

Species limits, patterns of secondary contact and a new species in the *Trogon rufus* complex (Aves: Trogonidae)

JEREMY KENNETH DICKENS^{1,2,*}, PIERRE-PAUL BITTON³, GUSTAVO A. BRAVO^{4,●} and LUÍS FÁBIO SILVEIRA¹

¹Museu de Zoologia da Universidade de São Paulo, 481 Av. Nazaré, Ipiranga, São Paulo, 04263-000, Brazil

²Fundación Para La Tierra, 321 Mariscal José Félix Estigarribia, Pilar, 2800, Ñeembucú, Paraguay

³Department of Psychology, Memorial University of Newfoundland, 232 Elizabeth Avenue, St. John's, NL A1B 3X9, Canada

⁴Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

Received 6 May 2019; revised 13 October 2020; accepted for publication 8 November 2020

The black-throated trogon, *Trogon rufus*, is a widespread, polytypic species-complex with a convoluted taxonomic history. Here, we integrated morphological, vocal and genetic datasets, including spectral data and digital quantification of barred plumage, to assess and redefine its species limits according to the foremost species concepts. We suggest the recognition of four named and one new species. *Trogon tenellus* and *T. cupreicauda* are divergent across Central and South America without geographic overlap or intermediates. *Trogon chrysochloros* in the Atlantic Forests of Brazil is phenotypically, genetically and ecologically distinct. In Amazonia, *Trogon rufus* consists of three phenotypically distinct subspecies intergrading with each other in a ring-like formation around central Amazonian rivers. *Trogon rufus rufus* in the Guiana Shield, *Trogon rufus amazonicus* in south-eastern Amazonia and *Trogon rufus sulphureus* in western Amazonia, with contact across the Lower Amazon and Madeira rivers, likely due to secondary contact between incompletely diverged lineages. The unique combination of song, morphology and mtDNA features of an unnamed, isolated population in the Atlantic Forest of north-eastern Brazil resulted in its description as a new species, known only from the type locality and considered here as Critically Endangered, requiring urgent conservation actions.

ADDITIONAL KEYWORDS: species boundaries – Neotropical – sibling species – divergence – alpha taxonomy – species delineation – taxonomic revision – evolutionary trends – new species – Aves.

INTRODUCTION

The trogons and quetzals (Trogoniformes) are a pantropically distributed order of birds consisting of a single family, the Trogonidae, which contains 43 species and 109 subspecies (Gill & Donsker, 2019). They are identified by the possession of a heterodactyl foot, in which digits one and two point posteriorly

(Collar, 2001), and are among the most colourful birds in the world. Males are patterned with hues of iridescent green, blue, violet and purple above (except in the Asian *Harpactes* Swainson, 1833), and a bright red, yellow or orange abdomen. Females have grey or brown plumage where males are iridescent

Originating in Eurasia during the Palaeogene (Kristoffersen, 2002; Mayr, 2005; Oliveros *et al.*, 2019), they are thought to have been widespread across Laurasia and Africa before becoming fragmented between the African, Asian and American tropics due to global cooling and changes in habitat during the Oligocene–Miocene (Oliveros *et al.*, 2019). Today, they are most diverse in the Neotropics with 29 species,

*Corresponding author. E-mail: jerdickens@gmail.com
[Version of record, published online XX XXXX XXXX;
<http://zoobank.org/> urn:lsid:zoobank.org:pub:BD62F699-AA76-4EE3-8B78-C4007112F103]

of which 24 species and 66 subspecies belong to the genus *Trogon* Brisson, 1760 (Gill & Donsker, 2019). This relatively high diversity is a result of their rapid diversification in South America following the ‘Great American Interchange’ coinciding with the closing of the Isthmus of Panama (DaCosta & Klicka, 2008). Although diversification is mostly attributed to divergence across geographic barriers, its sympatric occurrence in multiple lineages yielded classic patterns of trait sorting amongst South American species (Bitton, 2015). This is especially notable in the characteristic undertail pattern (black, white or barred), presence/absence of a white breast band and head colour.

Differences in these traits are, therefore, likely associated with taxonomic differences and they have featured prominently in trogon taxonomy, along with differences in tonality of iridescent plumage patches, bareparts’ coloration (especially eye-ring) and wing panel patterning (plain or barred) (Gould, 1838; Ridgway, 1911; Todd, 1943; Zimmer, 1948; Pinto, 1950; Collar, 2001). In particular, the distinctiveness of the undertail pattern between species has long raised suspicions over its involvement in species recognition (Collar, 2001). This was recently confirmed by Bitton & Doucet (2016), whilst Bitton & Doucet (2014) linked it to the tail-raising display – a multifunctional visual display that targets both con- and heterospecifics in the closely related species, *Trogon elegans* Gould, 1834. In terms of the tonality of iridescent plumage, this is known to be produced by the coherent scattering of light by melanosomes in the feather filaments (Durrer & Villiger, 1966). However, the variability in tonality and barring dimensions has never been investigated at the meta-population level but would likely offer insight into species limits.

In this context, *Trogon rufus* Gmelin, 1788 is widely distributed in the understory and mid-levels of humid forests from Honduras to northern Argentina, up to 1100 m above sea level (Collar, 2001). It was first described by Gmelin (1788) from female birds depicted and described by Buffon and d’Aubenton (1765–81) as ‘Le Couroucou à queue rousse’ and Latham (1782) as ‘Rufous Curucui’ from French Guiana and named after their reddish-brown colored upperparts. The male was initially described as *Trogon atricollis* Vieillot, 1817, until Gould (1838) realized that *Trogon rufus* and *T. atricollis* were in fact the same species.

It is easy to distinguish from its congeners by the unique combination of a green head in males, brown in females, and a yellow belly. However, with the collection of more material, it soon became recognized as notoriously variable across its distribution and resulted in the description of nine taxa. Of particular interest to past authors has been the uppertail colour,

which varies notably between populations (Gould, 1838; Ridgway, 1911; Todd, 1943; Zimmer, 1948; Pinto, 1950), whilst the dimensions of the barred patterning, collar presence/absence and body size have also featured prominently. Nevertheless, most accounts are highly speculative, usually because of the limited material available, leading to high levels of uncertainty in classifications.

The first new species to be split from the nominate was *Trogon sulphureus* Spix, 1824, described from a single male collected in Tabatinga, on the Rio Solimões, Brazil, which was distinguished by its shiny coppery (versus green) uppertail. A second coppery-tailed form from Santa Maria, on the left bank of the upper Amazon in Peru, was described as *Aganus devillei* Cabanis & Heine, 1863, but most authors found it to be consistent in morphology with *T. sulphureus*. Nevertheless, slight differences in the intensity of the copper sheen of the uppertail between specimens led to its intermittent resurrection (Stone, 1928; Zimmer, 1930; Gyldenstolpe, 1945) until Gyldenstolpe (1951) noted that the close proximity between the type localities, both on the left bank of the Rio Solimões, made it almost impossible for them to be different.

