

MICRASTUR GILVICOLLIS, A VALID SPECIES SYMPATRIC WITH *M. RUFICOLLIS* IN AMAZONIA

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For well over a hundred years the systematics of the smaller forms of the neotropical genus *Micrastur*, the forest falcons, has been a subject of controversy. General agreement has gradually resulted with respect to most of the taxa, but there is still confusion surrounding the forms *gilvicollis* and *plumbeus* and their relationship to *M. ruficollis*.

It is generally believed that all the small forest falcons inhabiting Amazonia belong to a single form under the name *gilvicollis*. This form has been considered a distinct species by Hellmayr (1910:410, 1921:178), Pinto (1935:96-99, 1947:322-328, 1964:91), Hellmayr and Conover (1949:255-258), Phelps and Phelps (1958:72), Meyer de Schauensee (1966:62), and Haverschmidt (1968:71). However, it has been treated as a geographic race of the widely distributed *M. ruficollis* by Sclater (1918:346), Hellmayr (1929:454), Peters (1931:278), Amadon (1964:19-22), Brown and Amadon (1968:750), and Meyer de Schauensee (1970:51).

The present paper provides morphological and acoustical evidence to show that, contrary to generally prevailing concepts, there are actually two very similar but specifically distinct forms (sibling species) of small *Micrastur* which are sympatric, even largely syntopic, throughout Amazonia. One of these is relatively homogeneous morphologically throughout the area and should bear the name *M. gilvicollis*. The other is in fact a form of *M. ruficollis* and intergrades with neighboring forms in some of the peripheral areas of Amazonia.

"Amazonia" is here used in the broad geographic sense to include not only the humid equatorial forests of the Amazon River basin, extending west to the base of the Andes in northern Bolivia, eastern Perú, eastern Ecuador, and southeastern Colombia, but also the Guianas and Venezuela south of the main Orinoco River, extensive areas of which constitute a biomic continuum with Amazonia proper and therefore show considerable avifaunistic affinity to it.

PREVIOUS TAXONOMIC TREATMENTS

The small forest falcons of Amazonia are gray; they do not exhibit the gray/rufous dichromatism which, to greater or lesser degree, characterizes *M. ruficollis* in many parts of its range. Further, although the underparts are barred with black or gray and white (as in all *M. ruficollis*), in Amazonian birds this is extremely variable in extent—from wholly barred underparts to barring only on the breast. This and other variable external features were used in earlier attempts to divide the Amazonian population into more than one taxon. All of these were found unacceptable and gradually the opinion prevailed that there was only one highly variable form. Hellmayr's position in this respect may have been influential during recent times, for he was firmly convinced that all the gray birds of Amazonia belonged to only one form, *gilvicollis*, which he treated first as a species (1910:410, 1921:178), and later as a race of *M. ruficollis* (1929:454).

Then Pinto presented evidence for considering *M. gilvicollis* specifically distinct. He based his opinion upon two gray specimens from the coastal belt of southern Bahia (well within the range of *M. r. ruficollis*) which he considered to be inseparable from the gray birds of Amazonia and, therefore, inescapably referable to that form (1947:325). (In agreement with Hellmayr, Pinto called all birds from Amazonia *gilvicollis*.) In express reliance on Pinto's findings, Hellmayr (in Hellmayr and Conover 1949:255-258) again granted species status to *gilvicollis*. Yet Pinto himself still had some doubts because of evidence of intergradation between the birds of Amazonia and *M. ruficollis* elsewhere in Brazil (1947:327).

Amadon, too, saw evidence "that around the entire borders of its huge Amazonia range the characters of *gilvicollis* blend with those of neighboring races [of *M. ruficollis*]" (1964:20); he therefore preferred to treat *gilvicollis* tentatively as a race of *M. ruficollis*.

In these and other treatments the concept

TABLE 1. Characteristics of adult *Micrastur* spp. specimens collected in Venezuela south of the main Orinoco River after recording their voices.

Catalog no. ^a	Sex	Voice ^b	Wing chord (mm)	Tail (mm)	Ratio: wing/tail	No. tail bars ^c	Color of	
							iris	facial skin ^d
Group R (<i>M. r. concentricus</i>)								
6306	♂	1	175	171	1.02	3	brown	y-o
6333	♂	1	177	159	1.11	3	brown	y-o
6213	♀	1	186	174	1.07	3	brown	y-o
Group G (<i>M. g. gilvicollis</i>)								
5197	♂	2	(173)	(134)	molting	(2)	white	r-o
5184	♂	2	181	149	1.22	2	white	r-o
6518	♂	2	181	145	1.25	2	white	r-o
(spirit coll.)	♂	e	180	150	1.20	3	white	r-o

^a Collection of the Estación Biológica de Rancho Grande.

^b 1 = Normal vocalizations similar to *M. ruficollis zonothorax* as well as to other races of *M. ruficollis*; 2 = normal vocalizations similar to each other but not similar to *M. ruficollis*.

^c The number of tail bars is the total white or light-colored transverse bars on the upper surface of the central rectrices, excluding the tip.

^d y-o = yellowish-orange; r-o = reddish-orange.

^e This bird was caught in a net and thus was not singing when caught. A bird with a type 2 voice did sing in this same spot at dawn of the morning the bird was netted.

that only one form of small *Micrastur* inhabits Amazonia prevails.

MATERIAL STUDIED

In the past few years I have collected for the Estación Biológica de Rancho Grande, Venezuela, six specimens of small *Micrastur* from the regions south of the main Orinoco River in Venezuela. All were in adult plumage. All were collected while "singing," after I had recorded their voices. For comparison, specimens of singing birds were also taken in north-central and western Venezuela, after their voices were recorded. The different recordings were compared aurally and audiospectrographically. Three of the specimens from south of the Orinoco had vocalizations similar to those recorded in north-central and western Venezuela, given by *M. ruficollis zonothorax*. The others had voices similar to each other but different from *M. r. zonothorax*.

The two groups thus derived from vocal characters proved to be different in other characters as well. To establish the fundamental differences between these two groups (R and G), the six specimens, together with another from the same area, taken in a net by G. Stuart Keith, are listed with their pertinent mensural and other characters (table 1).

Some 200 adult specimens of small *Micrastur* in various museums of the United States, Brazil and Venezuela were also examined; their measurements are given in table 2.

THE TWO SPECIES IN AMAZONIA

From table 1, it is readily seen that two different forms are involved: in addition to consistent differences in voice and in colors of soft parts, one of these forms is relatively short-winged and long-tailed while the other is the converse. Comparison of these with the many museum specimens of small *Micrastur* showed that the mensural proportions (wing/

tail ratio) of the Group R birds (with the *M. ruficollis*-type voice) correspond to those which are doubtless races of *M. ruficollis* throughout the extensive presently acknowledged range of this species (compare the ratios of Group R in table 1 with those of *ruficollis*, *zonothorax*, *guerilla*, and *interstes* in table 2).

Further, I found that throughout Amazonia, formerly considered not to be inhabited by *M. ruficollis* (except to the extent that certain authors treated *gilvicollis* as a race of *M. ruficollis*), there are numerous specimens that correspond to the Group R birds in wing/tail ratio (compare *concentricus* in table 2 with Group R in table 1), while other specimens from throughout Amazonia are similar in mensural proportions to the group G birds (compare *gilvicollis* of table 2 with Group G in table 1). Although there is considerable overlap in absolute measurements, the ratios of wing/tail of all specimens that correlate with the Group R birds are smaller than those of all specimens that correlate with the Group G birds. This striking difference is easily seen in figure 1. (Figure 1 was prepared before the material from Brazilian museums was added to table 2. The addition of these data increased the overlap in absolute measurements but did not affect the dichotomy of wing/tail ratios.)

It thus appears evident that there are two distinct forms of small *Micrastur* inhabiting Amazonia, one of which is a form of the widespread species *M. ruficollis*. There are three old names applicable to the birds of Ama-

TABLE 2. Measurements of adult specimens of *Micrastur* spp.

