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## Systematic Notes on the Bird Family Cracidae. No. 2 Relationships and Geographical Variation of *Ortalis vetula*, *Ortalis poliocephala*, and *Ortalis leucogastra*

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### INTRODUCTION

The Cracidae are a well-defined family of gallinaceous birds of tropical America, but the genus *Ortalis* penetrates well north of the Tropic of Cancer, reaching the lower Rio Grande Valley in Texas in the east and southern Sonora in the west (fig. 1). In the lower Rio Grande Valley it ascends to the region of Laredo, or to latitude 27° 30' N., and reaches about the same latitude in the west in the region of Alamos, but it does not inhabit the Mexican Plateau north of Mexico City. *Ortalis* is the most widely distributed genus in the family and breeds farthest north.

The forms of *Ortalis* that breed in Mexico north to Texas were divided into two species by Peters (1934), namely, *wagleri* Gray, 1867, in western Mexico from Sonora to Jalisco, and *vetula* Wagler, 1830, ranging from the Rio Grande in the east and Colima in the west to the Guatemalan border. In *vetula*, Peters included as subspecies *poliocephala* Wagler, 1830,

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and *leucogastra* Gould, 1843. This treatment is the "classical" one followed by Hellmayr and Conover (1942), Ridgway and Friedmann (1946), and Friedmann, Griscom, and Moore (1950), but it has been questioned in recent years by Wagner (1953) and Moore and Medina (1957) who gave good reasons for considering that *poliocephala* is not conspecific with *vetula*, although in the main it replaces *vetula* in western Mexico. Their reasons can be summarized as follows: the two birds differ distinctly morphologically and in their vocalizations, and they do not interbreed although their ranges come in contact and overlap to some extent.

Moore and Medina added that *leucogastra*, which inhabits coastal Chiapas (and which Wagner believes is a subspecies of *vetula*), is probably a separate species also, but they did not investigate this question. The main purpose of their paper was to show that *wagleri* is conspecific with *poliocephala*, because they discovered that the two forms, which hitherto had always been considered to be distinct species, interbreed in western Jalisco. Aldrich and Duvall (1955) have also excluded *wagleri*, *poliocephala*, and *leucogastra* from *vetula*, but their paper, which was designed for the needs of game technicians, did not discuss taxonomy.

The systematic status of the four forms was studied by me in detail with a large amount of material, and I have come to the same conclusion as Moore and Medina, namely, that *vetula* and *poliocephala* are separate species and that *wagleri* is conspecific with *poliocephala*. I agree also that *leucogastra* is a separate species. The three species differ very clearly and do not interbreed, although their ranges meet. The ranges also overlap slightly but, in the main, the three species represent one another geographically, a distributional pattern that characterizes all the other species of *Ortalis*.

The present paper consists of two sections. The first is devoted to a discussion of the distribution of the species and their characters; the second, to a discussion of the geographical variation.

## DISTRIBUTION

The distribution is shown in figures 1 and 2. The records are those of the specimens that I have examined, with five exceptions: a record for the State of Mexico, one from Puebla, and three from the Pacific lowlands of Chiapas. I had no specimens from these localities, but it seems important to include them because the State of Mexico is the correct type locality of nominate *poliocephala*, the record from Puebla is an extension of its range, and those from Chiapas suggest that the three species probably overlap in the region of Pijijiapan.

The type locality of *poliocephala* Wagler, described only from "Mexico,"

had been restricted to La Salada, Michoacan, by Ridgway and Friedmann (1946, p. 36), but, as Moore and Medina mentioned, Stresemann (1954, p. 89) showed later that the type had been collected by Deppe in August, 1826, at Real [de] Arriba in the State of Mexico. I could not find this locality, but it would appear to be not far from Temascaltepec, southwest of Toluca.

The records from the region of Pijijiapan are based on sound tapes recorded by L. Irby Davis on March 3 and 4, 1961, at localities about 21 kilometers apart. The spectrogram that I obtained from the tape recorded northwest of Pijijiapan is typical of *vetula* (fig. 6), but the bird recorded about 15 kilometers southeast of Pijijiapan is *leucogastra*. Hitherto, *vetula* seems to have been reported from coastal Chiapas only from Mapastepec, about 45 kilometers southeast of Pijijiapan, by Martín del Campo (1942, p. 700) in a report cited by Moore and Medina. This record may be doubtful, because Wagner, who had supplied it to Martín del Campo, failed to mention *vetula* in coastal Chiapas in the paper he published in 1953, and *vetula* is also not mentioned as occurring in this region by Alvarez del Toro (1964, p. 16) in the most recent list of the birds of Chiapas. It is significant, however, that Alvarez del Toro stated that *leucogastra* ranges north in the coastal region to Pijijiapan and *poliocephala* south to Pijijiapan. This brings the two species to the very region where Davis made his sound record of *vetula* and suggests that the three species meet and probably overlap.

Tonala constituted the southernmost record of *poliocephala* prior to the list of Alvarez del Toro. I have shown this locality on figure 2 because it had been questioned by Peters (1934, p. 19), who suggested that Tonala was perhaps an error for Tonila, Jalisco. The records of Wagner (1953) and Alvarez del Toro (*loc. cit.*) show, however, that *poliocephala* is found in the region of Tonala and south of it to Pijijiapan.

Furthermore, I found an old specimen of *leucogastra* in the collection of the British Museum labeled "Tuxtla, Chiapas, Richardson, March 17, 1897." I presume this refers to Tuxtla Gutierrez, the capital of Chiapas, but I doubt that it was collected there. I believe it was mislabeled, because *leucogastra* is not found in inland Chiapas. I suspect the bird was captured on the coast and brought, perhaps for sale at the market, to Tuxtla Gutierrez where Richardson secured it.

*Ortalis poliocephala* and *O. vetula* appear to overlap also on the Isthmus of Tehuantepec. Such overlapping had been suspected, and I have seen one specimen of each from this region which may have been taken at Santa Maria Chimalapa. Other specimens suggest that the zone of overlap extends farther west to the region of Matias Romero. Laurence C.

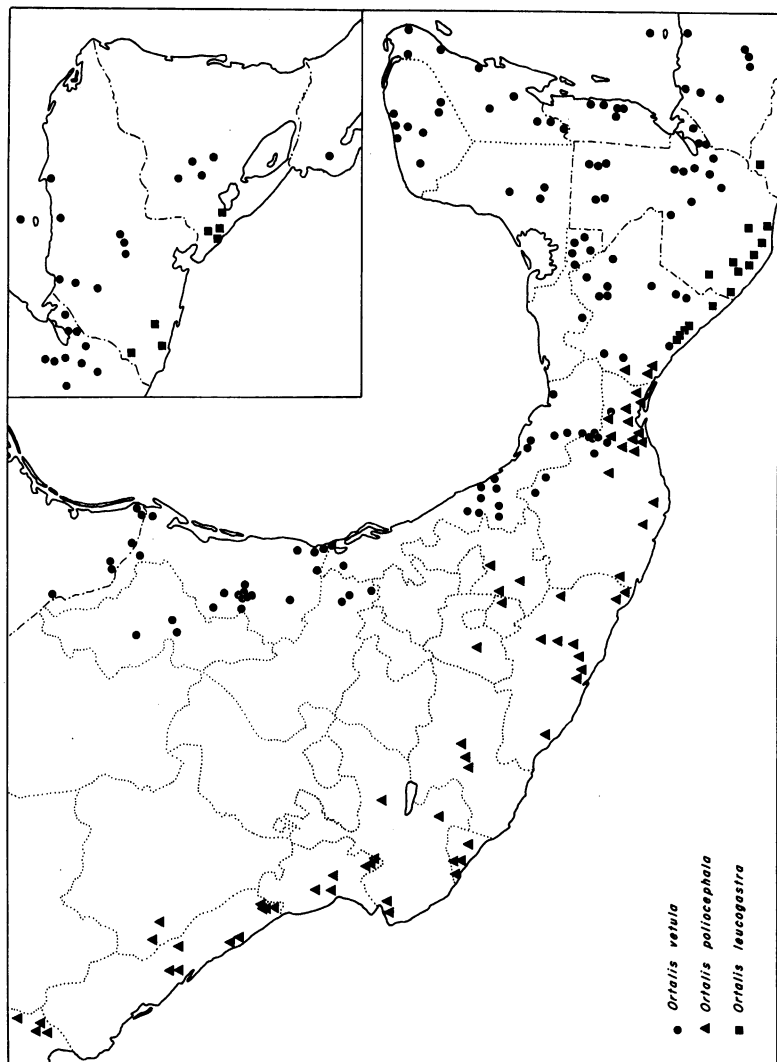


FIG. 1. Distribution of *Ortalis vetula*, *O. poliocephala*, and *O. leucogastra*.

Binford of Louisiana State University, who has been studying the birds of the isthmus in the field, writes to me that he believes the two species meet also in the region of El Barrio. Salvin and Godman (1902, p. 280) had reported *poliocephala* from El Barrio which is about 11 or 12 kilometers southwest of Matias Romero, or very near the locality indicated on figure 2 as "6 miles south [of] of Matias Romero." Moore and Medina (1957) mentioned also the overlap on the isthmus but gave no data.

The specimens of *poliocephala* and *vetula* mentioned above from Santa Maria Chimalapa are labeled merely "Chimalapa" and may not have been taken at the same locality, because there are two settlements by that name east of Matias Romero. Their full names are Santa Maria Chimalapa (the locality shown on fig. 2) and San Miguel Chimalapa, this second settlement being 22 kilometers south of Santa Maria. The specimen of *poliocephala* that is in the collection of the American Museum of Natural History was taken on March 8, 1890, by A. C. Buller, whereas the specimen of *vetula*, which is in the United States National Museum, was taken on March 12, 1869, by Sumichrast. I have not been able to reconstruct the itinerary of Buller in this region, but Binford, who has partially retraced the route of Sumichrast, believes that he very probably collected his specimen at Santa Maria Chimalapa. He says that he has found that Sumichrast collected at "Chimalapa" only on March 12, 1869, and that Sumichrast (Lawrence, 1875, p. 7) mentioned a "Santa Maria, Chimalapa." It is probable that the comma between the two parts of the name is misplaced or is perhaps a typographical error, as Binford believes. He states also that the two species could be found at Santa Maria because the ecological conditions at this locality are suitable for both.

The only specimens of *poliocephala* that I have seen from the State of Puebla were collected in the southwest at Rancho Papayo which is 10 miles south of Tehuitzingo, and at Tochimilco, 10 kilometers west of Atlixco, but I have also indicated Chachapa on the map, because it seems to be the easternmost record of *poliocephala*. Chachapa is about 11 kilometers east of the city of Puebla, and the record from this locality was published by Ferrari-Perez (1886, p. 175).

