A REVISION OF THE TUFTED FLYCATCHERS OF THE GENUS *MITREPHANES*

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ONE of the most attractive birds of Mexican forests is the tawny little crested pewee, *Mitrephanes phaeocercus,* commonly called the Tufted Flycatcher. When I gathered material for a study of variation in the Mexican forms, I also compared all additional specimens of the genus I could borrow. Altogether I assembled 728 specimens, including all the proposed forms and series from every country and Mexican state the bird has been reported from except Ecuador.

The genus name *Mitrephanes* was a substitute by Coues (1882) for *Mitrephorus* Sclater, 1859, preoccupied. Apparently no one has questioned the validity or limits of the genus, for the small, weak feet and tarsi, pycnaspidean (Ridgway, 1907: 346 calls it quasi-pycnaspidean or quasi-holospidean) tarsal envelopes, and pointed crest make a unique combination. Ridgway (1907) recognized five species, although he was able to examine only two. Hellmayr (1927) lumped the entire genus in a single species, as did Zimmer (1930; 1938*a*) in the most thorough revision thus far. Griscom (1932) restated the specificity of *M. berlepschi,* and Sutton and Burleigh (1940), while they did not discuss the South American forms, distinguished *M. aurantiiventris* (of southern Central America) as a species separate from *M. phaeocercus*. It should be noted that Zimmer had only 76 specimens altogether and Sutton and Burleigh only 38 from north of the Isthmus of Tehuantepec.

HABITS AND HABITAT

My own field experience with *Mitrephanes* has been confined to México. There *M. phaeocercus* inhabits the more humid parts of the pine–oak forest and cloud (subtropical) forest. In winter it lives in tropical deciduous forest, tropical evergreen forest, and tropical thorn forest as well as in lower-elevation pine forest and cloud forest; it deserts higher-elevation pine forest. All that I encountered in pine or pine–oak forests were foraging out from exposed perches at the rims of barrancas or mountain ridges. In cloud forest they were foraging out over openings or low trees and returning to perches 20 to 100 feet above the ground, in the manner of a pewee (*Contopus*).

Skutch (1960) states that from Guatemala to western Panamá the Tufted Flycatcher is a permanent resident of subtropical forest and of temperate pine–oak forest. He describes the behavior briefly, including evidence of a close relationship with the pewees. All localities in central and eastern Panamá reported in the literature and on specimen labels

(*M. p. viridus* and *M. p. eminulus*) are from elevations of 2,000 feet or more, apparently in the subtropical zone. But the few localities in which *M. p. berlepschi* has been found, in western Colombia and northwestern Ecuador, are near sea level in the humid tropical zone! On the other hand, *M. olivaceus* in Peru and Bolivia occurs in upper humid tropical and subtropical forests at elevations from 4,000 to 8,000 feet (Zimmer, 1938*a*).

The literature makes no mention of migration in *Mitrephanes* except within México, nor have I uncovered any evidence of such movement. In México a marked altitudinal migration occurs, first noted by Van Rossem (1945), from the high mountains to the tropical lowlands. It seems most marked in northwestern México, where the breeding range is in the pine and pine–oak forests of the Sierra Madre Occidental and outliers (at elevations of 5,200–10,000 feet) but the wintering range is from lower pine–oak forests (Babizos and Rancho Batel, Sinaloa; mountains west of Tepic, Nayarit; 6,400–3,400 feet) to sea level in thorn forest (Culiacán, Quelite, and Cacalotan, Sinaloa). In northeastern México Miller *et al.* (1957: 96) recorded a similar movement from cloud forest in spring down to tropical deciduous forest in winter, near Gómez Farías, Tamaulipas. Farther south I have examined winter specimens from near Valle Nacional, northern Oaxaca, 1,900 feet, tropical evergreen forest, and Jamaica Junction, southern Oaxaca, 3,000 feet, tropical deciduous forest.

One specimen apparently represents a definite migration from one breeding area to a wintering area chiefly populated by a different race. I collected CAS 618550, adult male, 6 October 1955, 6 miles west of Tepic, Nayarit, in mixed woodland at 3,600 feet. Unlike 12 other fall and winter specimens from Nayarit, it is referable to the race *burleighi* rather than *tenuirostris*. This bird must have flown at least 75 miles west from its interior breeding range, unless it represents an unusual dark variation of *tenuirostris*.

SPECIFIC LIMITS

All the forms of *Mitrephanes* are allopatric. When Zimmer (1930) described the juvenal plumage of Peruvian *M. olivaceus* as more similar to that of the Central American forms than is the adult plumage, he argued that this showed their essential conspecificity. As shown in the section on variation below, present evidence shows distinct discontinuities in variation. The most abrupt break occurs in Ecuador, between the coastal forest of western Colombia and northwestern Ecuador on the one hand and the eastern slope of the Andes in Peru on the other. Lesser breaks occur in Central America—one between Nicaragua and Costa Rica, and another between central and extreme eastern Panamá.

