

Morphology and vocalization support specific status of the Chestnut-headed Chachalaca, *Ortalis motmot ruficeps* (Wagler, 1830) (Aves; Galliformes; Cracidae)

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Abstract. The Little Chachalaca (*Ortalis motmot*) is a widely distributed species in the Amazon basin, typically found in riverine habitats. There are two disjunct populations: the northern *O. m. motmot* and the southern *O. m. ruficeps* (known as Chestnut-headed Chachalaca). Here we performed a vocal, morphological and plumage comparison between these two taxa. Birds present differences in tail coloration but are otherwise undiagnosable in terms of plumage. *Ortalis m. ruficeps* is, however, markedly smaller and lighter than *O. m. motmot*, with no overlap in size or weight. We also found vocal differences between *O. m. motmot* and *O. m. ruficeps*, no overlap in geographic distributions and no signs of hybridization across its range. Based on the available data, *Ortalis m. ruficeps* thus must be considered a valid species, endemic to Brazil.

Keywords. Morphology; Plumage; Voice; Little Chachalaca.

INTRODUCTION

Despite its large size, conspicuousness, ecological, social and economic importance, the cracids comprise a group of Galliformes of largely neglected taxonomy. The definition of many taxa within this family is presently supported by early 19th century analysis of few specimens and poorly analyzed populations. Despite the relatively large amount of available material in museums, just a handful of studies were performed based on good series of specimens thoroughly covering the species distribution. Unsurprisingly, recent studies using different sets of analytic tools (depending on the available material) have been demonstrating the need of revision of polytypic taxa, in order to discriminate true evolutionary entities from taxonomic rubbish, with the consequent uncovering of valid taxa of immediate conservation concern (e.g., Grau *et al.*, 2003; Silveira *et al.*, 2004; Costa *et al.*, 2017; Evangelista-Vargas *et al.*, 2017; Silveira *et al.*, 2017; Evangelista-Vargas & Silveira, 2018). For example, the recognition of *O. remota* as a critically endangered valid species (Silveira *et al.*, 2017) promptly ignited a series of

field studies directed to the conservation of the few remaining individuals.

Within the cracids, the chachalacas (genus *Ortalis* Merrem, 1786) exemplify well this taxonomic inflation, with five out of 15 of the accepted species being polytypic (*O. vetula*, *O. ruficauda*, *O. canicollis*, *O. guttata* and *O. motmot*; Silveira *et al.*, 2017). The Little Chachalaca, *O. motmot* (Linnaeus, 1766), currently counts with two recognized subspecies: the nominate *O. m. motmot* and *O. m. ruficeps* (Wagler, 1830). The latter was originally described as a full species (*Penelope ruficeps*) by Wagler (1830), based on a specimen from Pará state, northern Brazil. Wagler (1830) proposed that *O. ruficeps* was similar, but much smaller than *O. motmot*, and had the basal portion of the outer tail feathers colored bronzy brass. Sclater & Salvin (1870) and Allen (1876) agreed with Wagler (1830, 1832), using the name *Ortalis ruficeps*. In a subsequent study, Riker & Chapman (1891) presented *O. ruficeps* under the name *Ortalis motmot*, which was considered a mistake by Hellmayr & Conover (1942). Ogilvie-Grant (1893, 1897) used the name *Ortalis ruficeps* mentioning the outer tail feathers blackish glossed with green and tipped

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with chestnut. Ihering & Ihering (1907) and Heinroth (1922) subsequently kept the species rank of *O. ruficeps*.

The subordination of *O. ruficeps* to *O. motmot* was first proposed by Todd (1932), who analyzed a series of specimens from the lower Amazon. This author mentioned the smaller size and differences in head and tail coloration of *O. ruficeps* but suggested that it only represented a race of *O. motmot*. Peters (1934) agreed to this treatment and all subsequent authors followed suit, without presenting additional analyses (Pinto, 1938; Hellmayr & Conover, 1942; Pinto, 1964; Vaurie, 1965, 1968; Delacour & Amadon, 1973; Blake, 1977; Pinto, 1978; del Hoyo et al., 1994; Grantsau, 2010). These studies maintained a similar description and diversely pointed out to various diagnostic features of *O. ruficeps* in comparison with *O. motmot*: the smaller size (Hellmayr & Conover, 1942; Pinto, 1964; Delacour & Amadon, 1973; Grantsau, 2010); a lighter and/or brighter coloration of the crown in *O. ruficeps* (Hellmayr & Conover, 1942; Pinto, 1964); a redder coloration of the crown (Hellmayr & Conover, 1942; Blake, 1977); and a darker overall coloration (Pinto, 1964; Delacour & Amadon, 1973; Grantsau, 2010). Differences in the color of the external rectrices were also raised (Hellmayr & Conover, 1942; Blake, 1977), although Vaurie (1965) argued that this was a more subtle character. Sick (1985, 1997) was the only author who consistently kept the species rank for *O. ruficeps*.

Recent studies have shown that a closer examination of large cracids series can reveal several valid species within the subspecies of polytypic complexes (e.g., *Ortalis guttata*), in some instances with dramatic implications for conservation (Silveira et al., 2017). Therefore, in the present study, we conducted a thorough examination of the available museum skins of *O. m. motmot* and *O. m. ruficeps*, together with high quality photographs and vocalizations available in online repositories, in order to provide a taxonomic revision of these two supposed subspecies, with updated diagnoses and geographic distribution.

MATERIAL AND METHODS

We examined 147 specimens deposited in the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil), American Museum of Natural History (AMNH, New York, USA), Colección Ornitológica Phelps (COP, Caracas, Venezuela), Estación Biológica de Rancho Grande (Aragua, Venezuela), Field Museum of Natural History (FMNH, Chicago, USA), Muséum National d'Histoire Naturelle (MNHN, Paris, France), Museum für Naturkunde (MfN, Berlin, Germany), Naturalis Biodiversity Center (RMNH, Leiden, the Netherlands), and Staatliches Museum für Naturkunde Stuttgart (SMNS, Stuttgart, Germany), and we measured 76 of those specimens (51 *O. m. motmot* and 25 *O. m. ruficeps*, including males and females from Venezuela and Brazil deposited at COP and MZUSP, respectively).

We also obtained photographic records from the WikiAves platform (www.wikiaves.com.br) to comple-

ment the distribution map (31 localities). Finally, we gathered 40 voice recordings from Xeno-Canto (www.xeno-canto.org) and WikiAves, from which 18 were suitable for spectrographic analyses.