Hellmayr and Conover (1942, p. 170), and Ridgway and Friedmann (1946, p. 34), have given the erroneous impression that the ranges of *vetula* and *poliocephala* overlap or meet in Puebla by allocating a record of Ogilvie-Grant from coastal Veracruz to the state of Puebla. Ogilvie-Grant (1893, p. 513) had reported two specimens that had been collected by F. D. Godman in March [1888] at "Hacienda de los Atlixcos," but unfortunately he did not state where this locality was. Ridgway and

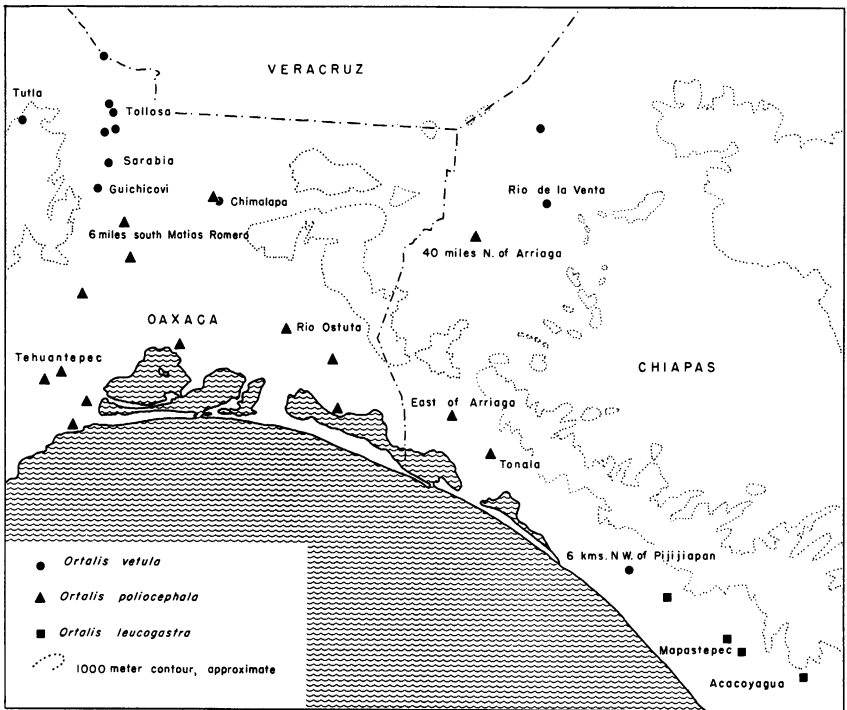


FIG. 2. Distribution of *Ortalis vetula*, *O. poliocephala*, and *O. leucogastra* on the Isthmus of Tehuantepec in Oaxaca, and in western and coastal Chiapas. Scale: 1,000,000.

Friedmann added "Puebla," and Hellmayr and Conover abbreviated the name, referring to the locality as "Atlixcos, Puebla," confusing it apparently with the town of Atlixco in Puebla. But the statements of Godman himself (1915, p. 10) leave little doubt that the hacienda was at or near the present village of Atlixcos in the foothills about 10 kilometers from the coast and about 37 kilometers southeast of Misantla. It does not appear on maps and was probably liquidated by the Mexican revolution. During the period concerned, Godman said that he was collecting southeast of Misantla "near the coast at the foot of the mountain range, which proved to be very good collecting ground and added considerably to our birds and insects." He cited no date or locality for this region, but the present village of Atlixcos is situated exactly in the region he mentioned. I have examined the two specimens concerned which are in the collection of the British Museum.

Hellmayr and Conover (*loc. cit.*) did not mention any other record of *vetula* from Puebla, but Ridgway and Friedmann (*loc. cit.*) added San José Acetano [*sic*] which, however, is in extreme northeastern Puebla and only 4 kilometers from the border of Veracruz in the region south of Papantla where *vetula* would be expected. This record was supplied by Ferrari-Perez also (1886, p. 176), and the correct spelling of the locality is San José Acateno.

Friedmann, Griscom, and Moore (1950, p. 70) stated that *vetula* occurs in Puebla but gave no information other than saying that the material exists in the collection of Moore. Dr. J. W. Hardy informs me that it consists of six specimens that were collected by Chester Lamb 30 miles east of Huauchinango at 1200 feet, and 5 miles north of Apapantilla at about 2200 feet. Five birds were taken between October 31 and November 29, 1942, at the first locality which would seem to be only about 20 miles from San José Acateno and at about the same elevation. Apapantilla, where the sixth was taken on May 15, 1943, is about 33 kilometers northeast of Huauchinango in extreme northeastern Puebla.

In short, the evidence available so far shows that *vetula* inhabits eastern Puebla but does not ascend to the plateau to meet *poliocephala*.

Friedmann, Griscom, and Moore remarked, in their definition of the range of *poliocephala*, that "the species also has been recorded from Jalisco and Guanajuato, the records possibly pertaining to this race," but all the specimens that I have seen from Jalisco are *wagleri*, or intermediate between it and nominate *poliocephala*, and I have been unable to trace any record from Guanajuato.

Southern Chihuahua has been included in the range of *wagleri* (or in that of *griseiceps* Van Rossem which is a synonym of *wagleri*) by nearly all authors, but no valid record seems to exist, although it is quite probable that *wagleri* penetrates a little way into southern Chihuahua in the region east of Alamos, Sonora. The basis for including Chihuahua seems to consist, in all cases, of a specimen collected on May 7, 1888, at "Hacienda de San Rafael, Chihuahua," by Abbott Frazar, but Van Rossem has shown (1945, p. 307) that this locality is actually in Sonora, about 2 miles west of the border of Chihuahua. The specimen was examined by me.

Not all the localities from which I have examined specimens are shown in figures 1 and 2, for the simple reason that I could not find some, while others are situated too near one another to be mapped with clarity. I doubt, however, that those that were not found would change the distribution significantly because they appear to be situated in the regions shown, judged by the general itinerary of the collector or other evidence.

A complete list of the specimens that I have seen is given at the end of this paper.

After this study had been completed and I was studying *O. garrula*, I found that Slud (1964, p. 76) had reported one specimen of *O. vetula* from Costa Rica. It was taken at Ballena in the lowlands of Guanacaste on August 19, 1929, by Austin Smith and is the first and only record of this species for Costa Rica, although Slud believes that he collected another specimen of *vetula* on the Nicoya Peninsula in 1950 which he misidentified at the time as *garrula* and prepared as a skeleton. The existence of the specimen from Ballena, which had not been reported hitherto in the literature, was made known to Slud by Alexander Wetmore. It is in the collection of the Museum of Zoology of the University of Michigan (No. 134911); it was kindly lent to me by Dr. Storer.

The fact that *O. vetula* apparently replaces *O. garrula* in northern Costa Rica raises an interesting question, because *vetula* was not known before south of the Department of Matagalpa in Nicaragua, or of about latitude 13° 25' N., where it meets *garrula*. There is a possibility that the range of *vetula* is continuous in western Nicaragua from Matagalpa to Guanacaste, but this would imply an extensive overlap of the ranges of *vetula* and *garrula* which, as stated above, would be unprecedented in *Ortalis*. I suspect, therefore, that *vetula* is not found in western Nicaragua south of the Department of Matagalpa, although it reoccurs again in Guanacaste where it replaces *garrula* for ecological reasons mentioned by Slud, namely, that *vetula* is better adapted to a region with a very prolonged dry season, such as Guanacaste, than is *garrula* which inhabits the rest of Costa Rica which is more humid than Guanacaste. My belief that the population of *vetula* in Guanacaste may be isolated from the rest of the range of the species is supported by the fact that the specimen from Ballena differs distinctly in coloration from the other populations of *vetula* that I have examined (see below for a discussion of the geographical variation of *vetula*).

I would have expected, however, to find *O. leucogastra* rather than *O. vetula* in Guanacaste, because the range of the former is restricted to the coastal region of the Pacific, but *leucogastra* does not seem to have been reported south of about the northwestern end of Lake Managua (see fig. 1 on which I have also entered the record of *vetula* from Guanacaste).

### MORPHOLOGICAL DIFFERENCES

The three species differ very clearly in their morphology, the differences involving size, proportions, and the structure of the body feathers. Differences in coloration exist also, but they do not appear to be of spe-



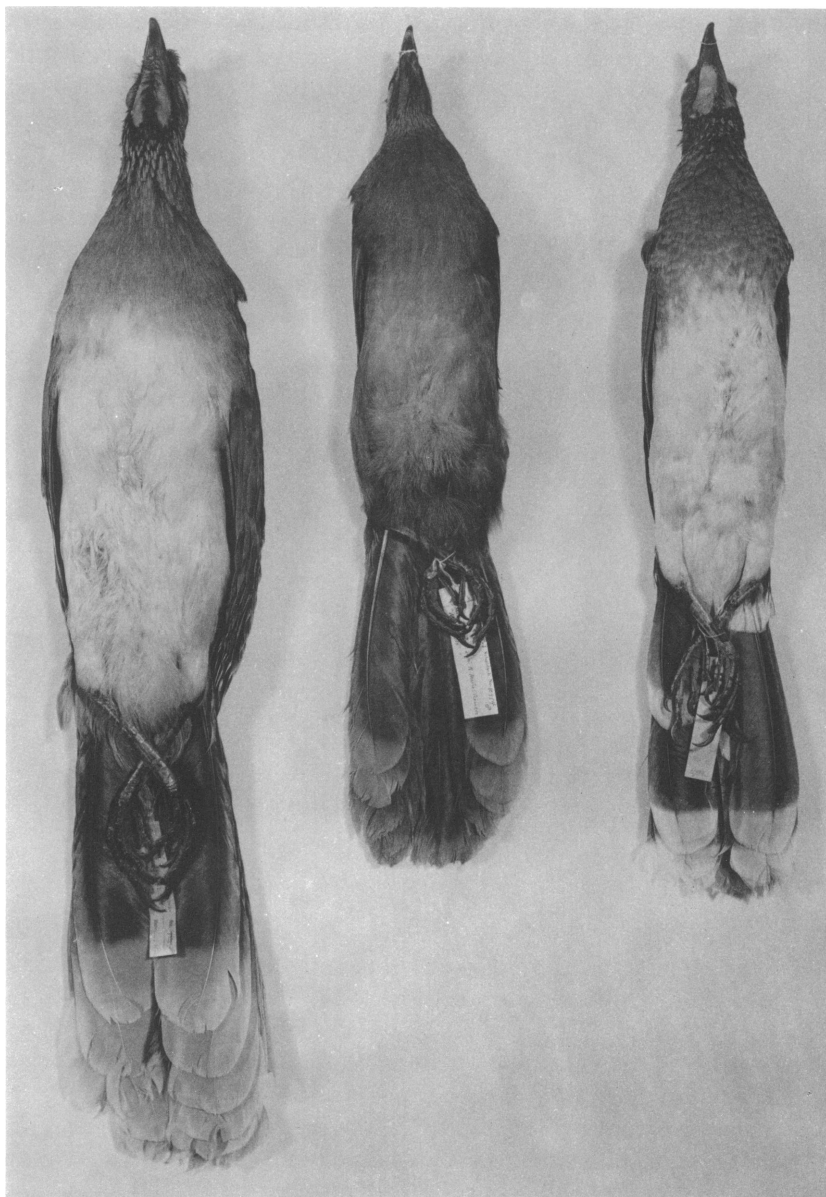


FIG. 3. *Ortalis poliocephala* (left), adult male, 5 miles northeast of Apatzingan, Michoacan; *O. vetula* (center), adult male, 24 miles north of Matias Romero, Chiapas; *O. leucogastra* (right), adult male, Finca el Espino, 15 miles south of Mazatenango, Department of Suchitepequez, Guatemala.

cific importance, except that *leucogastra* is distinctly more rufous brown, less olive gray, than *vetula* and *poliocephala* and the feathers of its mantle and breast are not uniform in pattern, as in the other two species, but faintly edged with gray.

