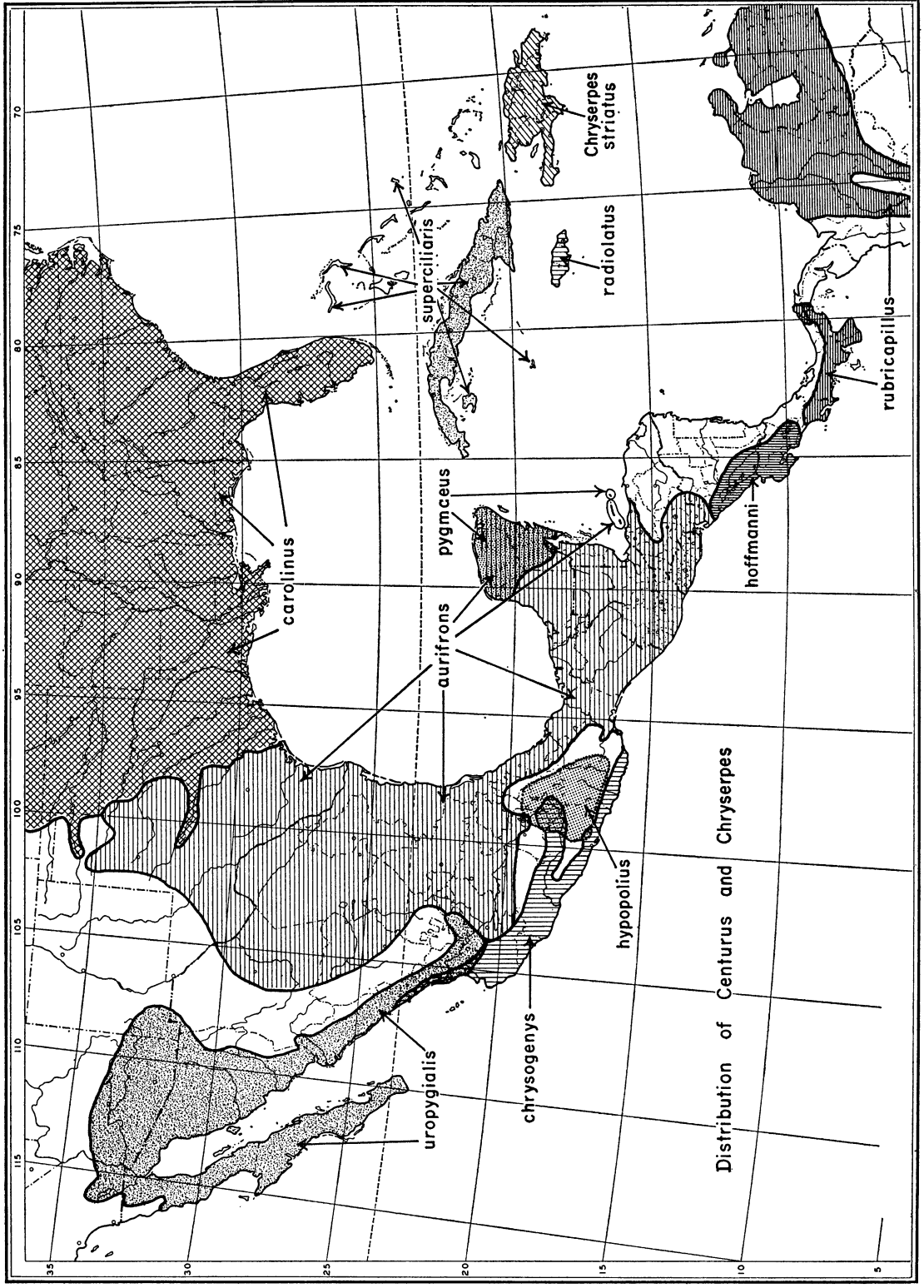


FIG. 1. Distribution of several species of woodpeckers of the genus *Centurus*.

GENERIC LIMITS

THERE IS LITTLE AGREEMENT among systematists as to the number of genera in which species of the *Centurus-Tripsurus-Melanerpes* complex are to be included. In many early classifications, as well as in some of recent date (Todd, 1946), three genera are maintained, but Peters (1948) has lumped all three under the name *Melanerpes*. Other workers have recognized two genera, combining *Tripsurus* with *Centurus* (Mexican Check-List Committee, 1957, p. 36) but maintaining *Melanerpes*, and still others (e.g., Wetmore, 1957, p. 51) unite *Tripsurus* and *Melanerpes* but regard *Centurus* as distinct.

In the generic diagnoses of *Tripsurus* and *Centurus* prepared by Ridgway (1914), there is no character or combination of characters providing clear distinction between the two groups of species. The tail is supposedly two-thirds as long as the wing in *Centurus* and less than one-half as long in *Tripsurus*, but, in fact, the tail is slightly less than one-half as long as the wing in *C. hoffmanni* and *C. rubricapillus*; and it is slightly more than one-half as long in *T. pucherani* (see table 1). The extent of feathering of the orbital region is another feature purportedly distinguishing the two groups: in *Tripsurus* this region is bare, and in species of *Centurus* it is supposedly well feathered. However, as acknowledged by Ridgway himself, this region is fully as bare in *C. chrysogenys* as in *T. pucherani*. Moreover, it is almost as extensively bare in *C. rubricapillus* and *C. superciliaris*, and an intermediate condition is seen in *C. hypopolius*. Similarly, the structure of feathers of the malar apex is variable in both genera and cannot serve as a diagnostic character. Nor do the shape and size of the nostril (supposedly broadly oval in *Centurus* and oval or ovate and smaller in *Tripsurus*) provide a basis for separation.

Wetmore (1957) argues for the maintenance of *Centurus* as a genus distinct from *Melanerpes* (in which he apparently includes *Tripsurus*) on the basis that the regularly barred back and the soft and "blended" breast feathers of *Centurus* contrast with the uniformly colored back and the hair-like feathers of the breast in "typical" *Melaner-*

TABLE 1
WING/TAIL RATIOS IN MALES of *Centurus*

Population	Wing/Tail ^a
<i>C. hoffmanni</i>	2.03
<i>C. aurifrons santacruzi</i>	
SE. Honduras-Nicaragua	
(33) ^b	1.68
El Salvador (32)	1.75
NW. Honduras (31)	1.76
S. Guatemala (30)	1.82
Central Guatemala (29)	1.76
SE. Chiapas (22)	1.77
Mean, samples 22, 29-33	1.76
<i>C. aurifrons dubius</i>	
Mean, samples 23, 25	1.65(1.62-1.69) ^c
<i>C. aurifrons grateloupensis</i>	
Mean, samples 12, 15, 16	1.69(1.68-1.70)
<i>C. aurifrons aurifrons</i>	
Mean, samples 3, 5, 10, 14	1.71(1.69-1.75)
<i>C. aurifrons polygrammus</i>	
Mean, samples 18-21	1.74(1.67-1.85)
<i>C. carolinus</i> (Texas)	1.64
<i>C. uropygialis</i>	
Sonora	1.58
Nayarit-Sinaloa	1.60
Jalisco-Aguascalientes	1.63
Zacatecas	1.70
<i>C. hypopolius</i> (Puebla)	1.56
<i>C. chrysogenys</i> (Nayarit)	1.71
<i>C. pygmaeus</i>	
Yucatán	1.70
Cozumel Island	1.62
Bonaca Island	1.72
<i>C. rubricapillus</i>	
Panamá	2.11
Isla El Rey	2.12
<i>C. pucherani</i> (Nicaragua)	1.92
<i>C. chrysauchen</i> (Costa Rica)	2.04

^a Calculated from mean wing and tail lengths of samples.

^b Numbers in parentheses refer to sample areas indicated in figure 2.

^c Range.

pes. He fails, however, to point out that these characters will not permit separation of *Tripsurus* and *Centurus*.

In urging that "such apparently well-characterized groups" as *Centurus* and *Tripsurus* should not be combined with *Melanerpes*, Todd (1946, p. 297) suggests that "more

weight should be given to color pattern." But when we compare the species assigned to *Centurus* and to *Tripsurus*, it is soon apparent that similarities in color and pattern between *Centurus chrysogenys* and *Tripsurus pucherani* actually provide the strongest argument for combining the two nominal genera. Specimens of these two woodpeckers are shown in plate 54. Similar features are: (1) dorsal barring of black and white; (2) extensive black on side of head (in males of *C. chrysogenys* this color is limited to the superciliary region, whereas it also extends over the postorbital region in *T. pucherani*; in females of both species, the black passes over the occipital region as a band, which is wider in *Tripsurus*); (3) yellow frontal region; (4) naked, black orbital region; (5) dark breast and throat; and (6) barred flanks, the bars being darker and more extensively distributed anteriorly in *Tripsurus*.

The chief difference in color between these species involves the presence of yellow on the malar region and chin in *C. chrysogenys* and its absence in *T. pucherani*, but this is a trivial difference, for the character is subject to geographic variation in *C. chrysogenys* and is, in fact, almost absent in birds from Morelos (R. T. Moore, 1950, p. 109). The amount of yellow on the malar region and chin also varies individually within wide limits in another species, *C. pygmaeus* (see p. 255).

Skutch (1943, 1948) has argued against combining *Tripsurus* and *Centurus* on the basis of "fundamental" differences in certain aspects of life history. In his studies of *C. rubricapillus*, *C. hoffmanni*, and *C. aurifrons* in Central America, Skutch notes (1948, pp. 257-258) the following features of life history contrasting with those of *Tripsurus*: (1) the male alone attends the nest at night, the female roosting elsewhere; (2) the nest is kept clean during incubation and the early part of the nestling period, but fecal matter is often allowed to accumulate as the nestlings grow older and the parents no longer enter the nest cavity to feed them; and (3) in *C. rubricapillus*, the young are not led back to roost in the nest after they fledge. (Information on this aspect of behavior is not available for *C. hoffmanni* and *C. aurifrons*.)

By way of contrast, in *T. pucherani*, *T. cruentatus*, and *T. chrysauchen*, Skutch finds

that (1) both the adult male and female usually sleep in the nest with their eggs or young (rarely roosting alone in separate cavities); (2) the nest is kept clean until the young take wing and later; and (3) fledglings return to roost in the nest cavity with their parents and may continue this habit until the approach of the next breeding season.

Although Skutch's observations are of considerable interest and should be extended to other woodpecker species, there is reason to doubt that the reported differences in life history of Central and South American species of *Tripsurus* and *Centurus* are in any sense "fundamental" or of unusual significance from a systematic standpoint. Also, we call attention to the fact that Skutch's conclusions in regard to generic classification were based on observations of only a few individuals representing less than half of the total number of species assigned to these genera. Hence, the degree of constancy of these differences in the two groups of species remains to be determined, and we note that at least one of the traits is subject to individual variation within a single species. Thus, for *T. chrysauchen*, Skutch reports several instances in which the female of a pair roosted in a cavity apart from that in which the male incubated and brooded at night, and he also found a female of *T. pucherani* roosting alone in a separate cavity while the male of the pair incubated. On this account, we are reluctant to attach much taxonomic significance to roosting locations.

Differences in nest sanitation are, as Skutch points out, related to the fact that the nesting cavity of the species of *Tripsurus* studied is used as a family "dormitory" (Skutch, 1961a) by the parent birds and fledged young of the species of *Tripsurus* studied but not by those of *Centurus*. Therefore, the basic question concerns the degree of taxonomic significance to be attached to differences in the length of time that fledglings remain with their parents. Since the time of dispersal of the young varies among species of some other genera of birds, it seems reasonable to suspect that it may have no particular value as a taxonomic character at the generic level in woodpeckers. For example, in wrens of the genus *Campylorhynchus* (Selander, MS), the young of some species (e.g., *C. brun-*

neicapillus) disperse from the parental territory soon after fledging, while in other species (e.g., *C. zonatus*) they remain for more than a year, being associated in family groups with their parents and assisting, as helpers at the nest, in rearing broods in the next breeding season (Skutch, 1935, 1961b). An intermediate condition is seen in *Campylorhynchus rufinucha*, in which, as in the species of *Tripsurus* studied by Skutch, the young of the year disperse at the beginning of the next breeding season. Interspecific variation in the time of dispersal of the young is also found in jays of the genus *Aphelocoma* (Pitelka, 1951a). In birds, the time of disbanding of family groups and dispersal of young is presumably adaptively related to structure and other aspects of the dynamics of the populations, but little is known of the nature of this relationship or of the selective forces that determine the time of dispersal.

Skutch (1948, p. 256) reports seeing individuals of *T. cruentatus* in Ecuador give a "magnificent exhibition of aërial flycatching, in their strong flight and intricate maneuvers rivalling the Neotropic Kingbirds (*Tyrannus melancholicus*) which were engaged in the same occupation at the same time." This observation is of special interest, since *Melanerpes erythrocephalus* frequently feeds in this fashion, while species of *Centurus* in México and the United States do little flycatching. In an earlier paper (Selander and Giller, 1959b) we suggested that the relatively long wing of *M. erythrocephalus* is an adaptation for stronger flight in connection with aerial feeding, and it now appears that the same may be true for species of *Tripsurus*. Skutch (1948, p. 226) mentions that *T. chrysauchen* captures insects on the wing, rising above treetops and twisting and looping in the air, and Slud (1960, p. 84) reports flycatching by *T. pucherani* in Costa Rica. At present we do not know whether these species indulge in this habit more frequently than does *C. rubricapillus* or other species of *Centurus*, although this seems likely.

In sum, one species (*chrysogenys*) invari-

ably placed in *Centurus* by taxonomists who maintain *Tripsurus* is obviously more closely allied to *T. pucherani* than to any species included in *Centurus*. If the genus *Tripsurus* is to be maintained, the species *chrysogenys* must be transferred to it from *Centurus*. Even if such transfer were made, however, further difficulties arise in the classifying of the species *hypopolius*, which, like *chrysogenys*, bridges the gap between "typical" *Tripsurus* and "typical" *Centurus*. It has invariably been assigned to *Centurus*, but, as noted below, it shows a resemblance to *chrysogenys* in plumage pattern, in relative reduction in size of the hyoid apparatus, and in some other features. At least pending comprehensive studies of internal anatomy and further investigations of life history and behavior, we see no course but to combine the two genera; *Tripsurus* Swainson (1837) is regarded as a synonym of *Centurus* Swainson (1837).

We have nothing to offer regarding the problem of the relationship between *Centurus* and *Melanerpes*, except to note that, in the series *C. pucherani-pulcher-chrysauchen-flavifrons*, there is progressive simplification of plumage pattern that involves the reduction of dorsal barring and the extension of red on the belly. This trend leads finally to *C. cruentatus* (including "*rubrifrons*," which is probably a color phase of *cruentatus* rather than a distinct species; Haverschmidt, 1957), a species resembling in several respects *Melanerpes portoricensis* of Puerto Rico. In *C. cruentatus*, the only vestiges of bars are light smudges on the outer webs of the outer rectrices and a few light bands at the tips of the inner secondaries. This trend in variation, together with the well-known similarity of pattern of the juvenal plumage of *Melanerpes erythrocephalus* to that of the juvenal and adult plumages of *Centurus* species (Amadon and Eckelberry, 1955, p. 74) suggests a close phyletic relationship between the groups of species presently classified in these separate nominal genera, but we are reluctant to lump the two until a more thorough study of the situation has been made.

GEOGRAPHIC VARIATION IN *CENTURUS* *AURIFRONS* (WAGLER)

MORPHOLOGIC VARIATION and systematic relationships among populations currently assigned to the species *C. aurifrons* have been considered in brief reviews by Ridgway (1881, 1914), Griscom (1932), and Wetmore (1943). The principal problem concerns the relationship of populations of red-naped and narrowly barred birds (*dubius*) occurring on the Yucatán Peninsula and yellow-naped and broadly barred birds of the Mexican Plateau and Texas (*aurifrons*) and the arid regions of the Isthmus of Tehuantepec and interior Chiapas (*polygrammus*). In addition, there is the related problem of the systematic status of the closely allied Costa Rican and Nicaraguan form *hoffmanni*, which is considered below.

Working with a total of 62 specimens, Ridgway (1881) correctly determined that two of the extreme types, *aurifrons* and *dubius*, are connected by intergradation of characters in specimens from Veracruz and Guatemala (*santacruzii* of the older literature), and on this basis he considered the whole complex to be a single species, relegating the nominal species *dubius* and *santacruzii* to races of *aurifrons*. However, this essentially modern treatment subsequently was abandoned by Ridgway (1885a, 1885b, 1887, 1888, and 1914) in favor of a more conservative scheme of classification similar to that adopted by Hargitt (1890) and Salvin and Godman (1888), in which four species, *aurifrons*, *polygrammus*, *dubius*, and *santacruzii*, were recog-

nized and specimens showing intermediacy of characters were regarded as interspecific hybrids.

Ridgway's second classification was accepted by Cory (1919) and many other authors, but, in 1932, Griscom, examining large series of specimens, reached conclusions almost identical to those originally stated by Ridgway in 1881, and a study by Wetmore (1943) later supported these findings. Nonetheless, some authors (Stone, 1932; Bond, 1936; Sutton, 1940; and Brodtkorb, 1943) continued to hold the more conservative view which maintains *dubius* and *santacruzii* as specifically distinct from *aurifrons*, and, as recently as 1951, Sutton again expressed the opinion that *dubius* and *aurifrons* are separate species. Meanwhile, several additional races were described, and in 1948 Peters recognized a total of 12 subspecies of *C. aurifrons* (in addition to *hoffmanni*, which was also regarded as a race of *C. aurifrons*).

Nothing would be gained at the present time by a review of the nomenclatural history of the *aurifrons* complex or by a discussion of the characteristics and distributions of the named races. Therefore, we propose for the moment to pass over the matter of subspecies and, instead, to examine individual and geographic variation in size and several characters of color and pattern in order to determine the extent of intergradation among these markedly differentiated, allopatric populations.

METHOD OF ANALYSIS OF VARIATION

Within the total geographic range of the *aurifrons* complex, 34 sample areas have been designated, as shown in figure 2. Our samples include specimens from all parts of the range except Roatán, Barbareta, and Utila Islands. To permit quantitative analysis of variation in color and pattern, we first determined the limits of variation in these characters, then selected series of reference specimens (listed in the Appendix) representing equally spaced steps or segments in total spans of variation. Specimens of *C. hoffmanni* were used to repre-

sent one category of belly color and one category of frontal region color, but all other reference specimens were *C. aurifrons*. The number of categories represented by reference specimens varied with the character, as follows:

NAPE COLOR: Fourteen categories, from yellow (category 0) to red (category 13).

FRONTAL REGION COLOR: Eight categories, from yellow (0) to red (7).

BELLY COLOR: Twelve categories, from yellow (0) to red (11). In analyzing variation

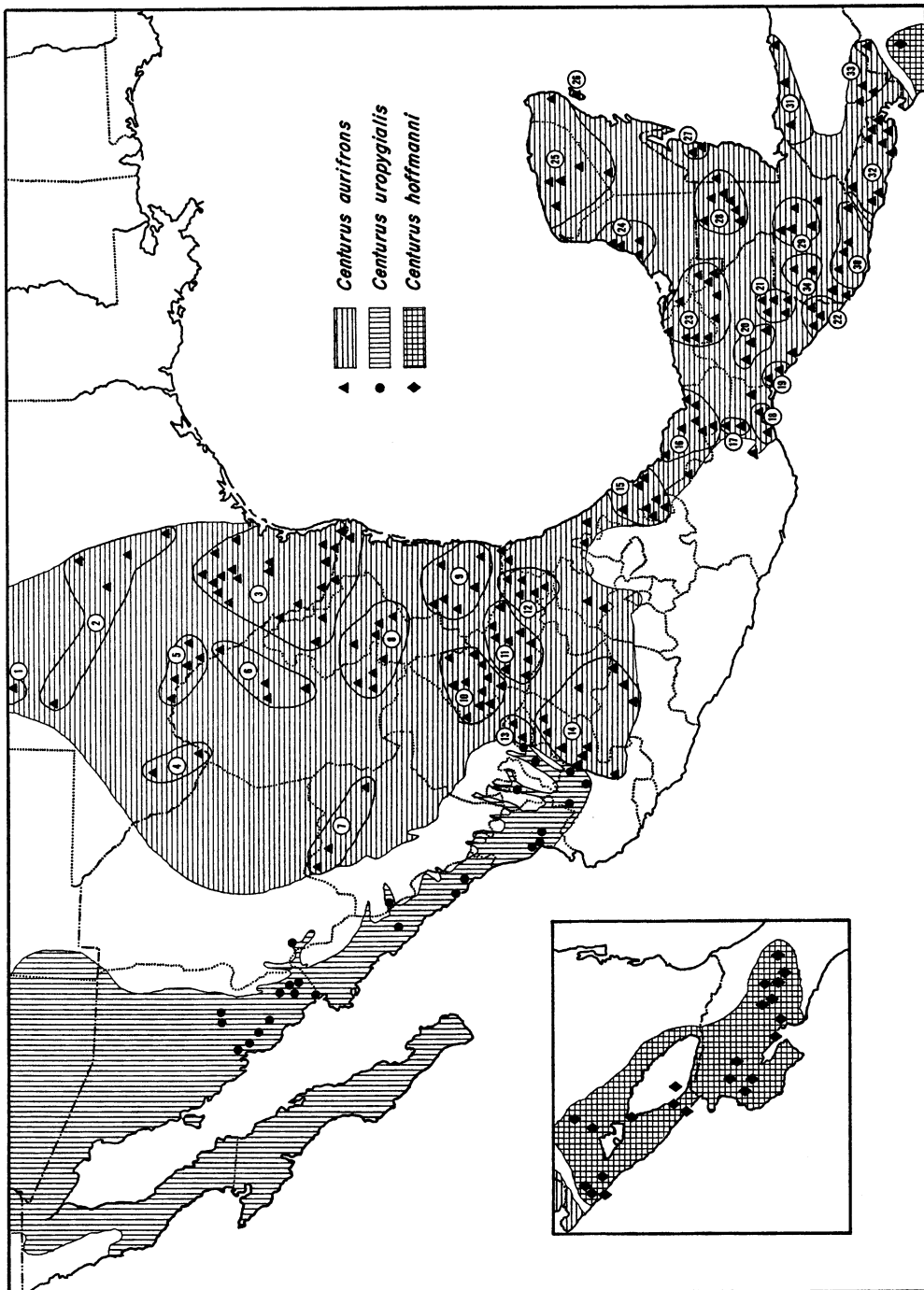


FIG. 2. Distribution of *Centurus aurifrons*, *Centurus uropygialis*, and *Centurus hoffmanni*. Symbols indicate localities of specimens examined. Sample areas used in analysis of variation in *C. aurifrons* are designated by numbers.

in this character, we considered only the hue of the color, not the value, intensity, or extent of distribution in the abdominal region.

DORSAL TAIL PATTERN: Seven categories, representing a range from maximum white barring and streaking (0) to black with no white marks (6).

Widths of white and black bars were measured in the center of the dorsal region. A number of standard linear measurements were made from the skins, including the arc of the unflattened wing and bill length from the anterior edge of the nostril to the tip of the bill. In addition, notes were taken on the color of the breast and flanks and on several other geographically variable characters of color and pattern for which quantitative treatment was not attempted.

Our analysis of geographic variation is

based almost entirely on adult males. The variation in females follows closely that shown by males, there being no significant sexual dimorphism in color or pattern except in the markings of the head. The female lacks the red coronal patch of the male, and, in all populations in which the nape of the male is not pure red, the nape color of the female is purer yellow than that of the male. There is a moderate degree of sexual dimorphism in size, with females averaging smaller than males in all linear dimensions.

There are no appreciable age differences in plumage or size following the postjuvinal molt, which involves complete replacement of the juvinal plumage. Because none of the species of *Centurus* is migratory, we have been able to use in our studies specimens taken at all seasons of the year.

VARIATION IN CHARACTERS

Individual and geographic variation in characters of color and pattern is shown in figures 3 through 7, and data on size are presented graphically in figures 8 through 11. In all figures, numbers following locality names refer to sample areas designated in figure 2. Available weights are presented in table 2.

NAPE COLOR: On the Mexican Plateau and in Texas, the nape of males is yellow or orange, with mean sample scores ranging from 2.5 in northwestern San Luis Potosí (sample 10, fig. 3) to 5.9 in northern Coahuila (sample 6). Individual variation is relatively great, as it is in other populations having a yellowish nape. Extending from northwestern San Luis Potosí to Campeche (sample 24), there is a cline in which yellow (2.5) passes through orange to an almost pure red (12.4), with the steepest gradient occurring between central San Luis Potosí (sample 11) and eastern San Luis Potosí (sample 12). The nape is red and shows little variability throughout the Yucatán Peninsula, but the color tends toward orange, with some individuals having a distinctly orange nape, in Guatemala (samples 28 to 30, and 34), southeastern Chiapas (sample 22), El Salvador (sample 32), and Honduras (samples 31 and 33).

Geographic variation in extent of connection between the highly colored coronal and nape regions in males parallels the clinal

changes seen in nape color. In Texas and over the Mexican Plateau, the red coronal patch is relatively narrow and is separated from the yellow or orange nape by a broad band of gray. In southern Tamaulipas and in central and eastern San Luis Potosí, the patch averages wider and usually has at least a narrow central connection with the nape. There is a much greater degree of confluence between colored areas in material from Veracruz, but many specimens have small gray patches in the occipital area between the crown and the nape. In birds from Tabasco, the Yucatán Peninsula, and Central America, the two colored areas are broadly joined and the coronal patch is also relatively wide.

On the Pacific side of the Isthmus of Tehuantepec (samples 17 to 19) and in central and eastern Chiapas (samples 20 and 21), nape color is on the yellow side, being similar to that of birds from the Mexican Plateau. This development reaches an extreme in eastern Chiapas (sample 21), where the color is almost pure yellow (0.4). As in other yellow-naped populations, the nape and coronal areas of the male are separated by a gray band.