We compared the birds in terms of plumage coloration, morphology and voice. For plumage coloration we analyzed the color of the crown, forehead, throat, chest, abdomen, flanks, crissum, mantle, wing coverts, primaries, tail coverts, external and central rectrices. For morphology we measured the exposed culmen, bill width and depth, and tarsus (nearest 0.01 mm) as well as the wing and tail length (nearest 0.1 cm). Finally, for the vocal analysis we measured the total syllable duration and the duration and spacing of each note, using the Software Raven Pro 1.5 (Bioacoustics Research Program, 2014).

Statistical analyses were conducted in R version 3.4.3 (R Core Team, 2017) for morphological and voice characters. We first tested separately whether each of the measurements and vocal characters were explained by taxa, sex and the interaction between taxa and sex (only taxa in the case of the vocal characters). Model selection was performed via stepwise backwards selection, dropping non-significant terms with the critical *p*-value corrected for multiple testing (Bonferroni correction = 0.05/number of tests) in each step. Next, we conducted a Principal Component Analysis on the standardized measurement values (mean centered at 0, standard error at 1) of the group of morphometry and voice characters. Missing values were replaced by zeros after the standardization (thus replaced by the mean value). Principal components 1 and 2 explained 81% of the variation for morphometrics and 62% for voice characters and were retained for subsequent analyses. Lastly, we conducted two analyses: a multivariate analysis of variance (MANOVA) with both PC1 and PC2 as response variables and two separate regressions for PC1 and PC2 separately (similar to the first analysis), once more with the critical *p*-value corrected for multiple testing.

RESULTS AND DISCUSSION

As previously reported in the literature (Wagler, 1832; Ogilvie-Grant, 1893, 1897; Hellmayr & Conover, 1942; Vaurie, 1965; Blake, 1977), *O. m. motmot* and *O. m. ruficeps* differ from each other in the coloration of the rectrices, but are identical in other plumage characters, with little intraspecific variation. The border of the external rectrices are tinged with olive dark brown in *O. m. ruficeps*, while they are reddish brown in *O. m. motmot* (Fig. 1).

We did not observe any of the other differences in plumage reported in earlier studies, even after analyzing a large number of specimens. We did observe a lighter crown color in a few specimens of *O. m. ruficeps* (MZUSP 17054, 22045, 22046, 22818, 22819, 46256), as previously reported (Todd, 1932; Hellmayr & Conover, 1942; Pinto, 1964), but in all other specimens the coloration was identical to *O. m. motmot*. Moreover, we did not observe differences in darkness or redness in other plumage characters (*contra* Hellmayr & Conover, 1942; Blake, 1977; Pinto, 1964; Delacour & Amadon, 1973; Grantsau, 2010).

On the other hand, and confirming what was reported in the literature since its original description (Wagler, 1830; Todd, 1932; Hellmayr & Conover, 1942; Pinto, 1964; Vaurie, 1965; Delacour & Amadon, 1973; Grantsau, 2010), *O. m. ruficeps* is smaller than *O. m. motmot* in almost every character analyzed and the differences are maintained even when sexes differ in size. Furthermore, there is no overlap in size range between the two taxa. When compared to *O. m. motmot*, *O. m. ruficeps* has a smaller culmen (10%; percentage difference between brackets), bill width (13%), tarsus (16%), wing (12%), and tail length (16%; see Appendix 1). *Ortalis m. ruficeps* is also significantly smaller when using the principal components PC1 and PC2, with males larger than females (Fig. 2, MANOVA: Taxon $F_{2,70} = 197.85$, $p < 0.01$, Sex $F_{2,69} = 6.46$, $p < 0.01$; see also Table 1 and Appendix 2). To complement our morphological analyses, we obtained the fresh mass from the label of ten specimens of *O. m. motmot* (from Venezuela

and Brazil deposited at MZUSP and EBRG) and a single record from the literature for *O. m. ruficeps* (Graves & Zusi, 1990). *Ortalis m. motmot* is heavier than *O. m. ruficeps*, weighing on average 476 g (ranging from 431 to 520 g, including males and females), while the sole adult male of *O. m. ruficeps* (Graves & Zusi, 1990) weighed 345 g, 27% lighter than the nominate form. Finally, contrasting to what is reported in the literature (del Hoyo *et al.*, 1994), individuals of *O. m. motmot* from Venezuela are not as small as *O. m. ruficeps*.

The vocalizations of *O. m. ruficeps* differ from those of *O. m. motmot*, but the results should be interpreted with some caution due to the limited sample available for *O. m. ruficeps*. The main difference of the song of *O. m. ruficeps* when compared with *O. m. motmot* is the longer syllable duration (Fig. 3, MANOVA: Taxon $F_{2,48} = 12.61$, $p < 0.01$), although the duration of each note varied among the two taxa (Appendix 3 and 4).