The difference in general size between *poliocephala* and the other two species is very marked and evident at a glance (fig. 3). *Poliocephala* has broader tail feathers, but the fact is not significant, as the width of the feathers is correlated with size. The measurements of the two subspecies of *poliocephala*, of *leucogastra*, and of two populations of *vetula*, which are about average in size, are given in table 1.

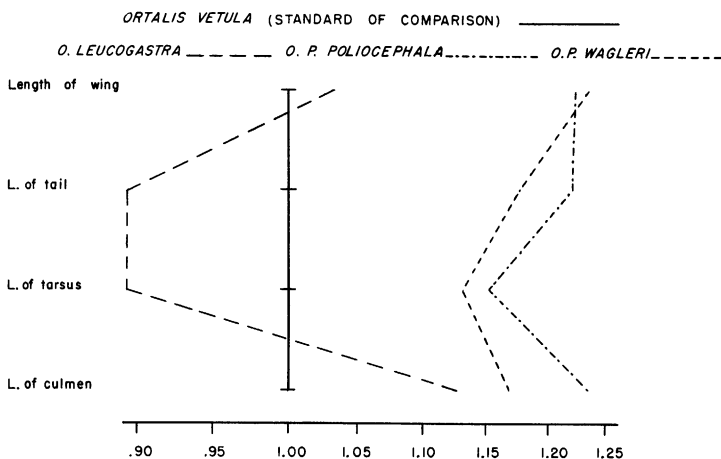


FIG. 4. Comparison by ratio diagram of the proportions of *Ortalis vetula*, *O. leucogastra*, *O. poliocephala poliocephala*, and *O. poliocephala wagleri*.

The differences in proportions are shown by figure 4 through the use of a logarithmic ratio diagram constructed in the manner explained by Amadon (1950, p. 258). The standard of comparison (ratio, 1.00) selected was the population of nominate *vetula* from central Veracruz which is topotypical and about average in size for the species.

It is evident from this diagram that the proportions of *leucogastra* are not at all similar to those of *vetula* and of the two subspecies of *poliocephala*. Its wing length is only slightly longer than that of *vetula*, but its tail and tarsus are shorter (table 1), which results in very different proportions (fig. 4), the tail and tarsus of *leucogastra* being only about 0.90 of *vetula*. On the other hand, the bill of *leucogastra* is longer; it is about 1.12 of *vetula*, and it is also relatively longer than that in the two races of *poliocephala*.

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF ADULT MALES IN *Ortalis vetula*, *Ortalis leucogastra*,  
AND *Ortalis poliocephala*

	<i>O. v. vetula</i>		<i>O. leucogastra</i>	<i>O. p. poliocephala</i>	<i>O. p. wagleri</i>
	Central Veracruz	S. Veracruz and Isthmus of Te- huantepec			
Wing					
Mean	210.2	205	217.6	256.5	259.3
Range	195-220	193-213	205-223	240-280	236-283
$\sigma$	7.03	5.97	4.62	10.20	12.0
<i>N</i>	15	22	26	28	30
Tail					
Mean	233.7	230.3	208.4	284.5	274.7
Range	220-253	215-250	198-220	260-318	247-295
$\sigma$	10.50	9.53	5.42	16.50	12.23
<i>N</i>	15	22	26	28	30
Tarsus					
Mean	60.2	58.8	53.5	69	67.5
Range	53-65	56-62	50-58	63-74	62-75
$\sigma$	3.12	2.02	2.03	2.90	3.14
<i>N</i>	15	22	26	28	30
Exposed culmen					
Mean	24.2	24.9	26	28.3	27
Range	22-27	22-28	23-30	26-32	22-30
$\sigma$	1.43	1.46	1.55	1.64	1.82
<i>N</i>	15	22	26	28	30

The proportions of the two forms of the latter are very similar (with the exception of a slight difference in the wing/tail ratio) and do not differ significantly from those of *vetula*, although the tarsus is relatively shorter.

The differences in proportion confirm my belief that *leucogastra* is much more distantly related to *vetula* and *poliocephala* than those two are to each other.

Further confirmation comes from the structure of the feathers and their coloration. In *poliocephala* and *vetula*, the structure of the body feathers is less integrated than in *leucogastra*, perhaps most evident on the breast. The feathers of *poliocephala* and *vetula* are more or less disintegrated and "hairy" at the tip or along the distal half of the feather, whereas those of *leucogastra* are more compact and are rounded at the tip. In addition, the tips of the feathers of *leucogastra* are faintly edged with

gray, as stated above, whereas those of *poliocephala* and *vetula* are concolorous with the rest of the feather. The appearance of the three birds is different (figs. 3 and 5), *leucogastra* having a smoother and more patterned plumage.

The structure of the feathers of the mantle and breast is similar in *vetula* and *poliocephala*, although *vetula* is a little more "hairy" and has also a more disintegrated and shorter crest, the crest being best developed in the northern populations (*wagleri*) of *poliocephala*. *Vetula* shows also some differences from *poliocephala* in feather structure. In nominate *poliocephala* and in *wagleri*, the feathers of the malar region and throat are stiffened and lanceolate in shape (fig. 5) and in nominate *poliocephala* (more so than in *wagleri*) become denuded of barbs as a rule on the feathered median strip of the throat, forming true bristles. But these specialized feathers are lacking, or virtually so, in *vetula*, although in some individuals the feathers of the lower throat retain a slight tendency to be lanceolated. When this tendency persists, the lanceolated feathers are very few and are always poorly developed and weak. The feathering of the lower throat of *leucogastra* is more similar to that of *vetula* and these two species differ at a glance (fig. 5) from *poliocephala*.

Moore and Medina (1957) seem to have been the first and only modern authors to consider that the difference in measurements and in the feathering of the throat between *poliocephala* and *vetula* were of specific importance. It seems surprising to me that the differences mentioned were not so considered before, but evidently the only character that was deemed to be of specific importance, before Moore and Medina, was the striking difference between *poliocephala* and *wagleri* in the coloration of the abdomen and tips of the tail. These parts are chestnut in *wagleri*, as against white, more or less tinged with ochraceous buff, in *poliocephala*. No other two forms within the genus differ so conspicuously in coloration, and Ridgway and Friedmann (1946) evidently did not consider them to be closely related because they separated *wagleri* from *poliocephala* in their list by the unrelated *O. garrula* and *O. ruficauda*. But, as Moore and Medina have shown, this conspicuous difference is not of specific importance, as *wagleri* and *poliocephala* are similar in other characters and are connected by an interbreeding population.

To return to *leucogastra*, this species seems to be more closely related to a group of South American species (*superciliaris*, *motmot*, and *guttata*) than it is to *vetula* and *poliocephala*. In *leucogastra*, and the three South American species, the feathers of the breast are or tend to be more rounded and compact than do those of the other species of *Ortalis*, and are faintly edged with gray, the pale edges being best developed in *guttata*

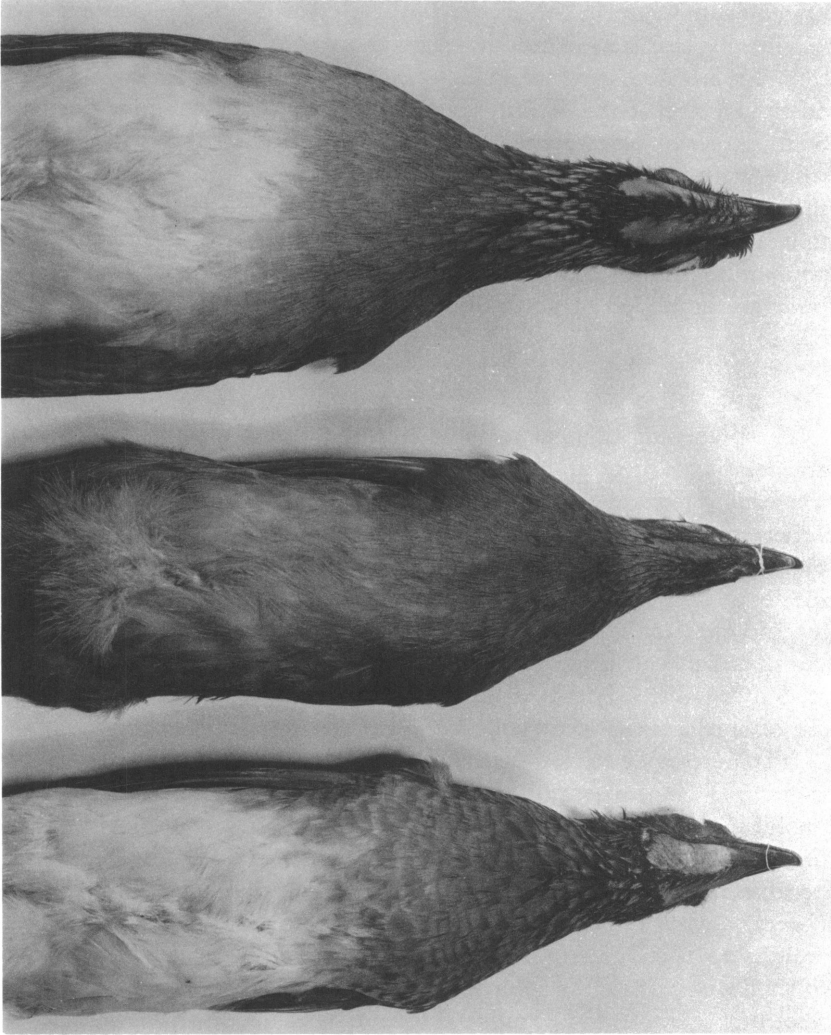


FIG. 5. Shape, structure, and coloration of the feathers of the throat and upper breast in *Ortalis poliocephala poliocephala* (top), adult male, 5 miles northeast of Apatzingan, Michoacan; *O. vetula* (center), adult male, 24 miles north of Matias Romero, Chiapas; *O. leucogastra* (bottom), adult male, Finca el Espino, 15 miles south of Mazatenango, Department of Suchitepequez, Guatemala.

where they are conspicuous and white or whitish. To be sure, the color of the tail differs, the outer tail feathers are rufous or chestnut to a variable extent in the three South American species, as against brown, broadly

tipped with white in *leucogastra*, but the color of the tail varies intra-specifically and hence does not appear to be a species character. The case of *poliocephala-wagleri* is mentioned above, and *O. ruficauda* shows another instance of this variation. In the latter, which inhabits northern South America from Santa Marta to Venezuela, the tail is tipped with white in the western part of the range (*ruficrissa*) but with chestnut in the east (nominate *ruficauda*). This difference was also long considered to be of specific importance but Phelps (1943) reported an intermediate population from the mountains east of Lake Maracaibo and now the two birds are adjudged to be conspecific (see Phelps and Phelps, 1958, pp. 82, 83).