The Central American form was then described as *Trogon tenellus* Cabanis, 1862, based on an immature male with a brown tail. However, since Grant (1892) first noted the uniquely bluer tail colour of the adult male and the broader barring on the undertail and wing panel compared to the nominate it has been recognized as valid by most subsequent authors. Similarly, *Trogonurus curucui cupreicauda* Chapman, 1914, from the Chocó and Magdalena Valley, was distinguished from *tenellus* and the nominate by its copper-bronze uppertail with greenish reflections. The undertail and wing panel barring were also noted as similar to *tenellus* but broader than the nominate, whilst it lacked the white breast band of these taxa and had a more deeply yellow abdomen. Subsequent authors have consistently upheld the validity of this taxon but maintained its subspecies status due to uncertainty over the fact that these distinctions represented species-level differences.

Unlike the aforementioned taxa, there has been wide disagreement about the validity and status of *Trogon chrysochloros* Pelzeln, 1856, described from a series of specimens from São Paulo state, Brazil. Pelzeln (1856, 1868) distinguished it from the nominate by its larger body size, presence of a vague white breast band and the finer barring of the upperwing coverts and outer tail secondaries, although he noted overlap in the coarseness of the barring and that the breast band could not yet be regarded as diagnostic due to the small sample size. Seemingly unaware of this, Bertoni described *Trogon splendidus* Bertoni, 1901, from

Paraguay based on similar differences, which [Cory \(1919\)](#) promptly synonymized with *T. chrysochloros*.

The validity of *T. chrysochloros* was questioned by a number of authors, including [Cabanis & Heine \(1863\)](#), [Grant \(1892\)](#), [Ihering \(1898\)](#), [Ihering & Ihering \(1907\)](#), [Ridgway \(1911\)](#), [Cory \(1919\)](#), [Sztolcman \(1926\)](#), [Pinto \(1932, 1935, 1938\)](#) and [Camargo \(1946\)](#). They noted similarity in coloration with *T. rufus*, and overlap in barring dimensions, body size and inconsistency in breast band presence/absence, so they treated *T. chrysochloros* as a synonym of *T. rufus*. On the other hand, authors including [Berlepsch & Ihering \(1885\)](#), [Hellmayr \(1906\)](#), [Stone \(1928\)](#), [Griscom & Greenway \(1941\)](#), [Todd \(1943\)](#), [Peters \(1945\)](#) and [Pinto \(1950, 1978\)](#) considered *T. chrysochloros* a subspecies of *T. rufus* based on the confirmation of differences described by [Pelzeln \(1856\)](#), whilst noting additional subtle differences, such as a more blue-green mantle ([Hellmayr, 1906](#)). However, [Pinto \(1935\)](#) noted the similarity in the smaller size and more citrus-yellow abdomen of specimens from Bahia, Brazil, in the Atlantic Forest, with specimens from Amazonia, so he synonymized these but maintained *T. chrysochloros* for specimens from the southern Atlantic Forest, which were consistently larger and had cadmium yellow abdomens. In addition, [Collar \(2001\)](#) presumed that records of *Trogon rufus* in the Atlantic forest of Alagoas, north-eastern Brazil, pertained to *T. chrysochloros* but lacked any material on which to base his judgement.

Finally, in Amazonia, a lot of disagreement and speculation arose regarding the validity of *Trogon r. amazonicus* [Todd, 1943](#) from ‘Lower Amazonia’. [Todd \(1943\)](#) described it based on differences in the uppertail colour, which he described as more coppery-bronze than *T. rufus* but less so than *T. sulphureus*. Nevertheless, he also acknowledged the intermediary nature of specimens from Manacapuru, on the south bank of the central Amazon, halfway between the type localities of *T. r. sulphureus* and *T. r. amazonicus*. In contrast, [Pinto \(1950\)](#) noted a specimen from the Rio Arapiuns, on the lower Rio Tapajos, within the distribution of *T. r. amazonicus*, that had a *T. rufus*-like green uppertail and, therefore, synonymised *T. r. amazonicus* with *T. rufus*, but conceded that most specimens in the region possessed more coppery uppertails. Nevertheless, despite this disagreement and without any further justifications of taxonomic validity or status, all major modern taxonomic sources ([Piacentini et al., 2015](#); [Gill & Donsker, 2019](#); [Remsen et al., 2020](#)) have maintained [Todd’s \(1943\)](#) classification of the following six subspecies ([Fig. 1](#)): *T. r. rufus* [Gmelin, 1788](#) in the Guiana Shield, *T. r. sulphureus* [Spix, 1824](#) in upper Amazonia (west of the Madeira and Branco Rivers), *T. r. chrysochloros* [Pelzeln, 1856](#) in the Atlantic forest (including Alagoas), *T. r. tenellus* [Cabanis, 1862](#) throughout Central

America, *T. r. cupreicauda* ([Chapman, 1914](#)) in the Chocó-Magdalena region and *T. r. amazonicus* [Todd, 1943](#) in lower Amazonia (east of the Madeira River).

However, since this last revision in 1943, a wealth of new museum specimens, song recordings and genetic sequences have become available, providing an excellent opportunity for a more comprehensive investigation of the species limits in the complex. The advent of novel technologies, particularly spectrometry for colour analysis, digital photographic analysis of plumage patterning ([McKay, 2013](#)), acoustic analyses of song recordings ([Payne, 1986](#); [Catchpole & Slater, 2003](#)) and molecular phylogenetics, also provide new ways to compare traits important for the distinction between species. Therefore, we aim to assess and redefine the species limits of the *Trogon rufus* complex by integrating comprehensive analyses of morphological, vocal and genetic characters.

MATERIAL AND METHODS

MORPHOLOGICAL ANALYSES

Material Examined: We examined 906 museum specimens identified as *Trogon rufus* (547 male, 359 females) housed at 17 different museums (see complete list in [Supporting Information, File S1](#)), including all available type specimens. JKD measured specimens in United States and Brazilian collections by hand and qualitatively assessed type specimens in European collections and specimens in the Colección Ornithologica Phelps in Venezuela via high-quality digital photographs, measuring only the barred patterning.