FRONTAL REGION COLOR: Variation in this character parallels that of nape color, except in Central America (samples 22, 30, 31, 32, and 33), where it shows a more marked shift

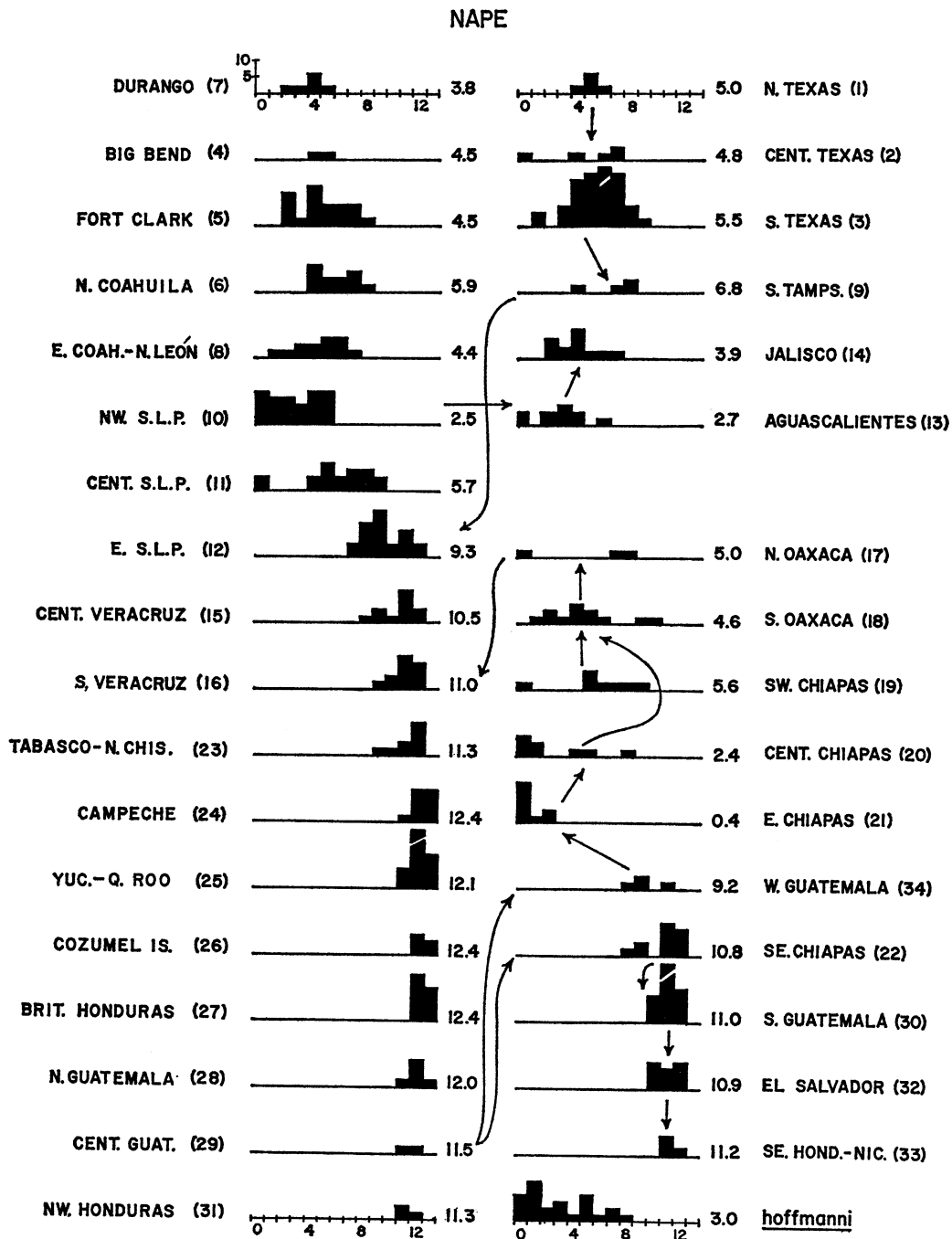


FIG. 3. Individual and geographic variation in nape color in males of *Centurus aurifrons* and *Centurus hoffmanni*. Categories of nape color are indicated in text; mean sample scores are shown at right of base lines of histograms. Numbers in parentheses refer to sample areas indicated in figure 2; arrows indicate geographic contact of populations sampled.

TABLE 2
WEIGHTS (IN GRAMS) OF *Centurus aurifrons*

Sample ^a	Males			Females		
	No.	Mean	Range	No.	Mean	Range
Central Texas (2)	—	—	—	1	90	—
S. Texas (3)	4	82.4	(79-85)	1	79	—
E. Coahuila-Nuevo León (8)	1	86	—	—	—	—
Aguascalientes (13)	9	90.5	(81-98)	10	77.6	(67-84)
Jalisco (14)	9	86.5	(77-96)	11	77.9	(66-83)
NW. San Luis Potosí (10)	21	86.5	(73-99)	10	77.9	(70-90)
Central San Luis Potosí (11)	8	82.6	(73-99)	4	72.8	(66-77)
E. San Luis Potosí (12)	10	85.2	(69-102)	7	73.8	(65-79)
Central Veracruz (15)	1	93	—	—	—	—
Tabasco-N. Chiapas (23)	2	81.5	(81-82)	1	72	—
Campeche (24)	1	85	—	—	—	—
Yucatán—Quintana Roo (25)	3	81.1	(79-83)	3	70.2	(66-74)
	9 ^b	87.7	(81-95)	8 ^b	76.4	(71-84)
Cozumel Island (26)	2 ^c	86.5	(84-89)	1 ^c	79	—
British Honduras (27)	2	88.8	(85-93)	—	—	—
N. Guatemala (28)	3	83.4	(82-85)	2	77.5	(77-78)
Central Guatemala (29)	—	—	—	1	80	—
SE. Guatemala (30)	1 ^d	92	—	2	86.0	(85-87)

^a Numbers in parentheses refer to sample areas indicated in figure 2.

^b Data from Paynter (1955, p. 165); specimens from Quintana Roo and Campeche.

^c Data from Paynter (1955, p. 166).

^d Data from Tashian (1953, p. 204).

to orange and yellow scores (fig. 5). Again there is a cline from yellow (1.4) to red (6.3) between northwestern San Luis Potosí and Campeche, and the population of eastern Chiapas represents an extreme in average expression of yellow (1.0).

BELLY COLOR: Variation in belly color (fig. 4) follows that of the two characters previously discussed, with two notable exceptions. First, in Texas and over the Mexican Plateau, belly color varies from yellow to orange, with an extreme on the yellow side being reached in western Texas (samples 4 and 5; scores, 1.0 and 0.9) rather than in northwestern San Luis Potosí. Second, the cline connecting the yellow-orange color of northwestern San Luis Potosí (2.9) and the red (10.5) of Campeche has its steepest gradient not in San Luis Potosí but between central and southern Veracruz (samples 15 and 16), where the shift is from an average score of 6.0 to one of 9.3. The transition from red to orange in Central America is roughly equivalent to that shown in the color of the frontal region; and, once

again, the purest yellow is found in birds from eastern Chiapas (1.3).

DORSAL TAIL PATTERN: Variation in dorsal tail pattern (fig. 5) is not correlated with that of characters previously considered. In most samples from the Mexican Plateau and Texas, well over half of the specimens fall in category 6, with no white markings present; mean sample scores range from 5.5 to 6.0. This character is slightly more variable in San Luis Potosí, and most specimens from central and southern Veracruz (samples 15 and 16) show some white marks. From Tabasco and northern Chiapas (sample 23) southeast to northern Guatemala, there is a return to an essentially unmarked condition (6.0). Then in Central America a shift to a moderate amount of white marking occurs, with mean sample scores ranging from 3.0 in southeastern Chiapas (sample 22) to 5.5 in central Guatemala (sample 29). The only populations in which conspicuous white markings represent the usual condition are those of the Pacific side of the Isthmus of Tehuantepec

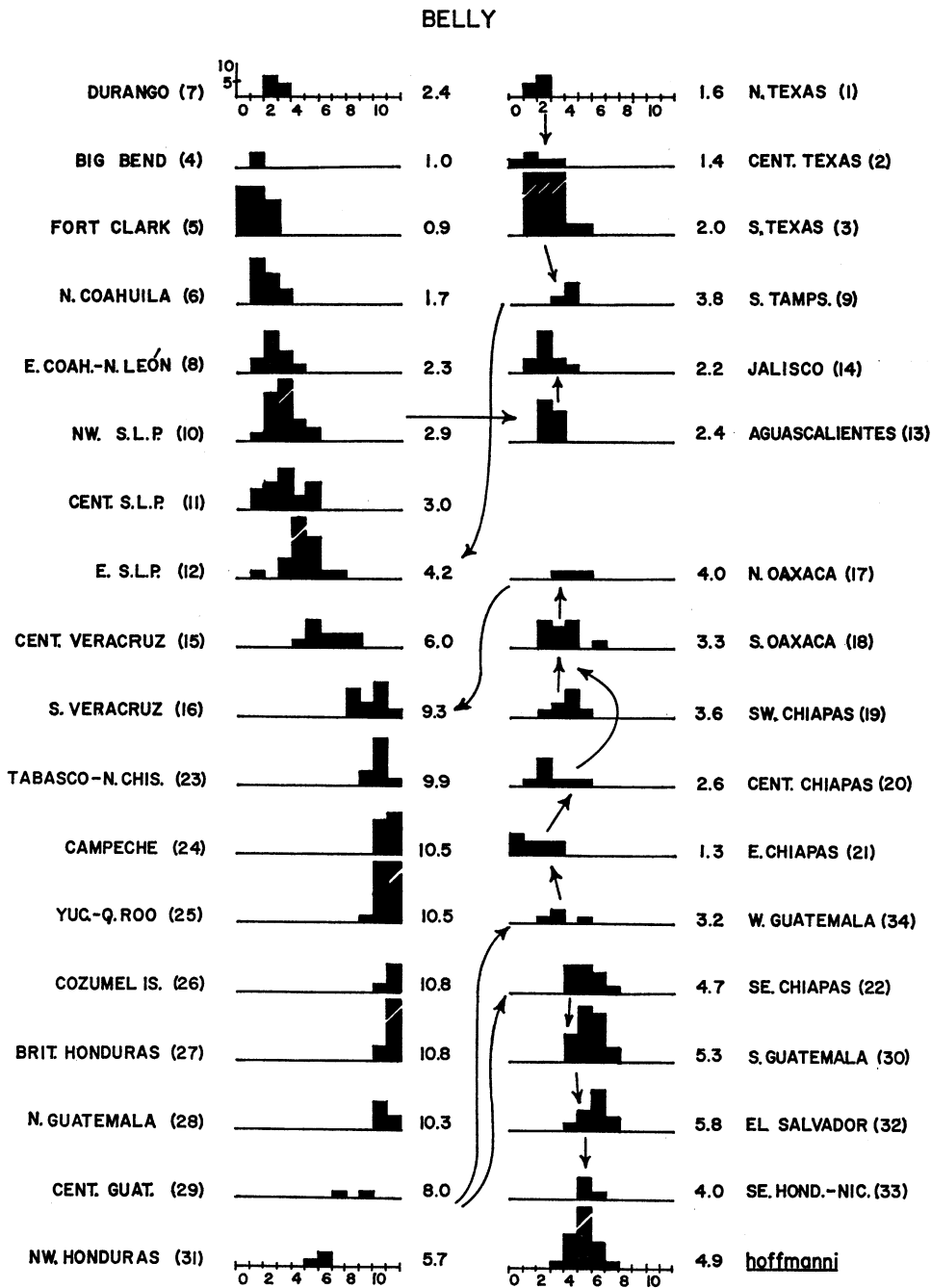


FIG. 4. Individual and geographic variation in belly color in males of *Centurus aurifrons* and *Centurus hoffmanni*. Categories of belly color are indicated in text; mean sample scores are shown at right of base lines of histograms. Numbers in parentheses refer to sample areas indicated in figure 2; arrows indicate geographic contact of populations sampled.

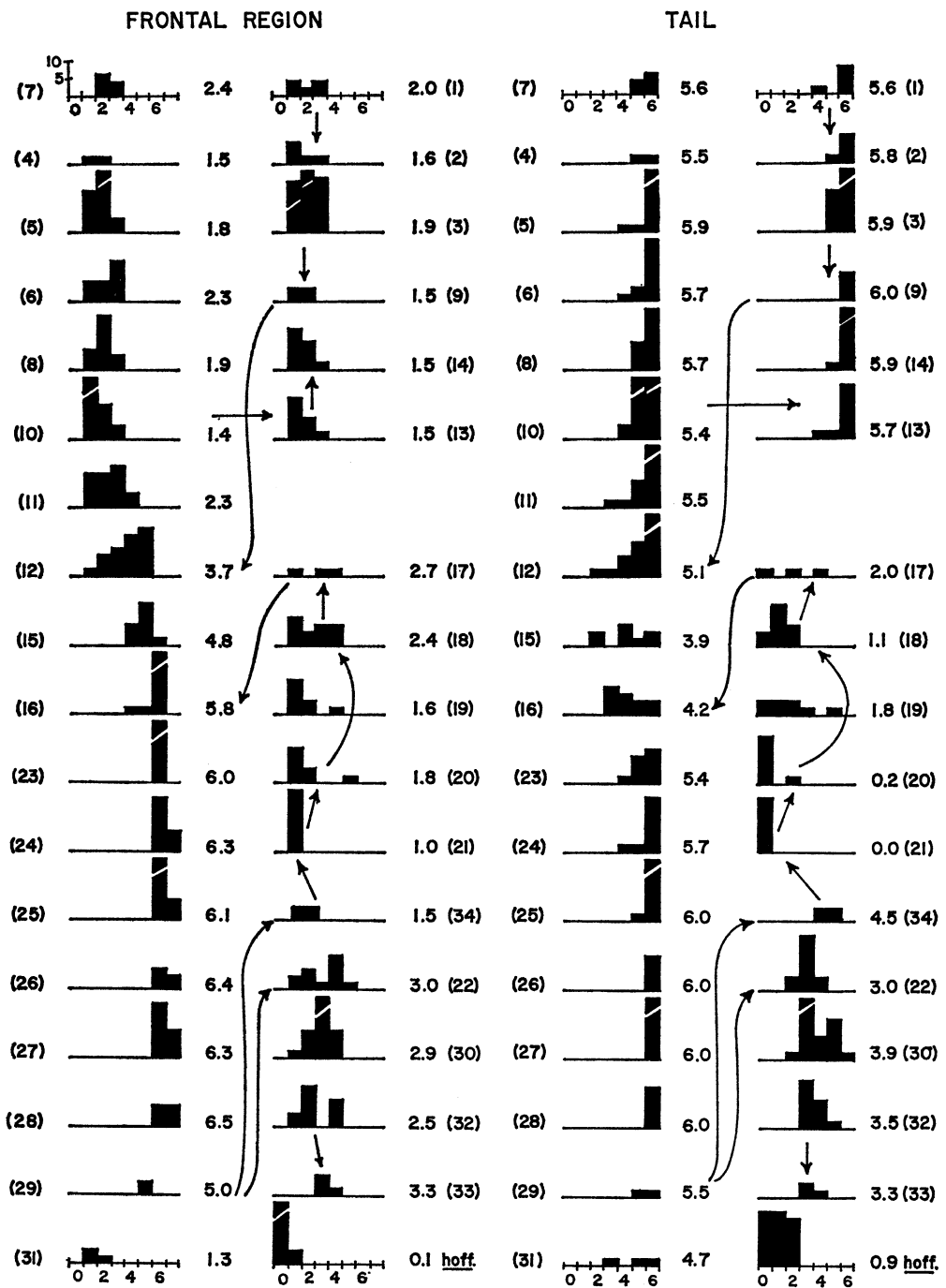


FIG. 5. Individual and geographic variation in frontal region color and dorsal tail pattern in males of *Centurus aurifrons* and *Centurus hoffmanni*. Categories of frontal region color and of dorsal tail pattern are indicated in text; mean sample scores are shown at right of base lines of histograms. Numbers in parentheses refer to sample areas indicated in figure 2; arrows indicate geographic contact of populations sampled.

and interior Chiapas (samples 17 to 21), and it will be noted that all specimens in the sample from eastern Chiapas fall in category 0.

DORSAL BARRING OF BLACK AND WHITE: The widest black bars are found in specimens from Texas and the Mexican Plateau, with a maximum mean width of 3.94 mm. being reached in the sample from Aguascalientes (fig. 6). Between central San Luis Potosí and southern Veracruz, there is clinal decrease in width from 3.73 to 2.65 mm. A moderate increase in width is apparent in southeastern Chiapas, El Salvador, and Honduras, with sample averages of 2.78 to 3.10 mm. Black bars are also moderately wide in samples from the Pacific side of the Isthmus of Tehuantepec and interior Chiapas, where average width ranges from 2.68 to 3.13 mm.

The width of the white bars (fig. 7) exhibits a pattern of geographic variation roughly comparable to that of the black bars. Again the most prominent bars are found in samples from Texas and the Mexican Plateau, but the clinal shift to narrower white bars begins in northwestern San Luis Potosí rather than in eastern San Luis Potosí, as in the case of the black bars. Width increases slightly in southeastern Chiapas and El Salvador but returns to a very narrow condition (1.13 mm.) in northwestern Honduras.

COLOR OF THE BREAST AND SIDES: The color of the under parts varies from light gray in Texas and on the Mexican Plateau to a much darker olive or brownish olive-gray in Central America and on Cozumel Island, and samples from the Yucatán Peninsula and southern Veracruz are more or less intermediate in this character. We note that the color is subject to considerable seasonal variation as a result of wear and soiling.

The gray color of the forehead and anterior superciliary region is no darker, and may in fact be lighter, in the ventrally dark birds of the Yucatán Peninsula and Central America than in specimens from populations having pale gray under parts, and these areas are almost white in some specimens from the

Yucatán Peninsula.

With respect to variation in size in the *aurifrons* complex, the following points seem worthy of comment.

WING LENGTH (FIG. 8): Among northern samples, wing length is greatest in northern Texas (sample 1) but is almost equaled by samples from Jalisco, Aguascalientes, and northwestern San Luis Potosí. Wing length decreases clinally from eastern San Luis Potosí south along the Caribbean coast of México to Tabasco and northern Chiapas (sample 23) but returns to moderate size on the Yucatán Peninsula and in Guatemala. It is large again in El Salvador but even smaller in southeastern Chiapas and in Honduras. In southern Oaxaca and interior Chiapas, wing length appears to vary clinally from 138.3 mm. in southern Oaxaca (sample 18) to 133.0 mm. in eastern Chiapas (sample 21).

TAIL LENGTH (FIG. 9): This character is less variable geographically than wing length. Again the maximum size is seen in northern Texas, but the tail length is actually rather uniform, averaging between 75 and 80 mm., in most samples from central and western Texas south to central Veracruz. Nearly maximum size is achieved on Cozumel Island, with clines connecting this population with shorter-tailed populations to the north and south.

BILL LENGTH (FIG. 10): This character shows a pattern of geographic variation not unlike that of wing length. Note that, whereas birds from southern Oaxaca and interior Chiapas have wing lengths almost equaling those of birds from Texas and the Mexican Plateau, in bill length they are distinctly smaller.

BILL DEPTH: This was the least variable linear dimension studied. The most notable feature is the comparatively large size in specimens from Cozumel Island and El Salvador.

TARSUS (FIG. 11): Variation in this character exhibits a pattern similar to that of bill length.

BLACK BARS

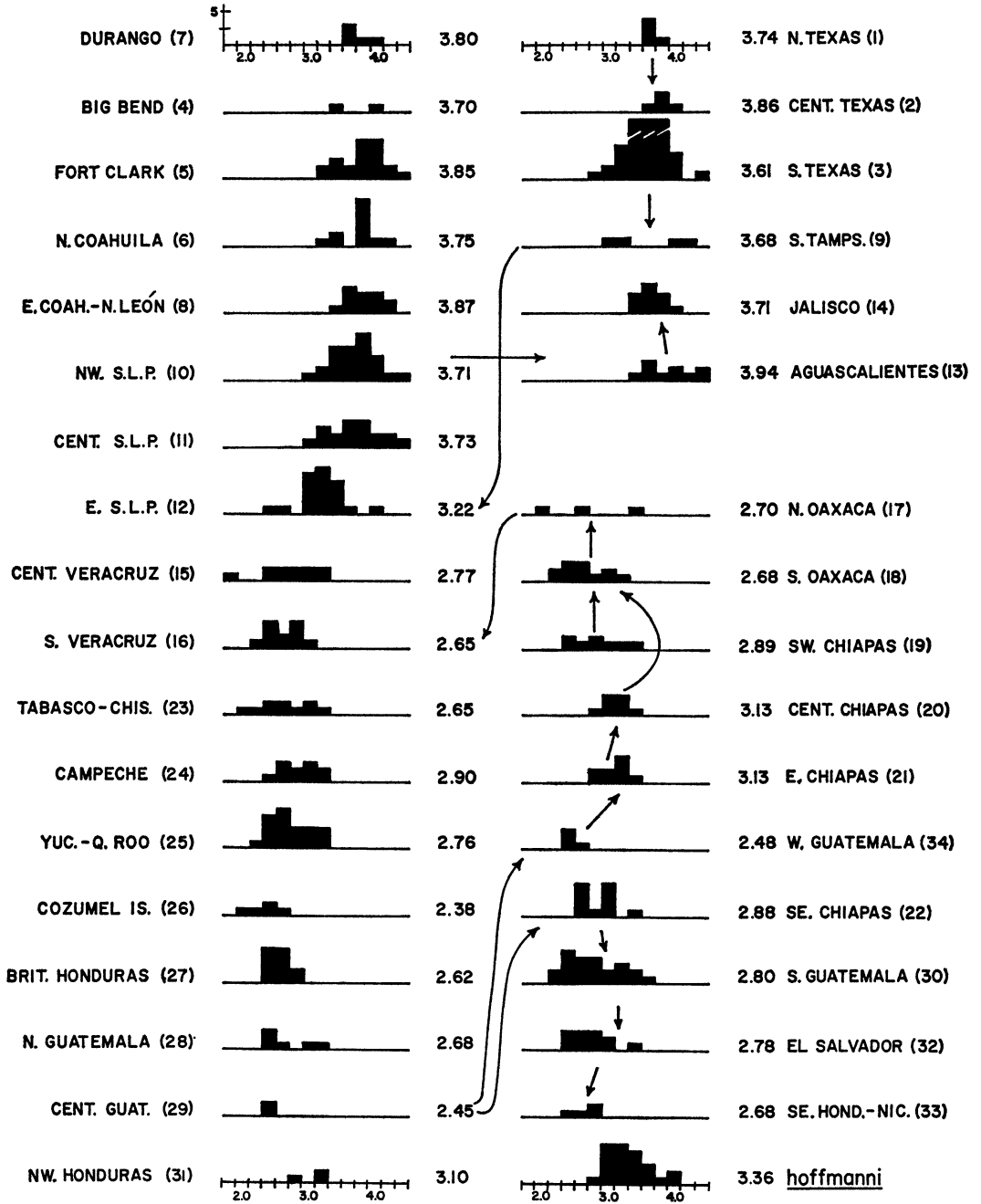


FIG. 6. Individual and geographic variation in width of dorsal black bars in males of *Centurus aurifrons* and *Centurus hoffmanni*. Mean measurements of samples are shown at right of base lines of histograms. Numbers in parentheses refer to sample areas indicated in figure 2; arrows indicate geographic contact of populations sampled.

WHITE BARS

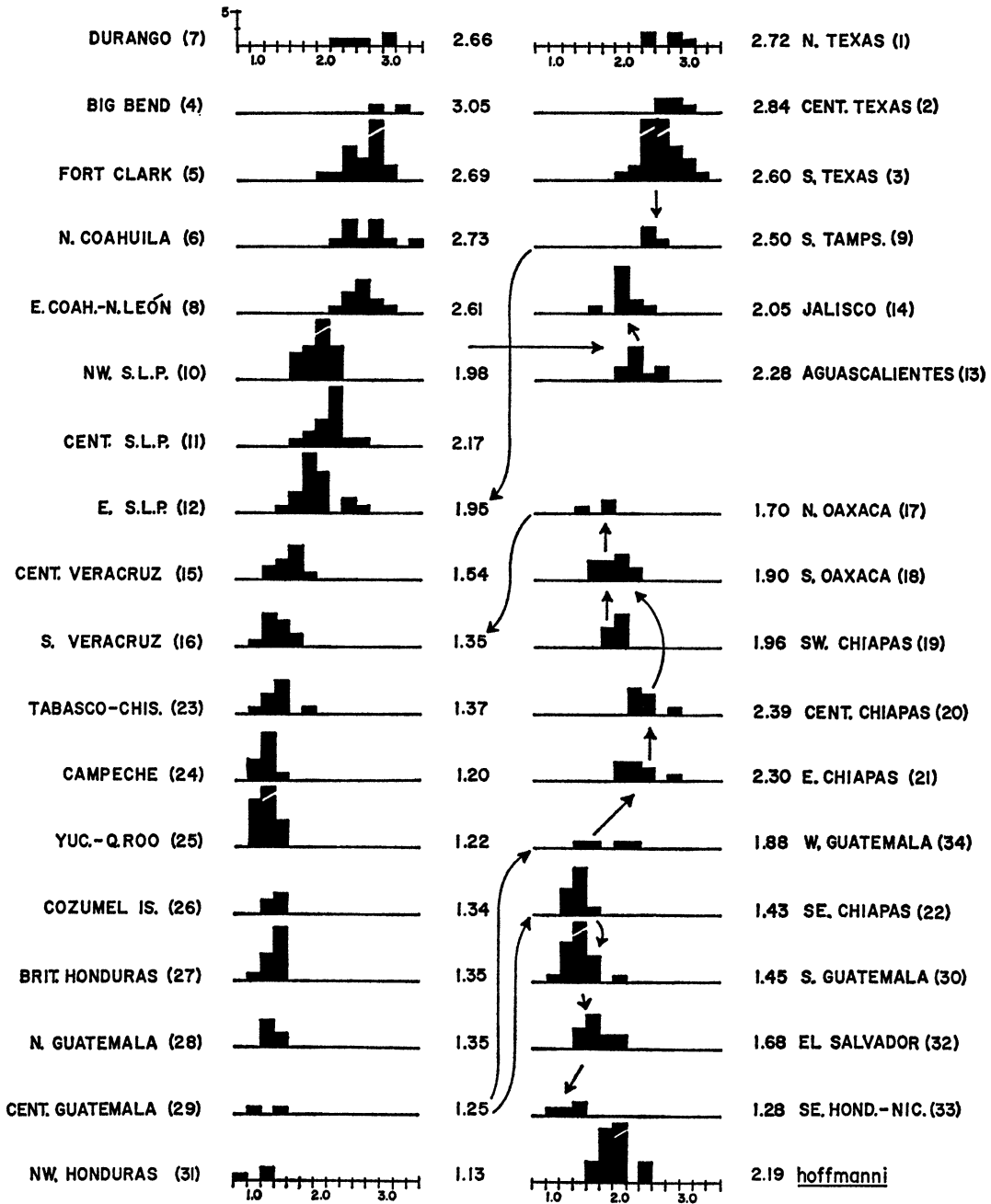


FIG. 7. Individual and geographic variation in width of dorsal white bars in males of *Centurus aurifrons* and *Centurus hoffmanni*. Mean measurements of samples are shown at right of base lines of histograms. Numbers in parentheses refer to sample areas indicated in figure 2; arrows indicate geographic contact of populations sampled.