### VOCALIZATIONS

The preceding discussion shows that the ranges of *vetula*, *poliocephala*, and *leucogastra* meet and overlap slightly, and also that the three species are well differentiated morphologically. The other species of *Ortalis* adhere to this pattern or are allopatric, and no species seem to interbreed, as hybrids are unknown. Taibel has shown, however, that the species of *Crax* with which he experimented readily interbreed in captivity and that their first- and also second-generation hybrids are fertile. He obtained the same results with three species of *Penelope* and concluded (1958, 1964) that these genera, and apparently *Ortalis* also, consist of only a single polytypic species.

It is quite evident, however, that all the species keep perfectly distinct in nature. The separation may be achieved variously, such as by morphological or behavioral differences or geographical or ecological isolation. Taibel minimized the importance of the morphological differences because they are not effective in captivity, but it seems to me that in *Crax*, at any rate, they must be important because the males of this genus are distinguished chiefly by vivid dissimilarities in the color of the bill or of its fleshy caruncles. Behavioral and ecological differences may exist also, but relevant comparative studies have not been made of the behavior and ecology of the Cracidae. Wagner (1953) mentioned ecological differences between *vetula* and *poliocephala* in Chiapas, but this question requires further study, as the ecological requirements of the two species appear to be essentially similar in other regions.

In other cracids that lack conspicuous secondary sexual characters and are similar to one another in appearance, the isolating mechanism may be a purely mechanical one. They simply never come together. The Cracidae are all very sedentary, and a large river may form a perfect barrier. For instance, in the case of *O. ruficauda* and *O. motmot* my study

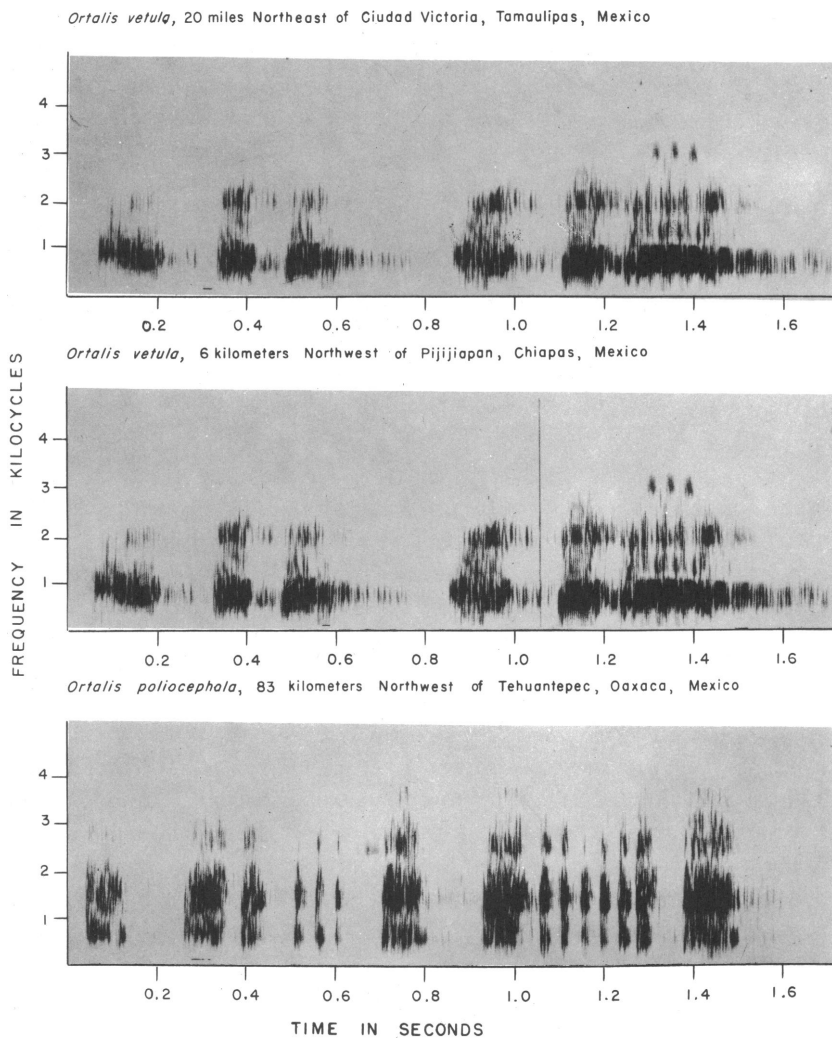


FIG. 6. Spectrograms of the song of *Ortalis vetula* and *O. poliocephala poliocephala*.

has shown that the range of the former extends to the north bank of the Orinoco, but not to the opposite bank where *ruficauda* is replaced by *motmot*. The two species never cross the river according to W. H. Phelps, Jr., who has discussed their distribution with me.

The three species of *Ortalis* of Mexico come in contact, and the very conspicuous difference in coloration between *wagleri* and *poliocephala* does

not prevent interbreeding. The most important isolating mechanism in this genus may very well consist of differences in vocalizations; all its species are noted for being extremely vocal.

It has been known for a long time that the vocalization of the birds (*vetula*) of eastern Mexico was quite different from that (*poliocephala*) of western Mexico. The difference was demonstrated by L. Irby Davis in 1952 at the annual meeting of the American Ornithologists Union, but he has not published his findings. Through the courtesy of Dr. P. P. Kellogg and of the Laboratory of Ornithology of Cornell University, I have been able to use most of the sound recordings made by Davis.

*Ortalis vetula* has a call, or "song," which consists of three syllables; that of *poliocephala* and *leucogastra* consists of four. Davis has interpreted the "song" of *vetula* as "slap-er-back," that of *poliocephala* as "cov-er-it-up," and the one of *leucogastra* as "get-to-the-woods," but to my ear the "songs" of *poliocephala* and *leucogastra* do not differ very much, although on the whole the "song" of *leucogastra* is somewhat less burry, with clearer intervals. The "song" of *wagleri* consists also of four syllables and to me sounds very similar to that of *poliocephala*. The same impression was obtained by the person (perhaps Davis himself) who noted in the catalogue of the Laboratory of Ornithology that it was "almost identical" with that of *poliocephala*.

These interpretations are suggestive, but the spectrograms (fig. 6) that I prepared from the tapes confirm that the "songs" of *vetula* and *poliocephala* are indeed very distinct. Five spectrograms from four localities ranging from the region north of Ciudad Victoria in Tamaulipas to Comitán, Chiapas, were made from the tapes of *vetula* and are all remarkably uniform. Six spectrograms from five localities ranging from the region of Manzanillo, Colima, to Arriaga, Chiapas, were made from the tapes of *poliocephala* and are consistent with, though less uniform than, the spectrograms of *vetula*.

The spectrograms prepared from the tapes of *wagleri* did not confirm the very close similarity to *poliocephala* mentioned above, but I am not able to assess their significance, and also that of the spectrograms of *leucogastra*, because of their great variation. I cannot determine the homology of these spectrograms to those of *vetula* and *poliocephala* (fig. 6), and therefore decided not to illustrate them.

I am baffled by the variation. For instance, the five spectrograms prepared from a tape of *leucogastra* recorded about 15 kilometers southwest of Pijijiapan, Chiapas, have two utterly different patterns, and, moreover, these patterns are different from those of two spectrograms prepared from each of two tapes of *leucogastra* recorded at different localities



south of Tapachula, Chiapas. From the range of *wagleri*, five spectrograms prepared from one tape recorded 17 miles east of San Blas, Nayarit, are fairly consistent, but they are very different from two made from another tape of *wagleri* recorded 34 miles northeast of Puerto Vallarta, Jalisco. All that I can say is that none of the spectrograms of *leucogastra* are similar to those of *vetula* and *poliocephala*, and that the five of *wagleri* from Nayarit (but not the two from Jalisco) show some similarity to the spectrograms of *poliocephala* but not very much. More recordings should be made, especially in the regions where the species meet, but for critical study they should be made under controlled conditions. One individual should be singled out and kept under visual observation at all times, with a blind if necessary, and then collected immediately for positive identification and to determine its sex.

### GEOGRAPHICAL VARIATION

This section discusses the geographical variation of *O. poliocephala* and *O. vetula* which are polytypic. *Ortalis leucogastra* shows no evidence of geographical variation.

#### *Ortalis poliocephala*

It is mentioned above that *poliocephala* consists of two forms which differ very conspicuously by the coloration of the abdomen and tips of the tail, these parts being chestnut in the populations (*wagleri*) that range from southern Sonora to Jalisco, whereas they are white, more or less tinged with ocraceous buff, in those (*poliocephala*) that range from Colima to Chiapas. These two forms were long considered to be distinct species and were believed to be separated by a gap in distribution in western Jalisco, but Moore and Medina have shown that this gap does not exist and that the two forms intergrade in the region between Puerto Vallarta, Jalisco, and western Colima. Their material from the zone of intergradation consisted of seven specimens, three from Colima and four from Puerto Vallarta and its region. The three from Colima and three from Puerto Vallarta and region were separated by them as a new subspecies which they named *Ortalis poliocephala lajuelae*, type locality, Lajuela, Colima. The new form is similar to nominate *poliocephala*, according to Moore and Medina, but darker and "somewhat intermediate" between it and *wagleri*. The seventh specimen, which is in the collection of the American Museum of Natural History, and is labeled "Bahia de Banderas, Jalisco," was referred by them to *wagleri* in their list of specimens. In my opinion, it should have been included in the new form, because

the itinerary of the collector (A. C. Buller) in the region of Bahia de Banderas shows that it must have been collected near Puerto Vallarta, and the account of this specimen given by Moore and Medina shows that it is intermediate also.

Moore and Medina's discussion of the individual variability of their specimens shows very clearly that they were dealing not with a well-defined and constant population but with individuals from a zone of secondary intergradation. The fact was recognized by Moore and Medina, but, no doubt, they thought that the description of *lajuelae* would emphasize the conspecificity of *wagleri* and *poliocephala*. Because I do not consider it good taxonomic practice to name an inconstant population from a zone of secondary intergradation, I prefer to synonymize *lajuelae* with nominate *poliocephala*, the specimens being on the whole more similar to the latter than to *wagleri*.

The birds that I have seen from the zone of secondary intergradation consist of the specimen from Bahia de Banderas, two from Puerto Vallarta of the type of *lajuelae* and of the paratype from the same locality, and of one from the Rio Armeria in Colima. The three specimens from Puerto Vallarta and Bahia de Banderas vary individually in the color of the under parts below the breast and slightly in the length of the crest which, however, is distinctly shorter than that of *wagleri*. The darkest specimen was taken at Puerto Vallarta and is very rufous on the lower breast and abdomen (being apparently much darker than any specimen seen by Moore and Medina) but is much less dark than *wagleri*. The specimen from Bahia de Banderas is distinctly paler but darker than the other specimen from Puerto Vallarta. The coloration of the "thighs," under tail coverts, and tips of the tail show the same range of variation. These three birds are all much more rufous than the two from Lajuella which also vary individually, the type of *lajuelae* being more darkly washed with cinnamon rufous than the paratype. The specimen from the Rio Armeria is about similar to the paler one from Lajuella. The specimens from the Rio Armeria and Lajuella are darker than nominate *poliocephala* and have a shorter crest than the three from Puerto Vallarta and Bahia de Banderas, their crest being about similar to that of nominate *poliocephala*. Thus, as we might expect, the hybrids taken on the border of the range of *wagleri* are more similar to it than those taken on the border of the range of nominate *poliocephala*, and vice versa.