Coloration: For 219 male specimens, representing more than 90% of our specimen-based localities, we obtained reflectance spectra of iridescent plumage patches (head, mantle, rump, chest, uppertail and subterminal tailband) over the ultraviolet-visible range (300–700 nm). We excluded abdomen colour as it fades and changes markedly after death. We used an Ocean Optics USB2000 spectrometer in conjunction with a PX-2 xenon lamp and a bifurcated fibre-optic probe (Ocean Optics, Dunedin, Florida, USA) fitted with a rubber tip that maintained a consistent distance between the fibre and feathers, and excluded ambient light. Measurements were taken in OceanView or Overture software (Ocean Optics) in relation to an Ocean Optics WS-1 diffuse pure white reflectance standard. We allowed the light source to warm up for 20 min prior to data collection to ensure constant light quality. Five reflectance spectra were measured per patch per individual directly from museum skins, avoiding areas that were dirty, ruffled or had lost feathers. We collected the measurements at the angle of maximum

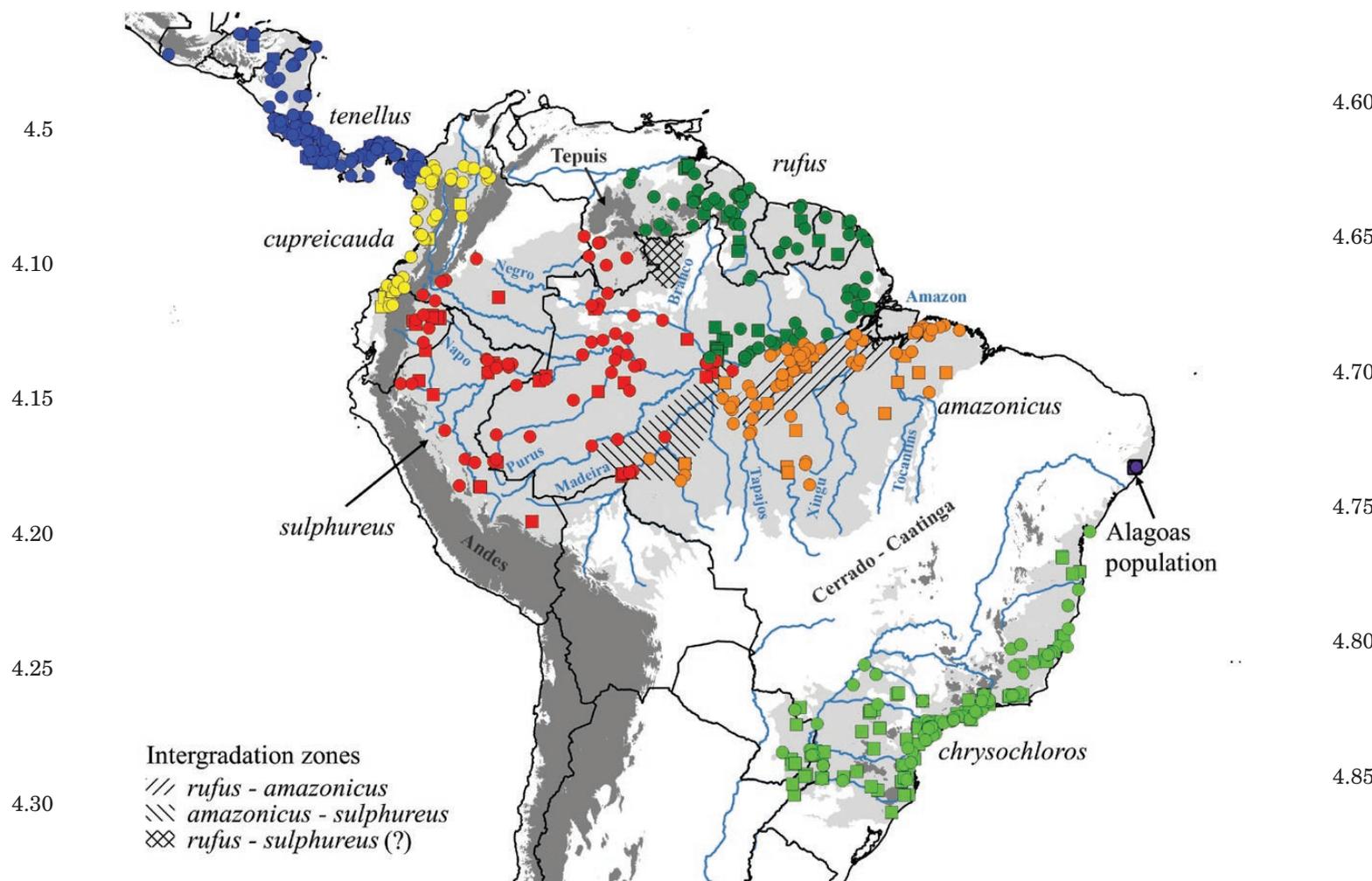


Figure 1. Localities of all examined museum skins (circles) and song recordings (squares) of species and subspecies in the *Trogon rufus* complex as well as the position of intergradation zones between Amazonian subspecies. Light grey = tropical and subtropical humid forests; dark grey = > 1000 m a.s.l., blue lines = major rivers.

reflectance to eliminate variation caused by changes in the angle of reflectance (Meadows *et al.*, 2011). The spectra were averaged in 1-nm steps and aggregated into mean curves per patch by individual. From these, the hue – wavelength at maximum reflectance, brightness – average area under the curve, and saturation – (value of maximum reflectance – value of minimum reflectance)/brightness, values were extracted for further use using the package pavo (Maia *et al.*, 2013) in R software (R Development Core Team, 2015).

Female coloration, we assessed qualitatively in preference to spectrometric analysis, due to the much lower level of colour variation observed and lack of iridescence. Since the brown colours displayed by females do not reflect light in the ultraviolet range, human assessment of colour would be near identical to that of birds (Håstad & Ödeen, 2008). We matched the colour of the head, mantle, chest and uppertail as

closely as possible to Munsell Soil Color Charts (Munsell Color [firm], 2010). These were transformed into x, y, z Cartesian coordinates for inclusion in quantitative analyses, as per Ruck & Brown (2015), based on the model developed by D’Andrade & Romney (2003).

Barring: We took RAW digital photographs of all adult specimens with intact undertail (343 M, 242 F) and wing panel (361 M, 203 F) barred plumage with a Nikon D60 camera and standard AF-S DX NIKKOR18-55 mm f/3.5–5.6G II ED lens and placed a standard ruler alongside each for scale. For consistency in scale, we took photographs with the lens exactly 50 cm above the ruler, with the camera secured in place using a tripod, and set the focal length to 45 mm. We used daylight to achieve optimal exposure. We then converted RAW images to lossless TIFF files using the adaptive homogeneity directed interpolation algorithm in DCRAW v.8.99,