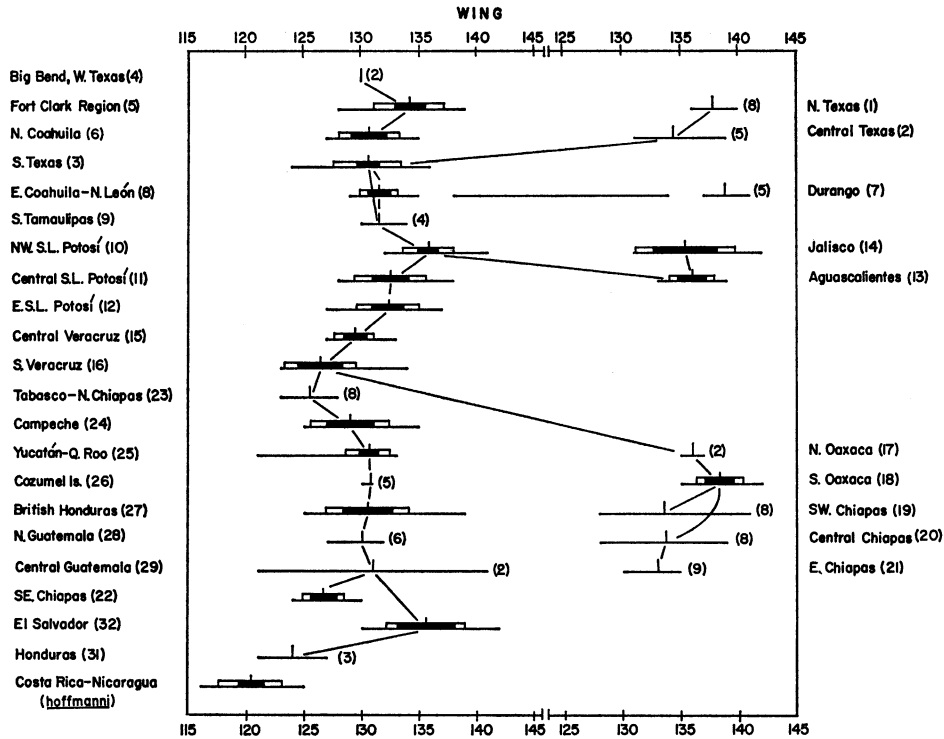


FIG. 8. Individual and geographic variation in wing length in males of *Centurus aurifrons* and *Centurus hoffmanni*. Diagrams show range, mean, standard deviation, and twice standard error of mean (solid rectangle). Geographic contact of populations is indicated by thin lines connecting means.

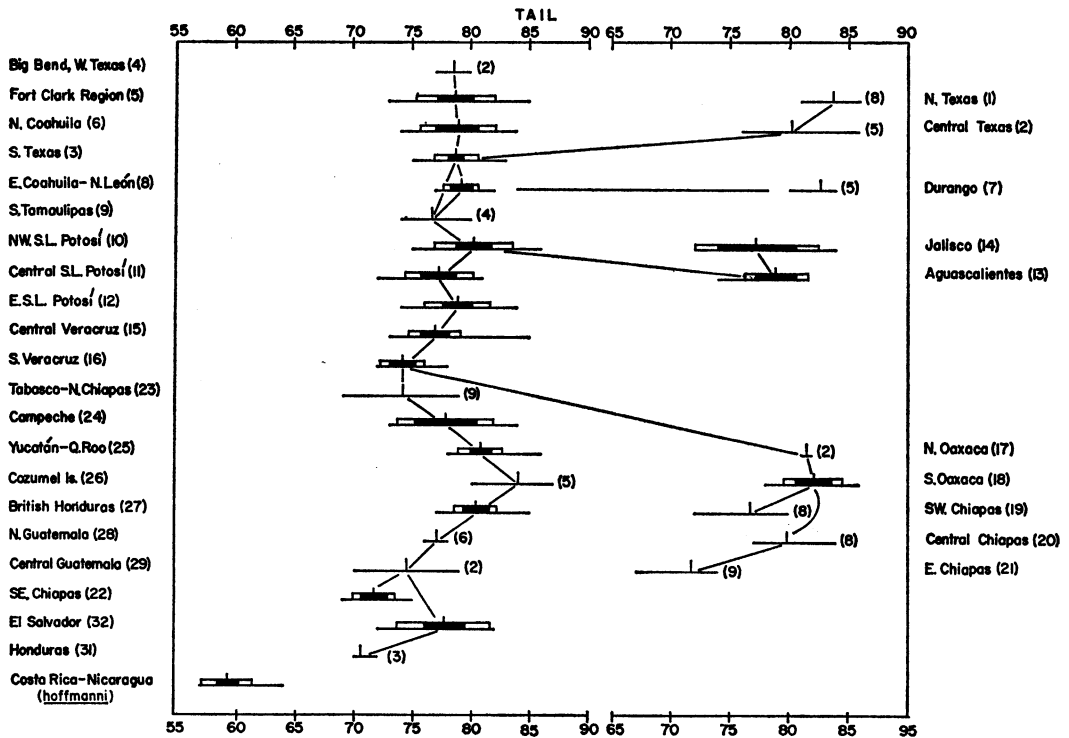


FIG. 9. Individual and geographic variation in tail length in males of *Centurus aurifrons* and *Centurus hoffmanni*. Diagrams show range, mean, standard deviation, and twice standard error of mean (solid rectangle). Geographic contact of populations is indicated by thin lines connecting means.

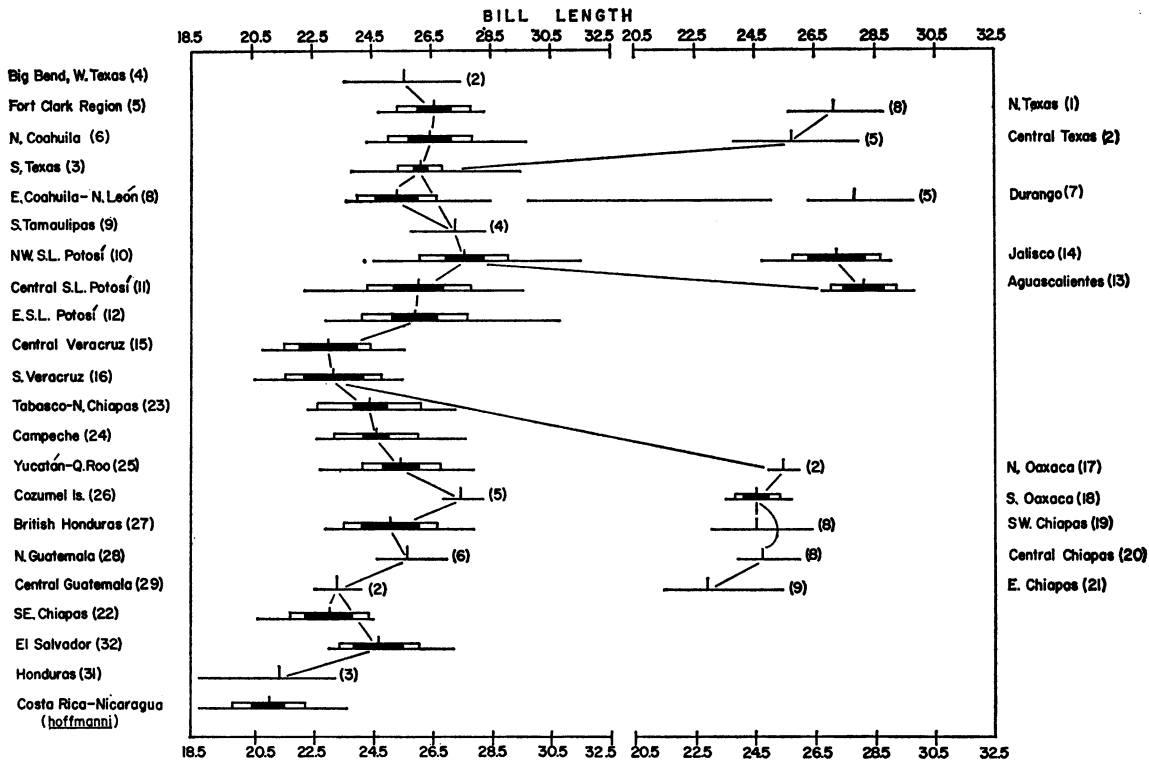


FIG. 10. Individual and geographic variation in bill length in males of *Centurus aurifrons* and *Centurus hoffmanni*. Diagrams show range, mean, standard deviation, and twice standard error of mean (solid rectangle). Geographic contact of populations is indicated by thin lines connecting means.

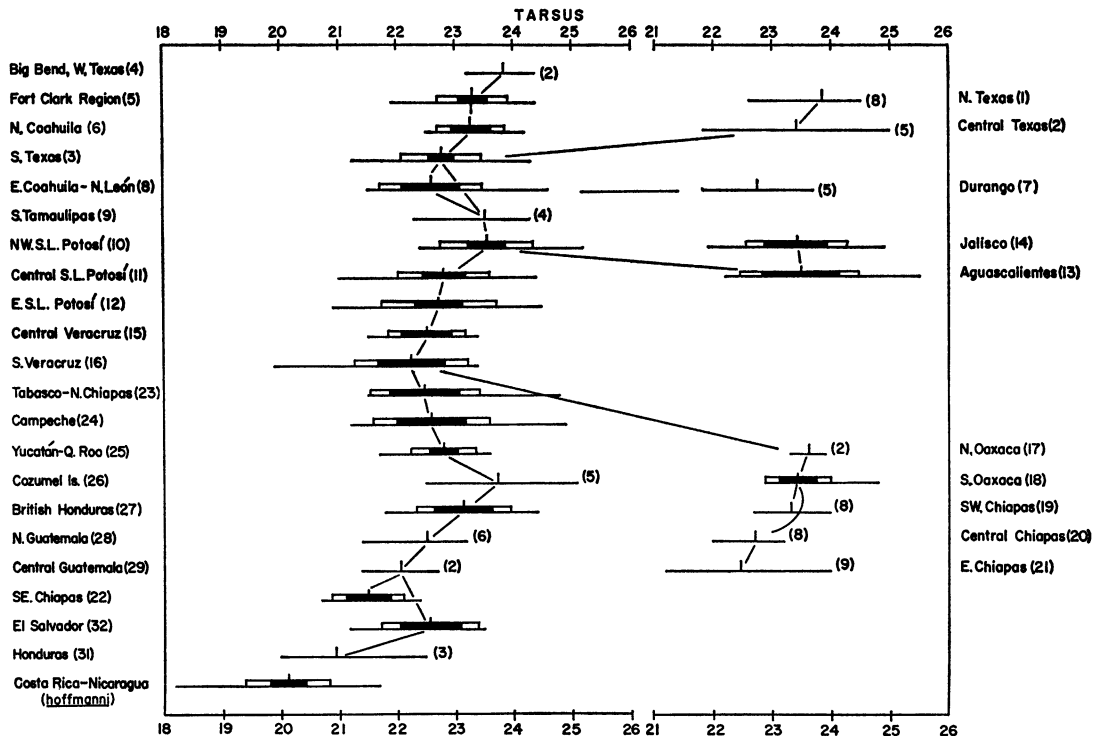


FIG. 11. Individual and geographic variation in tarsus length in males of *Centurus aurifrons* and *Centurus hoffmanni*. Diagrams show range, mean, standard deviation, and twice standard error of mean (solid rectangle). Geographic contact of populations is indicated by thin lines connecting means.

SUBSPECIES AND INTERGRADATION

In recent years the validity of the subspecies concept has been seriously questioned by a number of systematists and evolutionists (see discussions by Simpson, 1961, pp. 171–176; and Inger, 1961). If the category of subspecies is to have a continuing function in systematics, it is apparent that systematists must attempt to reach agreement on the definition of subspecies and the purpose the category is to serve. As a result of our work with *Centurus* and certain other genera of birds, we doubt the justification of the use of subspecific names as a “tool” in “describing” geographic variation in single characters or minor morphologic differences among populations. In our view, one proper function of the trinomial is to indicate a known or presumed conspecific relationship between allopatric populations that are sufficiently well differentiated in a number of morphologic, ecologic, physiologic, or behavioral characters as reasonably to suggest that they are to some meaningful degree semi-independent evolutionary units not distantly removed from the species level of evolution. Ideally, we should like to see the subspecific category used for the organization of geographic populations of a species into phylogenetic units, as suggested by Lidicker (1960, p. 161), but whether this can be accomplished for any large number of species remains to be determined. In any event, used in the manner suggested, the subspecific category at least serves the practical function of preventing morphologically or otherwise well-marked populations of a species from being elevated nomenclaturally to the species level, with the resultant obscuring of their true evolutionary relationships with populations from which they are not fully isolated by intrinsic barriers to genetic interchange (Mayr, 1954). In the final analysis, such use may prove to be the only justification for trinomials.

A dozen subspecies of *Centurus aurifrons* are currently recognized (Peters, 1948), but, considering the major features of geographic variation in this species, we believe that, at least as far as the continental populations are concerned, only four names should be applied. Thus, we find ourselves in the unusual position of advocating a return to a scheme of

classification essentially similar to that originally proposed by Ridgway in his first review of the species in 1881!

Centurus aurifrons aurifrons (WAGLER)

To populations distributed from Texas south over the Mexican Plateau to Jalisco, Michoacán, México, Hidalgo, and northwestern San Luis Potosí, we propose to apply the name *C. a. aurifrons* (Wagler, 1829, col. 512), with type locality at Ismiquilpam, Hidalgo. These populations are characterized by yellow to orange nape, frontal region, and belly; pale under parts; an absence (or at best slight development) of white markings on the tail; broad to moderately broad black and white barring dorsally; and relatively long wing and bill.

The name *C. a. incanescens* was proposed by Todd (1946, p. 298) for birds of the Big Bend area of Trans-Pecos Texas, with type locality 12 miles south of Marathon, Brewster County, and the range of this race was subsequently extended by Wetmore (1948) to include central Texas. Characters by which Todd sought to distinguish this race from *C. a. aurifrons* are: “underparts paler gray . . . ; crown also paler gray; forehead paler yellow; and nape orange rufous . . . to aniline yellow [versus ochraceous orange to Mars yellow in birds from the Mexican Plateau]; and yellow of underparts paler.”

Comparing moderate numbers of specimens from western and central Texas with a series from the Mexican Plateau, Wetmore (1948) found that the color of the frontal region, nape, and belly was not significantly different, a conclusion fully supported by our analysis of these characters (figs. 3–5). However, it was Wetmore’s opinion that *C. a. incanescens* could be maintained as a race on the basis of slightly paler gray under parts, narrower black and wider white dorsal barring, and an average difference in number of black markings on the upper tail coverts. We have not analyzed variation in the last of these characters, but it was evident from examination of our material that this is merely an average difference, as previously noted by Wetmore (1948). As shown in figure 6, the

width of the black bars actually shows little geographic variation from northern Texas south to Aguascalientes and Jalisco. It is true, however, that birds from northern and central Texas have wider white bars, on the average, than do specimens from the southern part of the Mexican Plateau (see fig. 7), and they tend to be paler gray ventrally. But in our opinion these differences do not constitute grounds for formal racial separation.

Centurus aurifrons dubius (CABOT)

To *Centurus a. dubius* (Cabot, 1844, p. 164), with type locality at Uxmal, Yucatán, we assign populations from Tabasco, northern Chiapas, and northern Guatemala north through the Yucatán Peninsula to Cozumel Island. Thus defined, the race *C. a. dubius* is characterized by red nape, with the coronal and nape regions confluent in males; red frontal region and belly; dorsal tail pattern with few if any white markings; moderately dark under parts; and narrow black and white dorsal barring. In size there is considerable variation among populations assigned to this race.

Birds from Cozumel Island, Yucatán, are, with some justification, generally distinguished racially as *C. a. leei* (Ridgway, 1885a, p. 22). In the characters of color and pattern we have studied in detail, birds from Cozumel Island are scarcely different in any degree from those of the adjacent mainland populations, but most specimens from the island are darker ventrally, and, as noted by Ridgway (1914), their upper tail coverts tend to be more heavily marked with black. In addition, some males show a tendency for fusion of the red crown and frontal regions, thus paralleling a condition more fully developed and consistent in the related species *C. carolinus* of the eastern United States. The sample from Cozumel Island averages slightly larger in all dimensions except wing length than those from mainland Yucatán, Quintana Roo, and British Honduras. But in the over-all picture of variation in *Centurus aurifrons*, the average morphologic differences between populations on the Yucatán mainland and Cozumel Island seem relatively minor, and we prefer not to apply a separate name to the latter population.

Centurus aurifrons grateloupensis (LESSON)

As indicated above in our discussion of patterns of variation, the characters of the strikingly marked races *C. a. aurifrons* and *C. a. dubius* (as herein defined) intergrade completely in clinal fashion over an extensive area from central San Luis Potosí south to southern Veracruz. Largely because it is convenient to have a name by which to refer to these intergradient populations, we follow general practice in recognizing *C. a. grateloupensis* (Lesson, 1839, p. 41), with type locality "Mexico," but, contrary to general practice, we would apply this name to all populations from central San Luis Potosí south to southern Veracruz. Wetmore (1943) and others recognize a second race, *C. a. veraecrucis* (Nelson, 1900, p. 259), with type locality at Coatzacoalcos, Veracruz, but we prefer to follow Griscom (1932) in considering it a synonym of *C. a. grateloupensis*.

Centurus aurifrons santacruzi BONAPARTE

Our analysis of characters has demonstrated considerable geographic variation in populations distributed from southeastern Chiapas east through southern and central Guatemala to El Salvador and Honduras. This variation is especially evident in linear dimensions, width of dorsal bars, and frontal region color, which ranges from yellow (mean sample score, 1.3) in northwestern Honduras to orange (5.0) in central Guatemala. However, dorsal tail pattern and color of the nape and belly are rather stable throughout Central America. It is noteworthy that Central American birds are closely matched in color and pattern by those of samples of *C. a. grateloupensis* from Veracruz. For example, mean scores for belly color range from 4.7 to 5.8 in Central America, and the mean sample score for birds from central Veracruz is 6.0. It seems consistent with our general plan of treatment to use only a single racial name, *C. a. santacruzi* (Bonaparte, 1837, p. 116), with type locality "Guatemala," for these populations.

Birds from the Caribbean slope of northern Honduras have been distinguished racially by Ridgway (1888, p. 582) as *C. a. pauper*, with type locality at Trujillo, Honduras, and this name has also been applied to birds from the

Motagua Valley of Guatemala (Skutch, 1945). Characters supposedly distinguishing *C. a. pauper* from *C. a. santacruzi* are smaller size and narrower white dorsal bars, but when birds from northern Honduras are compared with those from adjacent regions (Guatemala, El Salvador, and southeastern Chiapas), the following picture emerges: in length of wing, tail, bill, and tarsus, birds of the sample from Honduras average smaller than those of any other sample of the species *C. aurifrons*, although they are almost matched by the sample from southeastern Chiapas, and in bill depth the Honduran sample averages slightly smaller than samples from adjacent regions. The white bars on the back are narrower (1.13 mm.) than in any other sample, but the white bars of birds from southeastern Nicaragua are only slightly wider (1.28 mm.). Nape color (11.3) is probably not significantly different from that of birds from El Salvador (10.9), southeastern Chiapas (10.8), central Guatemala (11.5), and southern Guatemala (11.0); frontal region color (1.3) is slightly yellow, on the average, than in El Salvador (2.5), southeastern Chiapas (3.0), and southern Guatemala (2.9); belly color (5.7) is not significantly different from that of samples from El Salvador (5.8) and southern Guatemala (5.3); and the dorsal tail pattern (4.7), while darker than that of birds from El Salvador and southeastern Chiapas, is almost matched (5.5) in the sample from central Guatemala. All facts considered, there would seem to be little justification for nomenclatural separation of the northern Honduran population.

The name *fumosus* Nelson (1900, p. 258), with type locality at Huehuetán, Chiapas, is also regarded as a synonym of *santacruzi*, following Ridgway (1914) and other authors.

Three badly worn females from Progreso, Guatemala, have unusually yellowish napes and bellies (nape color near categories 5 and 6), which suggests some geographic differentiation in the arid district of the Motagua Valley, as previously noted by Griscom (1932, p. 229). Among Guatemalan specimens, only a female from Antigua (A.M.N.H. No. 394517) matches the Progreso birds.

Centurus aurifrons polygrammus CABANIS

We prefer to apply a single racial name, *C. a. polygrammus* (Cabanis, 1862, p. 326), with

type locality at San Bartolo[mé], Tehuantepec, Oaxaca, to the yellow-naped and boldly barred birds of the arid southern part of the Isthmus of Tehuantepec and the arid interior valley of Chiapas (samples 17 to 21, fig. 2), although it has been customary to recognize an additional race, *C. a. frontalis* Nelson, 1900, p. 257), with type locality at San Vicente, Chiapas. The relatively minor morphologic differences distinguishing these populations, some of which are shown in our analyses of characters, have been adequately discussed by Wetmore (1943), and "intergradation" is reported in a small sample of birds from the Monserrate region of Chiapas (Edwards and Lea, 1955, p. 44).

As herein defined, *C. a. polygrammus* is in most characters similar to *C. a. aurifrons*, from which it differs most conspicuously in having a greater amount of white in the tail.

POPULATIONS NOT REPRESENTED
BY SPECIMENS EXAMINED

Birds of the species *Centurus aurifrons* from Roatán and Barbareta Islands off the Caribbean coast of Honduras, are generally recognized as a distinct race, *C. a. canescens* (Salvin, 1889, p. 370), which reportedly is similar to *C. a. dubius* of the Yucatán Peninsula but differs in having wider white dorsal bars and the outer webs of the inner primaries spotted with white.

The population of *C. aurifrons* on Utila Island, Honduras, resembles that of the adjacent mainland (*C. a. santacruzi*) but has been distinguished racially by Bond (1936, p. 360), as *C. a. insulanus*, on the basis of the following characters: larger size; male with forehead and superciliary region decidedly white (versus gray in *C. a. santacruzi*); female with forehead and fore parts of crown whiter; and upper parts on the average "more extensively" barred with white. Bond also notes that there "is very little white on the rectrices, this sometimes entirely lacking," but the same is true for our small sample from the mainland. Measurements given by Bond indicate that the Utila Island birds are indeed larger than those from mainland Honduras, with wing lengths ranging from 130 to 138 mm. in three males and 127 to 128 mm. in three females; tail lengths are given as 75 to 85 mm. in males and 76 to 80 mm. in females (compare with sample 31 in figs. 8 and 9).

ZONES OF RACIAL INTERGRADATION

Our studies fully support the view that all populations of the *aurifrons* complex belong to a single species, since even the most highly differentiated forms have been shown to intergrade in zones of contact. We have already discussed in detail the complete and gradual transition from *C. a. aurifrons* of the Mexican Plateau to *C. a. dubius* of the Yucatán Peninsula through populations assigned to *C. a. grateloupensis*. There is also obvious clinal intergradation from *C. a. dubius* to the extreme *C. a. santacruzi* types of the Pacific slope of Central America through Guatemalan populations. In nape color (fig. 3), which is a representative character, there is a gradual cline from a mean sample score of 12.4 (almost pure red) in British Honduras through 12.0 in northern Guatemala, 11.5 in central Guatemala, and 11.0 in southern Guatemala to 10.8 in southeastern Chiapas and 10.9 in El Salvador.

Centurus a. polygrammus does not touch *C. a. aurifrons* geographically, but it is reasonable to assume that these two morphologically similar forms are conspecific, especially since the former appears not to be reproductively isolated from *C. a. santacruzi*, with which it is in contact at several points.

Between *C. a. polygrammus* of eastern Chiapas and *C. a. santacruzi* of the coastal region of southeastern Chiapas, the Sierra Madre de Chiapas, culminating in Volcán Tacaná on the Chiapas-Guatemala border, probably constitutes an almost absolute barrier to gene flow. Therefore it is not surprising to find that the two populations are, as our analysis has indicated, strikingly different in their characters. Similarly, specimens of *C. a. polygrammus* of eastern Chiapas differ conspicuously from birds in our sample of *C. a. santacruzi* from central Guatemala, but a series of four males and seven females from Sacapulas and Quiche, in central-western Guatemala (sample 34; fig. 2), although referable to *C. a. santacruzi*, definitely approaches *C. a. polygrammus* and tends to bridge the gap between the two. Intergradation is particularly evident in nape, belly, and frontal region colors (figs. 3-5), and one male (A.M.N.H. No. 406693) from Sacapulas has the red crown patch distinctly separate from the colored nape area, as in *C. a. polygrammus*. In size, specimens of *C. a.*

polygrammus from eastern Chiapas are only slightly larger than those of *C. a. santacruzi* from central and northern Guatemala, being in this respect intermediate between samples of the latter race and those of *C. a. polygrammus* from central Chiapas and Oaxaca.