Moore and Medina stated that the species "as a whole" shows good evidence of clinal variation, *wagleri* representing the dark extreme, "*lajuelae*" the intermediate, and nominate *poliocephala* the pale extreme, the birds of the lowlands of Guerrero and Oaxaca averaging smaller and

slightly darker than specimens taken at higher altitudes in Michoacan.

I believe, however, that it is misleading to interpret the variations of this species as a whole in terms of clinal variation, because its variation does not follow a regular gradient from north to south. The palest populations of *wagleri* are not found near the range of nominate *poliocephala* but in the more arid extreme north in Sonora, and nominate *poliocephala* merely shows slight local variations in coloration and size, the wing length averaging longer in birds taken at higher altitudes in any one region, but no geographical trend. *Ortalis poliocephala* does not normally ascend much above 4500 feet, except in Puebla and Morelos from which I have seen a specimen from Tochimilco, Puebla, which is at an elevation of a little over 6000 feet and one from Tetela del Volcan, Morelos, which is situated on the southern slopes of Popocatepetl at about 8000 feet. The bird from Tochimilco was not adult, but the one from Tetela del Volcan (an adult male) has the longest wing of any specimen that I have examined, measuring 280 mm. In southwestern Puebla, however, a male taken at about half of that altitude measured 261 mm.; birds from the coast average smaller, but the wing length of the males I measured reached 263 mm.

The specimens that I have seen from the range of *wagleri* vary geographically, the variation consisting of a slight clinal increase in saturation from north to south. Those from southern Sonora average paler and duller, a little more grayish above and on the head and breast, than birds from Sinaloa and Nayarit in comparative plumage. The latter average darkest, and birds from Jalisco are about similar to those of southern Sinaloa and Nayarit. All these differences are quite slight, however, and many individuals are indistinguishable.

Van Rossem (1934b, p. 431) separated the population of southern Sonora and northern Sinaloa as *griseiceps*, type locality, Alamos, but the variation is not sufficient to warrant nomenclatural recognition. The validity of *griseiceps* had already been questioned, and, after examining a large series, I synonymize this name with *wagleri* Gray, 1867. The latter was based on a specimen from "western Mexico," and this locality was restricted to San Blas, Nayarit, by Van Rossem (*loc. cit.*).

#### *Ortalis vetula*

*Ortalis vetula* varies geographically in color and size, the variation being predominantly clinal but relatively slight, as the range in color variation is narrow and the measurements show a great deal of overlap.

VARIATIONS IN COLORATION: The variation in the coloration has been

discussed extensively, but, as it has been considerably exaggerated by authors who often had no adequate comparative material, it seems best to describe it again, on the basis of a series of more than 400 specimens.

The palest populations are those of the lower Rio Grande Valley, northern Yucatan, and Utila Island off northern Honduras, but as they represent instances of parallel adaptation they need not be discussed together. At the northern end of the range, the birds of the lower Rio Grande Valley are relatively pale and dull. The forehead, crown, and nape are dull pale brownish gray (not brownish black as stated by Ridgway and Friedmann, 1946, p. 31) and do not contrast strongly with the color of the back, rump, and upper tail coverts which are dull olive-brown, with or without some admixture of gray. The throat and upper breast are also olive-brown, more or less tinged with gray, but are paler than the back, and the lower breast and abdomen are distinctly paler than the upper breast and throat, being more or less fulvous white. The center of the abdomen is more whitish, the sides and flanks are more fulvescent, and the under tail coverts are buffy brown. The tail is broadly tipped with dingy white, with or without a faint suggestion of gray or pale buff, with the exception of the central tail feathers which are indistinctly tipped with pale buffy brown or dingy white. Some authors, such as Miller and Griscom (1921a, p. 46), emphasize that this population and the one of northeastern Mexico are "characterized by snow-white tail-tips," but such is an exaggeration. Among the 86 specimens that I have seen from the lower Rio Grande Valley, I did not find a single one with "snow-white" tips and, indeed, very few in which the tips were really white.

A series of 62 specimens which was collected in Nuevo Leon (including the type of *mccalli* and other specimens from Boquilla), central and southern Tamaulipas, and southeastern San Luis Potosi is generally similar to the series from the Rio Grande but somewhat darker and more richly colored. In these specimens the crown and nape are darker, more sooty gray as a rule, and usually contrast more with the color of the back, which, together with the rump and upper tail coverts, is more fulvescent, less greenish and dull. The under parts are also darker and more fulvescent throughout than those of the birds from the Rio Grande, and no specimen is whitish on the center of the abdomen. The tail tips tend also to be more cloudy. The difference in the color of the abdomen was noted by Miller and Griscom (*loc. cit.*).

Some individuals in this series, chiefly from Nuevo Leon, are identical or virtually so with the birds of the Rio Grande, but it is interesting to note that all the darkest specimens were taken in the south, in southern

Tamaulipas, San Luis Potosi, and also northern Veracruz.

My series is unfortunately interrupted by a lack of specimens from the region which extends from Tampico and the Panuco River to the regions of Jalapa, Veracruz (the type locality of nominate *vetula*), and Cordoba, but there is no reason to suppose that the cline of increasing saturation is interrupted, because the specimens from the regions mentioned in central Veracruz are darker and more richly colored than those of Nuevo Leon, Tamaulipas, San Luis Potosi, and northern Veracruz. The crown and nape are darker, the upper parts are more brown and fulvescent, less olive, and the under parts are distinctly darker, more fulvescent, throughout. In the great majority of the specimens the tail tips are no longer whitish, but vary from grayish buff to dull and pale cinnamon.

The cline in coloration seems to end in central Veracruz. From there southward through southern Veracruz, Oaxaca, Tabasco, Chiapas, and Guatemala to Honduras and Nicaragua the populations do not become darker. They are all essentially similar to those of central Veracruz, although, to be sure, there is some evidence of local variation—for instance, in the central valley of Chiapas where the birds are somewhat paler on the abdomen than normal for the populations mentioned.

The similarity among the birds of central and southern Veracruz, Oaxaca, Tabasco, and the greater part of Chiapas has not been questioned, but some authors state that the birds of Guatemala, Honduras, and Nicaragua differ from nominate *vetula* by having darker tail tips, whereas other authors state that they differ only by being more uniform below. But the great majority of the specimens that I have examined from these three countries are identical with those from central Veracruz in every respect, although the tail tips, in an occasional specimen, are somewhat more rufous than average.

In the northern part of the Yucatan Peninsula, however, the population differs from nominate *vetula* by being distinctly paler throughout. It is more olive and grayish above, less brown and fulvescent, and is dull isabelline white on the abdomen, with a slight admixture of buff, not strongly rufescent as in nominate *vetula*, and the tips of the tail are more whitish, not buffy. This population (*pallidiventris*) shows some similarity to the populations (*mccalli*) of northeastern Mexico and Texas, but it is brighter, less dull above, and the pale area on its abdomen is purer white and in every case more extensive, but, on the other hand, the tips of the tail are darker.

The pale birds of the northern part of the peninsula are replaced southward by darker and more rufescent populations in Campeche,

Quintana Roo, the Peten, and British Honduras. The variation is probably clinal, but only in a broad sense, because the birds of the more central and southern parts of the peninsula vary a great deal individually and locally. Taken as a whole, they are, however, intermediate between *pallidiventrís* and nominate *vetula* and have been named *intermedia*.

Finally, we meet another pale population which is restricted to the relatively small island of Utila off northern Honduras. These birds (*deschauenseei*) are dull and grayish above and are very similar to *mccalli* from the Rio Grande Valley, except that they differ from them, or any other population of *mccalli*, by being more uniform in coloration below, more drab and ochraceous, and by having the tail tipped with grayish buff or dull cinnamon as in nominate *vetula*, not with white or whitish as in *mccalli*.

The discussion of the coloration concerns so far only geographical variation, but I have seen three specimens from Oaxaca which are very distinct from the local population and appear to be individual variants. They were taken at Tolloso from December 20, 1900, to January 5, 1901, and are fulvous brown and extremely dark. They were named *fulvicauda* by Miller and Griscom (1921a, p. 47), but specimens collected subsequently at Palomares, which is only 3 miles south of Tolloso, are normal in coloration and typical of nominate *vetula*. The physical conditions at the two localities are similar, and my belief that the three specimens are individual variants is strengthened by a similar, though very slightly paler, bird, taken very far away at Chamelecon, Honduras, on March 8, 1901.

I have not found another specimen similar to *fulvicauda*, but Griscom (1932, pp. 101–102) reported another which he says “is an extreme of the *fulvicauda* type” in his series of “thirty five specimens” from the eastern Alta Verapaz in Guatemala. I have examined this series (I find only 23 specimens, not 35), and the general coloration of this specimen is similar to that of nominate *vetula* from central Veracruz, not to the three *fulvicauda* from Oaxaca seen by Griscom. The tips of its tail are, however, more darkly tinged with cinnamon than specimens from central Veracruz, which was probably the reason for Griscom’s statement. He mentioned also that “about eight [other specimens] are nearer *fulvicauda*,” but, although this series shows some degree of individual variation, it does not differ essentially from nominate *vetula*, as Griscom agreed.

CORRELATION BETWEEN COLORATION AND RAINFALL: Brodkorb (1942) discussed the coloration of *vetula* and believed the degree of its saturation to be correlated with annual rainfall. He implied that this correlation is close and direct, but I find it so only in certain regions and within a defi-

nite limit. Beyond a certain critical point (apparently around 1500 mm. of rain) the coloration is no longer effectively correlated with prevailing humidity.

The specimens that I have seen from northeastern Mexico were collected within the isohyets of 500 to 1000; and those from northern Yucatan, between those of 500 to 1200. These birds are paler than specimens from Veracruz, Jalapa, and Cordoba that were collected within the isohyets of 1500 to 1600, but three specimens from Yajalon and Palenque in northern Chiapas (where the annual rainfall reaches 5400 mm., according to Brodkorb) are not darker than those of Veracruz, Jalapa, and Cordoba.

Three specimens may be insufficient for one to draw a conclusion, but the lack of correlation is well illustrated by the series of 33 specimens that I have examined from the Caribbean lowlands and highlands of Guatemala where the rainfall is very high. The birds of the lowlands are similar to those of the highlands, and to those from the regions mentioned in central Veracruz, although Vaurie and Vaurie (1949, p. 5) reported that at stations in the lowlands and highlands of Caribbean Guatemala the annual rainfall averages 3318 mm. at a station (Panzos) at 36 meters of altitude but increases to 5617 mm. at one at 725 meters above Panzos. The 33 specimens were taken in the lower Motagua Valley, on the slopes of the Sierra de las Minas, at Panzos on the lower Polochic River, and in the region above Panzos.

The correlation seems to be effective in the more arid belt of northern Yucatan, but I doubt that it can account for the local variations in coloration mentioned by Paynter (1955, p. 77) who agreed with Brodkorb. The specimens that he compared and discussed are few. A single bird from Vigia Chico is "almost exactly comparable to typical *O. v. pallidiventris*," whereas three out of four from Tabi are darker, the area around Vigia Chico being more arid than that at Tabi according to Paynter. But another single specimen from Laguna Chacanbacab is pale also, and its coloration approaches that of *pallidiventris*, according to Paynter, although I find that this locality is in a zone of comparatively high rainfall, lying about on the isohyet of 1600 in Tamayo's atlas (1949, map 7).