- standardizing settings across all images with output in raw colour using the custom white level of the original image. We then loaded TIFF images into IMAGEJ v.1.45r (Schneider *et al.*, 2012) for measurement of
- 5.5 barring traits and set the scale using the graduations on the ruler at 300× zoom. On the undertail, we measured the widths of the six outermost bars on rectrix 2 (three black, three white) and calculated the mean black and white bar widths. We then calculated barring density
- 5.10 (bars per cm) by converting the ratio between the number of bars (six) and the distance across them in mm to the number of bars in 10 mm. For the wing panel, we measured the widths of the eight outermost bars on the greater secondary wing-coverts (four black, four white, excluding that on the feather's edge) and calculated the mean black and white bar widths. We measured density by counting the number of black bars intersecting a 1-cm line drawn from the edge of two separate feathers in the greater secondary wing-coverts. In both the undertail and wing panel barring, we calculated the percentage area black as the sum of black bar widths as a percentage of the combined black and white bar widths.
- 5.15
- 5.20
- 5.25 *Morphometrics:* For 879 of the specimens examined, we obtained the following five measurements following Baldwin *et al.* (1931): wing length, tail length, total culmen length, height of bill at nostrils and width of bill at gape. We measured wing and tail lengths to the nearest millimetre with a standard ruler (0.5 mm precision). We varied from other authors by measuring the tail length from the tip of the longest rectrix to the internal base of the rectrices (which proved a constant landmark). For the bill, we measured characters to the nearest 0.1 mm with mechanical callipers. Additionally, we counted the number of serrations per side of the upper bill. Body mass was noted from the specimen tag.
- 5.30
- 5.35
- 5.40 *Bareparts' coloration:* We noted bill, iris, tarsus and eye-ring colours from specimen tags and/or associated photographs and allocated these to the following categories based on Munsell hues. For the eye-ring: blue, blue-grey, grey, white, green, green-yellow and yellow. For the tarsus: blue-grey, grey, purplish-grey, pinkish-grey, and olive. We supplemented data on bareparts' colours with footage from the following online digital archives: www.wikiaves.com.br, Internet Bird Collection (<http://ibc.lynxeds.com>), and Flickr.com, preceding January 2015, and various private contributions, using only clear images with undistorted colours.
- 5.45
- 5.50
- 5.55 *Additional discrete characters:* We recorded the presence (complete or inconspicuous) or absence of a white breast band, and the presence or absence and width of the black terminal tailband and subterminal tailband of greener coloration on the uppertail. We
- 5.56
- categorized the light brown wash on the undertail of females, as either absent, only basal to the outer rectrices, edging the black basal patch or extensive, when held in a natural position. 5.60
- DIET
- We recorded dietary preferences as either fruit or arthropods from stomach contents listed on specimen tags and photographs of feeding individuals from the above-mentioned digital archives. 5.65
- VOCAL ANALYSES
- 5.70 We examined 273 songs by separate individuals from 348 audio recordings in WAV format obtained from online and private audio collections (see complete list in [Supporting Information, File S2](#)). Prior to analysis, we rated the quality of recordings as A (loud, clear), B (relatively clear, little interference), C (relatively faint and/or with much interference) and D (barely audible) and only considered those rated A and B in the analyses. Due to the lack of information on sex for most recordings, and the lack of evidence for any major changes in song between sexes, and with and without playback in the preliminary analysis, we disregarded these factors in song selection. Using Raven Pro 1.5 (Center for Conservation Bioacoustics, 2014), we viewed song recordings as spectrograms with a frame length of 1024 points and sample rate of 44 100 Hz and counted the mean number of notes per phrase, which we averaged per individual. We then divided the song into two distinct parts: (1) the introductory (first) note and (2) loudsong (all more-or-less uniform notes following the first note). In the oscillogram view, we measured the time at the start and end of the first, second and final notes to the nearest millisecond. From these, we calculated the durations of the introductory note, loudsong notes (mean of second and final note durations) and the pause between the first and second notes. To calculate the loudsong pace (notes s⁻¹) we divided the number of loudsong notes by the time duration from the beginning of the second note to the end of the final note. To measure note frequencies, we selected the first, second and final notes of each phrase in the spectrogram using the on-screen cursor and opened the power spectrum for each note with the same parameters. For improved accuracy, we adjusted the upper and lower limits of the selected area to the inflection points of the curve and measured peak, high, low and 90% bandwidth frequencies (the frequency range around the peak frequency corresponding to 90% of the energy, in decibels) from the selection table. We calculated loudsong frequency values as the mean between the second and final note frequencies. 5.75 5.80 5.85 5.90 5.95 5.100 5.105 5.110 5.111 5.112

MOLECULAR ANALYSES

We sampled 29 vouchered specimens of the *Trogon rufus* complex (see [Supporting Information, File S3](#)), covering the total extent of its geographic distribution. We extracted total genomic DNA from muscle samples using the PureLink Genomic DNA Mini kit (Invitrogen Inc.) following guidelines by the manufacturer. We used standard methods ([Brumfield et al., 2007](#)) to amplify and obtain sequences for the mitochondrial gene NADH dehydrogenase subunit 2 (*ND2*, 1041 base pairs). Hot start polymerase chain reaction (PCR) amplifications were conducted at the Molecular Biology Lab (BioMol) of the University of São Paulo Museum of Zoology. Individual reactions contained approximately 50 ng of genomic template DNA, 1.5 mmol/L MgCl₂, 200 mmol/L dNTPs and 0.1 µL Platinum *Taq* DNA Polymerase (Invitrogen Inc.) in a total volume of 25 µL. The sequence of the forward primer (L5215) was 5'TAT CGG GCC CAT ACC CCG AAA AT3' (Hackett, 1996) and that of the reverse primer (H6313) was 5'CTC TTA TTT AAG GCT TTG AAG GC3' (Johnson & Sorenson, 1998). We conducted cycle-sequencing reactions using forward and reverse primers and obtained sequences at the Louisiana State University Genomics Facility on an Applied Biosystems 3130xl Genetic Analyzer. We obtained 25 additional sequences from GenBank to generate a final *ND2* matrix comprising 54 samples (see [Supporting Information, File S3](#)) with the following six outgroups: *Apaloderma vittatum* Shelley, 1882 (AY625222), *Harpactes diardii* (Temminck, 1832) (AY625214), *Priotelus roseigaster* (Vieillot, 1817) (AY625217), *Trogon collaris* Vieillot, 1817 (AY625196), *Trogon melanurus* Swainson, 1838 (AY625200) and *Trogon violaceus* Gmelin, 1788 (AY625205). In addition, we amplified the mitochondrial gene cytochrome b (*Cytb* 1143 bp) for the single individual from Alagoas following the protocol by [Brumfield et al. \(2007\)](#). We also obtained 33 *Cytb* sequences from GenBank corresponding to *Trogon rufus* (see [Supporting Information, File S3](#)). These two mitochondrial matrices have little overlap in the individuals they contain, therefore limiting our ability to concatenate both datasets. This sampling includes all currently recognized taxa within *Trogon rufus*.

We edited sequences and checked that they did not include stop codons or anomalous residues, using GENEIOUS v.11.1.4 (www.geneious.com; [Kearse et al., 2012](#)). We aligned sequences with the MAFFT v.7 multiple alignment plugin ([Kato & Standley, 2013](#)) implemented in GENEIOUS and deposited newly obtained sequences in GenBank under accession numbers MW367684–MW367713 (see [Supporting Information, File S3](#)).

Haplotype networks: For both *ND2* and *Cytb*, we built TCS haplotype networks ([Clement et al., 2000](#)) implemented in POPART ([Leigh & Bryant, 2015](#)). Outgroup samples and short ingroup sequences (< 1000 bp) were excluded from the analysis and matrices for both genes were trimmed to exclude any positions containing missing data (final matrix sizes: *ND2* – 1041 bp, 44 samples; *Cytb* – 1011 bp, 33 samples).