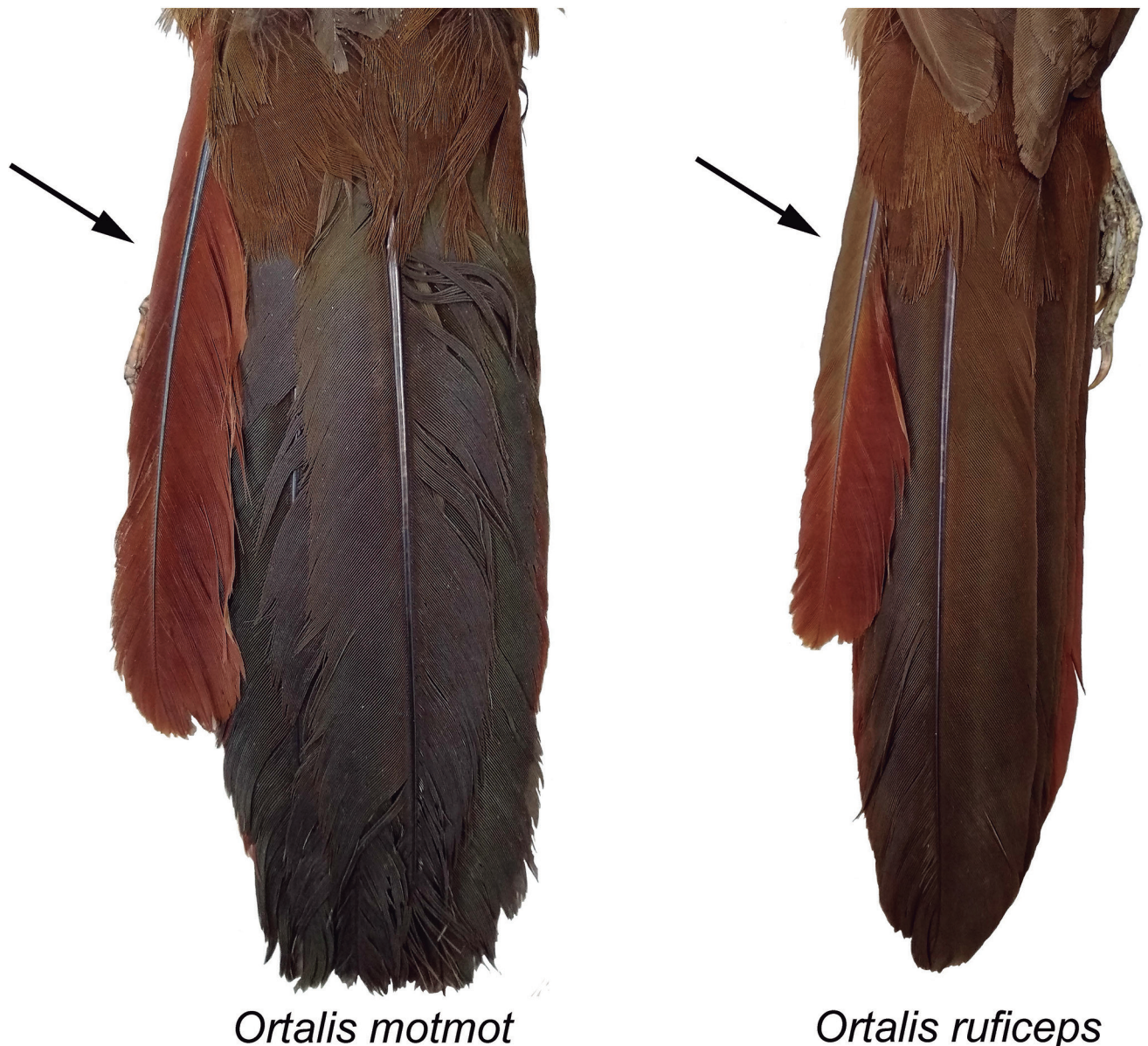


Figure 1. Photographs of the tail of *O. motmot* (MZUSP 82332) and *O. ruficeps* (MZUSP 102858) showing the color differences of the external rectrices (arrows). In *O. ruficeps* the border of the external rectrices are tinged with olive dark brown while in *O. motmot* they are reddish brown.

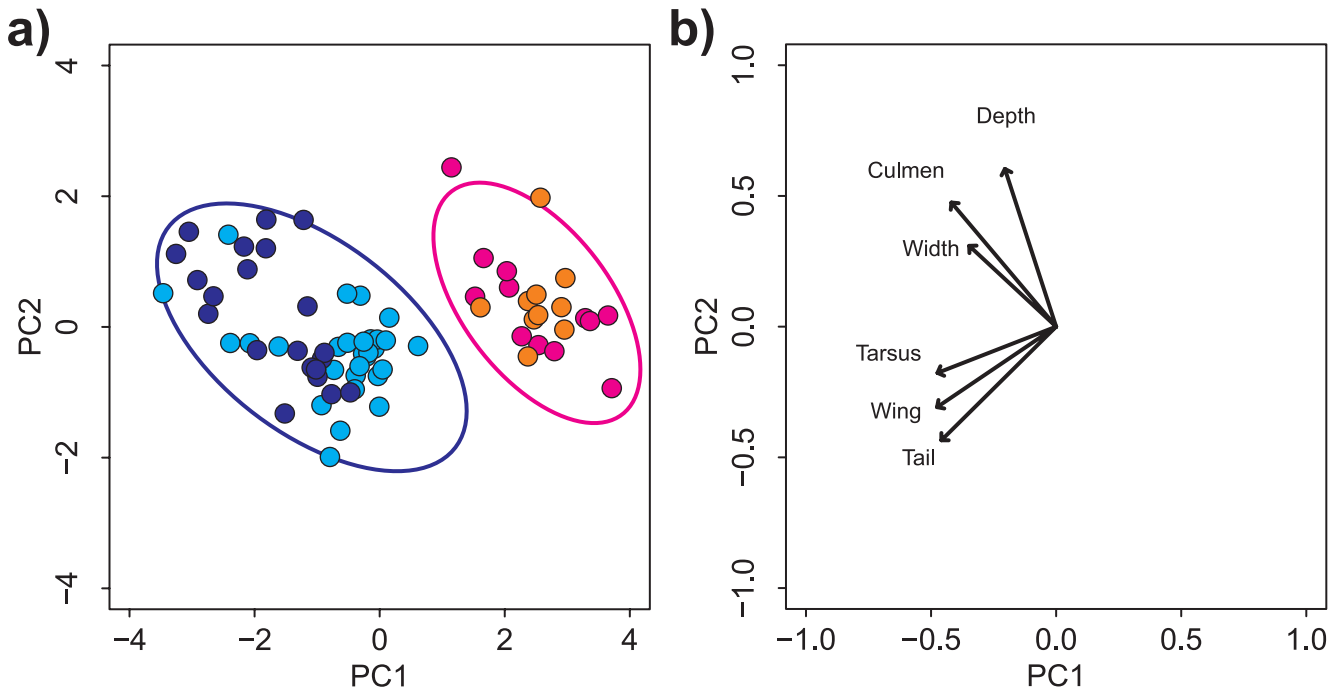


Figure 2. (a) Scatterplot of the two first components obtained from the Principal Component Analysis of the morphometric measurements. Blue: *O. motmot*, Red: *O. ruficeps*. Dark-colored symbols – males, light-colored symbols – females. Ellipses are 95% confidence ellipse (b) Loadings plot of the two first two first components obtained from the Principal Component Analysis of the morphometric measurements.