Beginning in eastern Chiapas and extending west through central Chiapas and southern and northern Oaxaca to southern Veracruz, evidence exists of clinal merging of characters of the races *C. a. polygrammus* and *C. a. grateloupensis*, with a marked shift occurring between the latter two regions. One specimen, a male (A.M.N.H. No. 388879) from Tequisistlán, Oaxaca, not included in our numbered samples (fig. 2), is a good intergrade between the races, as are several in our sample from northern Oaxaca, and the rather marked variability of the large sample of *C. a. polygrammus* from southern Oaxaca is presumed to reflect flow of genes south across the Isthmus of Tehuantepec from *C. a. grateloupensis*. Probably the steepest part of the gradient will be found near Matías Romero, where the arid vegetation types of the Pacific side of the Isthmus give way to the mesic and humid types of the Caribbean side (Selander, 1959, p. 403).

Intergradation between *C. a. santacruzi* of southeastern Chiapas and *C. a. polygrammus* of southwestern Chiapas probably occurs not far south of the Laguna de la Joya near Tonalá, a locality that marks the division between the arid and mesic sections of the Pacific coastal plain of Chiapas. Specimens from this region are too few in number fully to document this transition, but two specimens from Pijijiapan show intergradation, although on the whole they are referable to *C. a. santacruzi*.

As yet we have no data on intergradation between *C. a. polygrammus* and *C. a. dubius*, which presumably occurs in northern Chiapas just north of the hills forming the northern border of the central valley of Chiapas.

In sum, intergradation between morphologically dissimilar populations of the *C. aurifrons* complex clearly supports the hypothesis that *aurifrons*, *polygrammus*, *santacruzi*, *dubius*, and *grateloupensis* are races of a single, highly polytypic species. Presumably the insular forms *canescens* and *insulanus* are also races of this species.

ECOLOGIC DISTRIBUTION OF *CENTURUS AURIFRONS*

Over its extensive geographic range, this species occupies many of the major plant formations occurring from sea level to about 7500 feet elevation, but nowhere does it inhabit dense forest. The highest recorded elevation appears to be 7800 feet, which it reaches in Durango. The nominate race occurs for the most part in xeric Sonoran Zone associations, including mesquite and other arid woodlands in Texas (Hamilton, 1962b) and Tamaulipas (Sutton and Pettingill, 1942), mixed oak-juniper-mesquite woodland (Texas), arid pine-oak woodland (Sierra de Tamaulipas; Martin, Robins, and Heed, 1954), and the yucca-cactus-juniper-creosote bush association of Coahuila and San Luis Potosí. In addition, it is especially numerous wherever willows, cottonwoods, cypresses, or other riparian trees are found, as in Palo Duro Canyon, northern Texas, and in Zacatecas (Webster and Orr, 1954) and Nuevo León (Sutton and Pettingill, 1943). Where telephone or other poles are available for nesting, it may occur in areas where there are no large trees (Quillin and Holleman, 1918). In towns it nests and forages in elms, oaks, pecans, junipers, chinaberries, and other trees.

Centurus a. polygrammus, like *C. a. aurifrons*, which it closely resembles morphologically, also inhabits xeric and mesic vegetation types and is often associated with mesquite. Edwards and Lea (1955) found it in a variety of habitats on the central plateau of Chiapas.

Centurus a. grateloupensis inhabits both arid and humid tropical regions, occurring in tropical forest at Xilitla, San Luis Potosí (Davis, 1952), coffee plantations at medium

elevations in Veracruz, and coyol woodland on the arid coastal plain of central Veracruz.

Regarding the ecologic distribution of *C. a. dubius* on the Yucatán Peninsula, Paynter (1955) notes that it is chiefly an inhabitant of tall and moderately tall deciduous forest but also occurs in second growth in the rain forest. It is absent from the interior of heavy rain forest and from low scrub types. Van Tyne (1938) reports its occurrence in clearings in the forests of Petén, Guatemala, and we have found it common along humid forest edges and in humid woodland at Teapa, Tabasco, and Palenque, Chiapas.

Like *C. a. grateloupensis*, the Central American race *C. a. santacruzii* is confined chiefly to the tropical zone, within which it occurs in both humid and arid divisions and inhabits a variety of vegetation types. In the Guatemalan highlands, it occurs in coffee plantations at 3200 feet (Wetmore, 1941), and Tashian (1953) found it common at all localities that he visited in southeastern Guatemala. Deignan (1936) reports that it is abundant on the humid northern coast of Honduras, except in heavy forest. Skutch (1945) found it in the humid lower Motagua Valley; there are also a few records from the arid upper part of this valley. In El Salvador (Dickey and van Rossem, 1938) it is a common and generally distributed resident of all types of woodland in the Arid Lower Tropical Zone and occurs locally in the Arid Upper Tropical Zone up to 4500 feet; it is especially abundant in the lower coffee district, along hedgerows dividing cultivated fields, and about small farms of the lower hill country.

DISCUSSION

The barred pattern of the back and wings in *Centurus* is probably cryptic, and its geographic variation shows a reasonably close correlation with regional variation in climate and vegetation type. Boldly patterned types (*C. a. aurifrons* and *C. a. polygrammus*), which are in gross aspect much lighter than the narrowly barred types (*C. a. dubius* and *C. a. santacruzii*), are found in arid regions where light penetrates deep into the middle and lower strata of relatively open woodland

vegetation, and the background of trunks and branches to which the woodpeckers are exposed is relatively light in color. But in more humid regions where denser broad-leaved vegetation creates greater areas of shadow and where the color of the vegetation tends to be darker, the dark appearance of the narrowly barred forms is probably at a selective advantage. In similar fashion, we assume that the value and hue of the color of the breast and sides are adaptive, providing effective

counter-shading by being darker in more humid areas and lighter in those of greater aridity. Variation in the highly colored yellow or red belly may also be related to the problem of counter-shading, but, since the color of the belly is not correlated with that of other areas of the under parts, we suspect that it may have some social signal function as well.

In the genus *Centurus* as a whole, the extent of white barring on the tail tends to be directly related to the degree of boldness of the dorsal pattern, but even in *C. aurifrons* there are some notable exceptions. For example, conspicuous white tail bars occur in *C. a. polygrammus* but are lacking in both the boldly patterned *C. a. aurifrons* and the narrowly barred *C. a. dubius*. Since the tail is largely concealed by the wings when a woodpecker is perched, and the pattern is fully revealed only in flight or in display, it is possible that the pattern is relatively unimportant from the standpoint of concealment and has, instead, some significance as a "flash" signal.

The brightly colored, sexually dimorphic regions of the head presumably have major significance in sex and species "recognition" and in agonistic and courtship display. Even so, it may be that the dark red or orange frontal and nape regions of *C. a. dubius* and *C. a. santacruzi* have been selected because they are less conspicuous to predators against dark backgrounds than are the lighter yellow shades of other populations inhabiting more arid regions.

Wetmore (1943) believes that the red abdomen found in *C. a. dubius* is the primitive condition in the species, with the yellow and orange-yellow color in *C. a. santacruzi* and other races representing a secondary modification. The fact that the belly is red in species of "*Tripsurus*" and in several other species of *Centurus* may support this speculation, but it should be noted that the yellow-bellied and yellow-naped condition also occurs in several species of *Centurus*, including *C. hoffmanni*, *C. uropygialis*, and *C. chrysogenys*. Extensive speculation on this point seems unwarranted in view of the fact that yellow and red pig-

ments are biochemically similar carotenoids (Test, 1942; Fox, 1953; Rawles, 1960), the production of which may be modified by minor genetic changes, as evidenced by the wide range of individual variation found in a single population. Moreover, in flickers (*Colaptes*), as in certain other species of birds, variation in red and yellow pigments is influenced by diet (Lester Short, in conversation). There seems to be little justification in attaching much significance to a character so subject to variation and so easily modified genetically and environmentally.

To account for the present disjunct distribution of the yellow-naped and broadly barred, arid-adapted populations of *C. aurifrons* and the closely related species *C. hoffmanni* (see below), Wetmore (1943) has proposed that contact between yellow-naped and red-naped populations is secondary, and he would explain the gap in distribution between *C. a. polygrammus* and *C. hoffmanni* in terms of a crowding out and replacement of yellow-naped populations by an invasion of *C. a. santacruzi*. Most of the resemblances among *C. a. aurifrons*, *C. a. polygrammus*, and *C. hoffmanni* involve characters that are presumably adaptive in arid situations and could therefore have developed independently, but, considering also the close similarities of these forms in head pattern, we are inclined to accept Wetmore's hypothesis that these disjunct populations are monophyletic and were formerly connected by yellow-naped populations. In the case of the *C. a. aurifrons*-*C. a. polygrammus* disjunction, it is curious that there is not now a population of the *C. aurifrons* complex in the arid Pacific coastal region of southwestern México, where, instead, we find *C. chrysogenys*, a species resembling *C. a. aurifrons* in color and pattern but actually not at all closely related to it. Perhaps the hypothetical connecting population of the *C. aurifrons* complex was replaced by *C. chrysogenys*, the latter invading western México from the east, where a close relative, *C. pucherani*, is found today.

OTHER SPECIES OF *CENTURUS*

SYSTEMATIC STATUS OF *CENTURUS HOFFMANNI* CABANIS

IN THE ABSENCE of information on the behavior and ecology of *Centurus hoffmanni*, judgment of its systematic status must rest entirely on the unsatisfactory criterion of morphologic evidence. This form was described by Cabanis (1862, p. 322) as a distinct species, but it was soon lumped with *C. aurifrons*, to which it is closely allied, by Baird, Brewer, and Ridgway (1874) and Ridgway (1881). In more recent years, some authors (for example, Peters, 1948, and Eisenmann, 1955) have considered it a subspecies of *C. aurifrons*, while others, notably Griscom (1932) and Wetmore (1943), have suggested that it is specifically distinct. On the basis of our studies of *Centurus*, we would concur with the latter treatment, but solution of this problem must await further research in the field.

Centurus hoffmanni is probably in contact, if not locally sympatric, with *C. aurifrons santacruzi* in northwestern Nicaragua, where the two forms have been collected at localities only 55 miles apart (Jalapa and San Rafael del Norte) in a region lacking obvious barriers to distribution (fig. 2). Considering the nature of patterns of distribution and contact between *C. aurifrons* and *C. carolinus* in Texas (Selander and Giller, 1959b) and between *C. aurifrons* and *C. uropygialis* in west-central México (see below), we predict that *C. hoffmanni* and *C. aurifrons* will be found coming together in a very sharply defined zone, with no extensive area of sympatry.

It has been claimed (Salvin and Godman, 1888, p. 421) that specimens of *C. aurifrons santacruzi* from El Salvador show a "divergence" toward *C. hoffmanni* as regards amount of white in the tail, but in fact neither our large series from that region nor our small samples from southeastern Honduras and extreme northwestern Nicaragua (Jalapa) show evidence of intergradation with *C. hoffmanni* in this or any other character (see figs. 3-11). Nor do specimens of *C. hoffmanni* from Nicaragua differ in any significant degree from those of Costa Rica. Clearly this evidence strongly suggests that the two forms do not interbreed, if, as seems likely, they are in

contact in Nicaragua, but of course we cannot neglect the possibility of hybridization in a narrow zone, with no readily detectable introgression.

In color and pattern, *C. hoffmanni* shows a greater over-all resemblance to *C. a. polygrammus* than to any other population of *C. aurifrons* (pl. 53), but at the same time it does not differ greatly from certain populations of *C. a. aurifrons*. For example, nape color (fig. 3), which varies from yellow to orange (mean score, 3.0) in *C. hoffmanni*, is almost matched by samples of *C. a. aurifrons* from Jalisco (3.9) and northwestern San Luis Potosí (2.5). As noted by Wetmore (1943, p. 277), the red coronal patch of males of *C. hoffmanni* is usually more or less confluent with the yellow or orange color of the nape, whereas there is a bar of gray separating these two areas in *C. a. aurifrons* and *C. a. polygrammus*. The belly color (fig. 4) of *C. hoffmanni* (4.9) is on the average a less pure yellow than that of *C. a. polygrammus* (eastern Chiapas, 1.3) but is closely matched by that of *C. a. santacruzi* from southeastern Chiapas (4.7). The underparts are darker than those of *C. a. polygrammus* and those of *C. a. aurifrons*, yet lighter than those of *C. a. santacruzi*. The frontal region color (0.1) is a purer yellow than that of *C. a. polygrammus* (eastern Chiapas, 1.0) or that of any other population of *C. aurifrons* (fig. 5). The dorsal tail pattern shows a considerable amount of white (0.9), and, among samples of *C. aurifrons*, it is equaled only by *C. a. polygrammus* (mean scores of 0.0 to 1.8 in different samples). The black and white barring (figs. 6 and 7) is relatively heavy but averages somewhat narrower than that of *C. a. aurifrons* and *C. a. polygrammus*.

Individuals of *C. hoffmanni* are smaller than those of any population of *C. aurifrons* (figs. 8-11). The nearest approach is seen in *C. a. santacruzi* from northwestern Honduras, and it is significant that specimens of this race from El Salvador and southwestern Honduras are considerably larger than *C. hoffmanni*. Perhaps the most striking character of *C. hoffmanni* is its tail length, which is not only shorter than that of *C. aurifrons* but also

much shorter relative to wing length or to tarsal length. The wing to tail ratio for *C. hoffmanni* is 2.03, whereas comparable ratios for samples of the other species invariably are smaller, as shown in table 1. As noted previously by Griscom (1932), specimens of *C. a. santacruzii* from southern Guatemala approach *C. hoffmanni* in wing/tail proportion, but we find it significant that birds from El Salvador and Honduras do not, although in general the tail is slightly shorter relative to the wing in *C. a. santacruzii* and *C. a. polygrammus* than in more northern races.

ECOLOGIC DISTRIBUTION

Concerning the geographic and ecologic

distribution of *C. hoffmanni* in Costa Rica, Carriker (1910) notes: ". . . this species takes the place of . . . [*Centurus*] *pucherani* on the Pacific slope and the central plateau region, although the ranges of the two birds slightly overlap, the present bird occurring occasionally on the Caribbean slope (Juan Vinas and Guapiles). It is the common woodpecker of the highlands and the Pacific coast, although not so abundant in individuals as . . . *pucherani* on the eastern side. It is also found in more open country, rarely being seen in heavy forest." Cherrie reports that it occurs up to an altitude of 6500 feet in the interior. On the Pacific side of southern Costa Rica, *C. hoffmanni* is replaced by *C. chrysauchen*.

RELATIONSHIP OF *CENTURUS AURIFRONS* (WAGLER) AND *CENTURUS UROPYGIALIS* BAIRD

Modern classifications carry *Centurus aurifrons* and *C. uropygialis* as separate species, but this treatment has been questioned by van Rossem (1934, p. 410), who, on the basis of two "intermediate" specimens in the British Museum (Natural History), a female from Calvillo, Aguascalientes, and a male from "Santana," near Guadalajara, Jalisco, has suggested a conspecific relationship. Van Rossem has also called attention to the occurrence of traces of yellow in the nape patch and nasal region of specimens of *C. uropygialis*, a feature that could indicate interbreeding and introgression with *C. aurifrons*.

Before presenting our findings on the relationship of these species in zones of contact, we provide a brief review of the ecologic distribution of *C. uropygialis* for comparative purposes.

ECOLOGIC DISTRIBUTION OF *Centurus uropygialis*

This species inhabits arid regions and is in all respects a close ecologic counterpart of *C. a. aurifrons*. It has an altitudinal range from sea level to about 5000 feet but occurs primarily in tropical and Lower Sonoran zones below 3000 feet. In Baja California, it is common in many desert formations in which cactus and mesquite are dominant, especially where the large cardons are found, and it also nests in suburban gardens and in palms and yuccas (Bancroft, 1929). In southern

California, it inhabits timbered bottomlands of the Colorado River, desert washes where ironwood and paloverde reach large size, and desert mesas where there are large cacti (Grinnell and Miller, 1944). With the planting of cottonwoods and other trees in the Imperial Valley, it has extended its range northward in this century (van Rossem, 1932). In Arizona, it is the most common woodpecker in desert lowlands (Gilman, 1915), nesting commonly in saguaros and in other cacti in the Tucson area and also in trees within the city. It extends up into the lower part of the Transition Zone at 5000 feet in the Whetstone Mountains of Arizona, but it is more numerous in lowland valleys and on mesas (Smith, 1908). In Sonora, as throughout its range, it is found in cottonwoods, willows, and other riparian elements, and it also occurs in cactus associations (van Rossem, 1945).

Seven races of *C. uropygialis* are currently recognized (Mexican Check-List Committee, 1957), although, compared to *C. aurifrons*, this species is not by any means highly variable geographically.

CONTACT ZONES

There appears to be no contact between the two species in northern México, where *Centurus aurifrons* occupies much of the plateau and is separated from *C. uropygialis* by the Sierra Madre Occidental (fig. 2). But the race

C. uropygialis sulfuriventer penetrates inland in a series of low river basins and barrancas at the highly dissected southern tip of the Sierra Madre, establishing contact with *C. aurifrons aurifrons* in western Aguascalientes and central Jalisco (fig. 12).

AGUASCALIENTES CONTACT: Field work in this area was begun on June 9 and continued through June 14. In the vicinity of the city of Aguascalientes, we found only *C. aurifrons*, which was moderately common in riparian cottonwoods in agricultural areas and probably also occurred in cactus and yucca formations in gullies east of the city. Driving west from Aguascalientes on the road to Jalpa, Zacatecas, we entered the Calvillo Valley through a narrow pass about 33 kilometers west of Aguascalientes. Dry oak woodland was the dominant vegetation type on hillsides at the pass, but in arroyos this was replaced by a yucca-acacia-tuna cactus association in which a pair of *C. aurifrons* was taken and another individual was seen 34 kilometers west of Aguascalientes.

Between the pass and Calvillo, the valley widens and gradually decreases in elevation from 6000 to 5400 feet. At El Sauz, 38 kilometers west of Aguascalientes, both species were found together in small stands of cottonwoods and willows bordering two small reservoirs. Four pairs of *C. aurifrons* were seen, and seven adult specimens in breeding condition were collected. We also obtained an adult female and a juvenile of *C. uropygialis*.

From El Sauz, we continued west to La Panadera, a settlement on the Río de Malpaso (a tributary of the Río de Calvillo, which in turn flows into the Río Juchipila), 60 kilometers west of Aguascalientes, or about 2 kilometers east of Calvillo, where we camped on June 9 and 10. Both species were present in narrow stands, 40 to 50 feet tall, of riparian cottonwoods, willows, and *guamuchiles* along the Río de Malpaso, which at this locality is only a few yards wide, and a few birds were seen in orchards near houses. The results of our investigations at this locality can be summarized as follows:

Centurus uropygialis outnumbered *C. aurifrons* four to one: along a 2-mile stretch of the river, we found 20 individuals of *C. uropygialis* and five of *C. aurifrons*, and we also collected an adult female that appears to be an

interspecific hybrid (see below).

Adults were in breeding condition, and, with the exception of the hybrid, both members of pairs that were collected proved to belong to the same species. Pairs were spaced at intervals of approximately 50 yards along the river, and the habitat situations in which the two species occurred did not differ appreciably. Moreover, the spacing of pairs suggested that territories of the two species were mutually exclusive. We detected no differences in foraging behavior.

The vocalizations of the two species were similar, but identification was usually possible, since the calls of *C. uropygialis* were higher pitched and softer. The over-all degree of difference in the calls was roughly equivalent to that distinguishing the vocalizations of *C. aurifrons* and *C. carolinus* in their zone of contact in Texas (Selander and Giller, 1959b).

On June 11, camp was moved from La Panadera southwest to the settlement of La Cuesta, 5 miles southwest of Jalpa, Zacatecas, a locality on the Río Juchipila, approximately 30 miles from Calvillo. This region is more arid than that at Calvillo and lies at a lower elevation, approximately 5000 feet. At this locality, as in the Calvillo Valley, *Centurus* woodpeckers were confined to riparian habitats and trees near houses, none being observed in cactus and scrub vegetation on the hillsides, where they were replaced by the ladder-backed woodpecker (*Dendrocopos scalaris*). Thirty-four specimens of *Centurus* were collected, all of which are *C. uropygialis*; the other species was not recorded. Specimens of *C. uropygialis* were previously reported from the Jalpa area (Jalpa, Moyahua, and Apozol) by Webster (1958).

JALISCO CONTACT: An intensive search for another zone of contact between *Centurus* species was made in the Guadalajara region (fig. 12) from June 15 to 20. This heavily populated region has been so drastically altered by human activity that only a few areas of habitat suitable for *Centurus* remain; these consist of timber along streams and clumps of trees at settlements. We were able to obtain a series of *C. aurifrons* in willows and cypresses along the Río Grande de Santiago near the town of Puente Grande, 20 miles southeast of Guadalajara, and we found

C. uropygialis common in willows along irrigation canals in cane fields near La Vega, 21 miles west of Guadalajara, but we were unable to locate either species at Santa Ana Tepititlán, a locality that we presume to be the "Santana" (Sta. Ana) from which the "intermediate" specimen in the British Museum was obtained in 1889.

After a considerable period of searching, we discovered a previously unknown area of contact 5 miles northeast of Zapopan, on the rim of the Barranca de Oblatos of the Río Grande de Santiago, about 10 miles north of Guadalajara. The physiography and vegetation types of this barranca have already been described in connection with an avifaunal report (Selander and Giller, 1959a). In the barranca, the floor of which is at 3000 feet in elevation, only *C. uropygialis* was found, and here we collected a series of 12 specimens. On the rim of the barranca, at an elevation of about 5000 feet, both species occurred in a small grove of pecans, willows, mangos, and figs along a small stream. The surrounding area is covered with cactus and other typical arid plateau vegetation in which *C. aurifrons* occurs sparingly in the complete absence of the other species.

In the grove of mesic vegetation near the stream, *C. uropygialis* outnumbered *C. aurifrons* five to one, notwithstanding the fact that the locality is on the plateau at the extreme upper altitudinal limit of *C. uropygialis*, and the habitat is not greatly, if any, different from the habitats occupied by *C. aurifrons* elsewhere in the Guadalajara region. In this stand, we collected four adult males, five adult females, and four juveniles of *C. uropygialis*. Two adult females of *C. aurifrons* were taken, but males of this species were not seen.

MORPHOLOGIC DIFFERENCES AND HYBRIDIZATION

In comparing *Centurus a. aurifrons* from the Mexican Plateau with *C. uropygialis* from Jalisco, Nayarit, and southern Sinaloa, we noted the following differences:

1. SIZE (FIGS. 13, 14): *Centurus uropygialis* is smaller, especially in wing and bill length, but there is some overlap, sex for sex, in all dimensions, and particularly in the length of the tail, which is disproportionately large in

C. uropygialis and nearly equals that of *C. aurifrons*. Extremes of variation in body weight also show overlap.

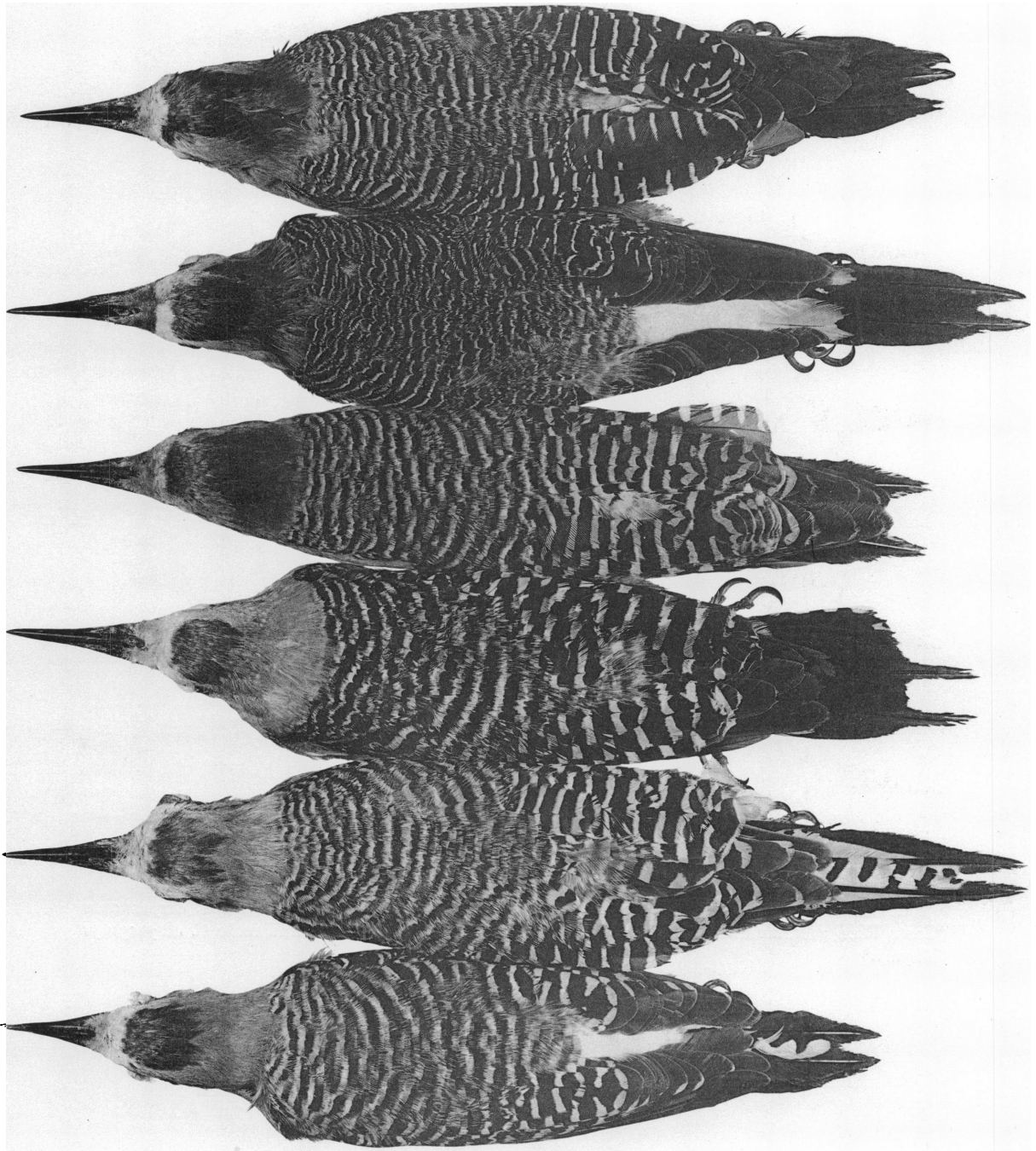
2. COLOR OF HEAD AND UNDER PARTS: These areas average somewhat browner and less neutral gray in *C. uropygialis*. In males of *C. aurifrons*, the frontal and nape regions are yellow or orange-yellow, and the red crown patch is relatively large; in males of *C. uropygialis*, the red crown patch is only three-quarters of the area of that of *C. aurifrons*, and the nape and frontal regions either lack yellow or are tinged with very pale brownish yellow. Similarly, in females of *C. uropygialis*, the nape and frontal regions normally lack yellow but may be tinged with pale brownish yellow.