Taxon	Sex	Wing chord (mm)			Tail (mm)			Ratio, wing/tail		
		n ^a	range	\bar{x}	n ^a	range	\bar{x}	n ^a	range	\bar{x}
<i>M. r. ruficollis</i>	♂	15	159-172	167	15	157-174	166	15	0.96-1.06	1.00
	♀	10	171-182	176	10	154-187	176	10	0.95-1.07	1.00
Type of <i>S. ruficollis</i> Vieillot ^b	♀		175			170			1.03	
<i>M. r. zonothorax</i>	♂	17	166-180	173	17	158-180	168	17	0.96-1.08	1.03
	♀	14	174-190	179	13	162-181	172	13	0.99-1.10	1.04
<i>M. r. guerilla</i>	♂	9	160-177	166	9	151-173	160	9	1.01-1.06	1.04
	♀	6	160-180	173	6	158-172	162	6	1.01-1.09	1.06
<i>M. r. interstes</i>	♂	19	157-172	165	17	146-167	154	17	1.02-1.11	1.07
	♀	14	160-179	171	12	149-170	158	11	1.04-1.12	1.09
<i>M. r. concentricus</i>	♂	23	157-178	169	23	140-171	157	23	0.99-1.14	1.08
	♀	14	170-186	177	13	151-174	162	13	1.05-1.15	1.10
Type of <i>Nisus concentricus</i> Lesson ^b	imm ♂		165			160			1.03	
Type of <i>M. pelzelni</i> Ridgway ^b	♂		6.50 inches; 165.1 mm			6.30 inches; 160 mm			1.03	
<i>M. g. gilvicollis</i>	♂	27	165-195	182	27	135-155	146	27	1.18-1.34	1.24
	♀	24	170-198	186	24	130-161	148	24	1.19-1.35	1.25
Type of <i>S. gilvicollis</i> Vieillot ^b	(-)		(“somewhat worn”) 185			155			1.19	
<i>M. g. plumbeus</i>	♂	4	163-187	173	3	123-133	129	3	1.29-1.33	1.31
	♀	4	172-180	176	4	134-140	135	4	1.23-1.34	1.30

^a Discrepancies in numbers of specimens derive from specimens that provided only one valid measurement, i.e., either wing or tail but not both, due to damage, wear, or molt.
^b Type of *M. pelzelni* measurements by Ridgway; *S. ruficollis*, *N. concentricus*, and *S. gilvicollis* types measured by Hellmayr, who may have measured the wings “flat.”

zonias: *gilvicollis* (Vieillot, 1817), *concentricus* (Lesson, 1830), and *pelzelni* Ridgway, 1875. I have not been able to examine the respective types, but the published information seems adequate to determine the proper allocation of these names. The mensural characteristics for the types, taken from Hellmayr (1921:178-179) and Ridgway (1875:495), are given in table 2. Hellmayr examined the types

of *ruficollis*, *gilvicollis*, and *concentricus* in the Paris Museum and presumably personally measured them; the measurements for *pelzelni* are no doubt Ridgway's own. It is probable that Hellmayr measured the wing flat and Ridgway measured the chord. Hellmayr's wing measurements would thus be longer but the difference would be small and would not affect the results.

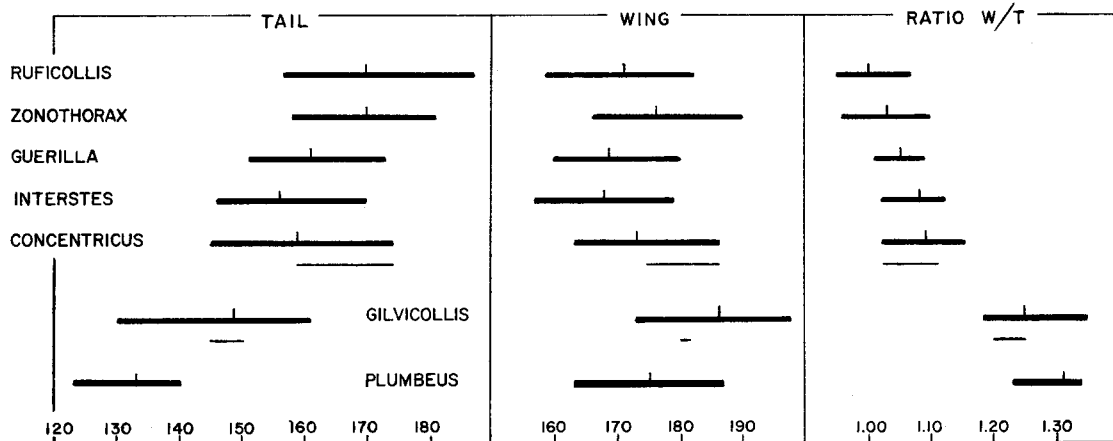


FIGURE 1. Mensural characteristics of taxa of *Micrastur*, combining males and females from Table 2. Thick horizontal lines represent range; vertical lines indicate means. Thin horizontal lines represent specimens of Table 1: Group R below *concentricus*, Group G below *gilvicollis*.

The type of *gilvicollis* Vieillot (locality uncertain; Cayenne designated by Hellmayr 1910:410) corresponds in mensural proportions to the long-winged, short-tailed form. Furthermore, specimen no. 470420 in The American Museum of Natural History in New York, labeled "Cayenne skin," bears a note in Hellmayr's own hand indicating that it compared favorably with the type of *Sparvius gilvicollis* Vieillot in the Paris Museum. This American Museum bird, unsexed but apparently an adult female, has measurements (wing 187, tail 149, w/t 1.25) that place it with the same long-winged, short-tailed form and its external appearance conforms. Thus it seems clear that *S. gilvicollis* Vieillot corresponds to the long-winged, short-tailed species, the name of which now becomes established as *Micrastur gilvicollis* (Vieillot).

It seems equally clear from the measurements given by Hellmayr and Ridgway that both remaining old names apply to the short-winged, long-tailed species. *Nisus concentricus* Lesson (Cayenne) has priority over *Micrastur pelzelni* Ridgway (Sarayacu, upper Ucayali, eastern Perú). The former is an immature bird, the latter, an adult. Using the earlier name, this form should be known as *Micrastur ruficollis concentricus* (Lesson). (Brown and Amadon 1968:750, applied the name *pelzelni* to a supposedly larger population of *M. ruficollis* in extreme western Amazonia. However, the measurements given [$\delta\delta$ 180–190, ♀♀ 190–200] apparently correspond to specimens of *M. gilvicollis*, for no specimen of *M. ruficollis concentricus*, which also inhabits extreme western Amazonia, has wings that long, compared sex for sex.)

It is noteworthy that Chubb (1916:222–224) separated the two species correctly, to judge from his descriptions; unfortunately, he used the name *interstes* for what is no doubt a specimen of the Guyana population of *M. r. concentricus*.

COMPARISON OF ADULT MORPHOLOGY

The two forms are very similar. There are some observable differences apart from the outstanding one of mensural proportions. They appear to be reasonably consistent but are small and relative, uncertain as taxonomic characters for identifying isolated specimens. Nonetheless, it is desirable to compare these sibling species in detail.

Upper parts. In general color, both forms are the same. No sexual difference is apparent. The back is blackish-gray and in many individuals the crown and nape are slightly

darker. The remiges have a brownish cast; the tail is considerably darker, almost black. Fresh feathers are grayer, old ones are browner.

The tail is tipped white and crossing it are two or three (occasionally one) narrow light bars. In the sample examined, about half of each form has two bars. One specimen of *concentricus* has one bar but eight *gilvicollis* show this, seven of them being from eastern Pará, Brazil. Occasional specimens of both forms have an incipient additional bar at the base of the rectrices. (The number of bars indicated is the absolute count, white tips and basal traces excluded; actually both forms usually have only two bars showing, tip excluded.) There is little sexual difference in number of bars. In *gilvicollis*, these are almost invariably clear white on the central pair of rectrices. However, in *concentricus* well over half the specimens show at least partial clouding of the bars on the central rectrices, some being almost obsolete.

Toward the western edge of Amazonia, the upper parts of *gilvicollis* appear somewhat grayer and paler than in *concentricus*, but in the central and eastern regions there is little or no difference. Three recent specimens of each form from Venezuela are inseparable as to species on the basis of dorsal color. Slight differences noted in other specimens may derive from differences of age and condition of the plumage.

Underparts. The gray bars of the breast seem to average a little less black, somewhat softer, often a bit browner in *gilvicollis*, but many specimens of both forms are quite similar. Sexual dimorphism in this barring is rather pronounced in *concentricus* (apparent too in some other races of *M. ruficollis*): in males the barring is finer than in females. A similar condition appears to apply in *gilvicollis* too, but it is not well defined in the material presently available to me. In general, however, *concentricus* males have the finest barring on the breast, *concentricus* females and *gilvicollis* males tend to be similar to each other in the coarser barring, while *gilvicollis* females may have the barring still more coarse.