A moderate course between the extreme points of view, which recognize four species or one, seems best to express the phylogeny of the genus. I would recognize two species—*M. phaeocercus* and *M. olivaceus*:

	phaeocercus	*olivaceus*
Range:	Northern México to northwestern Ecuador	Eastern Peru and Bolivia
Habitat:	Temperate pine and pine–oak forest, subtropical forest, and humid tropical forest	Subtropical forest and upper humid tropical forest
Size:	Larger to smaller	Larger than adjacent forms
Color:	Brown to yellowish green	Green—contrast marked with *phaeocerus* ventrally, but moderate dorsally

If an intermediate population exists, it may probably be found in the central Andes of Colombia.

Generic Relationships

Different authors have placed *Mitrephanes* with various other genera of flycatchers as the nearest relatives. Hellmayr (1927) put it in the subfamily Myiarchinae between *Cnemotriccus* and *Terenotriccus*. I compared skins of all 20 genera and most of the species included by Hellmayr in this subfamily except *Aphanotriccus* and *Praedo* (now usually lumped in the single genus *Aphanotriccus*), plus *Xenotriccus* Dwight and Griscom, 1927, and *Aechmolophus* Zimmer, 1938*b*, described subsequent to Hellmayr's work.

Mitrephanes is apparently a rather distinct genus, with closest relationships to *Pyrrhomyias* and *Contopus,* perhaps *Aechmolophus* and *Xenotriccus* next. I suggest the linear order *Nuttallornis, Contopus, Mitrephanes, Pyrrhomyias, Xenotriccus, Empidonax.* Table 1 compares all the genera of Myiarchinae that have any sort of a crest, even in one species. I have doubtless oversimplified some characteristics, for instance categorizing rictal bristles as short, moderate, or long. As noted above, Skutch (1960) described the behavior of *Mitrephanes* as rather similar to *Contopus*; but widely different from *Terenotriccus* and *Onychorhynchus.* Most recent authors merge *Blacicus* with *Contopus,* as I do here.

The genus *Aechmolophus* cannot be maintained; it should be lumped with *Xenotriccus.* The transfer is accordingly made: *Xenotriccus mexicanus* (Zimmer, 1938*b*) new combination. I studied 10 specimens of *X. mexicanus* and 3 of *X. callizonus,* all collected since Zimmer's work. These show that the differences between the two species in the shape of the crest and the shape of the tail are individual or seasonal. Valid dif-

TABLE 1

Comparison of Crested Genera of Myiarchine Flycatchers

	Myiarchus	*Contopus*	*Xenotriccus*	*Aechmolophus*	*Mitrephanes*	*Pyrrhomyias*	*Onychorhynchus*
Crest	None or slight	None or slight	Pointed, prominent	Pointed, prominent	Pointed, prominent	Bushy, slight	Fan shaped, large
Crown color	All dull	All dull	All dull	All dull	All dull	Bright patch	Bright patch
Bill	Large	Large	Small	Moderate	Small	Small	Large
Rictal bristles	Moderate	Short	Moderate	Moderate	Moderate	Short	Long
Nostril shape	Short or long ellipse	Long ellipse	—	Long ellipse	Long ellipse	Long ellipse	Long ellipse
Longest primary	8	9 (or 8)	7	8 (or 7)	8 (or 9)	8	7
Primary ten length compared to other primaries	Equal to 2 to between 4 and 5	Between 5 and 6 to between 7 and 8	Shorter than 1	Between 1 and 2 to between 2 and 3	Between 4 and 5 to between 5 and 6	Equal to 5 to between 5 and 6	Shorter than 1
Tail/wing ratio	0.85–0.94	0.75–0.84	1.03	0.95	0.81–0.84	—	0.82
Tarsus length (as per cent of wing length)	20–22	16–18	30	26–27	16–18	19	19–21
Tarsal scutellation	Proximal ⅓ holaspidean; distal exaspidean	All exaspidean or as in *Myiarchus*	Proximal ½ holaspidean; distal exaspidean	As in *Myiarchus*	All pycnaspidean	All pycnaspidean	All exaspidean
Syndactyly-fraction of basal phalanx of middle toe united to outer toe	¾	¾	—	¾	¾	¾	1 plus ¼ 2nd phalanx
Tail	Slightly double rounded, even, or slightly rounded	Slightly notched	Slightly rounded	Slightly rounded or slightly double rounded	Slightly notched	Slightly notched	Slightly rounded

ferences are of the same type and magnitude as those between the various species of *Empidonax*.

Molts and Plumages

Material is adequate from México for confident statements on molt in the races *phaeocercus, burleighi,* and *tenuirostris*. Adults have but one molt a year, a complete prebasic molt mainly in August. Evidence of some body molt was found as early as 4 July (a few fresh feathers in breast) and as late as 28 October (Allan Phillips specimen, label note "trace of molt on nape"). Only a few July adults show any molt, and most mid-September specimens appear to have completed their molt. A specimen I skinned 25 September showed no trace of molt. The order of molt beginnings is approximately: body feathers, inner primaries, rectrices, small wing feathers, tertials (about three-fourths of body plumage fresh by now), outer secondaries, crest.