3. UPPER TAIL CONVERTS: These feathers are regularly barred with black in *C. uropygialis*, whereas they are white or show black blotches or imperfect bars in *C. aurifrons*.

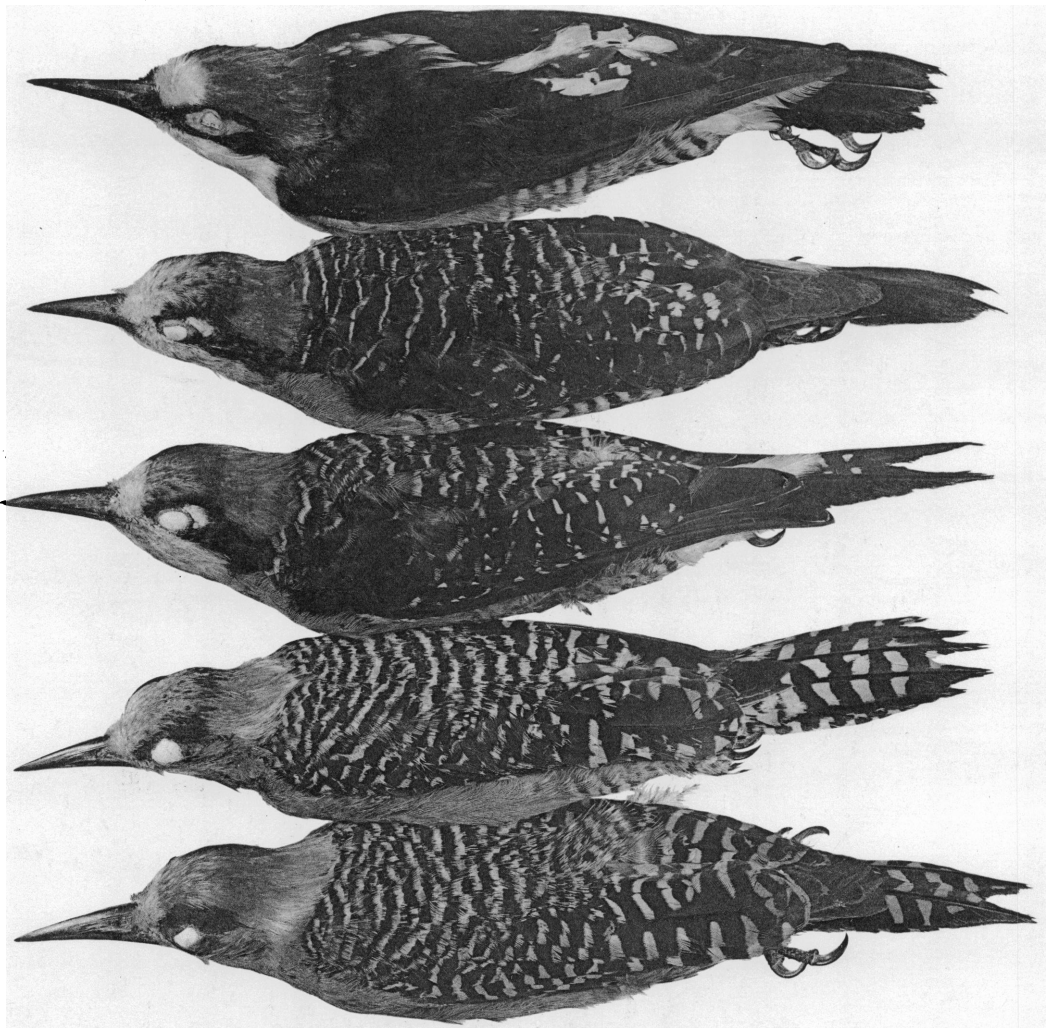
4. TAIL PATTERN: The dorsal tail pattern of *C. uropygialis* shows regular white bars on the inner webs of the central rectrices, and on the outer web there is either a series of white bars, a wide streak, or some intermediate condition. In *C. a. aurifrons*, the tail is black dorsally or has a few white smudges or small, imperfect bars on the inner webs of the central rectrices, and the outer webs of these feathers lack white. Ventrally, *C. uropygialis* has four or more white bars crossing both webs of the outer rectrix (number 5), whereas, in *C. a. aurifrons*, there are one or two white bars suggested by blotches of white, two more or less complete bars crossing both webs, and, rarely, a third incomplete bar on the inner web.

The hue, intensity, and distribution of yellow in the belly region are similar in both species, as are the pattern of dorsal barring and the dark barring on the thighs, posterior flanks, and under tail coverts.

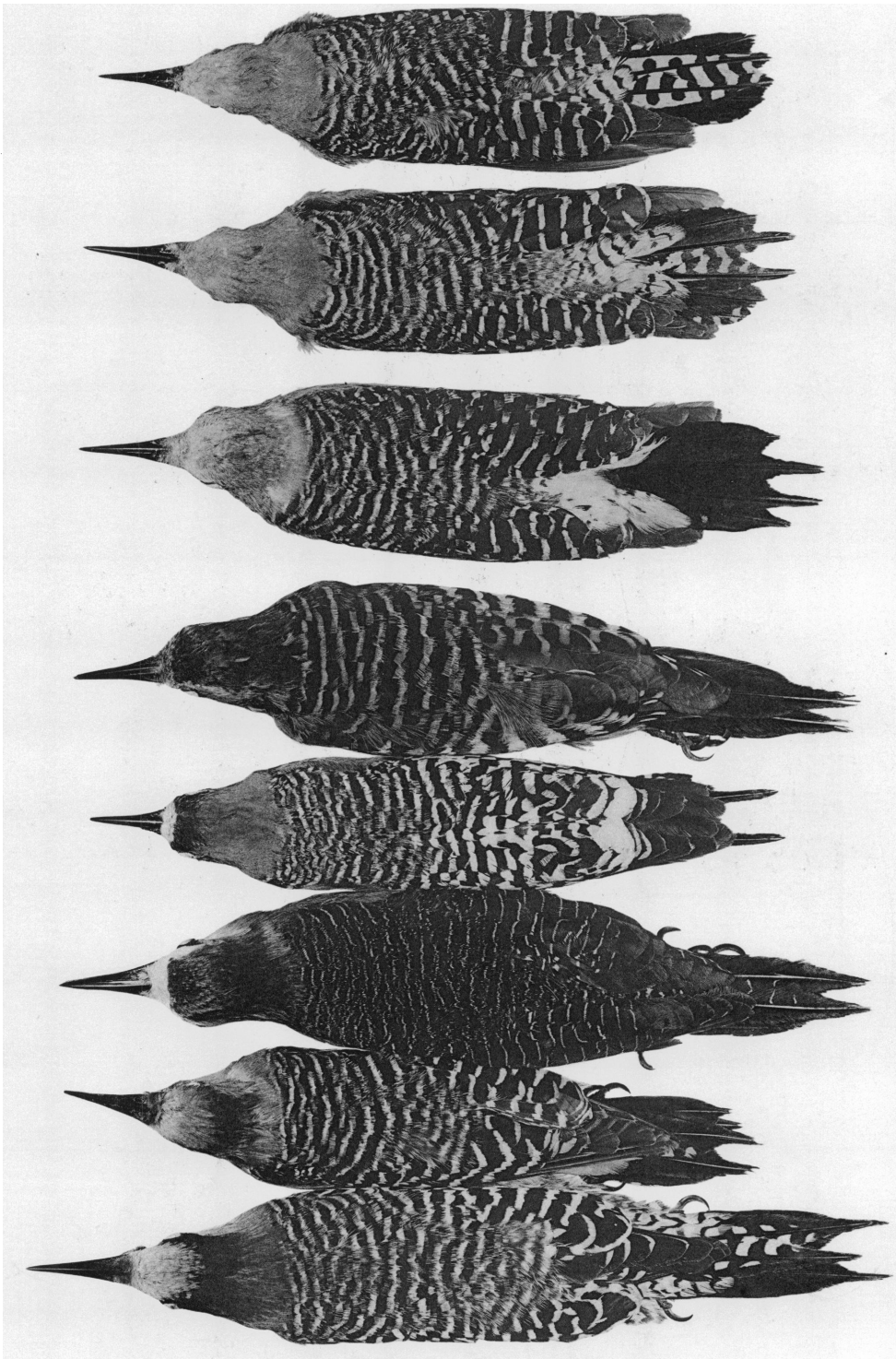
An examination of large series of specimens from the zones of contact in Aguascalientes and Jalisco fails to demonstrate an extensive intergradation of characters, a fact indicating that the two woodpeckers have evolved intrinsic reproductive isolating mechanisms and are to be classified as full species. The variation in size of specimens from the contact zones and adjacent regions is shown in figures 13 and 14; note that neither species



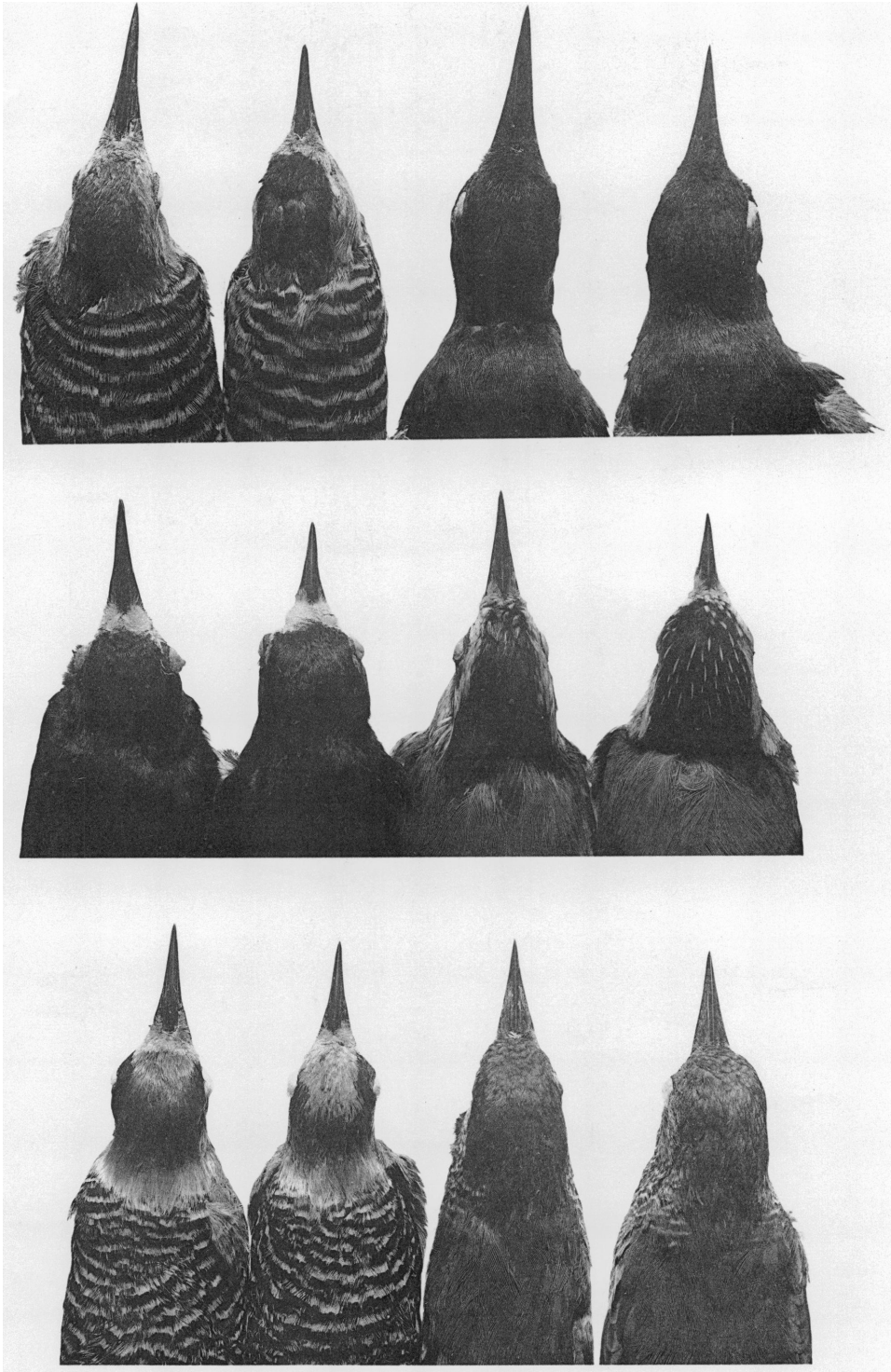
Adult male specimens of *Centurus aurifrons* and *Centurus hoffmanni* in dorsal view. From top to bottom: *Centurus a. santacruzi* (El Salvador); *C. a. dubius* (Yucatán); *C. a. grateloupensis* (San Luis Potosí); *C. a. aurifrons* (Aguas-calientes); *C. a. polygrammus* (Chiapas); and *C. hoffmanni* (Costa Rica)



Adult specimens of *Centurus* in dorsolateral view. *From top to bottom*: Male *C. chrysauchen* (Costa Rica); female and male *C. pucherani* (Costa Rica); and female and male *C. chrysogenys* (Nayarit)



Top to bottom, dorsal view: *Centurus uropygialis*, adult female, La Panadera, 2 kilometers east of Calvillo, Aguascalientes; presumed hybrid of *C. aurifrons* and *C. uropygialis*, adult female, same locality; *C. aurifrons*, adult female, same locality; *Chryserpes striatus*, male; *Centurus hypopolius*, male; *Centurus radiolatus*, male; *Centurus carolinus* (A.M.N.H. No. 39026), female variant from Florida, showing black occipital band; *Centurus s. superciliaris*, female



Interspecific variation in degree of sexual dimorphism in size of bill. Adult specimens in dorsal view. *Top row*: Left, male and female *Chryserpes striatus* (Hispaniola); right, male and female *Melanerpes herminieri* (Guadelupe Island, Lesser Antilles). *Middle row*: Left, male and female *Melanerpes portoricensis* (Puerto Rico); right, male and female *Xiphidiotopicus percussus* (Cuba). *Bottom row*: Left, male and female *Centurus chrysogenys* (Nayarit); right, male and female *Piculus rubiginosus* (Guatemala)

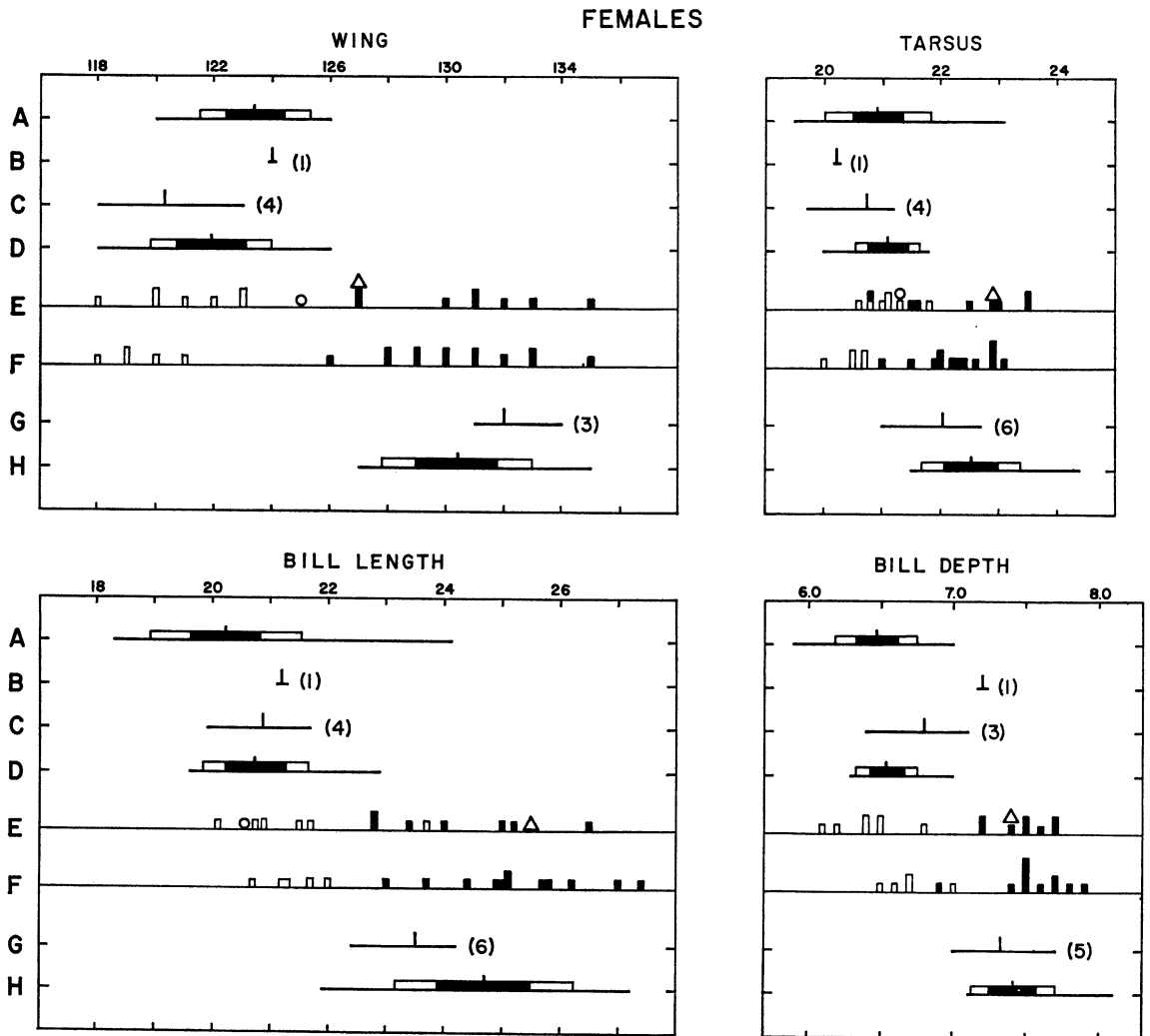


FIG. 14. Measurements of females of *Centurus uropygialis* and *Centurus aurifrons* from zones of sympatry and adjacent regions. Letters designate localities, as follows: A, southern Sonora (*C. uropygialis*); B, Sinaloa and Nayarit (*C. uropygialis*); C, La Vega and Bolaños, Jalisco (*C. uropygialis*); D, Jalpa region, Zacatecas (*C. uropygialis*); E, Calvillo Valley, Aguascalientes (open histograms, *C. uropygialis*; solid histograms, *C. aurifrons*; triangle, presumed interspecific hybrid, R.K.S. No. 3127; circle, presumed interspecific hybrid, B.M.N.H. No. 98-3-14-515); F, Guadalajara region (both species, as designated in E); G, northeastern Jalisco and central Aguascalientes (*C. aurifrons*); H, northwestern San Luis Potosí (*C. aurifrons*).

The distribution of specimens in the three classes is shown in table 3, in which it will be noted that yellow pigment is evident more frequently in worn than in unworn skins. In males, for example, 81 per cent of unworn skins but only 56 per cent of worn specimens fall into category 0, showing no trace of yellow on the nape. We also find yellow more often evident in males than in females.

With reference to the question of introgressive hybridization, we wish to emphasize the fact that, although the frequency of occurrence of yellow on the nape is perhaps slightly lower in birds from Baja California than in other samples, there is actually little geographic variation in this character in the species as a whole. If the occurrence of yellow in the nape region is a result of current or

relatively recent hybridization, it is difficult to explain the fact that yellow occurs as frequently in specimens from Arizona and California as in those from Aguascalientes, Zacatecas, and Jalisco, states near the zones of contact with *C. aurifrons*. A more plausible hypothesis is that the yellow represents a vestige of a character in the process of being lost in *C. uropygialis* or, in other words, a remnant of a character that was more fully developed in a population ancestral to present-day *C. uropygialis*.

PRESUMED HYBRIDS: The intermediate characters of three specimens from the zones of contact, the two in the British Museum mentioned by van Rossem (1934, p. 410) and one collected by us in 1958, suggest that intrinsic mechanisms isolating the two species reproductively are not fully effective and that occasional hybridization does occur.

Of the three questionable specimens, the one most likely to be a hybrid rather than merely an unusual variant of one of the species (see comments on this problem by Brown and Wilson, 1956) is an adult female (R.K.S. No. 3127; see pl. 55) taken at La Panadera, 2 kilometers east of Calvillo, on June 9, 1958. Its measurements are as follows: wing, 127; tail, 71; bill length, 25.5; bill depth, 7.4; tarsus, 22.9 mm.; weight, 82 grams. In weight and most linear dimensions (fig. 14), this specimen falls near the average for *C. aurifrons*, but the wing and tail lengths are near the observed minima for that species. The color of the head and under parts is matched by specimens of *C. aurifrons*, but in place of a conspicuous yellow nape crescent there is a narrow, dull grayish yellow patch quite unlike that seen in any other specimen of *C. aurifrons*; and in the nasal region just poste-

TABLE 3
VARIATION IN AMOUNT OF YELLOW ON NAPE IN *Centurus uropygialis*

Locality	Sex	Worn Specimens			Unworn Specimens				
		No.	0	1	2	No.	0	1	2
Aguascalientes (Calvillo Valley)	♂	10	5	4	1	—	—	—	—
	♀	7	5	1	1	—	—	—	—
Zacatecas (Jalpa)	♂	12	6	5	1	—	—	—	—
	♀	12	9	3	—	—	—	—	—
Jalisco (Guadalajara region)	♂	8	6	1	1	—	—	—	—
	♀	6	4	2	—	—	—	—	—
Sinaloa-Nayarit-W. Jalisco	♂	7	3	2	2	5	3	1	1
	♀	4	3	1	—	—	—	—	—
S. Sonora	♂	11	8	2	1	17	13	4	—
	♀	12	8	4	—	9	9	—	—
N. Sonora	♂	25	12	11	2	18	10	8	—
	♀	14	9	5	—	20	18	2	—
Arizona	♂	49	26	17	6	51	42	7	2
	♀	41	27	11	3	36	33	3	—
Nevada	♂	7	2	5	—	8	7	1	—
	♀	0	—	—	—	5	4	1	—
California	♂	17	8	7	2	17	14	3	—
	♀	16	11	5	—	18	15	3	—
N. and central Baja California	♂	11	7	3	1	9	8	1	—
	♀	6	5	—	1	6	6	—	—
S. Baja California	♂	41	28	10	3	29	27	2	—
	♀	32	26	6	—	11	11	—	—
Totals	♂	198	111	67	20	154	124	27	3
	♀	150	107	38	5	105	96	9	0
Percentages	♂	—	56	34	10	—	81	17	2
	♀	—	72	25	3	—	91	9	0

TABLE 4
 VARIATION IN DORSAL TAIL PATTERN IN *Centurus aurifrons* and *Centurus uropygialis*

Form, Sex, Age, Locality	No. of Specimens	Tail Pattern Categories											Mean Score	
		0	1	2	3	4	5	6	7	8	9	10		11
<i>Centurus aurifrons</i>														
♂ Adult, Aguas.-Jalisco	17	—	—	—	—	—	—	—	—	—	2	—	15	10.8
♂ Juvenal, Aguas.-Jalisco	3	—	—	—	—	—	—	—	—	—	—	—	3	11.0
♀ Adult, Aguas.-Jalisco	18	—	—	—	—	—	—	—	1	2	5	2	8	9.8
♀ Juvenal, Aguas.-Jalisco	3	—	—	—	—	—	—	—	1	—	—	—	2	9.7
Presumed interspecific hybrid														
♀ Adult (R.K.S. No. 3127)	1	—	—	—	—	—	—	1	—	—	—	—	—	6
<i>Centurus uropygialis</i>														
♂ Adult, Aguas.-Jal.-Zac.	32	1	3	3	11	11	3	—	—	—	—	—	—	3.2
♂ Juvenal, Aguas.-Jal.-Zac.	18	5	5	6	1	1	—	—	—	—	—	—	—	1.3
♀ Adult, Aguas.-Jal.-Zac.	29	4	5	9	5	5	1	—	—	—	—	—	—	2.2
♀ Juvenal, Aguas.-Jal.-Zac.	11	4	4	2	—	—	1	—	—	—	—	—	—	1.2
♂ Adult, Nayarit-S. Sinaloa	13	—	2	3	5	3	—	—	—	—	—	—	—	2.7
♀ Adult, Nayarit-S. Sinaloa	6	—	2	2	1	1	—	—	—	—	—	—	—	2.2

0 Full white bars on both webs of central rectrices

1 White bars confluent near outer margin of outer web on proximal half of feather, "trapping" incomplete bars of black (see specimen of *C. uropygialis*, pl. 55)

2 White bars confluent near outer margin along entire outer web

3 Broad streak of white on outer web, with small patches of black (representing greatly reduced bars) adjacent to rachis

4 Like category 3 but without patches of black

5 Streak of white on outer web shortened to three-quarters of length of web

6 Streak of white on outer web narrower than in category 5 and shortened to one-half of length of web (see hybrid specimen, pl. 55)

7 Four 3-4 mm.-wide white patches (representing incomplete bars) on inner web proximally

8 Four 2 mm.-wide patches of white near outer margin of inner web

9 Single 2-3 mm.-wide patch of white on inner web

10 Single 1 mm.-wide patch of white on inner web

11 No white markings on central rectrices (see specimen of *C. aurifrons*, pl. 55)

rior to the nostrils there are small patches of this same color. In the character of the nape and nasal region, the specimen falls nearer *C. uropygialis* than *C. aurifrons*, although it is not matched by any of several hundred specimens of the former species.