The extent of the barring is variable. In *gilvicollis* it may extend posteriorly from the breast to greater or lesser degree, especially over the flanks and tibia, even to the crissum (where it is usually quite sparse and limited to the lateral feathers), but most individuals are immaculate, or nearly so, on the belly. Many individuals of *concentricus* have barring extending equally over the entire underparts,

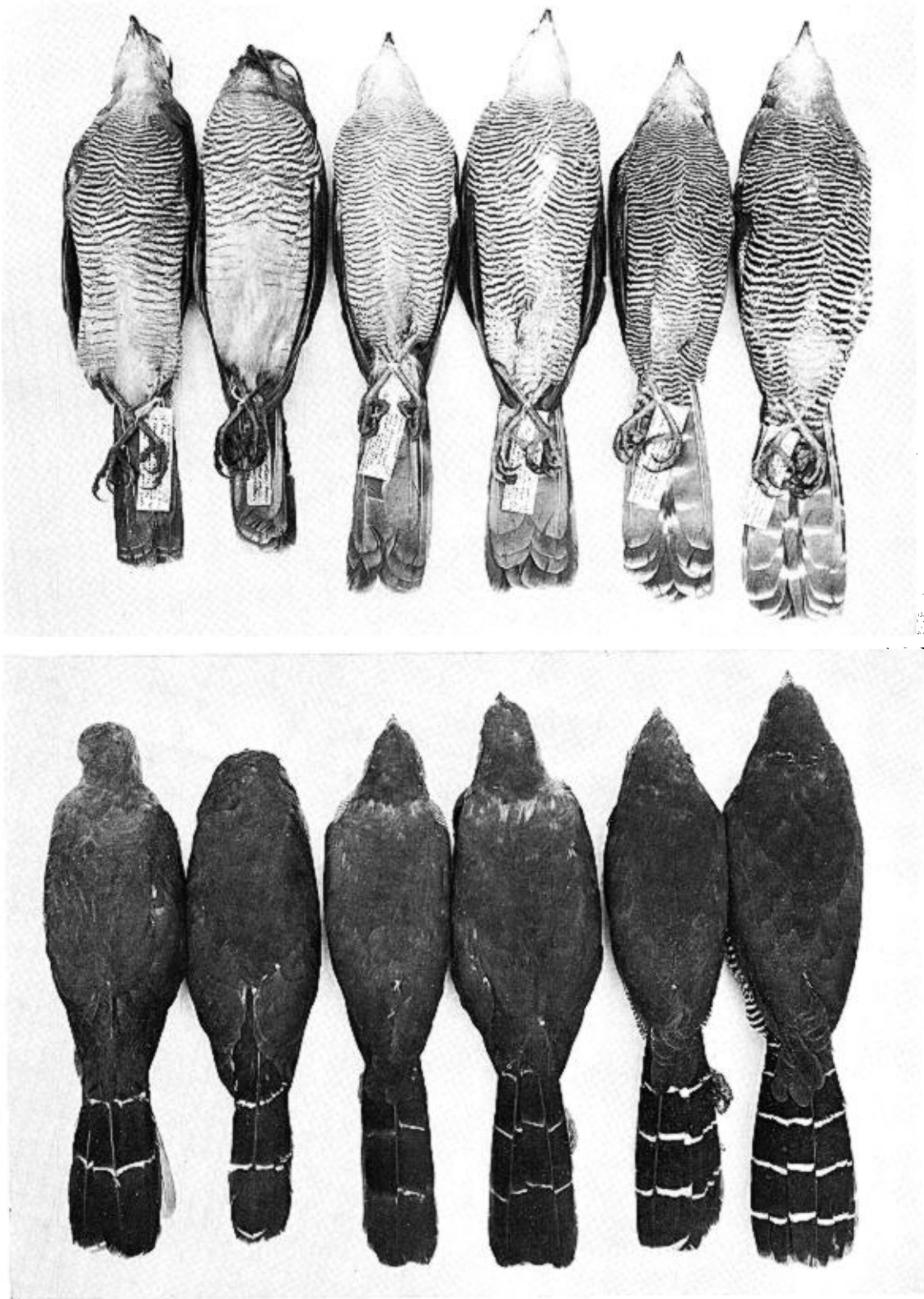


FIGURE 2. Photographs (ventral and dorsal) of selected specimens of *Micrastur gilvicollis* and *M. ruficollis*. Left to right: *M. gilvicollis gilvicollis* male, EBRC no. 5184, Rio Grande (El Palmar), Bolívar, Venezuela; female, AMNH no. 176810, Kamakusa, Guyana; *M. ruficollis concentricus* male, EBRC no. 6306, lower Rio Caura, Bolívar, Venezuela; female, EBRC no. 6213, Santa María (Upata), Bolívar, Venezuela; *M. ruficollis zonothorax* male, EBRC no. 5372, female no. 5370, both Rancho Grande, Aragua, Venezuela.

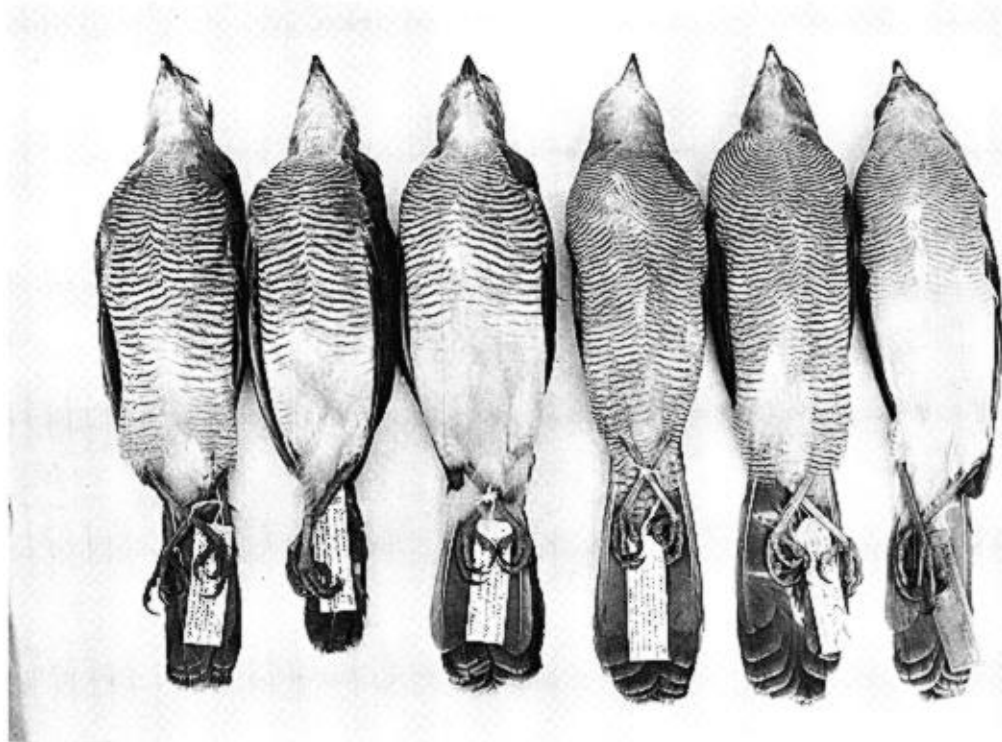


FIGURE 3. Variation in extent of ventral barring in the sibling forms of "Amazonia." Left to right: *M. g. gilvicollis*, three males: EBRG nos. 5184, 5197 and 6518, all Rio Grande (El Palmar), Bolívar, Venezuela; *M. ruficollis concentricus*, three males: EBRG no. 6333, lower Rio Caura, Bolívar, Venezuela; Phelps Coll. no. 29158, upper Rio Paragua, Bolívar, Venezuela; AMNH no. 288191, Limõal, Rio Tapajóz, Brazil.

but in 60% of the sample this becomes sparse or pale on the posterior parts, even obsolescent on the under tail coverts; in about half of these the lower belly has no barring. The sample suggests that along the Amazon, and extending into Perú, *concentricus* shows the greatest reduction in the barring of the posterior underparts. However, there are fully barred birds in this same area, while some white-bellied birds are found in the Guianas and Venezuela.

Figure 2 shows a pair each of *M. g. gilvicollis*, *M. r. concentricus*, and toptypical *M. r. zonothorax*. Variation in extent of barring of underparts is illustrated in figure 3. By way of further illustration from other regions and comparison with *M. r. ruficollis*, I refer to the excellent paper by Pinto (1947:322-328 and photos following 318). It is necessary to point out that specimens 18031, 20373, and 18030, portrayed by Pinto under *M. gilvicollis*, are actually *M. r. concentricus* (personally examined).