Judging from specimens and my own observations, most Mexican birds are hatched in June, with lesser numbers in May and July. The first prebasic molt extends from as early as 14 July (some fresh plumage in back) to 28 October (not discernible in skin, but Allan Phillips label note "light molt on head, neck, belly, and flanks"). In most cases the main change occurs in August.

The extent of the first prebasic molt varies; in most cases it includes all feathers except the primaries, secondaries, and rectrices. In about one-third of the specimens two or three juvenal (white-tipped) upper tail coverts are retained, and in fewer cases one or more tertials. Regarding the crest and the wing bars (secondary coverts), I am in doubt. The feathers of the crest are of such lax structure that I cannot tell whether slight white tips mark juvenal feathers or first basic plumage; these are present on two to six feathers in a few first year birds, November to February.

The aspect of the wing bars in first year birds, October to January, varies from dull dark brown (as in adult basic plumage) to pale buffy, and no molt is evident after October. In several instances of pale wing bars, the feathers are freshly acquired first basic, and probably, though not certainly, these coverts are always replaced.

As implied above, the juvenal plumage differs from the adult basic in that the feathers are generally barred or tipped with buff, which fades to white. In addition, the juvenal plumage is rustier or tawnier than the adult plumage in the brown races and more or less brown, rather than green, in the green races. The aspect of first year birds in fall and winter is identical with that of adults at the same seasons except that the rectrices and primaries are tipped slightly with white. Also some of the

upper tail coverts and crest feathers are sometimes tipped, and the edgings of the tertials and the wing bars are sometimes paler than in adult feathers. The last tipping to wear off is usually that on the rectrices, which persists even as late as March (one specimen). I am unable to detect any sign of prealternate molt at any age or season.

The material at hand is inadequate in seasonal distribution and in label information to allow decisive statements about molts in the Central and South American forms, but apparently the prebasic molt occurs in *olivaceus* in July and August and in *aurantiiventris* and *eminulus* in August and September.

GEOGRAPHIC VARIATION

Wing length.—Bergman's Rule is operative in both directions from the equator, but most changes are not abrupt. Table 2 shows a sharp break between Colombia and Peru with a nonoverlap gap of 4 mm (over twice the standard deviation), and lesser breaks (with slight overlap) between Colombia and eastern Panamá and between central and western Panamá.

TABLE 2
SUMMARY OF MALE WING MEASUREMENTS IN MILLIMETERS, *Mitrephanes*

Taxon	*Population*	*Sample size*	*Range*	*Mean*	*Standard deviation*	*Coefficient of variation*
tenuirostris	Sonora, Chihuahua	29	70–77	73.28	1.86	2.53
"	Sinaloa	39	69–77	72.15	1.82	2.53
"	Durango	19	69–75	72.95	1.61	2.21
"	Nayarit	13	68–74	71.31	1.82	2.55
burleighi	Zacatecas, Jalisco	11	69–75	72.09	1.83	2.54
"	Michoacán, Morelos, Est. México	35	68–75	71.86	1.96	2.73
"	Guerrero	14	69–76	72.71	1.95	2.68
"	Southern Oaxaca	7	72–75	73.71	—	—
phaeocercus	Hidalgo, Puebla, Tamaulipas, San Luis Potosí	20	68–75	70.90	1.76	2.49
"	Veracruz, Northern Oaxaca	21	64–74	70.00	2.37	3.39
nicaraguae	Chiapas, Guatemala	17	67–75	70.53	1.88	2.67
"	Honduras, El Salvador	30	65–73	68.77	2.16	3.13
"	Nicaragua	9	62–70	65.33	—	—
aurantiiventris	Costa Rica	30	61–70	64.47	2.56	3.96
"	Western Panamá	37	60–69	64.38	2.01	3.11
vividus	Central Panamá	9	58–64	61.00	—	—
eminulus	Eastern Panamá	11	59–65	61.73	1.82	2.95
berlepschi	Colombia	3	56–60	57.67	—	—
olivaceus	Peru, Bolivia	11	64–71	67.00	1.76	2.63

TABLE 3
SUMMARY OF MALE TAIL LENGTH IN MILLIMETERS, *Mitrephanes*

Taxon	*Population*	*Sample size*	*Range*	*Mean*	*Standard deviation*	*Coefficient of variation*
tenuirostris	Sonora, Chihuahua	29	58–65	60.96	1.63	2.67
"	Sinaloa, Durango	58	56–63	59.64	1.65	2.76
"	Nayarit	14	56–62	58.18	1.69	2.91
burleighi	Zacatecas, Jalisco, Michoacán, Morelos, Est. México	44	55–63	59.61	1.71	2.87
"	Guerrero, Southern Oaxaca	19	56–63	59.84	1.96	3.27
phaeocercus	Hidalgo, Puebla, Tamaulipas, San Luis Potosí	20	57–65	59.60	1.83	3.07
"	Veracruz, Northern Oaxaca	20	55–61	58.20	1.72	2.96
nicaraguae	Guatemala, Chiapas	18	54–63	59.39	2.30	3.88
"	Honduras, El Salvador	26	51–59	54.23	2.07	3.81
"	Nicaragua	9	50–56	53.22	—	—
aurantiiventris	Costa Rica, Western Panamá	63	47–55	51.63	1.91	3.71
vividus	Central Panamá	9	48–56	50.89	—	—
eminulus	Eastern Panamá	11	48–53	49.91	1.60	3.22
berlepschi	Colombia	3	49–55	51.67	—	—
olivaceus	Peru, Bolivia	11	53–58	55.55	1.50	2.71