Phylogenetic inference: We only performed phylogenetic gene tree inference within maximum-likelihood and Bayesian inference frameworks using *ND2* because haplotype networks for *ND2* and *Cytb* showed similar structures and a time-calibrated gene tree based on *Cytb* was recently published ([Smith et al., 2014](#)). We conducted the maximum-likelihood analysis with the GTR+ Γ model of nucleotide substitution and 999 bootstrap replicates implemented in RAxML 8.2.9 (Stamatakis, 2014) on the CIPRES Science Gateway v.3.3 ([Miller et al., 2010](#)). Based on the corrected Akaike Information Criterion (AICc; [Hurvich & Tsai, 1989](#)), we selected TRN+I+G+X as the best substitution model using the greedy algorithm ([Lanfear et al., 2012](#)) and PhyML v.3.0 ([Guindon et al., 2010](#)) implemented in PartitionFinder2 ([Lanfear et al., 2017](#)). We evaluated models of molecular evolution available in BEAST ([Drummond et al., 2012](#); [Bouckaert et al., 2014](#)) and did not assess any partitions in the sequence matrix because it has been shown that partitioning *ND2* by codon position on similar timescales has minimal impact on the estimation of topologies and speciation times when using relaxed clocks ([Smith & Klicka, 2013](#)). We estimated a time-calibrated gene tree within a Bayesian framework implemented in two independent runs of the program BEAST2 v.2.4.4 ([Drummond et al., 2012](#); [Bouckaert et al., 2014](#)) on the CIPRES Science Gateway v.3.3 ([Miller et al., 2010](#)). Based on the avian mtDNA substitution rate of 2.1%/My ([Weir & Schluter, 2008](#)), we used a log-normal relaxed molecular clock with a mean rate of 0.0105 (SD = 0.1) for mtDNA. We used a Yule prior with no restrictions on tree shape and a randomly generated tree as a starting tree. We ran analyses for a total of 100 million generations with a sampling frequency of 2500. We determined that replicate analyses converged (effective sample size values > 400) using TRACER v.1.7 ([Rambaut et al., 2018](#)). We used LogCombiner v.2.4.8 ([Bouckaert et al., 2014](#)) to merge the posterior distributions of trees from the two independent runs. Using TreeAnnotator v.2.4.4 ([Drummond et al., 2012](#); [Bouckaert et al., 2014](#)) and a burn-in of 20%, we estimated a posterior distribution of topologies and the maximum clade credibility (MCC) tree.

SPECIES DELIMITATION

We defined putative taxa based on congruence between groups of specimens with geographically consistent

morphological and vocal characters, and mitochondrial clades yielded by the molecular analysis. The taxonomic status of each taxa was determined by consideration of the criteria of the biological (Mayr, 1942; Paterson, 1985; Masters *et al.*, 1987), phylogenetic (Cracraft, 1983; Donoghue, 2016) and evolutionary (Wiley, 1978) species concepts.

STATISTICAL ANALYSES

We undertook all statistical analyses in R software (R Development Core Team, 2015) using a 95% probability level ($\alpha = 0.05$), excluding immatures and considering sexes separately. Prior to running any analyses, we checked all numeric variables for normal distribution using the Kolmogorov–Smirnov goodness-of-fit test and log-transformed all non-normally distributed variables. We then used linear discriminant function analyses to separately characterize the differences between putative taxa based on male morphology, female morphology and song datasets. For the song analysis, we excluded two-note phrases, as they lacked a measure of pace. For a more detailed synopsis of the differences between putative taxa, we used the Student–Newman–Keuls multiple comparisons test to reveal differences in their mean character states.

MAPPING

To visualize the geographic variation of phenotypic traits, we interpolated values of morphological and vocal characters using the inverse-distance squared function (distance coefficient set to 2, min/max values set to 5–95% of the cumulative load count), which were then visualized on a RGB colour scale in Quantum GIS (QGIS Development Team, 2019). To further elucidate trends, we created isophenes, or ‘phenotypic contour lines’ that express equal changes in the expression of a character across the species distribution, as first used by Haffer & Fitzpatrick (1985), by applying the ‘extract → contour lines’ function in QGIS to the raster of interpolated character values. Populations with consistent values of a character appear as ‘plateaus’ and are encircled by isophenes, whilst large changes between two adjacent groups appear as ‘valleys’ with the notable convergence of several isophenes in a parallel fashion. Widely spaced isophenes over an otherwise consistent population indicate gradual clinal variation, and dense convoluted isophenes, the mixing between characters with different values, or potential intergradation or hybrid zones. The extent of these intergradation zones was determined from minimum convex polygons created around all records possessing a mixture of traits between two adjacent taxa.

RESULTS

EXTERNAL MORPHOLOGY

Males: The discriminant analysis (Fig. 2A; Supporting Information, Table S1) properly assigned over 99% ($N = 125$) of specimens to the correct taxon. This included all specimens of *T. r. rufus* ($N = 14$), *T. r. sulphureus* ($N = 23$), *T. r. chrysochloros* ($N = 27$), *T. r. tenellus* ($N = 27$), *T. r. cupreicauda* ($N = 16$) and the Alagoas population ($N = 1$) with only a single specimen from the distribution of *T. r. amazonicus* ($N = 17$) assigned to *T. r. rufus*. All variables were predictors between taxa but bar widths accounted for the greatest loadings in all discriminant factors. Discriminant factor one accounted for 51.4% of the trace between taxa and factor two, 37.7%. In factor one, undertail black bar widths had the greatest negative loading and wing panel white bar widths the greatest positive loading. In factor two, the wing panel black bar widths had the greatest positive loading and wing panel white bar widths the greatest negative loading. The narrow white bars on the undertail and wing panel of *T. r. chrysochloros* make it highly diagnosable, as do the broad undertail black bars and narrow wing panel black bars of *T. r. tenellus*. Amazonian populations, were nearly completely differentiated by factor two, involving wing panel barring, due to the relatively narrow black and white bars of *T. r. rufus*, broad black and relatively broad white wing bars of *T. r. sulphureus*, and relatively narrow black and broad white bars of *T. r. amazonicus*. Individuals corresponding to *T. r. cupreicauda* had similarly broad white wing panel bars along with broader black and white bars on the undertail than *T. r. amazonicus*. Differences in bar widths correspond closely to barring densities and percentage areas black (Supporting Information, Table S3).