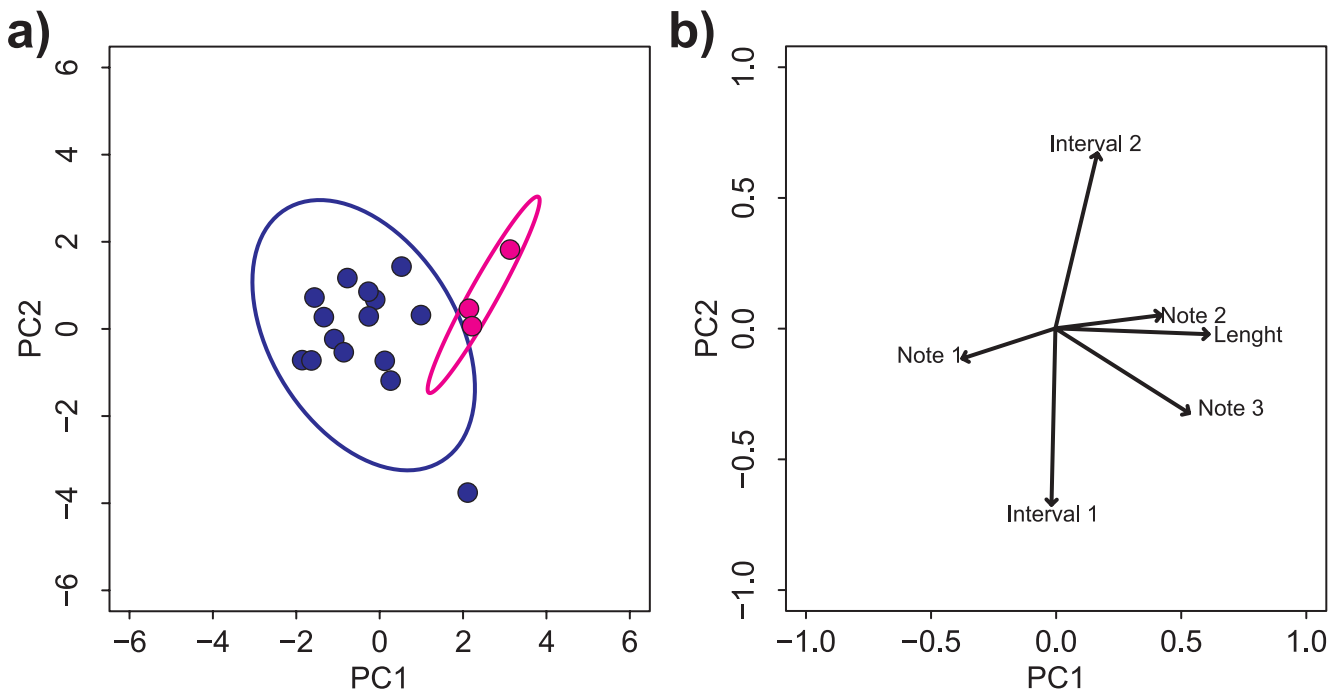


Figure 3. (a) Scatterplot of the two first components obtained from the Principal Component Analysis of the vocal characters. Blue: *O. motmot*, Red: *O. ruficeps*. Ellipses are 95% confidence ellipse (b) Loadings plot of the two first two first components obtained from the Principal Component Analysis of the vocal characters.

Ortalis m. motmot and *O. m. ruficeps* are common and locally abundant, being separated by the Amazon River. Populations of *O. m. ruficeps* occur south of the river (Pará and Mato Grosso states), following the courses of the rivers Tapajós, Xingu, Tocantins and Araguaia, while the distribution of *O. m. motmot* extends northward from the Amazon River, including the Brazilian states of Pará, Amazonas, Amapá and Roraima, as well as Guyana, French Guiana, Suriname and Venezuela (Fig. 4).

Although occurring mostly in riverine habitats, there is no sign of contact between northern and southern populations. Thus, these birds comprise another classic case in Amazonian biogeography of taxa separated by the course of the main rivers (Cracraft, 1985). A few specimens of *O. m. ruficeps* allegedly share the same localities of *O. m. motmot* specimens (Lago Cuipeua and Pinhel, both in Pará). These individuals were also noticed by Vaurie (1965), who regarded the localities as erroneous,

Table 1. Model results for the multiple regression analyses testing the effects of taxon and sex on the various morphometric measurements as well as means and standard errors (s.e.) for each taxon-sex combination. Statistics are given for each term at the point of exclusion of the term from the model. *P*-values in bold with an asterisk represent significance after a Bonferroni correction to account for multiple testing (critical *p*-value = 0.05/number of tests).

Bill culmen (mm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	67.00	7.79	< 0.01*
Taxon (<i>O. ruficeps</i>): Sex (male)	-2.00	0.72				
Taxon (<i>O. motmot</i>)	22.70	0.26				
Taxon (<i>O. ruficeps</i>)	21.26	0.44				
Sex (male)	1.42	0.40				
Bill width (mm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	48.00	4.5199	0.04
Taxon			1.00	50.00	39.33	< 0.01*
Sex			1.00	49.00	0.17	0.68
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.76	0.36				
Taxon (<i>O. motmot</i>)	9.16	0.12				
Taxon (<i>O. ruficeps</i>)	8.00	0.14				
Sex (male)	0.08	0.18				
Bill depth (mm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	45.00	1.16	0.29
Taxon			1.00	46.00	5.76	0.02
Sex			1.00	46.00	12.69	< 0.01*
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.44	0.41				
Taxon (<i>O. motmot</i>)	9.49	0.16				
Taxon (<i>O. ruficeps</i>)	9.00	0.19				
Sex (male)	0.71	0.20				
Tarsus (cm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	67.00	0.2958	0.59
Taxon			1.00	68.00	200.56	< 0.01*
Sex			1.00	68.00	10.28	< 0.01*
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.75	1.39				
Taxon (<i>O. motmot</i>)	57.25	0.47				
Taxon (<i>O. ruficeps</i>)	47.49	0.67				
Sex (male)	2.05	0.64				
Wing (cm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	69.00	1.15	0.29
Taxon			1.00	71.00	250.87	< 0.01*
Sex			1.00	70.00	6.19	0.02
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.31	0.29				
Taxon (<i>O. motmot</i>)	19.94	0.08				
Taxon (<i>O. ruficeps</i>)	17.57	0.12				
Sex (male)	0.33	0.13				
Tail (cm)	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	69.00	0.93	0.34
Taxon			1.00	71.00	191.85	< 0.01*
Sex			1.00	70.00	2.80	0.10
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.53	0.55				
Taxon (<i>O. motmot</i>)	24.52	0.15				
Taxon (<i>O. ruficeps</i>)	20.66	0.23				
Sex (male)	0.43	0.25				
PC1	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	69.00	5.75	0.02
Taxon			1.00	70.00	281.83	< 0.01*
Sex			1.00	70.00	13.10	< 0.01*
Taxon (<i>O. ruficeps</i>): Sex (male)	1.02	0.42				
Taxon (<i>O. motmot</i>)	-0.77	0.15				
Taxon (<i>O. ruficeps</i>)	2.91	0.21				
Sex (male)	-0.73	0.20				
PC2	Estimate	s.e.	ndf	ddf	F-test	p-value
Taxon : sex			1.00	69.00	2.18	0.14
Taxon			1.00	70.00	3.56	0.06
Sex			1.00	71.00	4.33	0.04
Taxon (<i>O. ruficeps</i>): Sex (male)	-0.60	0.41				
Taxon (<i>O. motmot</i>)	-0.19	0.13				
Taxon (<i>O. ruficeps</i>)	0.22	0.14				
Sex (male)	0.36	0.19				
PC1 and PC2 (MANOVA)	Residuals	Pillai	ndf	ddf	F-test	p-value
Taxon : sex	69.00	0.08	2	68	2.89	0.06
Taxon	70.00	0.85	2	70	197.85	< 0.01*
Sex	71.00	0.16	2	69	6.456	< 0.01*