A smooth cline extends from western Panamá north through Chiapas to northeastern México and from eastern México westward and thence northward as well as southward to Sonora and southern Oaxaca. Measurements of female wings average 2 to 4 mm less than those of males and show the same trends.

Tail length.—The shortest-tailed population is in eastern Panamá, and tail length increases in both directions from there. The sharpest break, or step, is between Honduras–El Salvador and Guatemala as shown in Table 3.

Bill length.—Length of bill was measured from the feathers. It actually doesn't vary much geographically (Table 4), but note that the shortest-billed population is also one of the longest-winged, and that the shortest-winged population is also one of the longest-billed. Thus the wing length/bill length ratio in northern *burleighi* is 8.4, in equatorial *berlepschi* 6.3.

Bill width.—The bill width was measured with a caliper at the center of the nostril. Unfortunately, differences in technique of the various preparators in closing the bill in this soft-billed flycatcher have badly obscured natural variation (note high coefficients of variation in Table 5).

TABLE 4
SUMMARY OF MALE BILL LENGTH IN MILLIMETERS, *Mitrephanes*

Taxon	*Population*	*Sample size*	*Range*	*Mean*	*Standard deviation*	*Coefficient of variation*
tenuirostris	Sonora, Chihuahua	31	8.1–9.6	8.79	.363	4.13
"	Sinaloa, Durango, Nayarit	74	8.0–9.7	8.78	.377	4.29
burleighi	Zacatecas, Jalisco, Michoacán, Morelos, Est. México	50	7.8–9.6	8.55	.408	4.77
"	Guerrero, Southern Oaxaca	21	7.9–9.4	8.71	.394	4.52
phaeocercus	Tamaulipas, San Luis Potosí, Hidalgo, Puebla, Veracruz, Northern Oaxaca	48	7.8–9.4	8.62	.402	4.67
nicaraguae	Chiapas, Guatemala	21	7.7–9.1	8.62	.379	4.41
"	Honduras, El Salvador, Nicaragua	36	7.8–9.9	8.84	.452	5.12
aurantiiventris	Costa Rica	30	8.0–9.6	8.82	.401	4.54
"	Western Panamá	39	8.2–10.0	9.13	.465	5.09
vividus	Central Panamá	9	7.9–9.7	8.63	—	—
eminulus	Eastern Panamá	11	8.4–9.5	8.98	.347	3.86
berlepschi	Colombia	3	8.8–9.4	9.13	—	—
olivaceus	Peru, Bolivia	11	8.3–9.5	9.09	.428	4.72

In an attempt to circumvent this problem, I separately calculated two samples collected only by Chester C. Lamb, one on the west coast of México and the other on the east coast (marked with an asterisk in Table 5). Apparently the difference in bill width between the populations of eastern and western México has been exaggerated in the past. The two smallest (shortest-winged) subspecies, *vividus* and *berlepschi,* have the broadest bills.

Color of underparts.—In this and following sections, "fresh-plumaged" birds are arbitrarily defined as those taken from the acquisition of mostly fresh body plumage in August through February. "Recent specimens" are arbitrarily defined as those taken since 1930. Statements on plumage color refer only to fresh, recent specimens, except in the few cases where noted otherwise.* Capitalized color names are those from Palmer and Reilly (1956), with whose color standard comparisons were made at all stages.

Five classes, with separation 100% from 100%, make simple, obvious divisions: (1) pale tawny—*tenuirostris, burleighi,* and *phaeocercus*; (2)

* In this and succeeding sections specimens marked with an asterisk are either too old (before 1931) or worn (after February) for truly valid color comparison; a few were used because no recent, fresh material from certain states exists.