Soft parts. All the *M. gilvicollis* I have collected (all adult males) had the iris white, the bare facial skin reddish-orange, and the legs yellowish-orange with the claws roughly "horn" or lighter. All the *M. ruficollis*,

whether *concentricus* or *zonothorax* (adults of both sexes), had the iris brown (varying from light brown or tan to dark brown) and the bare facial skin, and the legs yellowish-orange, the claws black or nearly so; three live, wild individuals of nominate *ruficollis*, seen well at close range, showed these same colors on the soft parts.

Few museum specimens of *M. gilvicollis* have the colors of soft parts indicated on the labels but those generally conform to my own observations: the iris is indicated as white, cream, straw, silver, or gray. One marked "yellow-orange" may have suffered blood incursion due to shot damage (a frequent occurrence in light-eyed species; one *gilvicollis* had both irises white when I retrieved it but a few minutes later one iris had turned yellow-orange, rather obviously due to blood incursion). Facial skin is indicated as red-orange or some similar hue, or sometimes simply orange.

Similarly, most of the specimens of *M. r. concentricus* that have soft part labeling have the iris color as brown or its variants, although two (15%) are marked as yellow (in other races of *M. ruficollis* about 45% of the adequately labeled birds have the iris indicated

as yellow, the rest, variations of brown). The facial skin is described as yellow or orange.

COMPARISON OF IMMATURES

Shortage of time for museum work in the United States did not permit detailed examination of many immature specimens. I did examine briefly a fine series at The American Museum of Natural History. Those considered to be *M. gilvicollis*, based on mensural proportions, proved to be, like the adults, a relatively homogeneous group. The base color of the underparts is white, with no sign of the fulvous coloring (varying from pale to quite saturated) found on many young of the races of *M. ruficollis*, including *concentricus*. (Some specimens of both *gilvicollis* and *concentricus* have a yellowish-buffy wash over the underparts, different from the fulvous color just mentioned. This appears to be random, affecting adults and immatures of both sexes, and is probably some kind of staining.) In both species the dark barring of the underparts is variable in extent and is more widely spaced than in adults; often the dark bars are more narrow too.

On the upper parts both forms are rather homogeneous within themselves but slightly different from each other; the presumed *M. gilvicollis* are mostly brownish-gray, the presumed *M. r. concentricus* more coffee or sooty brown. Variation brings the brownest *gilvicollis* close to the grayest *concentricus*. The crowns of both average darker than the backs. In both forms immatures are browner than adults, a difference quite noticeable in *concentricus*, especially among specimens from the same population; the difference is less conspicuous in *gilvicollis*.

Contrary to the adults, immature *concentricus* have very little tendency to clouding of the white tail bars. Absolute count was not made but immature *gilvicollis* have mostly two white bars showing, *concentricus* mostly three, tips excluded.

Examination disclosed a character for distinguishing between immatures of the two forms that appears almost as reliable as the wing/tail ratio. Immature *concentricus* have some, often considerable, white spotting (or discontinuous bars) on the upper tail coverts, sometimes concealed. Such markings are lacking on all immatures of *gilvicollis*.

A subsequent comparison in museums of Brazil and Venezuela of immatures from both countries corroborates the general impression I had received from the larger group in the American Museum. Specifically with regard

to light spotting on the upper tail coverts, I found that all of seven specimens of *M. gilvicollis* lack such marks (w/t ratios ranging 1.18–1.29). Of ten *M. r. concentricus* (w/t 0.99–1.13), eight show such spotting; two (w/t 1.03, 1.04) lack these marks, both being from Pará, Brazil. This may reflect intergradation with *M. r. ruficollis*, for two of nine immatures of that form also lack such spotting. (Three of six adult *M. r. concentricus* from eastern Pará show some rufous on the upper breast, indicating there probably is intergradation with *M. r. ruficollis* in that region.) White spotting on the upper tail coverts is present in all of nine immature *M. r. zonothorax* (w/t 0.97–1.08). Thus it appears that Amazonia birds having light spotting on the upper tail coverts may be confidently assigned to *M. r. concentricus*. Those lacking such marks are almost surely *M. gilvicollis*, unless from regions bordering on the range of *M. r. ruficollis*. This character serves further to confirm that the type of *Nisus concentricus* Lesson is an immature of the species *M. ruficollis*, for Hellmayr (1921:179) mentions "white transverse spots" on the upper tail coverts in describing the type.

The absolute number of white tail bars (tips excluded) in these immature specimens is two or three in *M. gilvicollis* (one specimen with one, from eastern Pará) and three or four in *M. r. concentricus*. Iris color of the latter is indicated as yellow, brown, and dark gray, while of *M. gilvicollis* it is white, except one labeled as brown. Younger birds may have brown irises, an ontogenetic sequence that holds for most light-eyed avian species.

BIOACOUSTICAL COMPARISONS

Although I believe the case for two sympatric species can stand on the differences in external morphology indicated, it was the birds' voices that provided the basis for uncovering these differences. The voices also contribute directly to the total evidence, as will now be set forth.

Terminology. I follow for the most part the terms suggested by Bondesen and Davis (1966), for I believe that they afford the most practical means now available for expressing verbally comparisons of sound spectrograms. Those terms most frequently used in this paper, the meanings of which may not be self-evident, are here defined; in some cases I reword slightly the original definition but try to retain the same meaning:

figure: sound which produces a single, complete, and distinct impression—usually

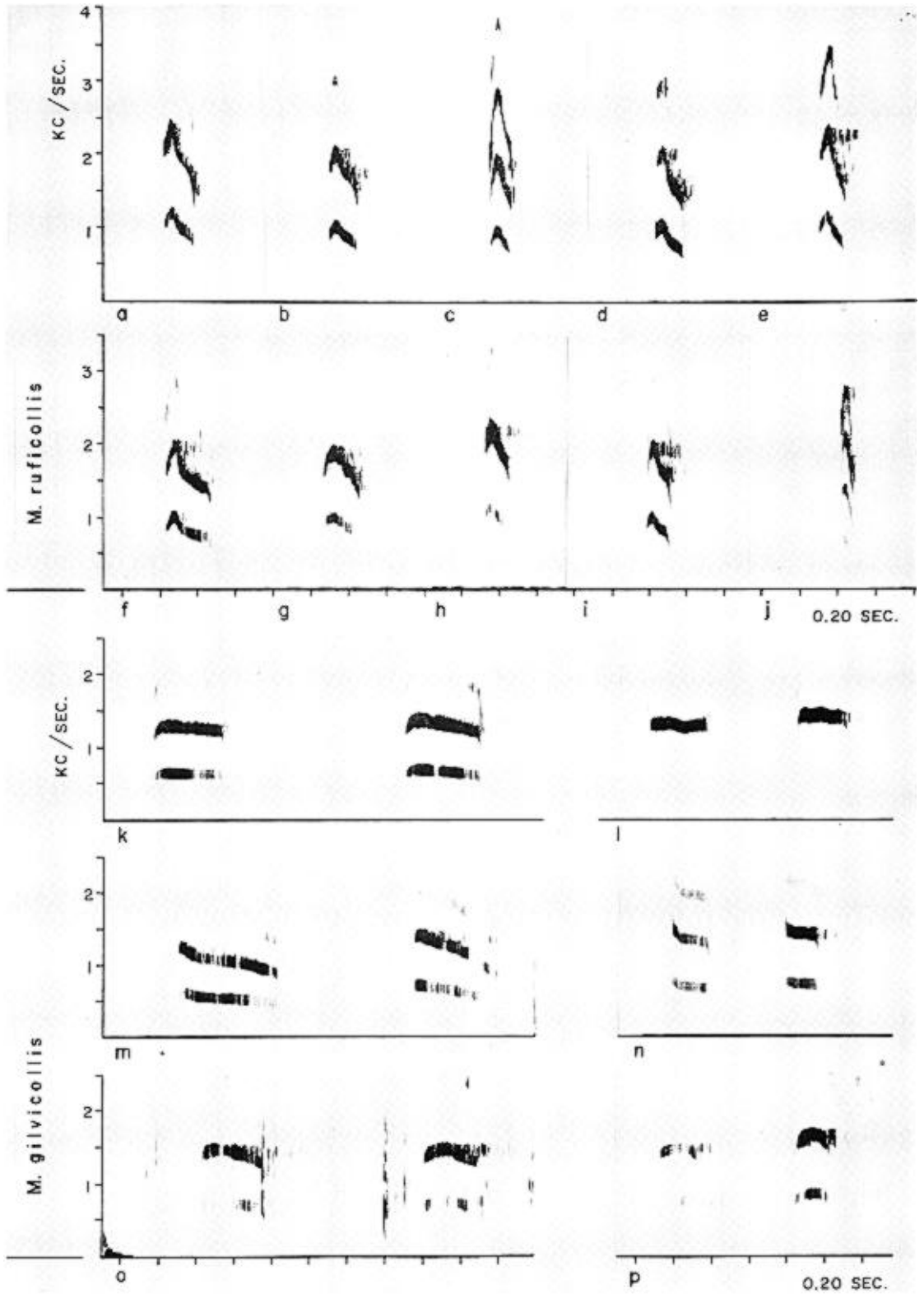


FIGURE 4. Sound spectrograms of single figures of *Micrastur ruficollis* (upper two rows) and 2-figure motifs of *M. gilvicollis* (lower three rows): *M. r. concentricus* (southeastern Venezuela), figures a and f; *M. r. zonothorax* (coastal mountains, northcentral Venezuela), figures d, e and h; *M. r. zonothorax* (Andes, western Venezuela), figures b and c; *M. r. interstes* (Costa Rica), figures g and i. Sound structure alteration under stress conditions is illustrated by figure j which is of the same individual that produced figure e (see text). The *M. g. gilvicollis* motifs (k through p) are of different individuals in the Imataca forest reserve (southeastern Venezuela).