The differences between taxa correlates strongly to the uppertail hue (Fig. 3A, Supporting Information, Tables S1, S2). It varies from distinctly bluer in *T. r. tenellus* to plain-green in *T. r. rufus* and the Alagoas specimen, warmer olive-green in *T. r. chrysochloros*, more coppery in *T. r. cupreicauda* and *T. r. amazonicus* and strongly coppery, even reddish, in *T. r. sulphureus* (Supporting Information, Fig. S1). Between Amazonian populations, only a handful of specimens south of the Amazon River, in the distribution of *T. r. amazonicus*, had uppertail hues equal to, or below, the maximum value in *T. r. rufus* (i.e. 585 nm, shiny olive-green), all originated from a limited area extending from the Madeira–Tapajos Interfluvium east to Belem (Fig. 3A). Three specimens (MZUSP 44168, CM 77942 and AMNH 429219) had hues of exactly 585 nm, whilst two (MCZ 22839 and 173839) were only slightly lower (573 and 576 nm). A further three of 64 qualitatively

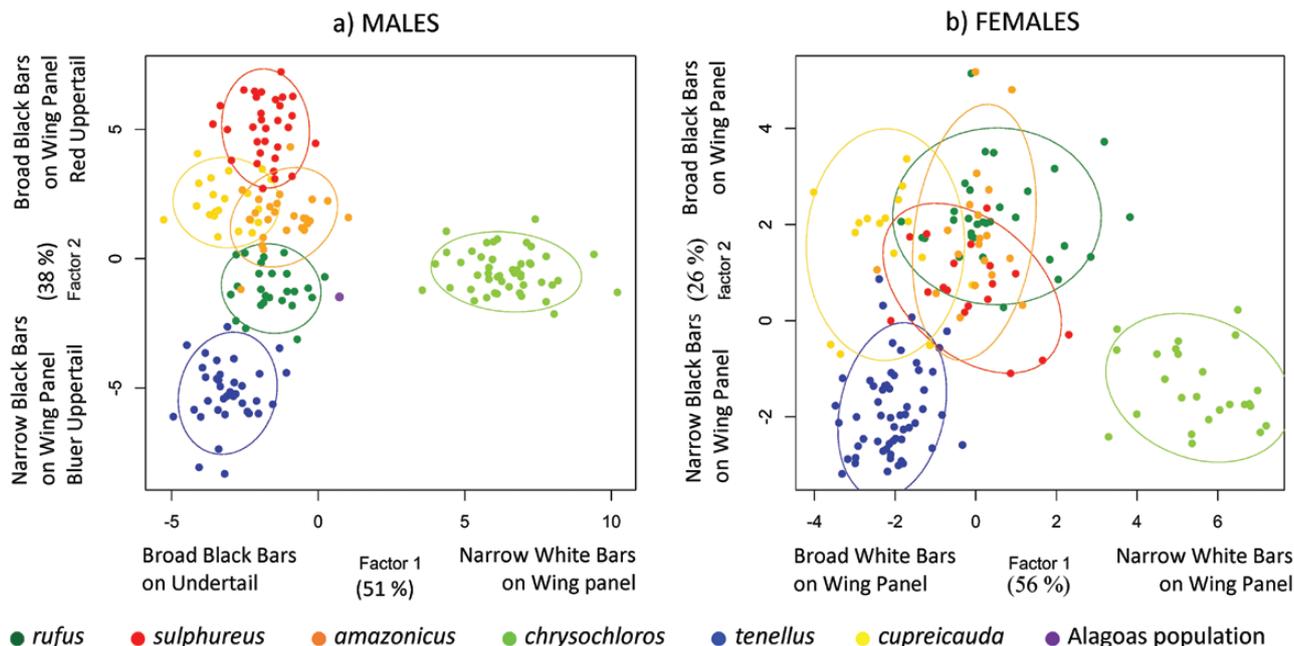


Figure 2. Linear discriminant factors one versus two of morphological characters between (A) adult males and (B) adult females in the *Trogon rufus* complex. Ellipses indicate 95% confidence intervals.

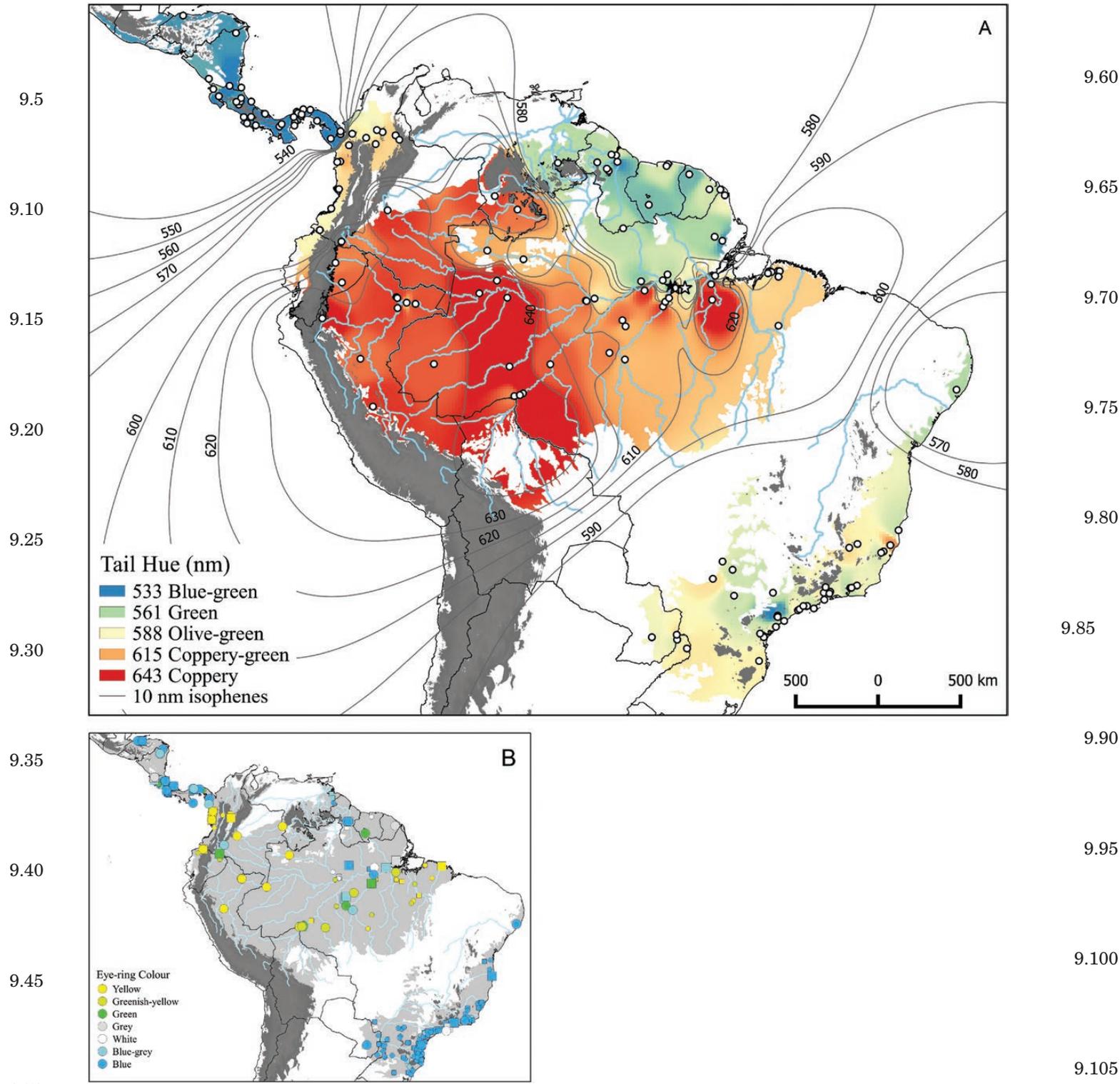
examined specimens (AMNH 288334, MPEG 22324; MPEG 75868) had similarly shiny-olive green uppertails. However, only a single specimen (MZUSP 32025, from the Rio Arapiuns, east of the mouth of the Rio Tapajos) fell well within the range of *T. r. rufus* at 550 nm. Furthermore, the greener subterminal tailband was also notably absent in *T. r. rufus* but present in *T. r. sulphureus* and *T. r. amazonicus*. The differentiation of all other iridescent plumage patches was only subtly between taxa (Supporting Information, Table S2) and we found no colour difference between the head and mantle, so henceforth consider them as a single homogenous plumage patch. Saturation also presented no differences between taxa, so was not considered further. However, we found a strong decrease in the hue of all patches with increasing elevation in *T. r. chrysochloros* (Supporting Information, Fig. S2).