which was later supported by Pinto (1978). These localities were also scrutinized by Wiley (2010), who raised a considerable suspicion of carelessness in labeling by the original collector A. Olalla. Thus, the correct provenance of these specimens is considered doubtful. Because of this and the lack of additional material indicating syntopy, we excluded these problematic localities from the map (Fig. 4).

Although uncommon in the taxonomy of recent birds, differences in dimensions of distinct and unrelated morphological traits are a strong indicative of the existence of distinct evolutionary lineages. Our expertise with osteology of Cracids (see Silveira, 2003; Grau *et al.*, 2005; Frank-Hoeflich *et al.*, 2007) show that modifications in skeleton and body size seem to evolve at a slower pace than plumage and voice, and finding these osteological differences, without overlap, strongly support the existence of two distinct species. Bone measurements and size differences are widely used and supported in paleontological studies to delineate species (*e.g.*, Olson 1974; Balouet & Olson 1987; Alvarenga *et al.*, 2002; Alvarenga & Olson, 2004; Mayr *et al.*, 2017), as well as in neontology to validate taxa with disjunct populations (Alvarenga *et al.*, 2002). Our extensive analysis of *O. m. motmot* and *O. m. ruficeps* show that the population south of the Amazon River differs considerably in size from birds from north of the Amazon, without overlap; differences in plumage and voice are also present, though of smaller magnitude. Based on these differences (size, plumage, and voice), coupled with the distinct geographical distribution, we therefore argue that *Ortalis ruficeps* (Wagler, 1830) should be treated as a valid species, distinct from *O. motmot*, as originally described and presented below.

Systematics

Order Galliformes

Family Cracidae

Genus *Ortalis* Merrem, 1786

Ortalis motmot (Linnaeus, 1766)

Phasianus motmot Linnaeus, 1766: 271.

Phasianus katraca Boddaert, 1783: 9.

Phasianus Parraka Gmelin, 1789: 740.

Phasianus Parraqua Latham, 1790: 632.

Phasianus Parrakoua Temminck, 1815: 695.

Penelope motmot Wagler, 1830: 1111.

Penelope paraca Schomburgk, 1848: 31.

Ortalis motmot Cabanis, 1849: 744; Sclater & Salvin, 1870: 532; Pelzeln, 1870: 285, 1873: 119; Brown, 1876: 373; Goeldi, 1897: 161.

Penelope Parrakoua: Burmeister, 1856: 341.

Ortalis motmot: Salvin, 1886: 175; Ogilvie-Grant, 1893: 505, 1897: 235; Goeldi, 1897: 156; Berlepsch & Hartert, 1902: 120; Hellmayr, 1907: 39; Berlepsch, 1908: 297; Sneathlaga, 1914: 56; Cherrie, 1916: 356; Chubb, 1916: 27; Beebe *et al.*, 1917: 127; Bangs & Penard, 1918: 40; Chapman, 1931: 61; Sick, 1985: 232; Sick, 1997, 2001: 277.