represented on a sound spectrogram as a continuous trace.

segment: a distinguishable part of a figure.

motif: a group of figures that has a special rhythmic or melodic character.

phrase: one or more motifs terminated as a unit by some form of cadence (melodic close or rhythmic pause).

pattern: the arrangement of sound energy in time, particularly as seen on a spectrogram or other visual representation of the sound; also applicable to the aural impression.

succession: repetition of figures or larger units.

frequency: the number of vibrations or cycles of a given sound in a unit of time (expressed herein in kilocycles per second: kc/sec).

pitch: the subjective interpretation of frequency. (This is influenced not only by the frequency but also by the intensity of the sound as well as by its harmonic content.)

Vocal patterns. The pattern most frequently heard from *M. ruficollis* is a prolonged succession of single figures, while a succession of 2-figure phrases is most often heard from *M. gilvicollis*. Various examples of the basic components of these vocal patterns are pictured in figure 4. The difference between the *M. ruficollis* figures and the figures of the *M. gilvicollis* motifs is quite apparent to the eye. To the ear, the former sound like sharp barks while the latter sound like laments.

Before pursuing further the vocal differences between the species, it is desirable to consider the acoustic evidence that links the form *concentricus* with the species *M. ruficollis*. In the upper two rows of figure 4 are spectrograms of the basic figure produced by nine different individuals. Two of these are of *concentricus*; the other seven are from three different, geographically separated populations representing two taxa (*zonothorax* and *interstes*) presently recognized as forms of the species *M. ruficollis*. These nine figures are essentially the same; the observable differences reflect individual variation.

Additional Venezuelan recordings of *concentricus* provide figures consistent with the patterns illustrated in figure 4. From elsewhere, a recording made near Manaus, Brazil, shows figures very similar to e (fig. 4); another from eastern Perú (Cerros del Sira, Dept. Huánuco), recently received from John S. Weske, shows figures like d.

Figure 5 illustrates that dawn song phrases of *concentricus* also correspond to those of other races. Aural comparison of recordings

of *guerilla*, the northernmost form of *M. ruficollis*, indicates that they fit the same pattern.

No recordings of nominate *ruficollis* (type locality designated as Rio de Janeiro by Hellmayr) were available when the illustrations for this paper were prepared. However, I was recently able to observe and record this form in eastern São Paulo and northern Rio Grande do Sul, Brazil. In the field it sounds the same as *M. r. concentricus* and *M. r. zonothorax*. Spectrograms show that the figures of single-figure succession (three different birds) lack the initial segment (i.e., the sharp rise in frequency at the beginning of the figure), and the second segment is kept short. They are like figures c and d (fig. 4) without the initial segment, or similar to the first figure of a 3-figure phrase (fig. 5, a). Otherwise, single-figure succession song is the same as in the other races. Dawn song phrases are quite like those illustrated in figure 5, although with a somewhat shorter interval between the figures of a phrase, particularly in the terminal motifs. The vocal differences indicated are minor and apparently not important to the birds themselves; *concentricus*, *zonothorax*, *interstes* and *guerilla* are all properly considered subspecies of *M. ruficollis*.

Figure 6 compares homologous vocalizations of *M. ruficollis* and *M. gilvicollis*, showing that differences similar to those demonstrated for the most frequently heard song patterns prevail throughout the normal repertoires—the *M. ruficollis* figures are shorter, sharper, and higher pitched. The vocalizations of *M. g. gilvicollis* and *M. r. concentricus* used to illustrate this paper were all recorded in Venezuela. Recordings recently made in Amazonian Brazil confirm the characteristic patterns of both species.

Both sexes of *M. ruficollis* are equally vocal and employ similar motifs. Apparently the only vocal difference between them is that the fundamental frequency of male voices is higher. The sex of the *M. ruficollis* individual that produced the 2-figure motif on figure 6 is not known but I suspect it to be male; the other three *M. ruficollis* patterns are known to be by females. On figure 4, known males produced a and e, while d was produced by a female. On figure 5, a is by a male and b, d, and f by females. As all singing individuals of *M. gilvicollis* collected have been male, I am unable to state sexual similarities or differences in the voice of this species. Frequently two birds are heard in a situation suggesting they may be a pair and one of those

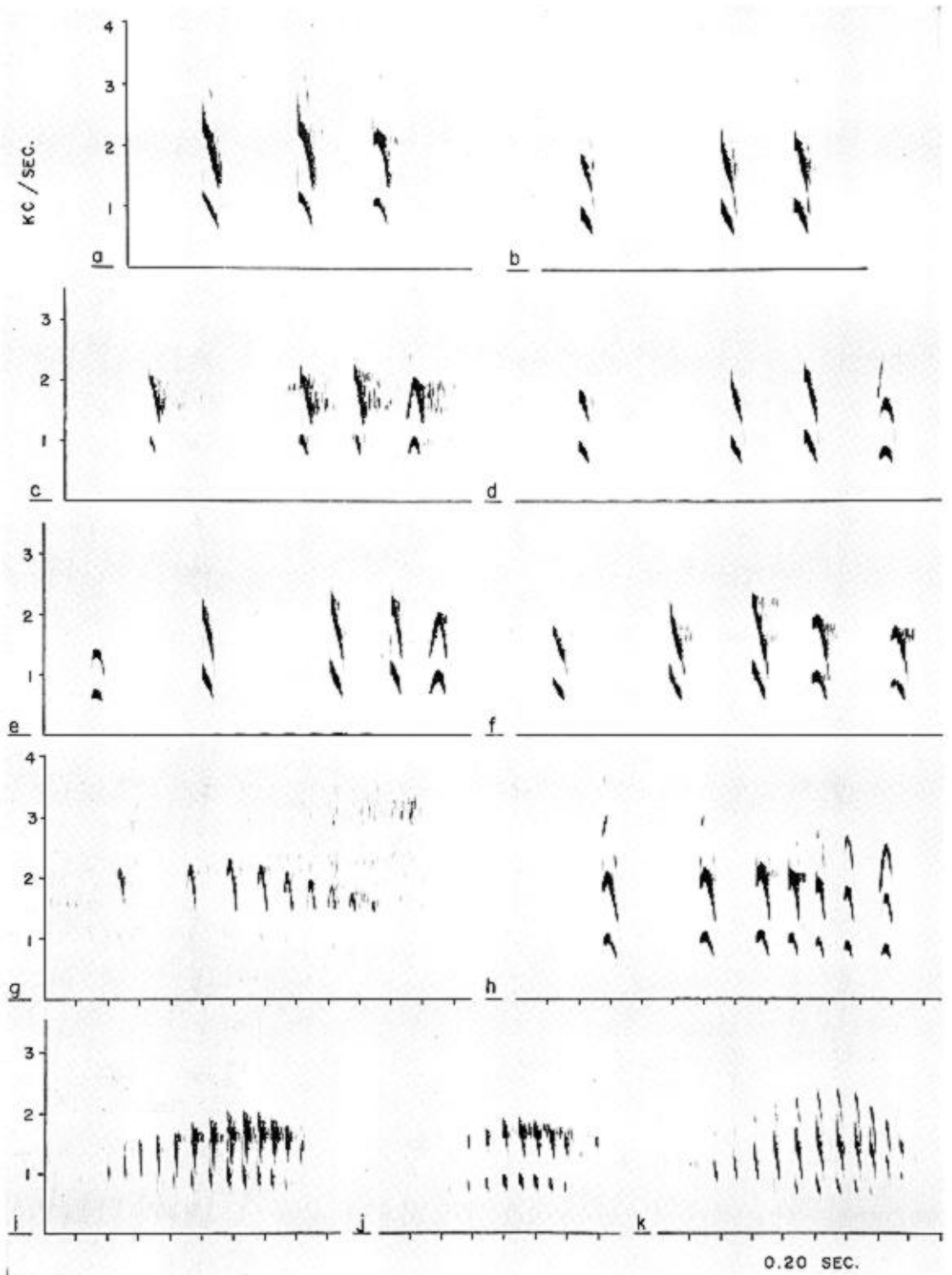


FIGURE 5. Dawn song phrases used by *Micrastur ruficollis*: *M. r. concentricus* (southeastern Venezuela), phrases b, d, e and i; *M. r. zonothorax* (northcentral and western Venezuela), phrases a, c, f, h and k; *M. r. interstes* (Costa Rica), phrases g and j.

seems to have a slightly higher voice than the other.