The specimens reported by Paynter (*loc. cit.*) from Quintana Roo and Campeche, and also those reported by Traylor (1941, p. 204) from Campeche, vary individually and locally. I believe that the variability (see below) of the populations from the more central and southern parts of the Yucatan Peninsula can be accounted for by the fact that these regions represent a zone of intergradation between nominate *vetula* and *pallidiventris*, rather than by variations in the annual rainfall.

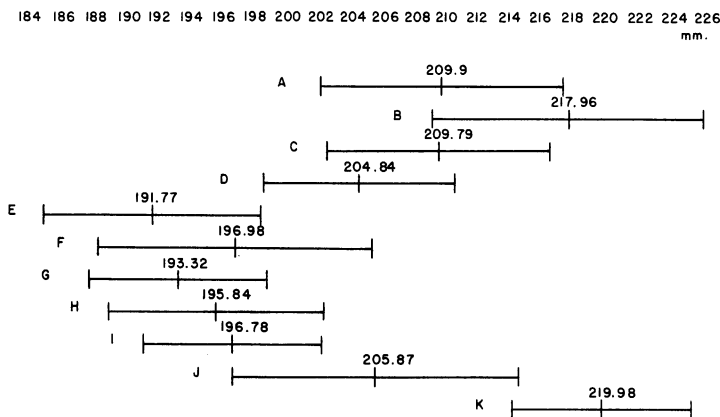


FIG. 7. Geographical variation of the length of the wing of adult males of *Ortalis vetula*. Vertical bars represent the statistical mean and one standard deviation above and below.

*Key:* A, Rio Grande Valley; B, Nuevo Leon, Tamaulipas, San Luis Potosi; C, central Veracruz; D, southern Veracruz and Isthmus of Tehuantepec; E, Tabasco, lowlands of northern Chiapas, and southern Campeche; F, Yucatan; G, central and southern Quintana Roo, British Honduras, Peten, and Motagua Valley; H, highlands of Chiapas; I, highlands of Guatemala; J, Honduras and Nicaragua; K, Utila Island.

**VARIATIONS IN SIZE:** The variations in size are shown in figures 7 to 10. They follow a simple pattern and can be discussed briefly.

The population of Utila Island has the longest wing but a distinctly short tail. This combination results in proportions that are different from those of the other populations, the ratio being 98 in the birds of Utila as against 87 to 90 for those of the mainland. The birds of Utila have also the biggest bill. Insular populations often have a bigger bill than their continental representatives, and hence this character may be termed "normal," but the very long wing of the birds of Utila, their different proportions, and the peculiarities of their coloration seem aberrant and probably reflect a faster rate of evolution induced by isolation on a small island. Utila is only 7½ miles in length by 3 in width and probably supports only a small population. It is only 19 miles from the mainland, but presumably this distance is sufficient to insure the isolation of its population because *Ortalis vetula* is noted for being very sedentary.

The variation of the mainland populations does not seem to follow closely any ecological rule. Color saturation does not increase beyond a certain point, as stated above, and the larger birds are not found farthest north (Rio Grande Valley) but farther south in Nuevo Leon, Tamauli-



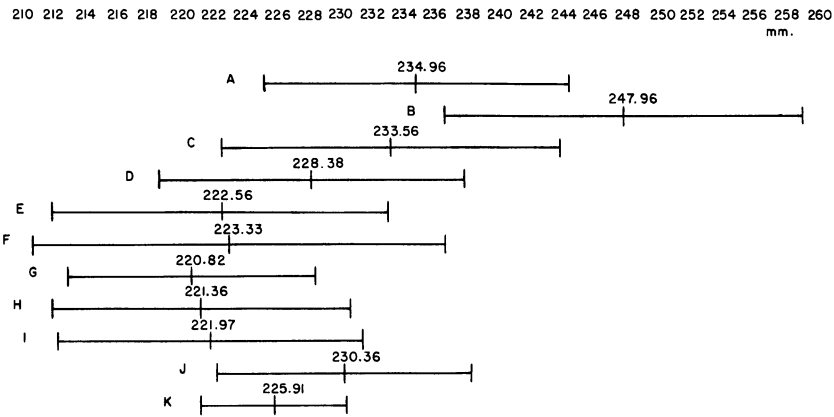


FIG. 8. Geographical variation of the length of the tail of adult males of *Ortalis vetula*. Vertical bars represent the statistical mean and one standard deviation above and below.

Key: A, Rio Grande Valley; B, Nuevo Leon, Tamaulipas, San Luis Potosi; C, central Veracruz; D, southern Veracruz and Isthmus of Tehuantepec; E, Tabasco, lowlands of northern Chiapas, and southern Campeche; F, Yucatan; G, central and southern Quintana Roo, British Honduras, Peten, and Motagua Valley; H, highlands of Chiapas; I, highlands of Guatemala; J, Honduras and Nicaragua; K, Utila Island.

pas, and San Luis Potosi. The length of the wing and that of the tail decrease clinally from these regions to the Caribbean lowlands of Mexico but increase again in northern Yucatan and still more so in Honduras and Nicaragua which represent the southernmost populations. The birds of the highlands of Chiapas and Guatemala are slightly bigger than those of the Caribbean lowlands of Mexico, but this increase may not be correlated with the higher altitude because the birds of very low-lying northern Yucatan are bigger than those of the highlands of Chiapas and Guatemala.

The variations in the lengths of the wing and tail on the mainland show the same trend, but the length of the tarsus, including that of the population of Utila, varies little. The length of the tarsus is actually rather uniform, although one would have expected greater adaptive variation more or less correlated with variations in habitat from arid scrub or chaparral to dense undergrowth on the edge of forests or mangroves.

The variations in the size of the bill are slight also and show no discernible trend other than in the case of the population of Utila Island noted above.

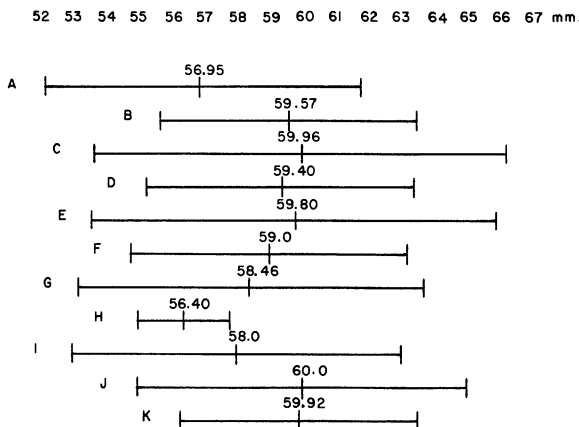


FIG. 9. Geographical variation of the length of the tarsus of adult males of *Ortalis vetula*. Vertical bars represent the statistical mean and two standard deviations above and below.

**Key:** A, Rio Grande Valley; B, Nuevo Leon, Tamaulipas, San Luis Potosi; C, central Veracruz; D, southern Veracruz and Isthmus of Tehuantepec; E, Tabasco, lowlands of northern Chiapas, and southern Campeche; F, Yucatan; G, central and southern Quintana Roo, British Honduras, Peten, and Motagua Valley; H, highlands of Chiapas; I, highlands of Guatemala; J, Honduras and Nicaragua; K, Utila Island.

The variations in size discussed above and illustrated in figures 7 to 10 are of adult males. The variation of the adult females is similar, but their measurements average consistently lower. For instance, the actual measurements in five populations are as follows:

**RIO GRANDE VALLEY:** Forty-six males, wing, 195–230 (210); tail, 215–265 (235.2); tarsus, 52–64 (56.7); exposed culmen, 20–25 (22.74); 30 females, respectively, 187–219 (200.9), 210–250 (229.5), 49–60 (54.6), 20–25 (22.2)

**SOUTHERN VERACRUZ AND ISTHMUS OF TEHUANTEPEC:** Twenty-two males, wing, 193–213 (205); tail, 215–250 (230.3); tarsus, 56–62 (58.8); exposed culmen, 22–28 (24.9); 16 females, respectively, 179–208 (191.8), 210–240 (220.3), 53–60 (56.7), 22–27 (24.1).

**NORTHERN YUCATAN:** Seventeen males, wing, 184–217 (197); tail, 205–252 (225); tarsus, 56–62 (59); exposed culmen, 22–26 (23.9); eight females, respectively, 184–195 (188.9), 202–235 (217), 53–60 (56.5), 22–25 (23.5)

**SOUTHERN QUINTANA ROO, BRITISH HONDURAS, PETEN, AND MOTAGUA VALLEY:** Twenty-three males, wing, 180–203 (194.4); tail, 205–244 (221.5); tarsus, 54–65 (58.3); exposed culmen, 21–28 (24.5); 17 females, respectively, 177–196 (188.6), 205–231 (217), 53–61 (56.6), 21–26 (23.4)

**UTILA ISLAND:** Seven males, wing, 213–229 (220); tail, 220–232 (226); tarsus, 57–63 (59.7); exposed culmen, 25–28 (26.3); five females, respectively, 190–216 (204.4), 210–230 (219), 56–60 (57.4), 22–26 (24.1)

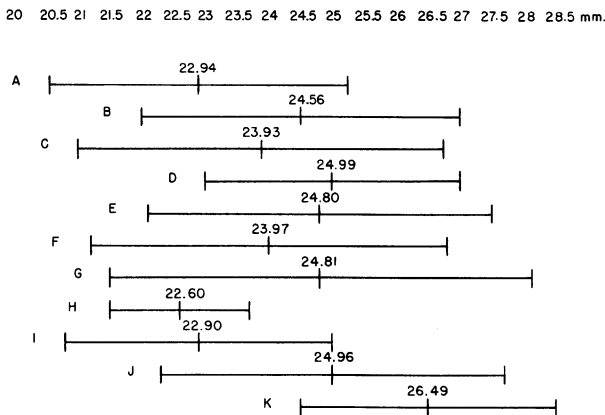


FIG. 10. Geographical variation of the length of the bill (exposed culmen) of *Ortalis vetula*. Vertical bars represent the statistical mean and two standard deviations above and below.

**Key:** A, Rio Grande Valley; B, Nuevo Leon, Tamaulipas, San Luis Potosi; C, central Veracruz; D, southern Veracruz and Isthmus of Tehuantepec; E, Tabasco, lowlands of northern Chiapas, and southern Campeche; F, Yucatan; G, central and southern Quintana Roo, British Honduras, Peten, and Motagua Valley; H, highlands of Chiapas; I, highlands of Guatemala; J, Honduras and Nicaragua; K, Utila Island.

**SUBSPECIES:** Nine subspecies have been named which, listed in chronological order with their type localities, are as follows: nominate *vetula* Wagler, 1830, vicinity of the city of Veracruz; *mccalli* Baird, 1858, Boquilla, Nuevo Leon; *plumbiceps* G. R. Gray, 1867, Omoa, Honduras; *pallidiventr*s Ridgway, 1887, Merida, Yucatan; *intermedia* Peters, 1913, Camp Mengel [= Alvaro Obregon], Quintana Roo; *jalapensis* Miller and Griscom, 1921, Jalapa, Veracruz; *fulvicauda* Miller and Griscom, 1921, Tolloso, Oaxaca; *deschauenseei* Bond, 1936, Utila Island, Honduras; and *vallicola* Brodkorb, 1942, Malpaso, Chiapas.