TABLE 5
SUMMARY OF MALE BILL WIDTH IN MILLIMETERS, *Mitrephanes*

Taxon	*Population*	*Sample size*	*Range*	*Mean*	*Standard deviation*	*Coefficient of variation*
tenuirostris	Sonora, Chihuahua	30	4.0–5.1	4.71	.252	5.35
"	Sinaloa, Durango	58	3.3–5.2	4.67	.289	6.20
"	Nayarit	16	3.8–5.2	4.76	.330	6.94
burleighi	Zacatecas, Jalisco, Michoacán, Est. México	45	4.2–5.4	4.72	.226	4.79
"	Guerrero, Southern Oaxaca	20	3.8–5.2	4.52	.400	8.87
phaeocercus	Tamaulipas, San Luis Potosí, Hidalgo, Puebla	20	4.6–5.6	5.02	.300	5.98
"	Veracruz, Northern Oaxaca	24	4.2–5.4	4.91	.401	8.17
nicaraguae	Chiapas, Guatemala	21	4.0–5.2	4.70	.291	6.21
"	Honduras, El Salvador, Nicaragua	39	3.2–5.4	4.46	.557	12.47
aurantiiventris	Costa Rica, Western Panamá	68	4.3–5.8	4.92	.300	6.09
vividus	Central Panamá	9	4.5–6.0	5.02	—	—
eminulus	Eastern Panamá	11	4.7–5.4	4.99	.178	3.57
berlepschi	Colombia	3	4.9–5.2	5.10	—	—
olivaceus	Peru, Bolovia	10	4.2–5.1	4.64	2.38	5.13
tenuirostris	*Lamb collected, Sinaloa	35	4.0–5.2	4.69	.244	5.22
phaeocercus	*Lamb collected, Puebla, Vera Cruz	9	4.6–5.4	4.90	.231	4.72

* Special groups—see text.

dark tawny—*nicaraguae*; (3) buffy yellow—*aurantiiventris* and *vividus*; (4) yellow—*eminulus* and *berlepschi*; (5) lime—*olivaceus*. In addition to color, the contrast between anterior underparts (throat and breast) and posterior underparts (belly, crissum, and under tail coverts) is moderate and the transition gradual in classes 1, 2, and 5, but prominent and sharp in classes 3 and 4. Within each class, the specimens may be analyzed thus:

(1) A gradual northwest to southeast cline of increasing darkness plotted in this order: 12 Sonora[1] → 42 Sinaloa, 1 Chihuahua, 10 Durango, 12 Nayarit, 1 Jalisco, 13 Michoacán, 15 Guerrero → 1 Nayarit, 2 Zacatecas, 2 Jalisco, 19 Est. México → 11 southern Oaxaca, 3 Tamaulipas → 5 Puebla, 13 Vera Cruz → 6 northern Oaxaca. Separation on

[1] Arrows separate series that may readily be distinguished by eye, but commas have no significance; numbers are the actual specimens in the compared series.

this character is 100% from 100% between the extremes (Sonora and northern Oaxaca) and about 90% from 90% between Sonora and Est. México or between Michoacán and Vera Cruz. Anterior underparts are medium, yellowish Tawny; posterior underparts are light, brownish Buffy Yellow in this class. A few worn (March) specimens* suggest that San Luis Potosí and Hidalgo belong near Est. México and Tamaulipas in the above series.

(2) I see very little internal geographic variation. The contrast with the darkest group (northern Oaxaca) above is relatively slight, although all individuals of (2) are clearly darker and most are yellower posteriorly. Anterior underparts are dark, yellow-brownish Tawny; posterior underparts are light, brownish Buffy Yellow in this class. Three old (February 1909) specimens* from Nicaragua are slightly paler and yellower than the 47 more recent ones from Chiapas, Guatemala, Honduras, and El Salvador.

(3) I see no geographic variation within the 39 specimens from Costa Rica and western Panamá, and the gap from class (2) is considerable. Anterior underparts are medium, between Buffy Brown and Buffy Yellow; posterior underparts are light Buffy Yellow. Six old (January 1926)* and seven worn (March 1951 and 1962) specimens* from central Panamá are duller and less buffy anteriorly and paler, less buffy, more purely yellow posteriorly.

(4) Two specimens from Cerro Tacarcuna, eastern Panamá, are warmer, more orangish on both areas than two specimens from southern Colombia. In this class the anterior underparts are medium, brownish Buffy Yellow; the posterior are pale Yellow. Seven worn old (March–June, 1912 and 1928) specimens* from Cana, eastern Panamá, show a distinct variance; they are colder, less buffy than those from Cerro Tacarcuna, although paler, less greenish anteriorly and less purely yellow posteriorly than specimens from Colombia, either northern* or southern.

(5) I can see no geographic variation within Peru (four specimens), not even when an old specimen* from Bolivia is added. This class is distinctly darker posteriorly and greener throughout than all the preceding. The anterior underparts are dark, olivaceous Yellow Lime; the posterior are light, grayish olivaceous Yellow Lime.

Color of upperparts.—Specimens compared were the same as those used for the ventral surface, above. Three major classes differ radically and obviously, segregation being 100% from 100%.

(1) Varying from pale to dark Olive and pale to dark Brownish Olive —México and Central America south to El Salvador.

(2) Approximately dark, yellow-limish Olive—Costa Rica and western Panamá.

(3) Varying from medium to dark olivaceous Yellow-Lime—eastern Panamá and South America.