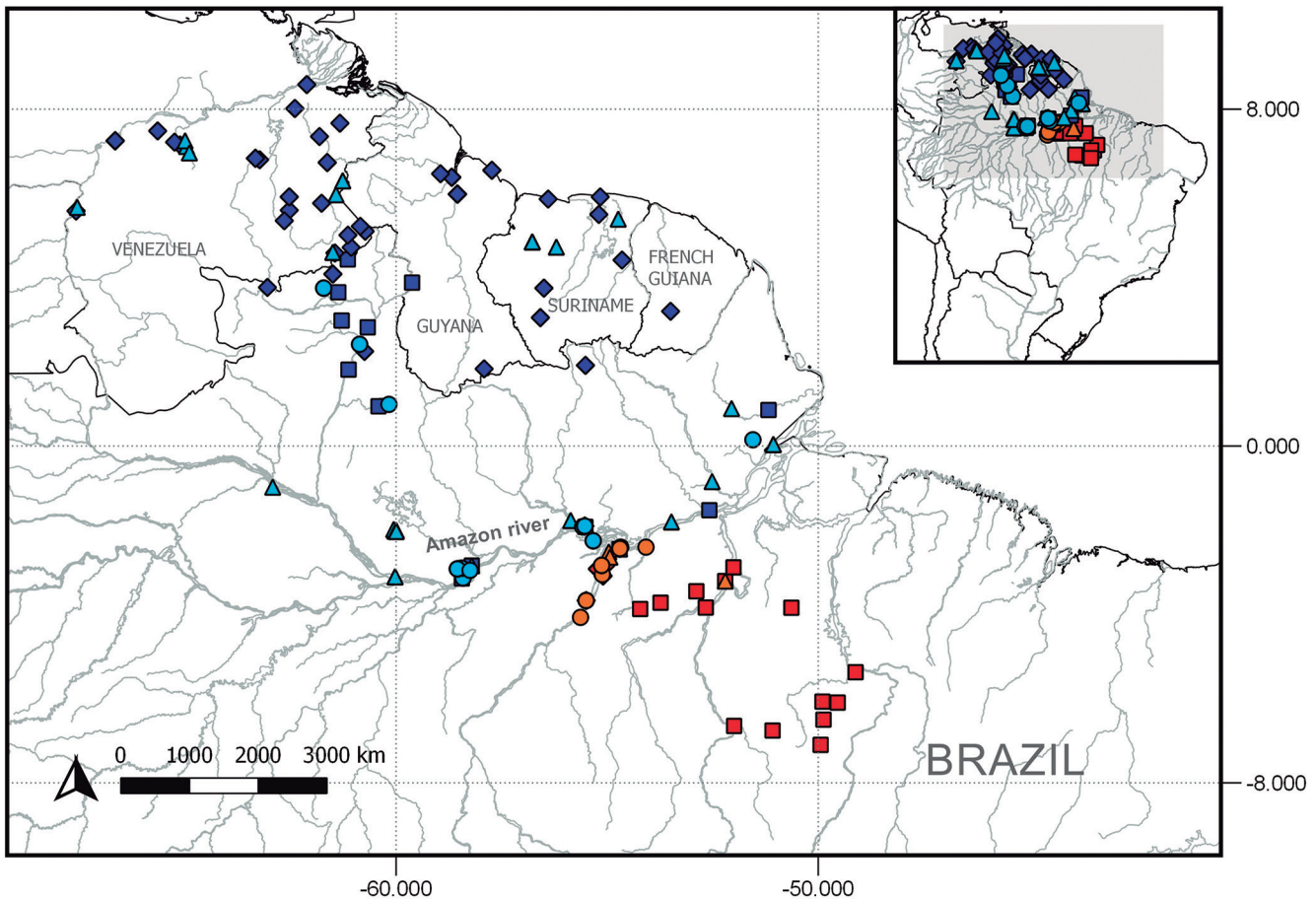


Figure 4. Distribution of *O. motmot* (blue and light blue) and of *O. ruficeps* (orange and red). Circles: measured specimens; triangles: vocalizations; diamonds: skins not measured; squares: photographs.

Ortalis katraça: Ihering & Ihering, 1907: 15.

Ortalis motmot motmot: Peters, 1934: 17; Hellmayr & Conover, 1942: 161; Pinto, 1964: 107; Vaurie, 1965: 19, 1968: 244; Delacour & Amadon, 1973: 116; Blake, 1977: 396; Pinto, 1978: 78; del Hoyo et al., 1994: 345; Grantsau, 2010: 63.

Type material: The species was described based on a specimen deposited in M. Réaumur's collection. Specimens from his collection eventually came to MNHN, but we were unable to locate an *Ortalis motmot* with compatible data in the MNHN collection, and we assume it is lost. See also Voisin et al. (2015).

Type locality: Cayenne, French Guiana.

Description: No sexual dimorphism in plumage color. Crown dark reddish brown. Forehead dark reddish brown. Bill gray. Throat yellowish red. Chest dark grayish brown. Abdomen, flanks and crissum pale brown. Mantle dark yellowish brown. Wing primaries and coverts dark brown. Tail coverts dark reddish brown. External rectrices dark reddish brown. Central rectrices dark brown. Males larger than females.

Measurements: See Table 1.

Voice: See Table 2.

Diagnosis: Similar to *O. ruficeps*, but border of external rectrices redder; size considerably larger (with no overlap); different vocalization (shorter syllable length, and consequently shorter song).

Distribution: Venezuela, Guyana, French Guiana, Suriname, and northern Brazil (Pará, Roraima, Amapá and Amazonas states).

Specimens examined (n = 111): BRAZIL: Amazonas: Comunidade Vila Nova, Macapá (MZUSP 82332); Rio Amazonas, Lago de Camaçari (MZUSP 22108, 22064, 22284); Rio Amazonas, Itacoatiara (MZUSP 22130, 22178); Rio Amazonas, Silves (MZUSP 22175, 22177, 22181, 21420); Rio Amazonas, Igarapé Anibá (MZUSP 21092, 22017, 22107, 22122, 22817). Pará: Rio Amazonas, Boca do canal Piava, 10 mi E Óbidos (FMNH 410726, 410727); Rio Trombetas, Jacaré (MZUSP 59839, 59840); Rio Amazonas, Jacuara (FMNH 422549); Lago Cuipeva (FMNH 410722, 410723, 410724, 410725); Lago Grande (MZUSP 10599, 10600, 10601); Rio Amazonas, Lago Cuiteuá (MZUSP 15693, 15694); Rio Amazonas, Igarapé Buiussú (MZUSP 22134). Roraima: BR-174, km 709 (MZUSP 81386), Rio Mucajaí (MZUSP 55750); Rio Jufari, Sitio Valdir (MZUSP 93582); Rio Mucajaí, São João da Boa Vista (MZUSP 55751); Serra da Lua, near Boa Vista (FMNH 46870, 46871, 46872, 46873); Serra Tepequém, V. Cabo Sobral, Amajari (MZUSP 79080, 79081, 79082). FRENCH GUIANA: Camopi (MNHN

Table 2. Model results for the simple regression analyses testing the effects of taxon on the vocal characters, as well as means and standard errors for each taxon. Statistics are given for each term at the point of exclusion of the term from the model. *P*-values in bold with an asterisk represent significance after a Bonferroni correction to account for multiple testing (critical *p*-value = 0.05/number of tests).

Total duration		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	10.33	< 0.01*
	mean				
<i>O. m. motmot</i>	0.47				
<i>O. m. ruficeps</i>	0.54				
Note 1		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	3.18	0.09
	mean				
<i>O. m. motmot</i>	0.11				
<i>O. m. ruficeps</i>	0.09				
Note 2		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	14.80	< 0.01*
	mean				
<i>O. m. motmot</i>	0.12				
<i>O. m. ruficeps</i>	0.16				
Note 3		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	3.38	0.08
	mean				
<i>O. m. motmot</i>	0.14				
<i>O. m. ruficeps</i>	0.17				
Interval 1		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	2.17	0.16
	mean				
<i>O. m. motmot</i>	0.03				
<i>O. m. ruficeps</i>	0.02				
Interval 2		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	1.39	0.25
	mean				
<i>O. m. motmot</i>	0.08				
<i>O. m. ruficeps</i>	0.10				
PC1		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	19.20	< 0.01*
	mean				
<i>O. m. motmot</i>	-0.48				
<i>O. m. ruficeps</i>	2.39				
PC2		ndf	ddf	F-test	<i>p</i> -value
Taxon		1.00	16.00	1.42	0.25
	mean				
<i>O. m. motmot</i>	-0.15				
<i>O. m. ruficeps</i>	0.76				