Morphometrically, the tail and wing lengths and number of bill serrations were strongly correlated to differences between taxa (Supporting Information, Tables S1, S4), due to the much larger size and highly serrated bill of *T. r. chrysochloros*, a feature shared by one of the two specimens from the Alagoas population (see below).

Females: The linear discriminant analysis of external morphology (Fig. 2B; Supporting Information, Table S5) properly assigned 92% of specimens to the correct taxon ($N = 165$). This included all specimens of *T. r. chrysochloros* ($N = 25$), 96% of *T. r. tenellus* ($N = 56$) with two improperly assigned to *T. r. cupreicauda*, 88%

of *T. r. cupreicauda* ($N = 16$), with one allocated to each *T. r. rufus* and *T. r. tenellus*, 90% of *rufus* ($N = 31$), with one allocated to each *T. r. amazonicus*, *T. r. sulphureus* and *T. r. cupreicauda*, 72% of *T. r. sulphureus* ($N = 18$) with two allocated as *T. r. rufus* and one each to *T. r. amazonicus*, *T. r. cupreicauda* and *T. r. tenellus*, and 94% of *T. r. amazonicus* ($N = 19$) with one assigned to *T. r. rufus*. All variables were predictors between taxa. Discriminant factor one accounted for 56.2% of the proportion of trace between taxa and factor two 25.8% (Supporting Information, Table S5). In both factors, the wing panel light brown bar widths had the greatest positive loading and the wing panel black bar widths the greatest negative loading. Individuals corresponding to *T. r. chrysochloros* are the most easily distinguished due to their distinctly narrow black and light brown wing panel bars and *T. r. tenellus* by their narrow wing panel black bars and moderate light brown bars. There is less differentiation between the remaining populations but *T. r. cupreicauda* is characterized by generally broader white bars, *T. r. rufus* generally has narrower light brown bars (comparable to *T. r. chrysochloros*) compared to *T. r. sulphureus* and *T. r. amazonicus*, whilst *T. r. amazonicus* overlaps in bar widths with *T. r. rufus* and *T. r. sulphureus*. These differences in wing panel bar widths correspond to differences in undertail barring dimensions (Supporting Information, Table S7).

Morphometric variables, namely tail and wing lengths and number of bill serrations, correlate the most strongly to discriminant factors between taxa (Table S5). This is mainly because all are distinctly



greater in *T. r. chrysochloros* but tail length also shows distinct structuring between remaining populations (Table 2; Supporting Information, Table S8) and is shortest in *T. r. tenellus* and *T. r. cupreicauda*, moderate in *T. r. rufus* and *T. r. amazonicus*, and slightly longer in *T. r. sulphureus*.

In terms of coloration, the extensive brown wash on the undertail is unique to *T. r. cupreicauda* (Fig. 6; Supporting Information, Fig. S5). Other strongly segregated coloration variables between taxa (Supporting Information, Tables S5, S6) include the head colour, with distinctly higher Munsell hue, chroma and value scores in *T. r. tenellus*, lower scores in *T. r. cupreicauda* and *T. r. rufus*, whilst only the Munsell value is higher in *T. r. chrysochloros*. The mantle is unique in *T. r. rufus* due to the generally lower hue and higher chroma. The chroma of the uppertail is also distinctly higher in *T. r. chrysochloros* and *T. r. amazonicus*, low in *T. r. cupreicauda* and intermediate in *T. r. tenellus*.

Bareparts: There was a strong correspondence between the possession of yellow to greenish-yellow eye-rings and olive tarsi in *T. r. sulphureus*, *T. r. amazonicus* and *T. r. cupreicauda* (Fig. 3B; Supporting Information, Fig. S7). However, there were notable exceptions of birds with blue, blue-grey or green eye-rings in the distribution of *T. r. amazonicus* in the region around the lower Rio Tapajos, especially the Madeira–Tapajos interfluvium, and, for *T. r. sulphureus*, along the eastern base of the Andes. In contrast, blue to blue-grey eye-rings and blue-grey tarsi were associated with *T. r. rufus*, *T. r. chrysochloros* and *T. r. tenellus* and the Alagoas population. White or grey eye-rings were mostly associated with grey or pinkish-grey tarsi, namely in *T. r. rufus* but also *T. r. tenellus* and *T. r. chrysochloros*. In general, female eye-ring and tarsus colours were simply duller renditions of colours in males (e.g. blue-grey vs. blue).

Breast band: The white breast band of males (Supporting Information, Fig. S6) was notably absent in > 90% of male specimens from within the distributions of *T. r. sulphureus* and *T. r. amazonicus* and all specimen and photographic records from the Alagoas population. Those with breast bands (< 10%; all inconspicuous) originated from the southern bank of the lower Amazon, in the distribution of *T. r. amazonicus*, and far western Amazonia, at the base of the Andes in *T. r. sulphureus*. In contrast, most specimens of *T. r. tenellus* and *T. r. chrysochloros* possessed breast bands but in *T. r. rufus* and *T. r. cupreicauda* it is variably present or absent.

VOCALIZATIONS

In the linear discriminant analysis of the song (Fig. 4A; Supporting Information, Table S9), 88% of songs were

properly allocated to taxon. This included 100% for *T. r. chrysochloros* ($N = 67$), *T. r. cupreicauda* ($N = 11$) and *T. r. tenellus* ($N = 15$). However, there was overlap among populations from Amazonia and Alagoas. The proportion of songs correctly assigned was 78% for *T. r. rufus* ($N = 32$) with six incorrectly returned as *T. r. sulphureus* and one as *T. r. tenellus*, 78% for *T. r. sulphureus* ($N = 37$) with eight incorrectly returned as *T. r. rufus*, 67% for *T. r. amazonicus* ($N = 9$) with two incorrectly allocated to *T. r. sulphureus* and one to the Alagoas population, and 60% for the Alagoas population ($N = 5$) with one incorrectly assigned to each *T. r. tenellus* and *T. r. sulphureus*. All variables were predictors of taxa and all, besides bandwidths, explained a moderate to large amount of the variation between them (Supporting Information, Table S9). Factor one accounted for 54.9% of the explained variation between taxa and factor two 23.2%. The pace of the song had by far the greatest loading in factor one and was slightly antagonistic to pause duration. Factor two was most heavily negatively loaded by the pace and mean loudsong note duration. Fast pace, short pause after the introductory note and short loudsong note durations were diagnostic of *T. r. chrysochloros*, whilst slow pace, long pause and short loudsong note durations were diagnostic of *T. r. cupreicauda*. All other taxa overlapped in factors one and two due to their shared slower pace, longer pause and longer loudsong note durations.