The tail pattern of this female is also intermediate and is not duplicated in any available specimen of either species. This is shown in table 4, in which specimens are assigned to 12 categories that represent progressive steps in the reduction of white on the central rectrices, a feature closely correlated with the amount of white on the ventral surface of the outer rectrices. (These are not the same categories of tail pattern used in the analysis of geographic variation in *C. aurifrons*, although a

few are more or less comparable.) Note that the female R.K.S. No. 3127 alone falls in category 6 between *C. aurifrons* (categories 7 to 11) and *C. uropygialis* (categories 0 to 5). The upper tail coverts of the presumed hybrid female are also intermediate in pattern (pl. 55), having black bars that are more perfectly formed than those of *C. aurifrons* yet narrower and less uniform in width than those of *C. uropygialis*.

In view of the obvious intermediacy of this specimen in a number of characters, the possibility of its being a variant of *C. aurifrons* or *C. uropygialis* seems remote, and we have accordingly identified it as an interspecific hybrid. It is worth recording that the bird was collected in the same tree with an adult

male of *C. uropygialis*, to which possibly it was mated; the male had a brood patch and testes measuring 5 mm. in length. In preparing the hybrid specimen, we found a fully formed brood patch and an ovary that was moderately enlarged and normal in appearance. These data strongly suggest that eggs had been laid. If in fact the bird is a hybrid, it seems probable that it is an F_1 , and the apparent absence of introgression in the Calvillo Valley populations sampled in 1958 would further suggest that the occasional hybrids formed are incapable of producing viable young.

The two presumed hybrids in the British Museum (Natural History) to which van Rossem (1934) referred were examined by us in 1958 but unfortunately were not available when we made our detailed analysis of variation in nape color and tail pattern in *C. uropygialis* and geographic variation in *C. aurifrons*. It is our opinion, however, that van Rossem (1934) was probably correct in interpreting these specimens as hybrids, although neither is so clearly intermediate in its characters as is our female from the Calvillo Valley.

The British Museum specimen from Calvillo (B.M.N.H. No. 98-3-14-515) is a female collected by W. B. Richardson in August, 1888. It was marked "imm." (immature) by the collector and is in a late stage of fall molt, either postjuvinal or postnuptial. It measured as follows: wing, 125; tail, 72; bill length, 20.6; and tarsus, 21.3 mm.; weight was not recorded by the collector, and bill depth cannot be measured. In most dimensions this specimen falls in a position intermediate between mean values for the two species (fig. 14). In color and pattern, it is *C. uropygialis*-

like, and the tail pattern does not differ from that seen in many specimens of *C. uropygialis*. However, the under parts and forehead are grayer (less brownish) than in any specimen of *C. uropygialis* in comparable plumage, and the nape appears to have much more yellow than do specimens of that species. Probably it would fall in category 3 of nape color, but a more critical appraisal of this feature is precluded by the fact that the feathers of the nape region are not fully grown.

The male specimen (B.M.N.H. No. 88-10-10-521) was collected at "Sta. Ana," Jalisco, on February 23, 1889, by W. Lloyd. It is marked "jv." (juvenile) by the collector but is actually an adult bird. It measured as follows: wing, 132; tail, 83; bill length, 23.9; bill depth, 8.1; and tarsus, 22.0 mm.; no weight is given. In wing length, it is intermediate between mean measurements of the two species (fig. 13). Our notes indicate that this specimen is also more or less intermediate in color and pattern but rather on the *C. uropygialis* side.

In conclusion, it may be of interest to record the incidence of hybrids in the two zones of contact. From the Calvillo Valley between Jalpa, Zacatecas, and the city of Aguascalientes, we have examined 15 adults of *C. aurifrons*, 18 adults and four juveniles of *C. uropygialis*, and the two presumed female hybrids. Hence, 5 per cent of the 39 specimens from the Calvillo Valley are hybrids. From "Sta. Ana" and our locality near Zapopan, Jalisco, we have examined 20 specimens (six adults of *C. aurifrons*, nine adults and four juveniles of *C. uropygialis*, and the one presumed male hybrid), 5 per cent of which show hybrid origin.

RELATIONSHIP OF *CENTURUS AURIFRONS* (WAGLER) AND *CENTURUS CAROLINUS* (LINNAEUS)

It has been suggested (Brodkorb, 1957) that these forms are conspecific but they are in fact full species, as demonstrated by sympatry in central Texas (Selander and Giller, 1959b).

All available breeding records of *Centurus* in Texas are shown in figure 15. Both *C. aurifrons* and *C. carolinus* have been found nesting in the same area at the following locali-

ties: Port Lavaca area, Calhoun County; Victoria area, Victoria County; Giddings, Lee County; Austin region, Travis County; San Angelo, Tom Green County; Colorado City, Mitchell County; Carbon area, Eastland County; and Vernon, Wilbarger County.

In winter *C. carolinus* tends to wander south and west of its breeding range, being reported at several localities in Nueces, Bee,

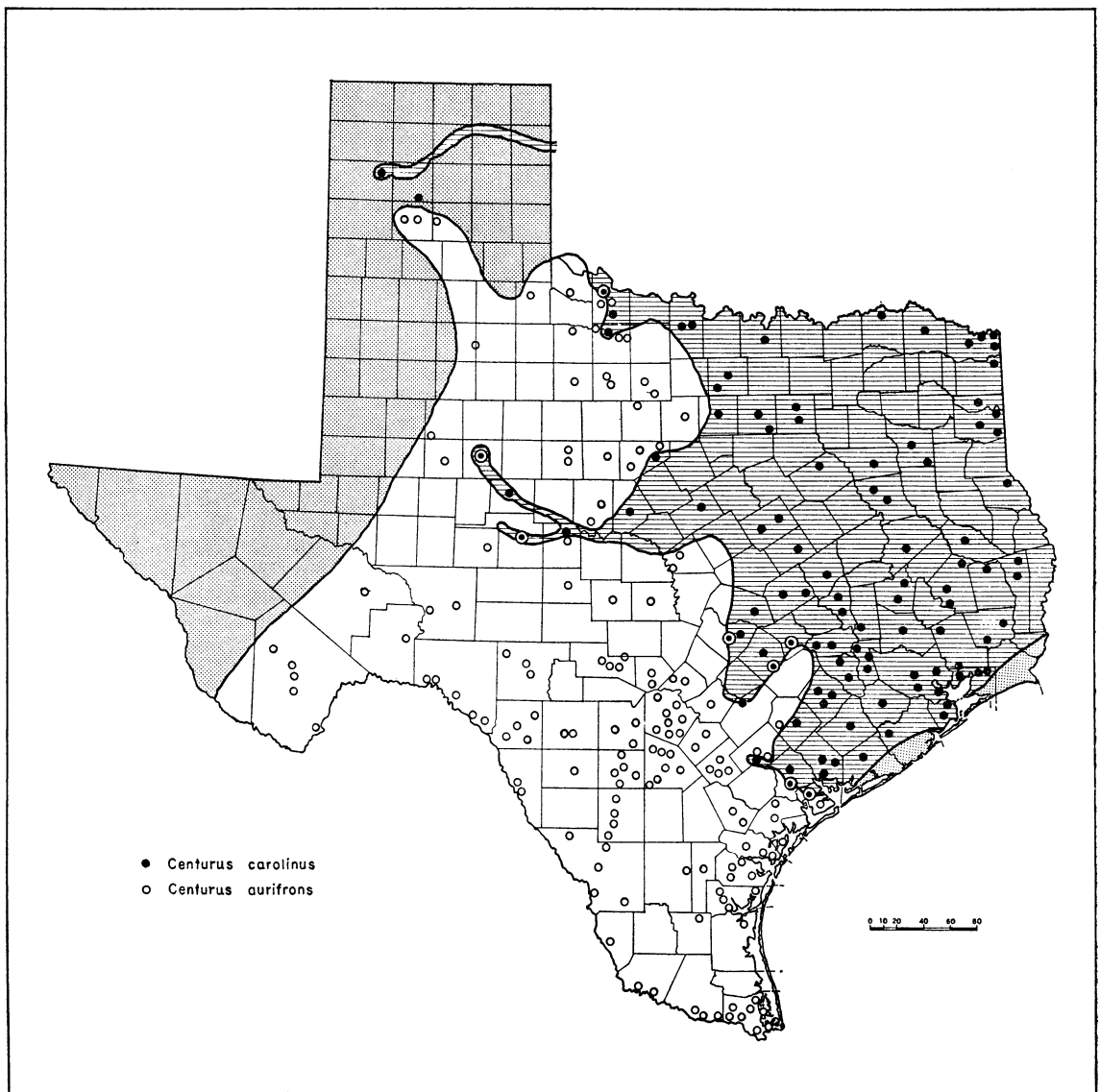


FIG. 15. Distribution of *Centurus carolinus* and *Centurus aurifrons* in Texas, based on specimens examined and numerous sight records.

Goliad, Aransas, San Antonio, Comal, and Kendall counties, and as far south as Brownsville and Starr counties along the Rio Grande.

In the zone of distributional overlap, which is, at least in the Austin region, only a few miles wide, both species are closely similar in size and in nesting and foraging behavior, and they hold mutually exclusive territories. Details concerning the habitat distribution and behavior of these species can be found in our earlier paper (1959b). Geographic varia-

tion in *C. carolinus* has been studied by Burleigh and Lowery (1944) and Koelz (1954); also, see remarks by Todd (1946).

At the time of our earlier report (Selander and Giller, 1959b), we had recorded no individual that suggested mixed ancestry, but in April, 1959, such a bird, a female, was seen on the campus of the University of Texas in Austin in company with, and apparently mated to, a male of *C. carolinus*. The dorsal tail pattern of the bird in question was typical

of that of *C. carolinus* in Texas, with conspicuous white bars on the central rectrices, but the nape was yellowish orange rather than red. This peculiar nape color suggested mixed ancestry, but the probability of the bird's being a hybrid is reduced by the fact that there are several similar specimens of *C. carolinus* in the collections of the American Museum of Natural History from localities far removed from the range of *C. aurifrons*. These are as follows:

- Female (A.M.N.H. No. 362499), Hillsboro, Iowa, February 2, 1899; nape pale yellowish orange
 Female (A.M.N.H. No. 362453), Eau Gallie, Florida, February 2, 1914; nape pale yellowish orange
 Two males (A.M.N.H. Nos. 362441, 362442), same locality, January 29, February 2, 1914; orange nape, frontal, and coronal regions
 Female (A.M.N.H. No. 362510), Danfuskie Island, South Carolina, November 24, 1904; nape orange
 Female (A.M.N.H. No. 362525), Warsaw, Illinois; nape orange
 Female (A.M.N.H. No. 362479), Delight, Arkansas, March 29, 1913; nape orange
 Female (A.M.N.H. No. 362435), Amelia Island, Florida, December 13, 1905; nape reddish orange

In view of these facts, and when it is considered that our questionable Texan bird had a tail pattern typical for *C. carolinus*, it is probable that it was an individual variant of that species rather than a hybrid. Without further explanation, Peterson (1960) has recently stated that hybrids between *C. carolinus* and *C. aurifrons* "are said to occur." Possibly this statement is based on sight records of variant individuals of the type just described, but, in any event, we have no knowledge of published reports of hybridization or of the existence of supposed hybrid specimens.

Centurus hypopolius (WAGLER)

Peters (1948) considered this form to be conspecific with *Centurus uropygialis*, but with few exceptions (Blake, 1953; Davis and Russell, 1953) recent authors (Sutton, 1951; Amadon and Eckelberry, 1955; Eisenmann, 1955; and Mexican Check-List Committee, 1957) have not followed this action. It is our opinion that, while *C. hypopolius* may have some not very distant phyletic connection

with *C. uropygialis*, it is highly unlikely that these two woodpeckers would interbreed if they were sympatric.

Centurus hypopolius resembles *C. uropygialis* in lacking highly colored nape and frontal regions, but it differs in lacking yellow on the belly. It is smaller than *C. uropygialis*, although there is a general similarity between the two species in body proportions, the wing and tail being comparatively long in both. The presence of a black superciliary patch, a relatively naked orbital ring, and a splotch of color (red) on the malar region suggests a relationship with *C. chrysogenys* rather than with *C. uropygialis*. The eye color of adults is also closer to that of *C. chrysogenys*: in *C. hypopolius* the adult iris is dull brown; in *C. chrysogenys*, burnt sienna or orange-brown; in *C. uropygialis*, reddish brown. In *C. aurifrons*, the iris is dark red in Mexican populations but may vary to reddish brown in Central American birds, according to Dickey and van Rossem (1938) and data on specimen tags. The iris is also dark red in *C. carolinus*. In juveniles of all species, the iris is dull brown.

There is considerable interspecific variation in the length and relative massiveness of the hyoid apparatus in *Centurus*. In skinning specimens we have noted a general similarity in *C. aurifrons*, *C. carolinus*, and *C. uropygialis* in this regard, but, in *C. chrysogenys* and even more markedly in *C. hypopolius*, this structure is relatively less massive and the horns are shorter.

The vocalizations of *C. hypopolius* were not studied in detail, but we recorded one distinctive call consisting of an indefinite number of harsh "che" notes delivered with rising inflection. This call was quite unlike any given by other species of *Centurus* with which we are familiar in the field. In their harshness the vocalizations of *C. hypopolius* suggest those of *C. chrysogenys*, but the calls are given more softly, being in this regard similar to those of *C. uropygialis*.

ECOLOGIC DISTRIBUTION: Throughout its relatively restricted geographic range in southwestern and central México (fig. 1), *C. hypopolius* occurs in arid regions and is found in habitats structurally similar to some of those occupied by *C. aurifrons* and *C. uropygialis* in northern México. It was common in yucca and cactus formations near Tepanco,

Puebla, in July, 1958, and Amadon and Eckelberry (1955) found it nesting in cactus along the highway near Izúcar de Matamoros, Puebla. Apparently it is in contact with *C. aurifrons* in the Valley of México, and it is also locally sympatric with *C. chrysogenys* in Guerrero, Morelos, and possibly southern Puebla (fig. 1). In Morelos, *C. hypopolius* is a common resident of the desert "chaparral," where it is frequently found on cacti, at medium elevations (up to 7000 feet), while *C. chrysogenys* is restricted to lower elevations (generally below 4700 feet) and has its center of distribution in riparian communities along the Río Balsas and its tributaries. However, locally the two species occur together, as at Alpuyecá, Morelos (Davis and Russell, 1953).

Centurus chrysogenys (VIGORS)

This handsome species (pl. 54) bears a superficial resemblance to the yellow-naped races of *Centurus aurifrons*, but as noted

above it actually seems to be not at all closely allied to the *aurifrons-uropygialis-carolinus* superspecies and apparently has closer phyletic ties with *C. pucherani* and other species of the "*Tripsurus*" group.

Geographic variation in this species has been studied by R. T. Moore (1950), who advocates the recognition of three races. The measurements of specimens that we have examined are shown in table 5.

In preparing specimens of *C. chrysogenys*, we noted the following peculiarities of structure and color as compared to *C. aurifrons*, *C. uropygialis*, and *C. carolinus*: iris of adults orange-brown (rather than red or reddish brown); orbital region naked; legs and feet with a more greenish (less bluish) cast; subcutaneous and body fat distinctly more orange (less yellow); head much more difficult to pass through neck in skinning, and skin bound to body by stronger fascia, especially dorsally on legs; hyoid apparatus relatively

TABLE 5
MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF *Centurus hypopolius*
AND *Centurus chrysogenys*

	No.	Wing	Tail	Bill Length	Bill Depth	Tarsus	Weight
<i>Centurus hypopolius</i>							
Puebla ^a							
♂ Adult	6	124.0 (122-125)	79.7 (77-86)	20.98 (19.7-22.6)	6.84 (6.4-7.8)	20.27 (19.5-21.1)	51.6 ^b (50-54)
♀ Adult	6	124.3 (122-128)	81.8 (76-88)	19.76 (18.4-21.3)	6.18 (6.0-6.5)	19.25 (18.4-20.5)	50.0 (46-54)
<i>Centurus chrysogenys</i>							
San Blas, Nayarit ^c							
♂ Adult	13	119.4 (117-123)	70.0 (68-71)	21.58 (19.5-24.5)	7.33 (6.9-7.5)	20.91 (20.4-22.4)	70.5 (65-73)
♀ Adult	14	115.1 (113-118)	68.6 (65-71)	18.80 (17.9-20.6)	6.75 (6.5-7.1)	19.77 (18.5-20.5)	62.6 (58-70)
Colima-S. Jalisco							
♂ Adult	4	120.3 (118-122)	67.0 (65-68)	21.48 (20.9-22.1)	7.40 (7.3-7.5)	21.38 (20.5-22.2)	76.8 (73-80)
♀ Adult	2	116.0 (115-117)	65.5 (63-68)	18.45 (18.4-18.5)	6.50 (6.5-6.5)	18.90 (18.6-19.2)	59.0 (54-64)
Guerrero ^d							
♂ Adult	8	125.3	71.4			21.4	
♀ Adult	4	121.6	70.2			20.8	

^a July 13, 1958.

^b Additional data from Davis and Russell (1953, p. 97): three adult males from Morelos, taken in July and August, weighed 48, 48, and 53 grams. An adult male from Mitla, Oaxaca, weighed 47 grams. Fifteen juvenal males in post-juvenal molt, collected on July 13, 1958, in Puebla, weighed 45.5 (41-51) grams.

^c June, 1958.

^d Data from Ridgway (1914, p. 90). Additional data: three adult males from Morelos weighed 80, 80, and 85 grams, and two adult females from Morelos weighed 68 and 73 grams (Davis and Russell, 1953, p. 97).

weaker in structure; and mucus-secreting glands (Gl. picorum; see Bock, 1961, p. 357) below rami of upper mandibles relatively smaller. The last two characters are associated with a relatively small bill, which suggests that this species does less excavating for food in trees than do the other species mentioned.

In the field we noted that *C. chrysogenys* was more prone to perch crosswise on twigs than were other species studied, but its general demeanor was not otherwise different. Vocalizations were loud and often rather harsher than those of the other species, and the "location call" was distinctive, consisting invariably of three or four notes (two or three short ones followed by a long one) rather than a rapidly pulsed series of seven or eight notes given by the other species (see Selander and Giller, 1959b, fig. 1, p. 111).

ECOLOGIC DISTRIBUTION: On the Pacific coastal plain of México, *C. chrysogenys* is an abundant resident of the Arid Tropical Zone, where it occurs in scrub land among giant cacti, as at Autlán, Jalisco (Zimmerman and Harry, 1951), along the edges of deciduous forest, and in association with a variety of palms. In the San Blas area, Nayarit, we found it common in mixed groves of palms, figs, and other trees along the coast. Nesting in coconut and other palms is also reported by Bailey (1906) and Lamb (1909). Commonly this species also nests in cacti (McLellan, 1927). As it ranges inland in the drainage basin of the Río Balsas and elsewhere, it appears to become restricted to riparian habitats. For example, 10 miles southwest of Juchitlán, Jalisco, we found it nesting in willows along a small stream, but it was absent from stands of tuna cactus on the surrounding hillsides. In Morelos, Davis and Russell (1953) noted that it is most common in riparian associations.

DISTRIBUTIONAL AND ECOLOGIC RELATIONSHIPS AMONG *Centurus chrysogenys*, *Centurus uropygialis*, AND *Centurus aurifrons*

Centurus chrysogenys breeds north in southern Sinaloa for an undertermined distance and has been taken as far north as Cosala, 75 miles north of Mazatlán. It is sympatric with *C. uropygialis* over a considerable area in Nayarit and southern Sinaloa. In the latter

state, *C. uropygialis* ranges from near sea level to 4000 feet, and records of *C. chrysogenys* indicate an altitudinal distribution from sea level to 3500 feet, as at Los Pieses and Cosala, although there is one doubtful report of its occurrence as high as 5000 feet (W. D. Miller, 1905). Both species have been taken at Mazatlán, Rosario, Labrados (McLellan, 1927), Escuinapa, and the "Rio Juanna Gomez" (W. D. Miller, 1905). In Nayarit, however, we found distinct altitudinal segregation of the species, with *C. chrysogenys* being confined to the coastal plain proper below 1000 feet, and *C. uropygialis* occupying medium-elevation slopes of the Sierra Madre between 1000 and 5000 feet (see figs. 12 and 16A). At the latter elevation near Guadalupe, *C. uropygialis* is in contact with *C. aurifrons*.

South of the range of *C. uropygialis* (the southernmost point of which is at Cocula, Jalisco; see fig. 12), *C. chrysogenys* ranges upward to 4500 feet, as shown in figure 16B and C, which is based on two road transects made in 1958, one (B) extending from Salinas, on the coast, northeast to Guadalajara through Autlán and Cocula, and another (C) extending from the Manzanillo area, Colima, north-northeast to Guadalajara through Colima, Ciudad Guzmán, and the Sayula basin. Upper tropical zone habitats in which *C. chrysogenys* was found at Tecotlán and at Pihuamo and Tuxpan were not visibly different from those occupied by *C. uropygialis* in Nayarit and in Jalisco west of Guadalajara. In the Manzanillo-Guadalajara transect, actual contact between *C. chrysogenys* and *C. aurifrons* was not recorded, but it undoubtedly occurs in the vicinity of San Sebastian, for we found *C. aurifrons* in a pecan orchard a mile north of that city, and *C. chrysogenys* was common in tropical riparian forest at Tuxpan and Pihuamo. The former locality is only 20 miles south of San Sebastian and in the same valley. Between San Sebastian and Tuxpan, the typical plateau flora is replaced by tropical vegetation in which banana and fig trees are common.

***Centurus rubricapillus* CABANIS AND *Centurus pygmaeus* RIDGWAY**

Centurus rubricapillus resembles *C. hoffmanni* and certain races of *C. aurifrons* in color and pattern but is much smaller than

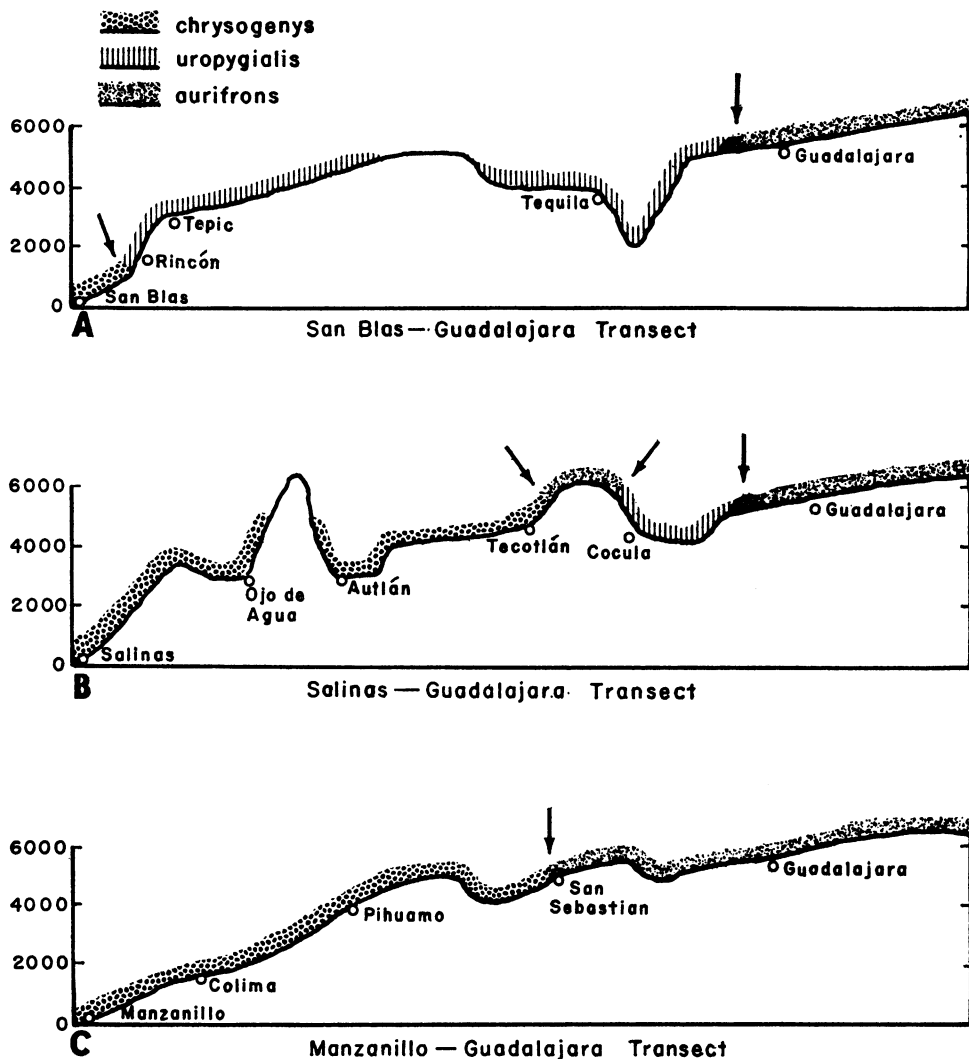


FIG. 16. Altitudinal distribution of three species of *Centurus* along three road transects in west-central México. Arrows indicate points of contact between species.

these forms. Geographic variation in *C. rubricapillus* has recently been reviewed by Wetmore (1957), who recognizes four subspecies, justifiably synonymizing several racial names based on individual rather than geographic variation. As in *C. aurifrons*, the color of the nape and belly varies from yellow to red, and there is in South American populations and in *C. r. seductus* of Isla El Rey, Pearl Islands, Panamá, a strong tendency for separation of the red coronal and the orange or yellow nape regions by an occipital band of gray. This tendency is most fully expressed in the race *C. r. paraguanae* of Venezuela, which is in

many respects a miniature of *C. aurifrons polygrammus*.