829); Saut Macaque (MNHN 757). GUYANA: Itabu Creek, Middle Base Camp (FMNH 120033); Rockstone (FMNH 105553); Rockstone, Essequibo River (FMNH 108052, 108053, 108054, 108055, 108056, 413176, 413177, 413178); Abary River (FMNH 190562, 190563); Kartabo Point (FMNH 408015, 408016, 408017); Oko Mts (FMNH 413179); Mahacai Creek (FMNH 32452, 32453); Trois Sauts (MNH 830). SURINAME: Savana Awarra – Wageningen (RMNH 65967-12); Lely Gebergte (RMNH 80449-13); Kayser Gebergte Airstrip, Zuid River (FMNH 422919, 422920); Wilhelmina Gebergte, West River (FMNH 423278, 423279); Paramaribo, vicinity (FMNH 47305); Republiek (RMNH 37980), Unknown locality (SMNS 2066). VENEZUELA: Caño

Cataniapo Atures (COP 20613, 20614); Sierra Pacaraima, Cerro Urutani (AMNH 812850, 812851, COP 73499); Arabapu Mt. Roraima (COP 4064, 4065); Caño Maniapure (EBRG 3618, 3619, 4300, 5665, 6578, 7421, 7520); Base Cerro Uaipan-Tepui (COP 42762); Campo Uriman Rio Caroni (COP 20614); Cerro Tigre Rio Chiguás (COP 15787); El Dorado (COP 17431, EBRG 2108, 2109); Falda, Cerro Cuquenán (COP 50112); Hato Sta. Tereza Rio Uairen (COP 44401); La Fáisca Cerro Paurai-Tepui (COP 32257); La Fáisca Mirra Cerro Paurai-Tepui (COP 32236); La Paragua (COP 15783, 15784, 15786); Mt. Auyan Tepui (COP 7855, 7856); Peso Callao (COP 74269); Ptari-Tepui Falda Sudoeste (COP 26862); Puerto Carretico Mato Caura (COP 51979); Reserva Florestal El Caura (EBRG 10618); San Ignacio de Yuruaní (EBRG 8648); Sierra Imataca Altiplanicie de Nuria (COP 16814); Sta. Rosalia Depto. Cedeño (COP 24983); Upata (EBRG 3985, 3996); Piacoa (FMNH 81436, 81437).

Photographs (n = 287): BRAZIL: Amazonas: Itacoatiara (1); Manaus (148); Presidente Figueiredo (53). Amapá: Ferreira Gomes (3); Macapá (4); Serra do Navio (5). Pará: Almeirim (2); Óbidos (2); Oriximiná (9); Prainha (1). Roraima: Alto Alegre (1); Amajari (42); Boa Vista (2); Caracará (7); Normandia (1); Pacaraima (1); Rorainópolis (2).

Voice samples. Used (n = 15): BRAZIL: Amazonas: Manaus (WA1119199, WA394390); Presidente Figueiredo (XC76224); Silves (WA1043482). Amapá: Macapá (WA135794, WA195670). Pará: Oriximiná (WA1797851); Prainha (WA583167). SURINAME: Foengoe Island (XC172162); Mozeskreek (XC272216, XC272217). VENEZUELA: Bolívar (XC226986); Caura (XC103386, XC226988); La Escalera (XC354952). **Not used (n = 20):** BRAZIL: Amazonas: Barcelos (WA23908); Manaus (WA154684, WA2063779, WA285768); Presidente Figueiredo (XC13320, XC227403, XC345471). Amapá: Laranjal do Jari (WA1725565); Macapá (WA148965) Serra do Navio (XC85264). FRENCH GUIANA: Armontabo (XC11783). SURINAME: Mapane (XC1065); Mozeskreek (XC272182, XC272183, XC272218). VENEZUELA: Bolívar (XC226985, XC227406, XC227407); Maripa (XC9925); Puerto Ayacucho (XC107593).

Ortalis ruficeps (Wagler, 1830)

Penelope ruficeps Wagler, 1830: 1111.

Ortalida ruficeps: Wagler, 1832: 1227; Sclater & Salvin, 1870: 533; Allen, 1876: 82.

Ortalida motmot: Riker & Chapman, 1891: 162.

Ortalis ruficeps: Ogilvie-Grant, 1893: 504, 1897: 236; Ihering & Ihering, 1907: 15; Sick, 1985: 232; Sick, 1997; 2001: 277.

Ortalis motmot ruficeps: Todd, 1932: 212; Peters, 1934: 17; Pinto, 1938: 100; Hellmayr & Conover, 1942: 161; Pinto, 1964: 108; Vaurie, 1965: 16, 1968: 244; Delacour & Amadon, 1973: 116; Blake, 1977: 396; Pinto, 1978: 78; del Hoyo et al., 1994: 345; Grantsau, 2010: 63.

Type specimen: MfN 11909, examined.

Type locality: Brazil, Pará state. A more precise locality was not given in the original description, but Erwin Stresemann (in Todd, 1932) argued that the collection site was probably around Cameté, Tocantins River, Pará state.

Description: No sexual dimorphism in plumage color. Crown dark reddish brown, lighter in a few specimens. Forehead dark reddish brown. Bill gray. Throat yellowish red. Chest dark grayish brown. Abdomen, flanks and crissum pale brown. Mantle dark yellowish brown. Wing primaries and coverts dark brown. Tail coverts dark reddish brown. External rectrices dark reddish brown with borders tinged dark brown. Central rectrices dark brown. Males larger than females.

Measurements: See Table 1.

Voice: See Table 2.

Diagnosis: Similar to *O. motmot*, but border of external rectrices less red; size distinctively smaller (with no overlap); different vocalization (longer syllable length, and consequently slower song).

Distribution: Brazil, south of Amazon River (Pará and Mato Grosso states).

Specimens examined (n = 36): BRAZIL: Pará: Rio Tapajós, Caxiricatuba (FMNH 410096, 410097); Rio Tapajós, Fordlândia (FMNH 422550, 422551; MZUSP 46266, 58096, 68851, 62591, 73244, 102858; Lago Cuipeua (FMNH 418533); Rio Amazonas, Foz do Rio Curuá (MZUSP 17054); Rio Tapajós (MZUSP 67928); Rio Tapajós, Pinhel (FMNH 411103, 411104, 411105); Rio Tapajós, Tauary (FMNH 410099, 410100); Rio Tapajós, Monte Cristo (MZUSP 46265); Rio Tapajós, Piquiatuba (MZUSP 22124, 22282, 22818); Rio Tapajós, Caxiricatuba (MZUSP 17053, 22045, 22046, 22088, 22103, 22123, 22125, 22126, 22131, 22132, 22133, 22819); Rio Tapajós, Santarém (FMNH 410098, MZUSP 46267).