The general trends of dorsal color are: (a) A prominent north to south cline of increasing greenness runs from northwestern México to Peru. In México north of Tehuantepec the trend is from the Pacific slope to the Atlantic slope, but in Central America no Pacific versus Atlantic slope differences are apparent. (b) A two-way cline of darkness decreases from maximum in Chiapas northwest and southeast to minimum, or pallor, in northwestern México and Peru. This seems to follow Gloger's Rule north from Chiapas, but to proceed almost inversely to Gloger's Rule from Chiapas southward. (Portig, 1965, gives Central American rainfalls; the climates involved are poorly known in South America.) (3) A slight cline of differing warmth (redness) in México grades from warmest in central western México to colder in eastern México and coldest in northwestern and southern México. Within each of the major classes these variations can be seen:

(1) In northwestern México grayness and pallor are extreme, and as far south as Nayarit and coastal Jalisco only slight warming appears. The color is yellowish Brownish Olive. In interior central México (Zacatecas, interior Jalisco, Michoacán, Est. México) and south to the Pacific coastal ranges of Guerrero and southern Oaxaca, colors are variable, but generally darker. Specifically a series from Zacatecas, interior Jalisco, and Nayarit (apparently a migrant from a breeding population of Zacatecas or Jalisco) is distinctly darker than any of 66 from Durango, Nayarit, etc., and warmer and darker than southern Oaxaca birds. A long series from Michoacán and Est. México is slightly paler than the preceding and the following groups, and also slightly duller, less green than the following. The Guerrero series is slightly darker again, and slightly greener; the southern Oaxaca group is grayer, less brownish than the three preceding groups. The populations from Zacatecas to southern Oaxaca are all a yellowish-brown Olive.

In eastern México lives the dark olive race *phaeocercus* (yellowish-brown Olive again in the color standard). Although 100% from 100% distinguishable from the Sonora to Nayarit series above (darker and greener), it is not prominently differentiated from the Zacatecas to Oaxaca series. To the north a series from Tamaulipas and northern Puebla is slightly paler and browner than that from west central Vera Cruz and northern Oaxaca, and the series from Vera Cruz is slightly greener than any other. As to distinction from Zacatecas to Oaxaca populations (*burleighi*), *phaeocercus* is slightly greener northward (Tamaulipas–Puebla versus Est. México–Michoacán) and slightly greener as well as darker

southward (Vera Cruz–northern Oaxaca versus Guerrero–southern Oaxaca), with the sharpest contrast in the state of Oaxaca.

The description by Sutton and Burleigh (1940) of *hidalgensis* was based upon a lack of enough freshly taken topotypes from Vera Cruz; here I must emphasize that all the specimens considered above were taken in 1941 or later except for some from Sonora and Sinaloa that date back as far as 1931. The March series from Hidalgo* and a single March bird from Cañada Grande, southern San Luis Potosí*, I have classified as worn but recent. The latter is precisely between Est. México *burleighi* and Tamaulipas–Hidalgo–Puebla *phaeocercus*. The former fit in perfectly with the October to February Tamaulipas–Puebla series and are, in fact, also indistinguishable from the palest individual from Vera Cruz. A special comparison* of all available recently taken March–April specimens from eastern Mexico (2 Tamaulipas, 3 San Luis Potosí, 6 Hidalgo, 6 Puebla, 7 Vera Cruz, 1 northern Oaxaca) confirmed the submergence of *hidalgensis*. The 5 greenest specimens came from Vera Cruz (4) and Puebla (1). In justification of Sutton and Burleigh's 1940 action, it should be noted that the only freshly taken topotype of *phaeocercus* available to them (Cornell 8294, 29 April 1939, Jalapa) is the brownest, least green recently taken Vera Cruz specimen I have seen—almost as brown as foxed skins of 1880.

South of the isthmus of Tehuantepec lives the darkest population, that of Chiapas, which is blackish Olive, distinctly darker than all populations to the north and averaging darker than series from Guatemala, Honduras, and El Salvador. Old specimens (1909) from Nicaragua* are indistinguishable from the paler individuals from Honduras and El Salvador.

(2) Little variation can be seen in this class, geographic or otherwise. However, the brownest single specimen, and also one of the darkest, is from Cartago province, central Costa Rica. The old (January 1926)* or somewhat worn (March 1951)* specimens from central Panamá are duller and greener and slightly darker than those from Costa Rica and western Panamá.

(3) A well marked cline of darkness and greenness occurs within this class. Eastern Panama specimens are the darkest, duskiest, least green; Colombian specimens are greener (near Lime but less yellowish) and paler; Peruvian specimens are still paler and greener. The gap between groups (2) and (3) is prominent, with the eastern Panamá birds distinctly greener than those from western and central Panamá.

Color of juvenal plumage.—A series of 43 specimens from all subspecies except *vividus* and *berlepschi* showed prominent geographical variation. Ventrally a smooth cline from pale Buffy Brown in Sonora darkened southeastwardly to deep tawny Buffy Brown to brownish Tawny in

Chiapas and Nicaragua; in Costa Rica and eastern Panamá the underparts were a little paler again and distinctly yellowish Buffy Brown; in Peru tawny Buffy Brown. Dorsally, a smooth cline ran from pale Sepia tipped with pale Tawny in Sonora, darker southeastward to dark Sepia tipped with Tawny in Chiapas, Guatemala, Nicaragua, and Honduras; in Costa Rica and eastern Panama the upperparts were a little paler again, and had more yellowish Tawny tippings. In Peru the upperparts were still paler and buffier, Buffy Brown tipped with pale Tawny.