Sequence and timing of vocalizations. Besides the basic differences in the form of the

individual figures used in natural vocalizations by the two species, there is a further difference in the development of their singing sessions.

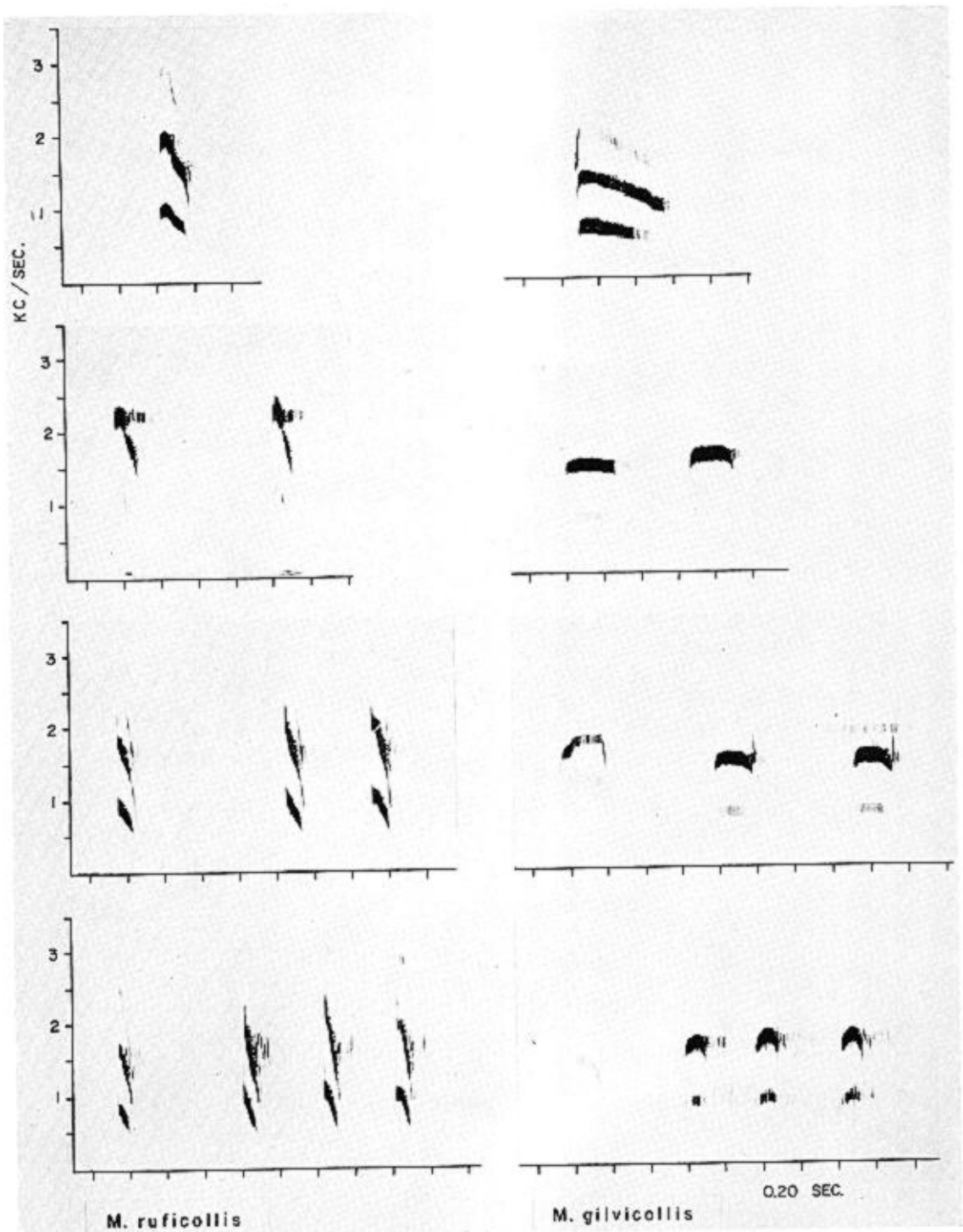


FIGURE 6. Comparison of homologous vocal motifs of *Micrastur ruficollis* (left) and *M. gilvicollis* (right).

M. gilvicollis sings mostly at dawn and in my experience is seldom heard after that. A song session begins typically with a succession of single figures, sometimes a few but often up to 20 or more. There is a slow acceleration in the tempo (a reduction in the interval between figures) as the song pro-

gresses, and a gradual shortening of the duration of the figures. The bird then changes to 2-figure phrases and continues this pattern for quite some time, during which the tempo slowly accelerates and the figures become shorter. Song often does not progress further, although one or more 3-figure phrases may be

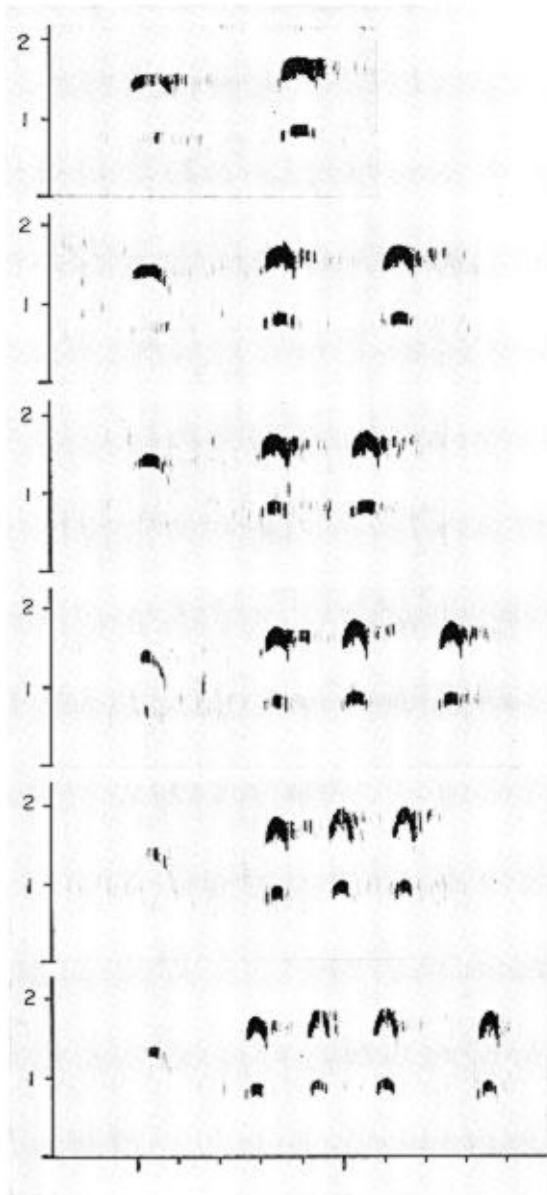


FIGURE 7. Progressive development of song pattern in *Micrastur gilvicollis*, explanation in text. Vertical scale kc/sec; horizontal scale 0.20 sec.

intermingled near the end. However, a bird may continue the song session with a period of 3-figure phrases and even go on to a period of 4-figure phrases that follows the same progressive pattern, perhaps including an odd 5-figure phrase near the end. This is illustrated in figure 7, beginning with a phrase from near the end of the 2-figure period and including sample phrases from the beginning and end of the succeeding periods. The transition from one period type to the next, during which phrases of adjacent periods are intermingled, may be rapid or rather protracted. Also, there

may be brief pauses between 1- and 2-figure periods or between 2- and 3-figure periods, with the bird sometimes changing perches.

The orderly, gradually accelerating development is typical of normal song in *M. gilvicollis* according to numerous observations involving at least nine individuals. However, I have also observed, particularly in the Río Negro region of southern Venezuela, song sessions in which a bird commenced with 2-figure phrases, then quickly began intermingling 3-figure phrases in an irregular manner, terminating the session with either 3-figure or 2-figure phrases. Such song periods showed little or no acceleration.