Seven of these subspecies were recognized by Ridgway and Friedmann (1946) in the most recent systematic treatment of the species as a whole, but I believe that the geographical variation, as summarized above, does not warrant the recognition of more than four subspecies: the aberrant *deschauenseei* from Utila Island, the well-differentiated *pallidiventr*s from northern Yucatan, *mccalli* from the lower Rio Grande Valley and north-eastern Mexico, and nominate *vetula* in the rest of the range. Ridgway and Friedmann (*ibid.*) synonymized *jalapensis* and *fulvicauda* with nominate *vetula*, and to its synonyms I add *plumbiceps*, *intermedia*, and *vallicola*.

The range of *mccalli* extends from the Rio Grande Valley south to

northern Veracruz and southeastern San Luis Potosi. I have not seen specimens from farther south, as stated above, until central Veracruz, but, as the variation is clinal, the limit of the range of *mccalli* can be drawn where I have mentioned. This is also the limit defined in the check list of the birds of Mexico by Friedmann, Griscom, and Moore (1950, p. 69).

Miller and Griscom (1921a) have synonymized *mccalli* with nominate *vetula*, but they were misled by the original description of nominate *vetula* and by the fact that Wagler had not indicated a definite locality in "Mexico." Wagler had mentioned that the tail of his specimen was tipped with white, and Miller and Griscom, believing that nominate *vetula* represented the population of northeastern Mexico, in which the tips of the tail are "white," restricted its type locality to Tampico, Tamaulipas, and described the birds of central Veracruz (in which the tail tips are buffy, as a rule) as *jalapensis*. They were soon informed by Hellmayr, however, that the type of nominate *vetula* had been collected near the city of Veracruz, and they accordingly corrected the type locality but unfortunately did not retract *jalapensis*.

Peters (1934, p. 19) retained *jalapensis* as a valid subspecies, but Van Rossem (1934a, p. 349) remarked that this name was probably a synonym of nominate *vetula* and that the correct name for the birds of the northeast was *mccalli*. Van Rossem did not reach a definite conclusion concerning *jalapensis* because it seemed to him that the type of nominate *vetula* was aberrant, but this question was discussed fully by Wetmore (1943, p. 245) who synonymized *jalapensis* with nominate *vetula*. This action has been followed ever since.

Griscom (1932, pp. 102–103) was the first to synonymize his own *fulvicauda* with nominate *vetula* (which he called *jalapensis*) because his series from Guatemala (which I have discussed above) led him to believe that *fulvicauda* was not a constant form, although he was not aware that it was based, as I believe, on individual variants. Friedmann, Griscom, and Moore (1950) suggested that *fulvicauda* may be a valid subspecies. They stated, "Additional material suggests that *O. v. fulvicauda* Miller and Griscom may be separable from [nominate *vetula*]." They gave no reference to any material or geographical clue, and the fact remains that specimens with the normal coloration of nominate *vetula* have been collected at virtually the same locality as the type series of *fulvicauda*.

The material that I have seen from the ranges of *plumbiceps* and *vallicola* shows that *plumbiceps* is not separable from nominate *vetula*, and that *vallicola* is only a local form which differs from nominate *vetula* merely by being slightly paler below than normal. This difference can be ac-

counted for by the fact that the central valley of Chiapas is more arid<sup>1</sup> than its surrounding highlands, but it is insufficient to warrant nomenclatural recognition.

I prefer not to recognize *intermedia*, although, generally speaking, most of the populations that have been referred to this form are intermediate in coloration between *pallidiventrís* and nominate *vetula*. The populations that have been referred to *intermedia* differ with nearly every author, but Campeche, western Tabasco, Atlantic slope of Chiapas, "western Guatemala," the Peten, southern Quintana Roo, and British Honduras have been included. These populations show a wide range of geographical and individual variation, from a population like the one from the Atlantic slope of Chiapas which Hellmayr and Conover (1942, p. 171) include in *intermedia* but which is identical to typical nominate *vetula*, to others that are more similar to *pallidiventrís*, or consist of individuals that bridge the gap in coloration between the latter and nominate *vetula*, or virtually so.

I find also that the population of western Tabasco, although slightly paler than normal for nominate *vetula*, is certainly much more similar to the latter in coloration than to any other form. Brodkorb (1943, p. 30) was correct in identifying it as *jalapensis* (i.e., nominate *vetula*; see above). Hellmayr and Conover (*loc. cit.*) included "western Guatemala to the Sierra Madre," but the species is not found in this region.

If we exclude the regions mentioned, we are left with Campeche, the Peten, southern Quintana Roo, and British Honduras. The specimens that I have seen from Campeche vary individually, but, with the exception of one bird from La Tuxpeña which is identical with some individuals of nominate *vetula* from Veracruz and Oaxaca, the rest of the series is pale and more similar to *pallidiventrís*. The original series of *intermedia* from southern Quintana Roo consisted of three specimens of which I have examined the two paratypes. These two birds are paler than nominate *vetula* but are more similar to it than they are to typical *pallidiventrís* from northern Yucatan. The rest of my series from southern Quintana Roo shows a rather wide range of individual variation, and this variation becomes even more pronounced in the series from British Honduras. A series from northern Peten is about similar to the birds of southern Quintana Roo but is somewhat paler and grayer throughout, less rufescent.

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<sup>1</sup> The annual rainfall of the valley "averages well below 1,000 mm," according to Brodkorb (1942, p. 182), but the series that I have seen (which includes the paratypes of *vallicola*) was collected between the isohyets of 1000 and 2000 (Tamayo, 1949, map 7).

In other words, the populations from the more central and southern parts of the Yucatan Peninsula are not homogeneous. They represent a zone of intergradation between nominate *vetula* and *pallidiventris*, and when we consider that the area involved is comparatively small, as Paynter (1955, p. 77) pointed out, and lacks "clear-cut barriers to stem the interchange of genes," it seems misleading to separate them as a distinct subspecies. Paynter recognized *intermedia*, and other authors may find it convenient to do so, but as this action seems undesirable I synonymize *intermedia* Peters with nominate *vetula* Wagler, the specimens on which *intermedia* was based being more similar to nominate *vetula* than to *pallidiventris*, as stated above.

The unique specimen from Costa Rica, which is mentioned in the distribution of the three species, differs from the specimens of any other population of *vetula* that I have examined by being more rufous brown on the back, wings, rump, and upper tail coverts, with scarcely a trace of olive, although it is similar to nominate *vetula* below. It may represent an undescribed and perhaps isolated subspecies, but the distribution of the species in Nicaragua requires further study, and more specimens are needed from Costa Rica for one to determine their range of individual variation. The measurements of this specimen, a female, are also larger than normal for nominate *vetula* (including "*plumbiceps*"), the wing length measuring 210, the tail 232 plus, the tarsus 61, and the exposed culmen 26, but these measurements are matched or exceeded by an occasional female of nominate *vetula* from Veracruz and Honduras in which the wing length may reach 216, the tail 240, the tarsus 62, and the exposed culmen 27.

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### SUMMARY

The chachalacas of Mexico belong to three species: *Ortalis vetula* Wagler, which ranges from the lower Rio Grande Valley southward through eastern and southern Mexico to Honduras, including the island of Utila, and northwestern Nicaragua, occurring again in Guanacaste in northwestern Costa Rica; *O. poliocephala* Wagler, which ranges from southern Sonora southward through western Mexico to the region of Pijijiapan in coastal Chiapas; and *O. leucogastra* Gould, which ranges from Pijijiapan southward in the coastal districts of the Pacific to northern Nicaragua.

The three were considered to be conspecific by all authors until Moore and Medina (1957) stated that *vetula* and *poliocephala*, and probably *leucogastra* also, were separate species.

The present paper confirms the opinion of Moore and Medina. It discusses the relationship of the three species and suggests that the nearest relatives of *leucogastra* are probably not *vetula* and *poliocephala* but a group of South American species (*superciliaris*, *motmot*, and *guttata*) with which it shares a morphological character that appears to be of phylogenetic importance in the genus *Ortalis*, namely, the structure and color pattern of the feathers of the breast.

The three species of Mexico are mainly geographical representatives, and their distribution in Mexico is discussed in detail, showing that the ranges of *vetula* and *poliocephala* meet and overlap slightly on the Isthmus of Tehuantepec, and that the ranges of all three species meet and probably overlap in the region of Pijijiapan in coastal Chiapas.

The morphological characters and the vocalizations of the three spe-

cies are analyzed. The morphological characters of the three species, and the vocalizations of *vetula* and *poliocephala*, are very distinct. The evidence concerning the vocalizations of *leucogastra* is inconclusive for technical reasons. It is suggested that differences in vocalizations may be the most important isolating mechanism in *Ortalis*.

The geographical variation is discussed. *Ortalis leucogastra* does not appear to vary geographically. *Ortalis poliocephala* consists of two subspecies (*wagleri* Gray, in the north of the range south to Jalisco, and nominate *poliocephala* south of *wagleri*); *wagleri* differs strikingly from nominate *poliocephala* by being chestnut, as against white, below the breast, and this difference was universally considered to be of specific importance until Moore and Medina (1957) reported that the two birds interbreed in western Jalisco.

The geographical variation of *vetula* is relatively slight and is clinal in some regions. In these and northern Yucatan, the degree of color saturation seems to be correlated with annual rainfall, but beyond a certain critical point (apparently around 1500 mm. of rain) the coloration is no longer correlated with humidity. Four subspecies are recognized in *vetula*: *mccalli* Baird, ranging from the Rio Grande Valley to northern Veracruz and southeastern San Luis Potosi; *pallidiventris* Ridgway, in the northern arid Yucatan Peninsula; *deschauenseei* Bond, on Utila Island; and nominate *vetula* in the rest of the range. Among the forms synonymized with nominate *vetula* is *intermedia* Peters, on the ground that this form represents morphologically unstable populations from a zone of integration between *pallidiventris* and nominate *vetula*.

## SPECIMENS EXAMINED

### *Ortalis leucogastra*

MEXICO: *Chiapas*: Huehuetan, 3 ♂, 2 ♀; Mapastepec, 3 ♂, 4 ♀; La Grada, 1 ♀; Acacoyagua, 4 ♂, 1 ♀; "Tuxtla," 1 ♂, (see text).

GUATEMALA: Volcan Tajumulco, 3500 feet, 1 ♂, 1 ♀; Retalhuleu, 2 unsexed; Tiquisate, 5 ♂, 1 ♀, 2 unsexed; Concepcion del Mar, Escuintla, 3 ♂, 7 ♀; El Zapote, "Costa Grande," 1 unsexed; San José, Escuintla, 5 ♂, 6 ♀; Finca Valledirios, Escuintla, 3 ♀, Finca Cipres, 1 ♀; Finca el Espino, 1 ♂; Hacienda California, 1 ♂, 3 ♀, no locality, 1 unsexed.

EL SALVADOR: Lake Ilopango, 1 ♀; La Libertad, 1 unsexed, no locality, 1 unsexed.