Other characters.—I am unable to correlate with geography the contrast between crest coloration and that of the back.

Discussion

The inverse relationship in Central and South America, the opposite of Gloger's Rule, might be explained by assuming that a shift from a brown to a greener color resulted in more additional protection than a shift from a paler to a darker shade. For a bird of the upper story of the forest like *Mitrephanes,* I prefer to express it in a different way. The green coloration would seem to be an adaptation to always-green subtropical and humid tropical forests and the brown or tawny-and-olive coloration to partly brown pine–oak forests, with this adaptation overriding Gloger's Rule.

Zimmer (1930) stated that the brown juvenal plumage in the southern forms of *Mitrephanes* indicates that the brown northern forms are nearer the ancestral type. I agree and suggest a hypothetical history of the genus. I suggest that the genus originated in the late Tertiary in Central America or Mexico, from the same section of the family Tyrannidae that gave rise in the same region at about the same time to *Contopus, Empidonax, Pyrrhomyias,* and *Xenotriccus.* The original form was brown in color and lived in temperate pine–oak forest. During one of the earlier glacial advances when temperate forests were extensive, it spread throughout much of Central America. During an interglacial period it was then restricted to isolated mountains; on one of these it developed green coloration as an adaptation to subtropical forest. Subsequently the green form spread southward into South America in almost continuous subtropical forest during Wisconsin times, only to have the range broken up again by the warming trend of Recent climatic change. (Martin, 1958, and Savage, 1966, discuss Pleistocene ecology in Central America.) The invasion of subtropical forest by brown forms to the north was a Recent event, unaccompanied by a radical color change. A lessening cline of slight dorsal greenness in the brown forms parallels the amount of subtropical forest habitat available, north from Nicaragua. This suggests a northwestward flow of green genes which gives out in Guerrero and San Luis Potosí along with the subtropical forest.

RESUME OF SPECIES AND SUBSPECIES

(All localities cited in this section refer to specimens examined.)

Mitrephanes phaeocercus tenuirostris Brewster 1888 (near Oposura, Sonora, México).

Paler throughout and averaging more slender billed than all other forms of the genus. Also larger (wing and tail lengths) than all other forms except *burleighi*.

Range: Mountains of northeastern Sonora (Oposura, Pinos Altos) and northwestern Chihuahua (Sierra Nácori, Bravo, Mina Abundancia, Jesús María) south along the western flank of the Sierra Madre Occidental in Chihuahua, Durango, and Sinaloa to Nayarit (Santa Teresa, mountains west of Tepic) and coastal Jalisco (Sierra Autlán). Descends in winter to low valleys and the coastal plain.

Mitrephanes phaeocercus burleighi Phillips 1966 (Rio Molino near San Miguel Suchistepec, southern Oaxaca, México).

Darker than *tenuirostris* throughout; also the southern populations (Guerrero and Oaxaca) are slightly greener dorsally and the northern populations are duller, browner dorsally.

Range: Sierra Madre Occidental, Sierra Madre del Sur, and most of Trans-volcanic Range; from western Zacatecas (west of Milpillas, Monte Escobedo) and central Jalisco (Tapalpa, Mezamitla) east through Michoacán to western Est. México (Villa Victoria, Temascaltepec) and northern Morelos (Coajomulco); south to near the Pacific coast of Michoacán (Coalcomán), Guerrero (Omilteme, Cerro Teotepec), and Oaxaca (near Lachao, Rio Molino). Descending to the valleys in winter and even migrating almost to the coast in Nayarit (mountain west of Tepic).

Remarks: This race is a weak one, but recognizing it is convenient; the alternative would be to regard the entire series of populations as intermediate between *tenuirostris* and *phaeocercus*. As constituted, about 90% of all individuals can be distinguished in fresh plumage (100% of certain populations). Too few recently taken specimens exist to define precisely the subspecific boundaries in Jalisco or in Oaxaca. To the east, specimens from southern San Luis Potosí (Cañada Grande) and extreme western Puebla (Los Venerables) are intermediate between *burleighi* and *phaeocercus*.

Mitrephanes phaeocercus phaeocercus Sclater 1859 (Córdoba, Vera Cruz, México).

Greener than *burleighi* dorsally and darker ventrally; smaller (wing and tail lengths) than *tenuirostris* and *burleighi*; also darker dorsally than *burleighi* southward.

Range: Sierra Madre Oriental from southern Tamaulipas (Rancho Cielo) and southeastern San Luis Potosí (near Xilitla) south through Hidalgo, eastern Puebla, and western Vera Cruz, in eastern mountains southeast to Cerro Zempoaltepec, Oaxaca (Moctum, Totonotepec), and central Oaxaca (Cerro San Felipe, 24 miles northwest of Oaxaca City, 15 miles west of Oaxaca City). Descending to the valleys in winter.