Whether *C. pygmaeus* of the northern Yucatán Peninsula and Cozumel Island and its dark insular representative, *tysoni*, on Bonaca Island, Honduras, are conspecific with *C. rubricapillus* is problematical, since these forms are allopatric (fig. 1). Peters (1948) and several others combine the two, but in Wetmore's opinion (1957) the narrower dorsal barring and the disproportionately longer tail (table 1) of *C. pygmaeus* argue for specific status. Perhaps the wisest course is to follow Wetmore until close simi-

larity in courtship, vocalizations, and other aspects of the behavior of these forms is demonstrated.

In color and pattern, *C. pygmaeus* is remarkably similar to *C. a. dubius*, with which it is sympatric (see below). It is in fact a miniature of that form and differs in color and pattern from *C. rubricapillus* in much the same way that *C. a. dubius* differs from *C. a. santacruzii*.

Parenthetically, we wish to state that, for reasons given in part elsewhere in this report, we cannot accept Sutton's suggestion (1951) that *pygmaeus* "represents" *C. aurifrons* and that the other Yucatán form, *dubius*, is specifically distinct from *C. aurifrons*.

ANTILLEAN SPECIES OF *CENTURUS*

Centurus superciliaris (TEMMINCK)

When Peters' (1948) readiness to lump allopatric forms in the genus (for example, *uropygialis* and *hypopolius*; *rubricapillus* and *pygmaeus*; and *aurifrons* and *hoffmanni*) is considered, it is surprising that he maintained the Grand Cayman form, *caymanensis*, as a species distinct from *C. superciliaris* of Cuba and its racial representatives on the Isle of Pines (*C. s. murceus*), Abaco Island (*C. s. blakei*), Watling Island (*C. s. nyeanus*), and Great Bahama (*C. s. bahamensis*). These forms possess a superciliary (or supraauricular) patch of black, which in the female is joined on each side by a black occipital band. In characterizing *caymanensis*, Ridgway (1914) correctly noted that there is "no trace of black superciliary spot," but he neglected to mention that an occipital band of black is suggested in females, the feathers of this region being black medially but grayish at the tips. In *C. s. nyeanus*, the superciliary spot is almost completely masked by grayish feather tips, and, except for this feature and the more conspicuous wash of yellow dorsally in *caymanensis*, the two forms are closely similar. Bridging the gap between *C. s. nyeanus* and *C. s. superciliaris* of Cuba, both as regards prominence of the black superciliary spot and body size, are the forms *C. s. blakei* and *C. s. bahamensis*. We therefore see no course but to regard the whole complex as a single species, although one might justifiably entertain doubts as to whether the most dissimilar

Adults of *C. pygmaeus* are highly variable with respect to the distribution and intensity of yellow pigment on the frontal region, malar region, and chin. In a series of 47 specimens examined, 32 had the entire frontal region intense yellow or orange-yellow, and the color extended posteriorly to the malar region and chin. In many of these 32 specimens there was yellow pigment around the eye, and in a few a spot of yellow was also present on the auriculars. In 10 specimens only the nasal tufts were yellow and the color was much less intense, and five specimens exhibited an intermediate condition, with a moderate amount of yellow in the frontal region but little on the malar region or chin.

forms, *superciliaris* and *caymanensis*, would interbreed and successfully exchange genes if they were brought into sympatry.

The striking over-all resemblance of *C. s. nyeanus* and *C. carolinus* of the eastern United States is not properly emphasized by Ridgway (1914), who compared the former only with other Antillean woodpeckers. They are similar in size, although the tail in *C. s. nyeanus* is on the average disproportionately short. Indeed, were it not for the aforementioned black superciliary spot, the more extensively bare orbital region, and the lighter forehead of *C. s. nyeanus*, it would be difficult to distinguish specimens of the two forms.

In examining large series of specimens of *C. carolinus*, one finds further evidence of close relationship between *C. carolinus* and the *C. superciliaris* complex in the form of individual variants showing slight to moderate development of the black occipital band characteristic of females of the latter species. Frequently in *C. carolinus* the gray of the occipital region is "intermixed" with black, as previously noted by Ridgway (1914), but occasionally there is a continuous black band, as in a female (A.M.N.H. No. 39026) from Sebastian River, Florida (see pl. 55), and in females from Silsbee, Texas (A.M.N.H. No. 362524), Sapelo Island, Georgia (A.M.N.H. No. 362495), and Hawkinsville, Florida (A.M.N.H. No. 367476).

A similar black occipital band is also weakly indicated by a few partly black feath-

ers in approximately 10 per cent of female specimens of *C. aurifrons* from Cozumel Island and the Yucatán Peninsula.

In *C. superciliaris*, as in *C. carolinus*, the adult iris is red or reddish brown, and the tarsus and toes are olive.

Centurus radiolatus (WAGLER)

The Jamaican form of *Centurus* resembles *C. aurifrons dubius*, showing in its white forehead and sides of the head and in its dark under parts "exaggeration" of characters present in that race of *C. aurifrons* (compare pls. 53 and 55). The belly varies from yellow to red, and the iris is red.

THE STATUS OF *Chryserpes striatus* (MÜLLER)

The Haitian Woodpecker (pl. 55) is so unusual in color and in some aspects of structure that it is difficult to judge its affinities. Recent classifications, including that of Bond (1956, 1961), carry it as a *Centurus*, but without question it is not closely allied to any species of that genus or of *Melanerpes*, and there would seem to be much justification for placing it in its own monotypic genus, *Cryserpes*, as W. D. Miller (1915) has advocated, at least until morphologic and behavioral studies provide further clues to its relationships with other woodpeckers. There is some possibility that its affinities are with "*Chloronerpes*" (= *Piculus*, part, of Peters, 1948). In *Chryserpes*, features not found in *Centurus* include the absence of barring on the flanks and under tail coverts; the absence of a highly colored frontal region, despite the fact that the nape (as well as the coronal and occipital regions in the male) is red; the short, red upper tail coverts; and the unusual olive and yellow colors of the body plumage and wings. The *Centurus*-like barred pattern of the dorsum and wings was probably acquired independently in *Chryserpes*, the resemblance to species of *Centurus* being a matter of convergence. As compared with species of *Centurus*, the bill of *striatus* is straighter and the culmen is more sharply ridged, and the color of the bill is peculiar, the lower mandible being horn color or gray basally rather than

black. Also, the iris color is unusual, being bright yellow or gold in adults. Other structural peculiarities of *Chryserpes striatus* have been described by W. D. Miller (1915).

One characteristic of *Chryserpes* that sets it apart from *Centurus* is an unusually marked degree of sexual dimorphism in bill size, a feature that, surprisingly enough, was overlooked by W. D. Miller (1915) and other authors. The possible adaptive significance of this feature is discussed below.

Information on the ecologic distribution and habits of this woodpecker is summarized by Wetmore and Swales (1931) and Wetmore and Lincoln (1933). It is reportedly one of the most common and widely distributed native birds of Hispaniola, inhabiting mangrove swamps and swampy woods on the coast, desert and thorn scrub lowland vegetation types, coffee plantations, wooded hillsides, and pinelands of the interior hills and mountains, "seemingly with no preference" (Wetmore and Swales, 1931, p. 291). It nests in cacti, palms, and a variety of trees.

Of special interest is a report by Wetmore (Wetmore and Lincoln, 1933) of colonial nesting in *Chryserpes*, a feature in which it differs from *Centurus* species: "At Terrier Rouge . . . these birds were surprisingly abundant . . . and we were astonished to find a dozen pairs going in and out of nesting holes in a single dead tree trunk standing in an open space, the holes being 3 to 10 meters from the ground and in some cases less than a meter apart. There was no question that the woodpeckers were colonizing, as the trunk was a veritable apartment house with the birds clambering actively over its surface and flying back and forth to near-by woodland."

Vocalizations of *Chryserpes* have been described (Wetmore and Swales, 1931) as loud, rollicking, rolling calls, often interspersed with tree-toad-like guttural sounds, suggestive of the calls of flickers (*Colaptes*), ant-eating woodpeckers (*Balanosphyra*), and the red-headed woodpecker (*Melanerpes erythrocephalus*). Elsewhere Wetmore (Wetmore and Lincoln, 1933, p. 44) mentions the "laughing" calls of the Haitian woodpecker and notes that this species does not "drum" as do species of *Centurus*.

DISCUSSION

SIGNIFICANCE OF ECOLOGIC RANGE IN DISTRIBUTION AND SPECIATION

MUCH MODERN SYSTEMATIC RESEARCH deals with congeneric species in zones of secondary contact where there is active testing of reproductive isolating mechanisms (A. H. Miller, 1955a) and where overlapping ecologic spheres may lead to interspecific interactions, including not only competition in the strict sense of the endeavor of individuals to obtain a common resource in short supply (Milne, 1961) but also aggressive and other interference interactions (Hutchinson and MacArthur, 1959; Ripley, 1961) which may not be related to resources in short supply but which in any event result in decreased population density of one or both species. If populations evolving in geographic isolation are to coexist as species after establishing secondary contact, they must be reproductively isolated to maintain their adaptive genetic systems, and at the same time there is some reason for believing that they must be ecologically isolated (compatible) through segregation to different habitats or by exploitation of different niches within the same general habitat type (Lack, 1947, p. 146). In short, they must differ in their ecologic spheres (A. H. Miller, 1955b; Dixon, 1961) or ranges, and in using these terms we refer to aspects of the Grinnelian and Eltonian "niche" (Udvardy, 1959) as well as to the habitat distribution of a species.

There is presently considerable disagreement among systematists regarding the importance of population interactions in the origin and development of reproductive isolating mechanisms (see, for example, Blair, 1958; J. A. Moore, 1957; Mayr, 1959; Bogert, 1960; Sibley, 1961). There is no greater harmony among views concerning the degree of significance to be attached to competitive and other interactions in the evolution of ecologic isolation between species. Proponents of density-independent and "probabilistic" theories of population control (Andrewartha and Birch, 1954) and certain other ecologists (Udvardy, 1951; Bowman, 1961) have argued that it is not necessary to invoke competition as a cause of ecologic segregation of sympatric species, since different habits and preferences

developed in geographic isolation will lead the two newly evolved species to select different sorts of places in which to live once secondary contact is established. (This argument is analogous to that of systematists who maintain that reproductive isolating mechanisms are fully perfected in geographic isolation and need not, therefore, be reënforced by selection when secondary contact is established.) However, an alternative and perhaps more convincing view, first developed in detail for birds by Lack (1944, 1949), holds that competitive interactions in zones of secondary contact play a fundamental role in the divergence of ecologic ranges. More importantly, this latter view maintains that the limits of the ecologic sphere of a species may ultimately be set by competitive pressures of other, sympatric species, although they may be determined proximally by instinctive or conditioned preferences (A. H. Miller, 1942).

Admittedly, most of the evidence for interspecific competition in wild populations is indirect, but in the opinion of many workers it is compelling. Among various lines of evidence are numerous examples of expansions of ecologic ranges and unusual numerical relationships of species belonging to unbalanced faunas of oceanic islands or isolated mountains (Amadon, 1950; Lack and Southern, 1949; A. H. Miller, 1955b; Crowell, 1961); the demonstration (Pitelka, 1951b) of competition for space in the form of interspecific territorialism leading to mutual depression of population densities in Allen and Anna hummingbirds (*Calypte anna* and *Selasphorus sasin*); and the demonstration of striking niche specificity among groups of sympatric congeners (Hartley, 1953; Gibb, 1954; Betts, 1955; and Dixon, 1961, on *Parus*; MacArthur, 1958, on *Dendroica*; and Cade, 1960, on *Falco*). In addition, we must at least cite recent contributions of MacArthur (1957), Hutchinson (1958), and Elton (1946), among others, to the problem of the role of interspecific competition in community organization and evolution. Of particular interest is MacArthur's demonstration that a

model based on the assumption of contiguous but non-overlapping niches fits the data on abundance of bird species in tropical forests better than do models based on other assumptions. This finding, in conjunction with Lack's conclusion (1954) that food supply is a major factor in the limiting of population size in birds, argues strongly for competition as an important factor in community organization.

In regard to the problem of reproductive isolation, it is clear that the efficiency of an isolating mechanism developed prior to a secondary contact of populations may be critical in determining the subsequent course of evolutionary development of the populations, especially when two populations become sympatric over a very limited area. When the zone of sympatry is narrow and the isolating mechanisms are less than fully effective, a stable situation may arise in which selection prevents extensive introgression and the two populations remain connected by a narrow zone of hybridization. Even if the hybrids are selectively inferior to the parental types, selection cannot enhance the isolation. Dispersal of pure types into the contact zone constantly disrupts the effects of reënforcing selection, and at the same time there is little chance that the reënforced genotypes will spread back into pure allopatric segments of the parental populations, since they are there selectively neutral if, indeed, not disadvantageous (J. A. Moore, 1957).

In similar fashion, the outcome of secondary contacts between species faced with the problem of making ecologic adjustments to reduce competition and other forms of interference may depend on the degree of ecologic isolation attained at the time contact is established. It may also depend on the degree of habitat diversity in the zone of sympatry (Amadon, 1950; Dixon, 1961; Hamilton, 1962a) and on the extent of the area over which sympatry is initially established, which in turn may be related to the character of gradients of environmental factors in the region of contact. Considering the general problem of ecologic isolation in birds, we may lump the results of secondary contacts of species into four categories: (1) If two species have evolved sufficiently distinctive ecologic spheres, extensive sympatry may be established with minor if any adjustments in forag-

ing behavior, habitat selection, and morphology (bill size). (2) When two species with similar ecologic spheres meet over an extensive area that provides sufficient habitat diversity to permit displacement, selection may promote unilateral or mutual "exaggeration" of morphologic and behavioral differences functioning to lessen detrimental interactions. (An example is provided by Vaurie's study, 1951, of nuthatches of the genus *Sitta*.) (3) When species having similar ecologic spheres become secondarily sympatric in a region of narrow habitat diversity, an adjustment involving displacement of characters may not be possible, and one species will ultimately replace the other as a result of interspecific competition. (4) A fourth possible outcome of the interaction of closely related species involves the meeting of species of such similar behavior and structure that they are ecologically incompatible within normal ranges of habitat diversity. Even in areas of gently sloping environmental gradients, a sharp line of contact between adjacent ranges is established, with little if any actual sympatry. In the absence of sympatry, reënforcement of incipient ecologic isolation cannot be effected, and the situation may remain stable for long periods, with neither species being able to invade the range of the other.

Our studies of *Centurus* have revealed no unequivocal evidence of reënforcement of either reproductive or ecologic isolating mechanisms. However, patterns of geographic distribution among *Centurus* species provide circumstantial evidence that closely related, morphologically similar species may be ecologically incompatible. Indeed, the allopatric distribution of closely related species is sufficiently marked to suggest that these woodpeckers may encounter special problems in achieving the ecologic adjustments necessary for sympatry.

Within the group of species usually placed in the genus *Centurus* (*sensu stricto*, as distinct from the "*Tripsurus*" group), there is only one case of sympatry over an extensive area. This occurs on the Yucatán Peninsula and Cozumel Island (see fig. 1), where *C. aurifrons dubius* is sympatric with *C. pygmaeus*. It is significant, we believe, that the two woodpeckers are markedly dissimilar in size, being in fact extremes in this regard

within the genus as a whole. The larger form, *C. a. dubius*, has an average body weight of 87 grams (table 2), while the smaller species weighs only 47 grams, and in bill length and other linear dimensions the two sympatric species show no overlap whatever.

Ecologic distribution and foraging behavior of these species have not been studied in detail, but the conspicuous size differences suggest that the sizes if not the types of food taken are different, and the isolating effect of the presumed feeding difference appears to be supported by partial habitat isolation. According to Paynter (1955, p. 165), *C. aurifrons*, which is the most abundant woodpecker on the Yucatán Peninsula, is most common in tall and moderately tall deciduous forest and in second growth within the zone of rain forest, whereas *C. pygmaeus* is most common in short and moderately tall deciduous forest and in coastal scrub. The latter species occurs only sparingly in the tall forest habitat "preferred" by *C. aurifrons*. Thus the species reach greatest population densities in different habitats, but both are found in the same stands of vegetation, in which, however, they exhibit stratal separation in foraging, the smaller species foraging usually within a few feet of the ground (Blake, 1953, p. 298), while the larger species forages at higher levels.

In sum, ecologic isolation between these sympatric species is apparently achieved by habitat segregation, stratal separation for foraging, and, as suggested by differences in size, specialization on food of different sizes and perhaps types.

The two species are similar in color and pattern and show parallel variation geographically, each being ventrally dark on Cozumel Island. Griscom (1926, p. 9) reports that the notes of the smaller species are distinctly weaker than those of the larger species. Nothing is known of their territorial relationships.

The distributional relationships of *C. chrysoegenys* and *C. hypopolius* are discussed above (p. 252). There is some overlap in ranges, but effective ecologic isolation is achieved by marked habitat differences. In the region of sympatry, the two species exhibit a considerable size difference (e.g., the weights of males of *C. hypopolius* range from 48 to 53 grams; those of males of *C. chrysoegenys*, from 80 to 85

grams). The degree of size difference is less than that between *C. aurifrons* and *C. pygmaeus* on the Yucatán Peninsula but considerably greater than that between *C. aurifrons* and *C. uropygialis*, species that are allopatric.

All other cases of sympatry over a considerable area involve one species belonging to the *Centurus* group and one belonging to the "*Tripsurus*" section of the genus. For example, *C. pucherani* (a "*Tripsurus*" type), ranging from Colombia north through the Caribbean side of Central America, Oaxaca, and Puebla, is sympatric with *C. aurifrons* in southeastern México. Little is known of *C. pucherani* in México, but to judge from published reports it is decidedly rare and is confined to rain-forest habitats, whereas *C. aurifrons* is abundant and exhibits a much greater latitude in habitat selection. South of the range of *C. aurifrons*, *C. pucherani* is reportedly abundant in "semi-open" rain forest in Costa Rica (Slud, 1960, p. 98) and has also been reported from rain forest in Nicaragua (Howell, 1957, p. 87). It is probably not without significance that *C. pucherani* and the race of *C. aurifrons* with which it is sympatric in southeastern México differ markedly in size. Wing length in *C. pucherani* from México averages 112 mm. in males and 110 mm. in females; bill lengths are 24.0 mm. for males, 23.3 mm. for females. Corresponding measurements for *C. aurifrons dubius* from the same region are: wing length, 133 mm. in males, 127 mm. in females; bill length, 32.2 mm. in males, and 28.3 mm. in females (measurements from Ridgway, 1914).

Too few data are available to warrant a discussion of ecologic relationships among the widely distributed species *Centurus rubricapillus* and three "*Tripsurus*" types with which it is sympatric: *C. chrysauchen* in Costa Rica and Panamá; *C. pulcher* (*C. chrysauchen pulcher*, according to Peters, 1948, p. 166) in Colombia; and *C. cruentatus* in Venezuela. Available data on the contact between *C. rubricapillus* and *C. chrysauchen* in Central America indicate isolation by marked habitat differences (Carriker, 1910; Skutch, 1948; Aldrich and Bole, 1937, p. 81).

Within the *Centurus carolinis-aurifrons-uropygialis* complex (superspecies), sharply defined zones of contact suggest that distribu-

tional limitations are imposed by interspecific interactions. In Texas, *C. aurifrons* ranges north to the Panhandle and east to the central part of the state, where it is in contact with *C. carolinus* along a broad front in a region environmentally intermediate between semiarid areas to the southwest and mesic areas to the east (fig. 15). Nowhere is there extensive overlap in ranges, but locally, as at Austin, the species are sympatric in a zone from 2 to 5 miles wide (Selander and Giller, 1959b). The two species populations undoubtedly are adapted to different ranges of temperature, humidity, and other environmental factors, but the fact that both occur in normal population densities up to the line of contact suggests that neither is at its limits of tolerance for these factors.

The two species in Texas are nearly identical in all linear dimensions and in weight but show consistent differences in tail pattern and in coloration of the head, the nape being red in *C. carolinus* and yellow or orange-yellow in *C. aurifrons*. The vocalizations are distinctive, although not markedly dissimilar, and are thought to serve, along with the morphologic differences, as a basis for species discrimination. As noted above, hybridization or heterospecific pairing is unknown.

Where the two species meet, the frequency of contact of individuals is limited by the occurrence of *C. aurifrons* in more xeric habitats, such as mesquite woodland, and *C. carolinus* in more mesic situations, such as oak woodland. But locally they occupy the same stands of vegetation, which demonstrates a significant overlap in habitat occurrence and in other aspects of their ecologic ranges. Moreover, within these stands, the two species behave territorially as a single species population, manifesting intense interspecific territorialism.

When all lines of evidence are considered, it is difficult to escape the conclusion that *C. aurifrons* and *C. carolinus* are ecologically incompatible. This is not to suggest that *C. aurifrons* would immediately occupy all of the range of *C. carolinus* if the latter were removed. But in view of the close similarities of the two species and the high degree of ecologic adaptability exhibited by *C. aurifrons* within its present large geographic range, there is reason to believe that occupancy of some or

all parts of *C. carolinus* territory in the eastern United States is easily within the evolutionary potential of *C. aurifrons*. Ecologic incompatibility of species is also suggested by the distributional relationships of *C. aurifrons* and *C. uropygialis*, as discussed above. (A comparable situation that involves apparent ecologic incompatibility of two species of pocket gophers of the genus *Geomys* has been studied by Kennerly, 1959; and Stresemann, 1939, cites several cases in which the presence of one species of bird seems to exclude other species from the area; see also Kendeigh and Baldwin, 1937.)

In the *Centurus carolinus-aurifrons-uropygialis* complex, as in the genus as a whole, the evolution of reproductive isolating mechanisms apparently tends to proceed more rapidly than does the evolution of ecologic isolation, with the result that the distribution and, hence, indirectly the evolution, of these species may be influenced to a significant degree by interspecific interactions with congeners.

In concluding this section, we wish to take the opportunity to amend and clarify our views on the ecologic significance of interspecific territorialism in birds (Simmons, 1951). Like several other authors, we have been guilty of assuming that species manifesting interspecific territorialism are necessarily demonstrating ecologic incompatibility (Selander and Giller, 1959b), but it now seems probable that in certain cases this type of interspecific response may merely be the fortuitous result of behavioral or morphologic similarities releasing territorial behavior. If the appearance, displays, or vocalizations (social releasers) of two species establishing sympatry are sufficiently similar, individuals of one species will respond to those of the other species as to their own species, and mutually exclusive territories will be established. Some competition for space may result. When the resulting spacial segregation of the two species is advantageous to one or both species in reducing competition for food or some other resource provided by the territory, selection will act to maintain the common social releasers and response mechanisms which insure interspecific territorialism (Dixon, 1961, p. 200). But if the mutually exclusive spacing is unnecessary in terms of

reducing interspecific competition for food or other resource, it seems probable that selection would act to eliminate the interspecific response by reducing the degree of similarity in appearance or behavior of the two species. However, where the zone of sympatry is very

narrow, the disruptive effect of gene flow from large populations adjacent to the zone may prevent selection from reducing the similarities, and interspecific territorialism may persist although it serves no useful ecological function.

SEXUAL DIMORPHISM IN SIZE

Species of *Centurus* and other genera of woodpeckers show an impressive degree of variation in sexual dimorphism in size, particularly in bill dimensions (pl. 56). Among species considered in the present report, extremes are represented by *Centurus hypopolius*, in which there is no significant sexual difference in bill size, and *Chryserpes striatus*, in which the bill of the female is markedly shorter than that of the male. In table 6, sexual dimorphism in wing, tail, tarsus, and bill length is shown for *Centurus* species and for several other genera of New World woodpeckers. To express dimorphism, we have calculated the percentage difference between mean measurements of males and females. From these data the following conclusions emerge: (1) The degree of sexual dimorphism varies within wide limits among various genera, species, and subspecies. Unfortunately, weights are not available for all forms that we wish to compare, but tarsal length may serve as a moderately accurate index to general body size. (2) In most species of woodpeckers, males average slightly larger than females, the difference in tarsal length amounting to about 5 per cent on the average. In a few species, the female is as large as or slightly larger than the male. (3) There is no apparent relationship between general body size and degree of sexual dimorphism in bill length or other dimensions; that is, larger species are not necessarily more dimorphic than smaller species. (4) In the great majority of species, sexual dimorphism in size is greater in bill length than in other dimensions, amounting on the average to about 9 per cent. Moreover, there is a greater range of intraspecific and interspecific variation in degree of dimorphism in bill length than in other linear dimensions. Similar findings are reported for the Hawaiian honeycreepers (Drepaniidae) by Amadon (1950, p. 187), but in the Icteridae sexual dimorphism in length of wing and

tail exceeds that of bill length (Selander, 1958). (5) When we select those forms that show unusually large degrees (16% to 21%) of sexual dimorphism in bill length, the interesting fact emerges that four of the six forms are insular endemics and the two remaining forms occur in an insular-like situation on the southern end of the peninsula of Baja California. Maximum dimorphism is shown by *Chryserpes striatus* of Hispaniola, in which bill length of the female is 21.3 per cent less than that of the male, notwithstanding the fact that sexual difference is only 9.6 per cent in tarsal length and is even less in other body dimensions. Relatively great sexual differences are also seen in bill depth (12.1%) and bill width (11.7%). When data on bill length in *Chryserpes* are graphed (fig. 17), it is evident that there is no observed overlap between the sexes.