NICARAGUA: Momotombo, 2 ♀; Chinandega, 2 ♀ San Geronimo, Chinandega, 1 ♂; Corinto, 1 ♀.

### *Ortalis poliocephala*

MEXICO: *Sonora*: Hacienda de San Rafael, 1 ♀; Alamos, 1 ♂, 3 ♀; Guicoroba, 3 ♂, 3 ♀. *Durango*: Chacala, 2 ♂, 1 ♀; Sayupa, 1 ♀. *Sinaloa*: El Molino, 30 miles



southwest of Culiacan, 3 ♂, 1 ♀; 25 miles south of Culiacan, 1 ♂, 1 ♀; Mazatlan, 1 ♂, 2 ♀; Presidio de Mazatlan, 1 ♂, 1 ♀; Plomosas, 1 downy chick; Escuinapa, 9 ♂, 9 ♀, 1 unsexed; Los Pielas, 3 ♂, 3 ♀; Arroyo de Lemones, 2 ♀; Jalpa, 1 ♀; Papachal, 1 ♂; Quotla, 1 ♂, 1 ♀; Los Robles, 1 ♀; Juana Gomez River, 3 downy chicks. *Nayarit*: Santiago, 1 ♀; San Blas, 1 ♀, 2 unsexed; Arroyo de Platanos, near Amatlan de Cañas, 1 ♂; Rio Ameca near Amatlan de Cañas, 1 ♂; Estancia, near Amatlan de Cañas, 1 ♀; Rio de Salvatierra, 1 ♂; Rancho San Pablo, Sierra de Alica, 1 ♂. *Jalisco*: Puerto Vallarta, 1 ♂, 1 ♀; Bahia de Banderas near Puerto Vallarta, 1 ♀; Barranca de Portillo near Guadalajara, 2 ♂, 1 ♀; Los Masos, 1 ♀. *Colima*: Lajueta, 1 ♂ (type of *O. p. lajuetae*), 1 ♀; Manzanillo, 1 ♀; Rio Armeria, 1 ♀. *Michoacan*: 5 miles northeast of Apatzingan, 2 ♂, 1 ♀; Tafetan, 1 ♀; La Salada, 3 ♂, 1 ♀, 1 unsexed; Hacienda de las Trochas, Tupila River, 1 ♂. *Morelos*: Tetela del Volcan, 1 ♂. *Puebla*: Tochimilco, 1 ♂; Rancho Papayo, 10 miles south of Tehuiztingo, 1 ♂, 1 ♀. *Guerrero*: Cuajinicualapa, 3 ♂; Chilpancingo, 1 ♂; Mexcala, 1 ♂; Papayo, 4 ♂; Tlalixtaquilla, 1 ♀; Ometepec, 1 ♂; Camaron, 1 ♂; Zihuatanejo, 2 ♂; Dos Arroyos, 2 downy chicks. *Oaxaca*: Punta Paloma, 10 miles south of Tapanatepec, 2 ♂; Rio Patos, 6 miles west of Tapanatepec, 2 ♀; Tehuantepec, 1 ♂, 1 ♀; Los Tejedos, west of Tehuantepec, 1 ♂; Ostuta River, 5 miles west of Zanatepec, 1 ♀; Huilotepec, 1 ♀, 5 unsexed young; Chicapa, 1 ♂; Llano Grande, 1 ♂, 1 ♀; Pluma, 1 ♀; Salina Cruz, 1 ♀; San Geronimo, 1 ♀; Chihuitan, 1 ♂; Santa Maria Chimalapa, 1 ♀ (see text); Rio Grande, 6 miles south of Matias Romero, 1 ♂. *Chiapas*: Hacienda Monserrate, 40 miles north of Arriaga, 1 ♂. Also seen: Western Mexico (type of *O. p. wagleri*); central Mexico, 1 ♀.

*Ortalis vetula*

UNITED STATES: *Texas*: Brownsville, 32 ♂, 13 ♀; Lomita Ranch, 3 ♂, 6 ♀, 2 downy chicks; Laredo, 1 ♂, 1 ♀; Rio Grande City, 1 ♀; Arroyo Colorado, 1 ♀; Arroyo Vertha, 2 ♂; Hidalgo, 8 ♂, 1 ♀; 8 miles northwest of Point Isabel, 1 ♀; Cameron County, no locality, 7 ♂, 5 ♀.

MEXICO: *Nuevo Leon*: Boquilla, 4 ♂ (including type of *mccalli*), 2 ♀; Rio Camachi, 2 ♂; Montemorelos, 1 ♂, 2 ♀; Salinas, 1 ♂, 1 ♀. *Tamaulipas*: Camargo, 1 ♀; Matamoros, 1 ♂, 1 ♀, Villagran, 2 ♂; Ciudad Victoria, 2 ♂, 1 ♀; Sierra Madre above Ciudad Victoria, 2 ♂; Tampico, 6 ♀; Aldama, 1 ♂; Rio Corona near Guemez, 1 ♀; Rio Sabinas near Gomez Farias, 3 ♂; Rio Martinez, 1 ♀; Rio Cruz, 1 ♂; Rio Tamesi near Rayon, 1 ♂; Rio Pilon, 1 ♂, 1 ♀; Santa Engracia, 4 ♂, 1 ♀; Presas, 1 ♂; Altamira, 3 ♂; near Altamira, 1 ♂, 1 ♀; no locality, 2 downy chicks. *San Luis Potosi*: Valles, 3 ♂, 3 ♀; El Bonito, 10 miles south of Valles, 1 ♀; Rio Verde, 1 ♀; near Tamazunchale, 1 ♀. *Veracruz*: Rio Panuco, 1 ♂; Jalapa, 1 ♀ (type of *jalapensis*), 1 unsexed; Hacienda Tortugas, 1 ♀; Hacienda de los Atlixcos, 2 ♂; Vega del Casadero, 2 ♂, 2 ♀; Plan del Rio, 1 ♂; Jico, 2 ♂; Cordoba, 1 ♂; La Antigua, 1 unsexed; Veracruz, 1 ♂, 2 ♀; Mirado near Veracruz, 1 unsexed; Laguna Larga, 1 ♂; Tres Zapotes, 5 ♂, 3 ♀; Ojochico, 3 ♂, 1 ♀; Achotal, 1 ♂; Paso Nuevo, 2 ♂, 4 ♀, 2 unsexed; Veracruz-Oaxaca border, 1 ♂; no locality, 1 ♂. *Oaxaca*: Soyaltepec, 1 ♀; Palomares, 1 ♂, 1 ♀; Tuxtepec, 3 ♂, 3 ♀; Guichicovi, 1 ♂; Tolloso, 3 ♂ (including type of *fulvicauda*), Tutla, 2 ♂, 3 ♀; Sarabia, 1 ♀; Montebello, 24 miles north of Matias Romero, 2 ♂, 1 ♀; 18 miles north of Matias Romero, 1 ♀; Santa Maria Chimalapa, 1 ♂. *Chiapas*: Yajalon, 1 ♂; Palenque, 2 ♀; San Cayetano, 2 ♀; El Ocote, Ocozacoautla, east bank of Rio de la Venta, 2 ♂, 1 ♀; Laxholob, Ocosingo, 1 ♀;

Laguna Ocotol, 1 ♂, 3 ♀; Malpaso, Siltepec, 1 ♀; Moriscal, 1 ♂, 1 ♀. *Tabasco*: Teapa, 2 ♀; Montecristo, 1 ♂; Balancan, 1 ♂, 1 ♀; 15 kilometers north of Reforma, 1 ♂; La Palma, 1 ♂; Tenosique, 1 ♂. *Campeche*: Apazote near Yohaltun, 1 ♂, 1 ♀; Matamoros, 1 ♂, 3 ♀; La Tuxpeña, 2 ♂ 2 ♀, 1 unsexed. *Yucatan*: Merida, 2 ♂ (including type of *pallidiventris*), 1 unsexed; Santa Clara, 1 ♂; Xocempich, 1 ♀; Chichen Itza, 16 ♂, 6 ♀; Izamal, 2 unsexed; Rio Lagartos, 1 ♀; San Felipe, 1 ♀; Temax, 1 unsexed; northern Yucatan, no locality, 2 unsexed. *Quintana Roo*: Cozumel Island, 5 unsexed<sup>1</sup>; Holbox Island, 4 unsexed; Mujeres Island, 2 unsexed; Meco "Island," 2 unsexed; El Meco (now Puerto Juarez), 1 ♂, 2 ♀; Coba, 2 ♀; Chunyaxche, 1 unsexed; Acomal, 1 unsexed; Camp Mengel, 2 unsexed; 46 kilometers west of Chetumal, 1 ♂; Tabi, 1 ♀; Estero Franco, 3 kilometers below Dos Bocas, 1 ♂, 2 ♀; 15 kilometers northwest of Kantunilkin, 1 ♂, 1 ♀; 15 kilometers northwest of Xtocomo, 1 ♂, 1 ♀.

BRITISH HONDURAS: Middlesex, 1 ♂; 22-mile station on the Stann Creek railroad, 1 unsexed; near Belize, 1 unsexed; Freetown, Sittee River, 4 ♂; near Manatee Lagoon, 2 ♀; Benque Ceiba, 1 ♂.

GUATEMALA: Tikal, 1 ♀; Uaxactun, 5 ♂, 2 ♀; 10 miles east of Uaxactun, 1 ♀; Chuntuqui, 1 ♂, 2 ♀; Sacchich, 1 ♂; Finca Chama, 1 ♂; Finca Sepacuite, 6 ♂, 2 ♀; Secanquim, 9 ♂, 6 ♀; Coban, 1 ♂, 2 unsexed; Panzos, 1 unsexed; Sierra de las Minas, 2 ♂, 1 ♀; Progreso, 1 ♂, 1 ♀; Los Amates, 2 ♂, 1 ♀; Gualan, 1 ♀; Quirigua, 1 ♂; Bobos, 3 ♂; Peten, no locality, 1 ♂; no locality, 2 unsexed.

HONDURAS: Utila Island, 7 ♂ (including type of *deschauensei*), 6 ♀; Omoa, 1 unsexed (type of *plumbiceps*); La Ceiba, 5 ♂, 2 ♀; Chamelecon, 1 ♀; Chamelecon River, 1 ♀; Trujillo, 1 ♂; Lake Yojoa, 1 ♂; El Jaral, Lake Yojoa, 1 ♀; Cantoral, 1 ♂; Monte Redondo, near Archaga, 1 ♂, 1 ♀; La Flor, near Archaga, 1 ♀; no locality, 2 unsexed.

NICARAGUA: San Rafael del Norte, 1 ♀; El Tanque, Matagalpa, 1 ♂; Matagalpa, 1 ♂; San Blas, 35 miles south of Metapa, 1 ♀.

COSTA RICA: Ballena, Guanacaste, 1 ♀.

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<sup>1</sup> The unsexed specimens listed from the islands are in the collection of the British Museum and were all collected by Gaumer allegedly in 1879 on Cozumel and in 1885 on Holbox, Mujeres, and Meco. Paynter (1955, p. 79) has questioned the authenticity of these records from Cozumel, Holbox, and Mujeres. Gaumer was apparently not always trustworthy, but these specimens are identical with *O. v. pallidiventris* taken at assured localities in northern Yucatan.

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