M. ruficollis differs vocally in many respects. While it too is most vocal at dawn, it may be heard at other times, especially during the early morning and at dusk. The order in which it may reproduce its repertoire is not predictable except in general terms. The composition most frequently heard is a succession of the single figures portrayed on figures 4 and 6. These are repeated with reasonably regular tempo at about 2-second intervals (1.5 to 3-second intervals observed as extremes). In a variation, an individual will emit phrases comprised of two to six such figures, the interval between figures being in that case only about one second and between phrases several seconds. I do not know the significance of this rather rare variation, which is not to be confused with dawn song. The few occasions when I have heard it have been during the early morning hours, not at dawn.

During certain times of the year *M. ruficollis* also uses compositions of a different type, homologous to dawn songs as used by many avian species. Some of the phrases commonly used are illustrated on figure 5; the phrases on figure 6, comparing *M. ruficollis* and *M. gilvicollis* motifs, are also dawn song phrases. Even during the times in their yearly cycle when dawn song is frequently and profusely used, such phrases are usually, although not always, preceded by a period of single-figure succession, sometimes of many minutes duration. If dawn song is to follow, shortly before the change the tempo may accelerate somewhat and with a brief transition of one to three 2-figure phrases the bird will start a period of 3-figure phrases. After only a few such phrases, the song session may cease; or it may continue with successive periods of phrases, each with the next greater number of figures per phrase, ceasing at any point along the line. A rather common development proceeds with a fairly rapid transition from 3-figure phrases up to multi-figure phrases such

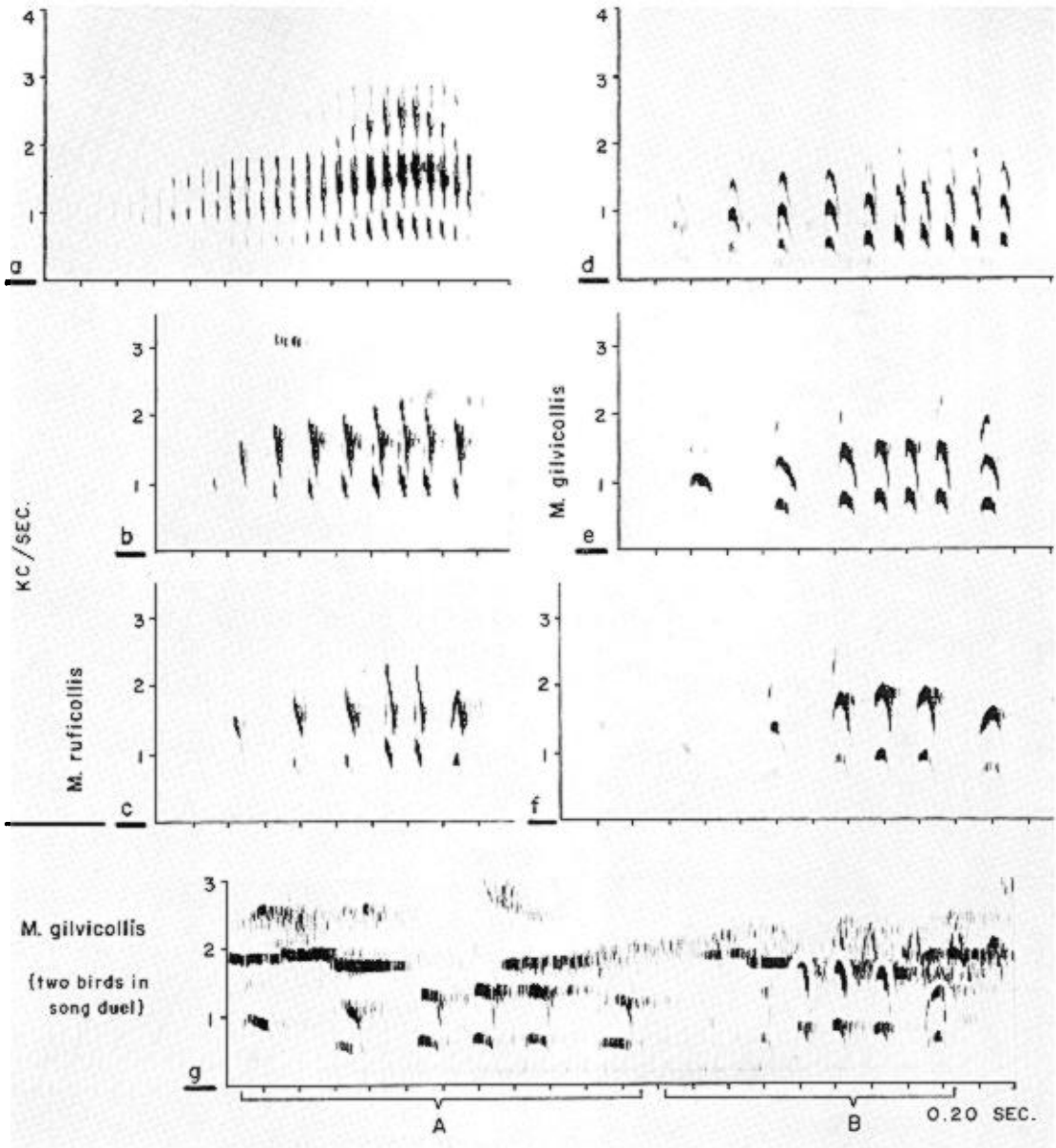


FIGURE 8. Vocalizations under stress, explanation in text.

as g and h, which may then be repeated for a long period.

It is not unusual for a bird to revert to single-figure succession after a period of dawn song phrases, or to inject such a period amid a total singing session. In such cases the change is usually made by halting (temporary cessation) rather than by vocal transition. Actually, halting occurs fairly frequently, especially during or at the end of the initial period of single-figure succession. Dawn song initiated after halting may begin with any type of phrase and proceed forward or backward.

Birds do not necessarily remain on the same

perch during a dawn song session. When stimulated by the singing of neighboring individuals, their session is often enriched and prolonged and they may change perches frequently, indicating there may be some territorial aspect to this activity.

Vocal alterations under stress conditions. Vocal changes may occur under the stress of direct intraspecific territorial conflict. I have seldom observed such conflicts. However, the conditions can be simulated by playing, within a responsive individual's territory, recordings of the species' vocal repertoire.

In vocal reactions of *M. ruficollis* to such intrusion, the individual figures comprising a

pattern are more sharply accented and of shorter duration than normal, and the fundamental frequency is usually lower. See figure 4, where sound figure e is one of a natural single-figure succession, while j is from a single-figure succession by the same bird after I played back to it some of its own song. Similar alteration occurs in the other patterns at the time of maximum stress. As the period of any given pattern-type progresses, the bird's tension apparently decreases (assuming that playback has been discontinued) and the figures gradually approach more normal form. An absolute peak in stress appears to be expressed by phrase a on figure 8. Phrases b and c represent the retardation of such a phrase as tension gradually subsides.

Experience with *M. gilvicollis* is somewhat similar. The maximum vocal expression of stress I have induced is represented in phrase d (fig. 8), and that from only one individual. Phrase e is the pattern after the same bird had relaxed somewhat. The maximum expression of stress that I could invoke from another individual is very similar to e, while f is its pattern after tension had lessened.

I chanced to record part of a situation that may represent natural conflict; one phrase by each participating bird is shown in spectrogram g. Because of extraneous sounds, it was difficult to produce a clear spectrogram from this recording, so I have delineated the second harmonic of the final four figures of the 7-figure phrase of bird B. The similarity of this phrase to phrase f is striking; the two phrases would appear to be of the same individual. Actually, the bird that produced f was recorded and collected almost 2 years before the other recording was made.

If we compare the homologous phrases of the two species under stress conditions, we see that the difference between them is of the same nature as observed when comparing natural vocal compositions. However, it can be seen too that many of the figures of *M. gilvicollis* phrase d (fig. 8) are very similar to the figures of *M. ruficollis* phrases b and d (fig. 5). Further, the complete *M. gilvicollis* phrase e (fig. 8) has a very close counterpart in *M. ruficollis* phrase h (fig. 5). This is the closest vocal approach between the two species that I have been able to find. But in this case we are comparing vocalizations produced in a highly altered neurological state with others produced under normal conditions, which is hardly a proper comparison. *M. gilvicollis* phrase f (fig. 8) is already different from any phrase produced by *M. ruficollis*—a difference

apparent even to an experienced human ear and very likely more so to the birds themselves.