Photographs (n = 125): BRAZIL: Pará: Altamira (9); Canaã dos Carajás (1); Curionópolis (3); Marabá (1); Medicilândia (1); Ourilândia do Norte (1); Pacajá (1); Parauapebas (19); Placas (1); Santarém (9); São Félix do Xingu (3); Uruará (1); Vitória do Xingu (7); Xinguara (5).

Voice samples. Used (n = 3): Pará: Belterra (WA757077); Santarém (XC312921, XC95103). **Not used (n = 2):** Pará: Altamira (WA1629138); Santarém (WA2288948).

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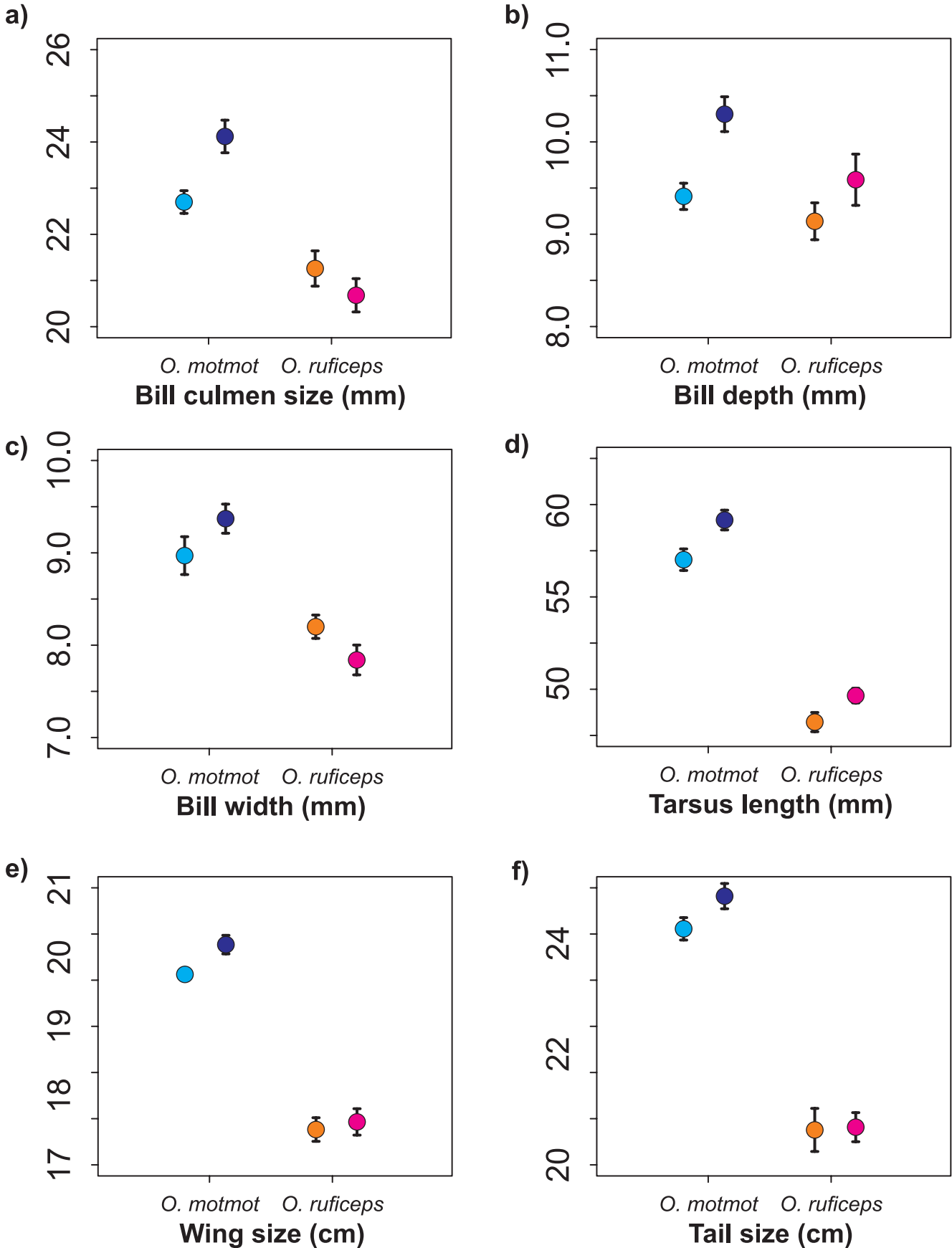
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APPENDIX 1

Results of the individual analysis testing for the differences in size of bill (a-c), tarsus (d), wing (e) and tail (f) between the two taxa (and also testing for sex differences). Blue: *O. motmot*; red: *O. ruficeps*. Dark-coloured symbols: males; light-coloured symbols: females.



APPENDIX 2

Outcomes of the principal component analysis for morphometrics.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.90	0.84	0.67	0.54	0.37	0.36
Proportion of Variance	0.68	0.13	0.08	0.05	0.03	0.02
Cumulative Proportion	0.68	0.81	0.90	0.95	0.98	1.00
Bill culmen	-0.42	0.47	-0.52	0.32	-0.27	-0.40
Bill depth	-0.20	0.60	0.75	0.05	0.12	-0.09
Bill width	-0.35	0.31	-0.26	-0.72	0.11	0.43
Tarsus	-0.47	-0.18	-0.07	0.48	0.62	0.35
Wing	-0.48	-0.31	0.26	0.10	-0.70	0.34
Tail	-0.46	-0.43	0.14	-0.37	0.19	-0.64

APPENDIX 3

Outcomes of the principal component analysis for song.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.49	1.23	1.07	0.83	0.65	0.06
Proportion of Variance	0.37	0.25	0.19	0.12	0.07	0.00
Cumulative Proportion	0.37	0.62	0.81	0.93	1.00	1.00
Total syllable length	0.61	-0.02	-0.22	-0.38	0.19	0.63
Note 1	-0.37	-0.11	-0.65	-0.33	0.52	-0.22
Note 2	0.42	0.05	-0.64	0.22	-0.49	-0.35
Note 3	0.53	-0.32	0.25	0.19	0.53	-0.48
Interval 1	-0.02	-0.67	0.15	-0.58	-0.41	-0.17
Interval 2	0.17	0.66	0.20	-0.58	-0.02	-0.40

APPENDIX 4

Results of the individual analysis testing for the differences in song and note duration between the two taxa. Blue: *O. motmot*, Red: *O. ruficeps*.