Mitrephanes phaeocercus nicaraguae Miller and Griscom 1925 (San Rafael del Norte, Nicaragua).

Darker than *phaeocercus* throughout, and also smaller. The southernmost population, from Nicaragua, is also somewhat yellower on the posterior underparts; the tail is shorter from Honduras south.

Range: Mountains of northern Chiapas (5 miles north of Jitotol) southeast through Chiapas, Guatemala, El Salvador, and Honduras to northeastern Nicaragua (San Rafael del Norte, Matagalpa). Permanent resident in temperate and subtropical forests according to Skutch (1960) and specimen labels.

Remarks: The submergence of the familiar race *quercinus* Dickey and Van Rossem (1927) is a direct result of the large amount of material now available from Central America. The shorter wing claimed by Miller and Griscom as a distinction for *nicaraguae* from a Guatemala series is not great (see Table 2), and the shorter tail

is shared by the series from El Salvador, whence *quercinus* was described. The color characters claimed by Dickey and Van Rossem are slight to my eye, but no fresh specimens from Nicaragua and El Salvador have been seen, and it is not clear whether Van Rossem, Griscom, or anyone else compared the Salvador and Nicaragua series directly when they were still unfaded. If the present subspecies is to be split, the new form must certainly be described from Chiapas, so that size variation is coordinated with color, and freshly taken specimens from Nicaragua and El Salvador must be compared.

Mitrephanes phaeocercus aurantiiventris (Lawrence 1867) (Tabacales, Costa Rica).

Distinctly yellower ventrally and greener dorsally than *nicaraguae*; also averaging smaller.

Range: Mountains of north-central Costa Rica (Villa Quesada, Alajuela Province) to eastern Panamá (throughout mountains of Chiriquí Province). Permanent resident in temperate and subtropical forests according to Skutch (1960) and specimen labels.

Mitrephanes phaeocercus vividus (Griscom 1927) (mountains behind Chitré, Chitré Province, Panamá).

Smaller than *aurantiiventris*; also duller, darker, and greener dorsally, duller and less buffy on anterior underparts, paler and more purely yellow on posterior underparts.

Range: Permanent resident of subtropical mountain forests of the central part of Panamá, in the provinces of Chitré (mountains behind Chitré), Coclé (Cerro La India Dormida, Head of Rio Guabel), and Panamá (Cerro Compana).

Mitrephanes phaeocercus eminulus (Nelson 1912) (Cana, Darién Province, Panamá).

Averaging longer winged than *vividus*; also greener and paler dorsally and distinctly yellower ventrally.

Range: Permanent resident of subtropical zone in eastern Panamá, in Darién Province (Cerro Malí, Cerro Tacarcuna, Cerro Pirre = Cana).

Remarks: As noted above, the population of Cerro Pirre differs in one character—less buffy underparts—from that of the Cerro Tacarcuna area to the north. On the basis of present material this would not justify the description of a new race.

Mitrephanes phaeocercus berlepschi (Hartert 1902) (Bulún, Ecuador).

Shorter winged than any other race; as compared with *eminulus,* tail averaging slightly longer, yellower, less orangish ventrally, and greener and paler dorsally.

Range: Humid tropical forest of the Pacific coast of Colombia (Mungarido and Malugita, Choco; La Guayancana, Nariño) and northwestern Ecuador.

Mitrephanes olivaceus Berlepsch and Stolzmann 1894 (Gorrita del Sol, Junín Province, Peru).

Larger than *berlepschi* and greener throughout; also paler dorsally and much darker on posterior underparts.

Range: Subtropical and upper humid tropical forests of the eastern slope of the Andes from northern Peru (Rio Jelashte, San Martín Province) to eastern Bolivia (Quebrada Honda).

Specimens Examined

Mitrephanes phaeocercus tenuirostris—México: Sonora 25, Chihuahua 21, Sinaloa 62, Durango 38, Nayarit 34, Jalisco 1.

M. p. burleighi—México: Zacatecas 4, Jalisco 20, Michoacán 44, Est. México 25, Morelos 14, Nayarit 1, Guerrero 32, Oaxaca 20.

M. p. phaeocercus (including intergrades with *burleighi*)—*México*: Tamaulipas 5, San Luis Potosí 17, Hidalgo 7, Puebla 13, Vera Cruz 37, Oaxaca 11.

M. p. nicaraguae—México: Chiapas 25, *Guatemala* 19; *Honduras* 50; *El Salvador* 7; *Nicaragua* 13.

M. p. aurantiiventris—Costa Rica 50; *Panamá*: Chiriquí 73.

M. p. vividus—Panamá: Chitré 6; Coclé 5, Prov. Panamá 1.

M. p. eminulus—Panamá: Darién 20.

M. p. berlepschi—Colombia: Choco 2; Nariño 2.

M. olivaceus—Peru: San Martín 2, Huánuco 3, Junín 7, Cusco 3, Puno 1; *Bolivia:* Cochabamba 1.

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