In summary, I believe the bioacoustical evidence shows clearly that two distinct species are involved. At the same time it seems also to point to a very close phylogenetic relationship, as suggested by the immediately preceding comparisons under stress conditions, and further by the sharing of several closely comparable motifs in natural song (fig. 6), even though these motifs are composed of differently formed figures.

ECOLOGICAL COMPARISONS

It is evident from the localities on the labels of various museum specimens that *M. g. gilvicollis* and *M. r. concentricus* are sympatric. To a considerable degree they are also syntopic, and in several localities in Venezuela and Brazil I have found both forms together. However, there are distinguishable ecological preferences. *Gilvicollis* is limited to humid evergreen forests, especially, and perhaps exclusively, those that remain humid throughout the year; it is found even in very humid regions. *Concentricus* appears to avoid the latter, but is found in the normally humid evergreen forests, as well as those that suffer a fairly prolonged dry season during part of the year; it also occupies seasonally deciduous woodlands (where I have found it when these are in foliage, but not when they are bare) that are not too far removed from evergreen forests. Because of its greater tolerance, *concentricus* is more widely dispersed throughout the range than is *gilvicollis*.

The altitudinal distribution of *M. gilvicollis* cannot yet be certainly defined. The few adequately labeled museum specimens are from relatively low areas. My contacts with it are all below 800 m. However, in some recordings made by Weske at an elevation of about 1600 m near Huanhuachayo, Apurímac-Ene valley region, Perú, I detect faintly in the background what seems to be 2-figure succession song typical of *M. gilvicollis*.

I know *M. r. concentricus* from as low as 30 m, while *M. ruficollis* as a species ranges commonly to 2000–2500 m (one record of 3000 m).

The two forms are of similar size, with no appreciable consistent difference in size of feet or bill. The different wing/tail proportions may indicate different modes of foraging, but I have no field observations that suggest this; their food items, as indicated by stomach contents, are rather similar. Of the specimens I collected, one female *concentricus* contained

remnants of a bird and a crab; a male had the same plus a lizard; one male *gilvicollis* contained remains of a bird. The prey birds, in all three cases, appeared to be nestlings, which is interesting but may be coincidence. The small forest falcons do take adult birds when they can. The netted bird included in table 1 became entangled when it struck at an adult woodcreeper (*Xiphorhynchus pardalotus*), that was in the net. Two specimen labels of *M. gilvicollis* indicated stomach contents of arachnids, insects, and a lizard. One *M. r. zonothorax* that I examined had eaten a small opossum (*Marmosa* sp.) and various arthropods; another contained remnants of a large coleopteran. This scanty evidence would indicate that the small forest-falcons may subsist largely on prey less agile than normal, healthy adult birds (see also Slud 1964: 71; Wetmore 1965:270).

DISTRIBUTION

In this paper no attempt is made to subdivide into geographical races either of these sibling species. For the present, *M. ruficollis concentricus* may be considered to range over Amazonia in the broad sense previously defined, with the following additions: in Brazil south of the Amazon River to an arbitrary line at 13° S, east to the Rio Araguaia and from its confluence with the R. Tocantins, northeast along the border between the states of Pará and Maranhão; in Bolivia in the lowlands in Pando and Beni (presumed; specimens from Cochabamba and Santa Cruz seem to be intergrades with another form of *M. ruficollis* and while possibly best assigned to *concentricus*, for the present I exclude them); in Perú, extending up the Huallaga valley, in addition to the Amazonian departments of Loreto and Madre de Dios (populations in the Apurímac-Ene valley as well as others in marginal Amazonian Perú may be assignable to *concentricus* but this has yet to be determined). I have seen no specimens from Amazonian Colombia, but as there are some from adjacent Ecuador and Perú the range probably includes the region south of the Guaviare River, possibly extending north toward the Meta in suitable areas along the Orinoco and its Colombian tributaries. Neither have I seen specimens from Surinam, although some of the descriptive material given by Haverschmidt (1968: 71) under *M. gilvicollis* appears to correspond more to *M. r. concentricus*. As specimens of this form are known from Guyana and Cayenne, it is probable that *M. r. concentricus* occurs in Surinam.

Specifically within Venezuela, *M. r. concentricus* is found in appropriate forested areas south of the main Orinoco River: southeastern Territorio Delta Amacuro, the whole state of Bolívar, and northern Territorio Amazonas. The report of *M. r. zonothorax* from south of the Orinoco (Phelps and Phelps 1958:71-72; Meyer de Schauensee 1966:62) is based on a specimen of *M. r. concentricus*.

The overall range of *M. g. gilvicollis* appears to parallel very closely that indicated for *M. r. concentricus*, although its narrower ecological tolerance restricts its distribution within the total range. The southernmost record in central Brazil is at about 11° S on the Rio Teles Pires (upper Tapajóz). In Venezuela it is known from various localities in southeastern Terr. Delta Amacuro, Bolívar (except the northwestern part), and Terr. Amazonas.

Three specimens from the humid, forested coastal region in southern Bahia and northern Espirito Santo (north side of Rio Dôce) correspond in all respects to *M. gilvicollis*. The Bahia specimens were reported previously by Pinto (op. cit.). This population seems now to be isolated from the main population of *M. gilvicollis* in Amazonia; it is, however, sympatric with a part of the population of *M. r. ruficollis*.

STATUS OF MICRASTUR PLUMBEUS

Still open is the status of this form from extreme northwestern South America—Colombia and Ecuador west of the Andes. Like *M. gilvicollis*, it has a short tail and proportionately long wings. Its wing/tail ratio falls at the upper limits of this character in *M. gilvicollis* and is thus totally different from that of *M. ruficollis* (see table 2). Also, as its range lies within that of *M. r. interstes*, it would seem to be specifically distinct from *M. ruficollis*. Its apparent limitation to humid forest corresponds to the ecological preferences of *M. gilvicollis*.

The little information available indicates that the iris color is reddish, brownish, or yellowish-gray in *plumbeus*; there are also some minor differences in color and pattern of the plumage that distinguish it from *M. gilvicollis*, but like the eastern Pará population of that species (cf. p. 402) it seems most often to have only one light tail bar. There is an absolute lack of bioacoustical information of this rare bird which, if available, could help determine its systematic position.

Considering that *plumbeus* may have been completely isolated from *gilvicollis* for a long time, it is arguable that it should be recognized

as a separate species. It is so treated in Brown and Amadon (1968:750), where, however, *gilvicollis* is considered a race of *M. ruficollis*. Lacking sufficient information to permit a clear-cut decision, and in view of the wing/tail ratio, it is perhaps better to treat it tentatively as a subspecies of *M. gilvicollis*, as done by Hellmayr and Conover (1949:259). Meyer de Schauensee followed these authors in his 1966 work and Brown and Amadon in 1970.

SUMMARY

Evidence is presented to show that, contrary to most previous concepts, there are actually two very similar but specifically distinct forms of small, barred *Micrastur* that inhabit Amazonia (*sensu lato*). These sibling species, which are sympatric and even syntopic, differ from each other in vocal characters, colors of soft parts, and mensural proportions (wing/tail ratio). One of them, proportionately long-winged and short-tailed, should bear the name *Micrastur g. gilvicollis* (Vieillot). The other, short-winged and long-tailed, possesses vocal similarities to, and shows morphological intergradation with, surrounding forms of the species *M. ruficollis* and should be called *M. ruficollis concentricus* (Lesson).

These two Amazonian species are compared morphologically, vocally, and ecologically. The most reliable method for separating museum specimens is by the wing/tail ratio. Immatures of both siblings are described briefly. Presence of white spotting (often concealed) on the upper tail coverts of most immature *M. r. concentricus* (and other races of *M. ruficollis*), and lack of these marks on all immature *M. g. gilvicollis*, provides a reasonably reliable character, in addition to that of mensural proportions, for distinguishing between them.

The northwestern South American form *plumbeus* is considered tentatively to be a geographic race of *M. gilvicollis*.

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ADDENDA

The presence of both *M. ruficollis concentricus* and *M. g. gilvicollis* in amazonian Colombia is confirmed by two specimens of the former and one of the latter from the Sierra Macarena, Meta. The latter, from Pico Rengifo (1500 m), is also the first confirmed record for *M. gilvicollis* at such a high elevation.

E. R. Blake, Field Museum of Natural History, and D. W. Snow, British Museum (Natural History), kindly supplied the pertinent data permitting identification of these three specimens, the reporting of which by Blake (*Fieldiana:Zool.*, 44:69-112, 1962) had previously escaped my attention.

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