In *Melanerpes portoricensis* of Puerto Rico and *Melanerpes herminieri* of Guadalupe Island, Lesser Antilles, dimorphism in body size, as reflected by tarsal length or wing length, is slightly greater than in other woodpeckers studied (with the possible exception of *Chryserpes*), and dimorphism in bill length greatly exceeds that of other dimensions, being about 19 per cent. In *Xiphidiopicus percussus* of Cuba, the tarsal length difference amounts to only 1.7 per cent, yet in bill length the female is 15.2 per cent smaller than the male.

Sexual dimorphism in *Centurus uropygialis* appears to be slightly greater than in any other species of *Centurus*, and dimorphism in bill length reaches an extreme in *C. u. brewsteri* of southern Baja California, in which it is 16.7 per cent; the nearest approach is in *C. u. uropygialis* of western México, with 12.9 per cent difference in bill length. *Dendrocopos scalaris* also shows marked dimorphism in bill length in southern Baja California.

It is also noteworthy that the piculet

Nesocittes micromegas, a genus and species endemic to Hispaniola and Gonave Island, is dimorphic in size (with the female being larger than the male), whereas species of the continental piculet genus *Picumnus* are essentially non-dimorphic in size.

In discussing factors affecting sexual differences in size in birds, Amadon (1950, 1953, 1959) has called attention to unusual degrees of sexual dimorphism in certain Hawaiian honeycreepers and in the West African sunbird *Cyanomitra thomensis* of São Tomé Island:

	WING	BILL LENGTH
<i>Pseudonestor xanthophrys</i>	9	23
<i>Hemignathus procerus</i>	5	22
<i>Cyanomitra thomensis</i>	12	27

It is of some interest that the degree of dimorphism in these insular species is roughly equivalent to that found in *Chryserypes striatus*

and the insular species of *Melanerpes*, and in these forms (as in the woodpeckers mentioned) dimorphism in bill length greatly exceeds that in wing length and in dimensions of other body parts. As Amadon has noted (1950, p. 188), the significance of increased dimorphism in these species is obscure; but, since two of the three are larger than related forms having less marked sexual differences in size, he does consider the possibility that we are dealing with cases of non-selective allometry (Rensch, 1950) in which ontogenetic growth rates responsible for sexual dimorphism in size in adults have been continued phylogenetically to some extent in rapidly evolving insular forms perhaps subject to a minimum of competition and predation. But, as did Amadon (1959, p. 533), we believe that a purely allometric interpretation of this phenomenon is unsatisfactory, for, although allometric factors may well be involved as a mechanism by which evolutionary changes in

TABLE 6
SEXUAL DIMORPHISM IN SIZE IN WOODPECKERS
(Percentage difference between mean measurements of males and females.^a)

Form	Locality	Sample Size ^b	Wing	Tail	Bill Length ^c	Tarsus
<i>Melanerpes portoricensis</i>	Puerto Rico	20-18 ^d	4.9	5.9	18.9	10.0
<i>Melanerpes herminieri</i>	Guadelupe Island, Lesser Antilles	20-13 ^d	6.2	1.2	19.0	11.3
<i>Melanerpes erythrocephalus</i>	E. United States	32-21	2.2	1.6	2.6	4.8
<i>Balanosphyra f. formicivorus</i>	México	41-44	4.4	1.3	6.7	6.2
<i>Asyndesmus lewis</i>	W. United States	16-14	2.5	5.4	3.7	3.5
<i>Chryserypes striatus</i>	Hispaniola	53-54 ^d	4.4	+3.8	21.3	9.6
<i>Xiphidiopicus p. percussus</i>	Cuba	10-10	1.8	+4.0	15.2	1.7
<i>Xiphidiopicus p. insulae-pinorum</i>	Isle of Pines	4-4	1.1	+4.5	13.8	5.9
<i>Piculus rubiginosus yucatanicus</i>	SE. México-Central America	18-24	1.3	2.4	5.1	1.4
<i>Veniliornis fumigatus sanguinolentus</i>	SE. México-Panamá	31-17	0.1	1.6	4.7	2.9
<i>Centurus s. superciliaris</i>	Cuba	10-10	1.9	0.8	10.8	3.1
<i>Centurus s. blakei</i>	Abaco Island	10- 9	2.8	0.9	11.3	4.8
<i>Centurus s. caymanensis</i>	Grand Cayman	10- 9	3.1	1.4	9.5	5.1
<i>Centurus carolinus</i>	E. United States	41-40	2.1	0.8	7.4	4.1
<i>Centurus radiolatus</i>	Jamaica	10-10	2.0	2.7	6.2	4.0
<i>Centurus aurifrons dubius</i>	Yucatán Peninsula	14-15	4.6	3.6	12.1	7.2
<i>Centurus a. aurifrons</i>	N. México-Texas	40-32	3.2	3.6	7.9	3.0
<i>Centurus a. polygrammus</i>	Oaxaca-Chiapas	12-10	4.2	5.0	12.3	6.3
<i>Centurus a. santacruzi</i>	Central America	12-10	1.2	0.3	7.6	2.2
<i>Centurus hoffmanni</i>	Costa Rica-Nicaragua	13-18	1.8	3.7	9.9	4.4
<i>Centurus rubricapillus seductus</i>	Isla El Rey	10- 8	2.0	1.6	10.4	6.3
<i>Centurus rubricapillus rubricapillus</i>	Panamá-Costa Rica	20-20	4.1	5.7	11.4	3.7

TABLE 6—(Continued)

Form	Locality	Sample Size	Wing	Tail	Bill Length	Tarsus
<i>Centurus pygmaeus rubricomus</i>	Yucatán	10-10	1.4	1.1	11.6	3.7
<i>Centurus uropygialis brewsteri</i>	Baja California	10-10	3.8	6.0	16.7	7.1
<i>Centurus u. uropygialis</i>	W. México-Arizona	33-21	2.4	9.9	12.9	5.3
<i>Centurus hypopolius</i>	Central México	7-4	1.1	+4.2	0.8	5.4
<i>Centurus c. chrysogenys</i>	Sinaloa-Nayarit	10-10	1.6	1.8	7.1	4.2
<i>Centurus p. pucherani</i>	Honduras-Panamá	30-15	1.1	0.7	6.6	3.0
<i>Centurus chrysauchen</i>	Panamá-Costa Rica	15-11	2.0	2.7	9.3	3.6
<i>Centurus flavifrons</i>	South America	12-11 ^a	—	—	5.1	—
<i>Centurus "rubrifrons"</i> ^f	South America	15-10 ^a	—	—	9.6	—
<i>Neoceus fernandinae</i>	Cuba	5-5	2.0	4.1	6.6	1.0
<i>Colaptes auratus chrysocaulosus</i>	Cuba	10-10	0.8	1.1	2.1	1.1
<i>Colaptes a. auratus</i>	SE. United States	22-22	0.4	1.4	4.1	2.2
<i>Colaptes c. chrysoides</i>	S. Baja California	10-8	1.6	4.9	2.3	+1.1
<i>Colaptes c. mearnsi</i>	Calif.-New Mexico	10-10	0.9	1.3	3.2	0.4
<i>Colaptes cafer rufipileus</i>	Guadalupe Island	6-7	+1.7	+0.4	+0.2	+2.6
<i>Colaptes cafer cafer</i>	California	10-10	1.8	3.0	4.0	7.7
<i>Colaptes cafer saturator</i>	NW. United States	10-10	1.7	1.4	5.3	4.3
<i>Colaptes mexicanoides</i>	Chiapas-Guatemala	16-8	2.0	1.1	6.8	3.8
<i>Dendrocopos scalaris lucasanus</i>	S. Baja California	10-10	2.7	+1.3	15.6	7.3
<i>Dendrocopos s. eremicus</i>	N. Baja California	10-5	4.9	1.6	11.2	7.4
<i>Dendrocopos s. cactophilus</i>	SW. United States— N. Sonora	35-36	2.4	+2.6	12.8	5.5
<i>Nesocittes micromegas</i>	Hispaniola	10-10	+4.3	+6.4	+9.6	+2.9
<i>Picumnus olivaceus flavotinctus</i>	Costa Rica	10-10	0.8	0.0	0.0	0.0

^a Measurements from Ridgway (1914), except as noted.

^b Indicates numbers of males and females measured; for example, "20-18" designates a sample of 20 males and 18 females.

^c Exposed culmen, not culmen measured from anterior rim of nostril.

^d Specimens in the American Museum of Natural History, Museum of Comparative Zoölogy, and the United States National Museum.

^e Specimens in the American Museum of Natural History.

^f See page 221 for nomenclature.

dimorphism are effected, it is our view that bill size in the two sexes would remain under the influence and control of selective forces at all times. In any event, in the case of the Caribbean woodpeckers, it seems unlikely that the marked sexual dimorphism in bill size can be attributed to non-selective positive allometry accompanying increase in body size, for the insular birds are not larger than less dimorphic continental types with which they can be compared.

In the absence of information indicating that the mating system is anything but monogamous in the insular woodpeckers, it does not seem possible to invoke increased sexual selection as a causative agent in the increased sexual dimorphism in size. Moreover, the fact that dimorphism in size of bill outstrips that

of wing length and tarsal length does not seem consistent with such a hypothesis.

It would be interesting to know if increased dimorphism in bill size in the insular woodpeckers has been achieved by unilateral or by mutual displacement in the sexes. Since body weights are not available, bill size relative to body mass cannot be compared directly, but comparison of relative bill size is possible if we assume that tarsal length is indicative of body mass. In *Melanerpes* bill length/tarsus ratios (table 7) indicate that in insular types the bill of the male is relatively longer and the bill of the female is relatively shorter than in the continental congener *M. erythrocephalus* and the related continental form *Balanosphyra formicivorus*. *Chryserpes* has no known close relative for comparison, but when it is

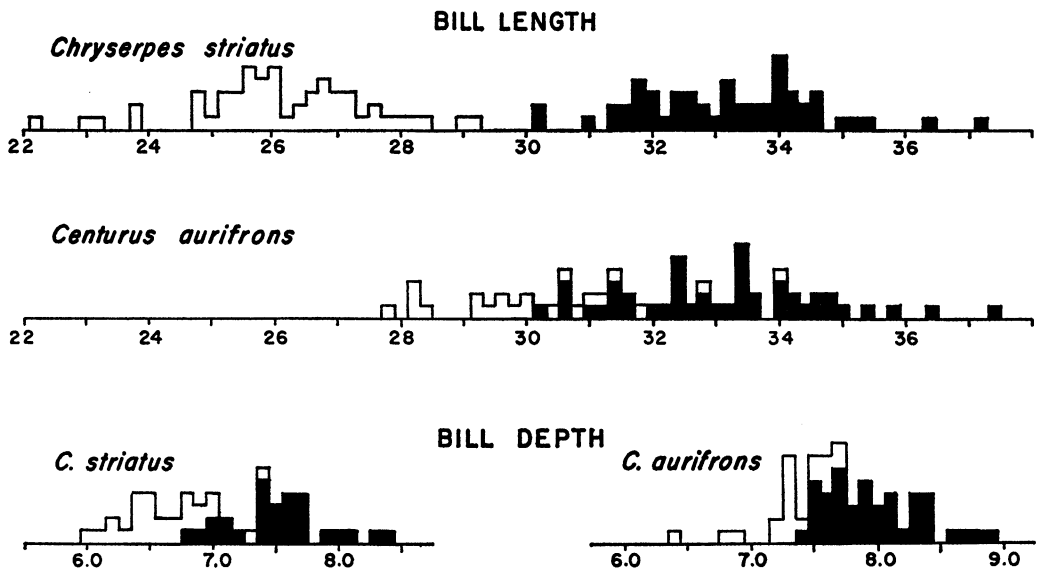


FIG. 17. Comparison of bill dimensions in *Chryserpes striatus* and *Centurus a. aurifrons* (sample area 3: southern Texas, Tamaulipas, and Nuevo León). Dark squares, males; light squares, females. Scale is in millimeters.

compared with the continental species *Centurus aurifrons*, there is, as in the case of *Melanerpes*, a suggestion of a two-way displacement in bill size. Apparently evolution of the insular types from less dimorphic ancestral forms has involved a decrease in the relative size of the bill in the female and an increase in the relative size of the bill in the male. We may tentatively conclude that the increased sexual dimorphism in bill size in these woodpeckers has been achieved by a mutual, two-way displacement, but this hypothesis requires testing by a comparison of the ratios of bill length to body mass.

POSSIBLE ADAPTIVE SIGNIFICANCE

Although the bill of birds is primarily a feeding device, it has a number of secondary functions, including its use as an aggressive weapon or object of display and as a tool in nest building. Therefore, evolution of bill size may be determined by a variety of selective forces, and it is likely that the functional significance and adaptiveness of sexual dimorphism in bill size and in other dimensions in woodpeckers will remain unknown until comparative studies of ecology and behavior of the insular and continental types are available. Possibly the increased dimorphism in

the insular species is related to major differences in the roles of the sexes in construction of roost or nest cavities, but it is at least equally probable that the dimorphism is somehow related to sexual differences in foraging behavior.

Some examples of sexual dimorphism in size that is apparently related to differences in foraging and feeding behavior in birds have been given by Rand (1952) and Storer (1952), who regard such differences as a means of reducing intraspecific competition for food (but see critical comments by Cade, 1960, pp. 241-246). The classical case is the now-extinct *Heterolocha acutirostris*, in which the long, thrasher-like bill of the female was used for probing into crevices, while the shorter, icterid-like bill of the male was used for digging into wood for insects. If selection can produce extreme sexual differentiation of the degree shown by *Heterolocha*, it seems entirely reasonable to expect lesser degrees of difference arising by selection in other species of birds.

In populations showing increased sexual dimorphism in bill size, variability within each sex group will determine whether or not the total span of bill length (or other dimension) for the combined sexes is also increased.

The comparison (table 8) of coefficients of variability in bill dimensions in *Chryserpes striatus* and *Centurus a. aurifrons* (sample area 3) suggests that increased dimorphism in *Chryserpes* has not been accompanied by a change in variability within either sex group. Since variability is approximately equal in the two species, increased dimorphism in bill length in *Chryserpes* to a point of non-overlap between the sexes results in an increase of approximately one-third in the total span of bill lengths in the population (see fig. 17).

If the total span in bill dimensions is related to the total span of sizes or types of food items taken, the increased sexual dimorphism in *Chryserpes* may have the following ecologic significance: (1) the total span of food sizes or types taken by the population is increased over that taken by *Centurus aurifrons* and other moderately dimorphic woodpeckers; and (2) the degree of overlap in food taken by the two sexes is reduced as each sex specializes to a greater degree on a separate range of food sizes or types. If food supply is limiting to woodpecker populations, non-overlap in sizes or types of food items taken by the sexes may facilitate maintenance of optimally large

TABLE 7
BILL LENGTH/TARSUS RATIOS
IN SEVERAL WOODPECKERS

Species	Sex	Bill Length/ Tarsus
Insular species		
<i>Melanerpes portoricensis</i>	♂	1.27
	♀	1.15
<i>Melanerpes herminieri</i>	♂	1.28
	♀	1.17
<i>Chryserpes striatus</i>	♂	1.42
	♀	1.23
Continental species		
<i>Melanerpes erythrocephalus</i>	♂	1.19
	♀	1.21
<i>Balanosphyra formicivorus</i>	♂	1.20
	♀	1.19
<i>Centurus aurifrons</i>	♂	1.36
	♀	1.28

TABLE 8
COEFFICIENTS OF VARIABILITY

Species	Sex	Bill length	Bill depth
<i>Chryserpes striatus</i>	♂	4.29	5.25
	♀	5.39	5.23
<i>Centurus aurifrons</i>	♂	2.87-5.86	2.47-4.92

populations. Thus reduced competition for food between the sexes could have selective value on both the individual and population level.

In attempting to develop a working hypothesis to account for interspecific variation in degree of sexual dimorphism in size in woodpeckers, we have been impressed with the fact that the most striking dimorphism is shown by three insular species, each of which is the only resident species of typical woodpecker on its respective island. Thus *Chryserpes striatus* is the only woodpecker of Hispaniola, apart from the endemic piculet *Nesocittes*, which is nuthatch-like in foraging habits, and the yellow-bellied sapsucker, which is a winter visitant; on Puerto Rico, where *Melanerpes portoricensis* is the only resident form, the sapsucker occurs as a rare winter visitant; and apparently no other species but the resident *Melanerpes herminieri* is known from Guadelupe Island (Bond, 1961). Since these islands are ecologically diversified and therefore seemingly provide habitats for several woodpecker species, it is tempting to speculate that freedom from competition with species of similar adaptive type has permitted the insular species to achieve a wider and more thorough exploitation of available food resources through evolutionary divergence of the sexes with regard to foraging behavior, which in turn has been accompanied by increased sexual dimorphism in size, and particularly in bill dimensions. However, it may be gratuitous to assume that unoccupied "woodpecker niches" are available on these islands. If one is willing to assume for the sake of argument that the food supply in habitats occupied by the insular forms is relatively poor, it seems possible that the increased sexual dimorphism and presumed reduction in intraspecific competition for food represents an adaptive response

essential to the maintenance of the resident populations and is quite unrelated to the absence of competition with other woodpecker species. In other words, it is possible that the insular forms have managed to survive in otherwise suboptimal habitats through adaptations that minimize the extent of overlap between the sexes in exploitation of limited food resources.

In future investigations into the adaptive significance of sexual dimorphism in bill dimensions in birds, it will be desirable to determine if increased sexual dimorphism is a

phenomenon of general occurrence among insular species. A preliminary survey of the passerine avifauna of the Antilles, based on size data in the literature, suggests that it is not, for none of the species appears to be clearly more dimorphic than related continental forms. This evidence strongly suggests that the marked dimorphism in certain insular woodpeckers does not exemplify a principle of broad application to insular faunal types but instead is somehow related to factors that are peculiar to woodpecker behavior or ecology.

SUMMARY

THIS STUDY is concerned with the systematic relationships among certain populations of woodpeckers of the genus *Centurus* occurring in the United States, México, and Central America. Significant conclusions arising from this investigation, which has involved field work in México in 1958 and examination of large numbers of museum specimens, are as follows:

The generic name *Tripsurus* is regarded as a synonym of *Centurus*, since there is no known character or combination of characters that distinguishes species currently assigned to these two nominal genera. Moreover, one species, *chrysogenys*, that is invariably assigned to *Centurus* is actually more closely related to species currently assigned to *Tripsurus*. *Centurus* (*sensu lato*) is closely allied with, and possibly inseparable from, *Melanerpes*.

Quantitative analysis of morphologic characters of specimens that represent populations of the *aurifrons* complex fully supports the view of Ridgway (1881) and Griscom (1932) that these populations belong to a single, highly polytypic species, since even the most strongly differentiated forms (*C. a. aurifrons* and *C. a. dubius*) intergrade in zones of contact. It is advocated that the number of subspecies for continental populations be limited to five; these are *C. a. aurifrons* (including *C. a. incanescens* of recent classifications), *C. a. dubius* (including *C. a. leei* of Cozumel Island, Yucatán), *C. a. grateloupenensis* (including *C. a. veraecrucis*), *C. a. santacruzii* (including *C. a. pauper* and *C. a. fumosus*), and *C. a. polygrammus* (including *C. a. frontalis*).

The color and pattern of the plumage in *Centurus* species are presumably cryptic, and geographic variation in these characters shows a reasonably close correlation with regional variation in climate and vegetation type. The brightly colored, sexually dimorphic areas of the head (and perhaps also the brightly colored belly region) presumably have epigamic significance.

It is probable that *Centurus hoffmanni* of Costa Rica and Nicaragua is specifically

distinct from *C. aurifrons*.

Field work in restricted zones of sympatry between *Centurus aurifrons* and *C. uropygialis* in Aguascalientes and Jalisco indicates that the two forms are specifically distinct. Approximately 5 per cent of the specimens taken in the zones of sympatry show evidence of hybrid origin, but gene exchange between the two forms is not extensive, if in fact it occurs at all. The presence of traces of yellow pigment on the nape of specimens of *C. uropygialis* throughout its range is interpreted not as evidence of present-day introgression of genes from *C. aurifrons* but as a vestige of a character more fully developed in a population ancestral to *C. uropygialis* and currently being lost in that species.

A specific relationship of *Centurus aurifrons* and *C. carolinus* is demonstrated by their sympatry without interbreeding in a narrow zone in Texas.

Contrary to the suggestion of Peters (1948), *Centurus hypopolius* is probably not conspecific with *C. uropygialis*, and it may be more closely allied to *C. chrysogenys*, with which it is sympatric in Puebla and Morelos.

The Haitian woodpecker, *Chryserpes striatus*, which has been assigned to *Centurus* by Bond and others, is not closely allied to any species of *Centurus* or *Melanerpes* and should be placed in the monotypic genus *Chryserpes*, as advocated by W. D. Miller, pending further study of its relationships.

The significance of ecologic range or amplitude in distribution and speciation in birds is discussed. For *Centurus* it is suggested that the evolution of reproductive isolating mechanisms tends to proceed more rapidly than does the evolution of ecologic isolation, with the result that competition and other interspecific interactions prevent extensive sympatry of closely related species of the genus.

The possible ecologic significance of increased degrees of sexual dimorphism in size, particularly in bill length, in certain insular woodpeckers is discussed, but, in the absence of comparative ecologic and behavioral studies, no satisfactory explanation of the phenomenon can be given.

APPENDIX

Reference specimens used in the analysis of color and pattern in *C. aurifrons* and *C. hoffmanni* (p. 222) are listed below, with category numbers in parentheses. All specimens are adult males of *C. aurifrons*, except as noted.

NAPE COLOR: Fourteen categories: (0) M.Z.U.M. No. 109172; 10 kilometers west of Tuxtla Gutiérrez, 800 meters, Chiapas, March 24, 1941. (1) M.Z.U.M. No. 109173; 10 kilometers west of Tuxtla Gutiérrez, 800 meters, Chiapas, March 24, 1941. (2) U.S.N.M. No. 193916; Canjob, Chiapas, March 26, 1904. (3) R.K.S. No. 3188; 5 kilometers west of Aguascalientes, Aguascalientes, June 14, 1958. (4) R.K.S. No. 3203; Puente Grande, Río Santiago, Jalisco, June 16, 1958. (5) D.C. No. 23495; Sabinas, Coahuila, February 15, 1910. (6) U.S.N.M. No. 183337; Nuevo Laredo, Tamaulipas, December 29, 1901. (7) R.K.S. No. 3060; 11 miles southeast of Pear-sall, Frio County, Texas, March 22, 1958. (8) M.Z.L.S.U. No. 11274; 1 mile west by north of Xilitla, 2500 feet, San Luis Potosí, January 27, 1947. (9) M.Z.L.S.U. No. 18067; Rancho Sabinal, 200 feet, San Luis Potosí, November 16, 1951. (10) D.C. No. 16593; Mt. Cacaguatique, Dept. San Miguel, El Salvador, December 14, 1925. (11) M.Z.U.M. No. 109179; 8 kilometers southwest of Veracruz, Veracruz, March 21, 1941. (12) D.C. No. 16546; Mt. Cacaguatique, Dept. San Miguel, El Salvador, December 10, 1925. (13) M.Z.U.M. No. 70584; Cayo, British Honduras, March 16, 1931.

FRONTAL REGION COLOR: Eight categories: (0) U.S.N.M. No. 132513; Turrialba, Costa Rica, May (*C. hoffmanni*). (1) U.S.N.M. No. 154936; Lagos, Jalisco, June 27, 1896. (2) U.S.N.M. No. 158579; Forlon, Tamaulipas, May 28, 1898. (3) M.Z.L.S.U. No. 11261; 1 mile west (by highway) of Huizache, 4300 feet, San Luis Potosí, February 16, 1948. (4) M.Z.U.M. No. 109180; 8 kilometers

southwest of Veracruz, Veracruz, March 13, 1941. (5) M.Z.L.S.U. No. 11276; Axtla River [= Río Huichihuayan], San Luis Potosí, April 29, 1948. (6) U.S.N.M. No. 359746; Tres Zapotes, Veracruz, March 7, 1940. (7) M.Z.U.M. No. 137879; Belize town, British Honduras, January.

BELLY COLOR: Twelve categories: (0) U.S.-N.M. No. 193924; San Vicente, Chiapas, April. (1) M.V.Z. No. 124893; 11 miles northwest of Jourdanton, 700 feet, Atascosa County, Texas, January 30, 1952. (2) M.V.Z. No. 124891; 11 miles northwest of Jourdanton, Atascosa County, Texas, January 30, 1952. (3) M.V.Z. No. 41531; Brownsville, Texas, January 27, 1911. (4) M.Z.L.S.U. No. 15217; Tepeyac, San Luis Potosí, June 14, 1950. (5) U.S.N.M. No. 34898; San Jose?, Costa Rica, no date (*C. hoffmanni*). (6) D.C. No. 16563; Mt. Cacaguatique, Dept. San Miguel, El Salvador, December 11, 1925. (7) M.Z.U.M. No. 107699; Esperanza, Escuintla, Chiapas, January 2, 1940. (8) Female, U.S.N.M. no. 154831; Guichicovi, Oaxaca, June 24, 1895. (9) M.Z.U.M. No. 108032; Panzos, 30 meters, Guatemala, March 5, 1940. (10) M.Z.U.M. No. 100194; Minatiltlán, Veracruz, April 26, 1939. (11) U.S.N.M. No. 167436; Cozumel Island, Yucatán, April.

DORSAL TAIL PATTERN: Seven categories: (0) M.Z.U.M. No. 109171; 4 kilometers west of Tuxtla Gutiérrez, 800 meters, Chiapas, April 21, 1941. (1) U.S.N.M. No. 57836; Chihintan [?], Tehuantepec, Oaxaca, November 20, 1868. (2) M.Z.U.M. No. 137894; Tehuantepec, Oaxaca, December 21, 1916. (3) M.Z.U.M. No. 102385; Unión Juárez, 1300 meters, Volcán Tacaná, Chiapas, March 18, 1939. (4) U.S.N.M. No. 359745; Tres Zapotes camp, Veracruz, January 20, 1940. (5) M.Z.L.S.U. No. 16905; Puente de Dios, San Luis Potosí, March 25, 1957. (6) M.Z.U.M. No. 137886; Belize town, British Honduras, April 10, 1931.

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