When we compared only populations east of the Andes in the linear discriminant analysis, it properly assigned 100% of recordings pertaining to the Alagoas population, whilst the proportions for *T. r. chrysochloros* and Amazonian populations remained the same (Fig. 4B; Supporting Information, Table S10). More specifically, the Alagoas population differed from *T. r. chrysochloros* in ten of 13 characters, *T. r. rufus* in six of 13, *T. r. sulphureus* in two of 13 and *T. r. amazonicus* in five of 13 characters (Supporting Information, Table S11).

The number of notes per phrase was distinctly high in both *T. r. chrysochloros* and *T. r. cupreicauda*, low in *T. r. rufus*, *T. r. sulphureus* and *T. r. tenellus*, and moderate in *T. r. amazonicus* and the Alagoas population (Table 3; Supporting Information, Table S11). There is strong correlation between the introductory note and loudsong note durations. In terms of note frequencies, the peak, high and low frequencies of both introductory and loudsong notes were all highest in *T. r. chrysochloros*, slightly less high in *T. r. tenellus*, low in *T. r. rufus*, *T. r. sulphureus* and *T. r. amazonicus*, and moderate in *T. r. cupreicauda* and the Alagoas population. Between Amazonian populations, frequencies were highest in *T. r. sulphureus*, followed by *T. r. amazonicus*, and distinctly lower in *T. r. rufus*. The bandwidth values of both introductory and loudsong notes were highest in the Alagoas population, *T. r. chrysochloros* and *T. r. cupreicauda*, low in Amazonian populations, and

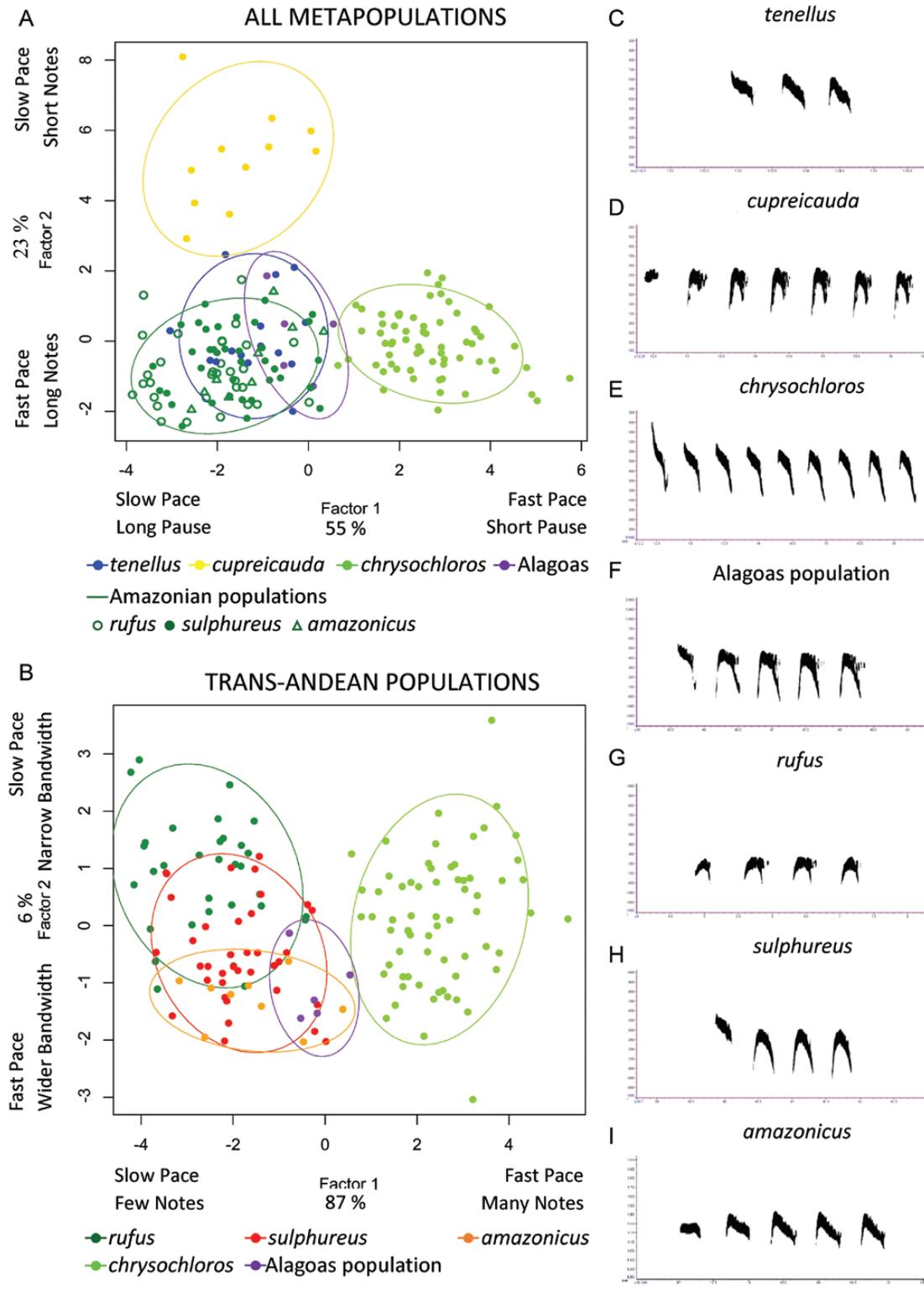


Figure 4. Linear discriminant factors one versus two of songs between (A) all populations in the *Trogon rufus* complex (different colours represent metapopulations and different marker shapes Amazonian populations) and (B) trans-Andean populations. Ellipses indicate 95% confidence intervals. C–I, show typical songs of: C, *Trogon tenellus* (ML57352, Costa Rica); D, *T. cupreicauda* (XC7020, W Ecuador); E, *T. chrysochloros* (XC85456, São Paulo, Brazil); F, Alagoas population (ML181311, Alagoas, Brazil); G, *T. r. rufus* (XC 119312, Amazonas, Brazil); H, *T. r. sulphureus* (ML30944, Peru); I, *T. r. amazonicus* (XC20747, Pará, Brazil).

low for the introductory note but high for the loudsong notes in *T. r. tenellus*.

The occurrence frequency of two-note phrases in recordings is different between taxa ($\chi^2 = 40.2$, d.f. = 6, $P < 0.001$) at 30.6% in *T. r. tenellus*, 20.8% in *T. r. rufus*, 10.3% in *T. r. sulphureus* and zero in *T. r. chrysochloros*, *T. r. cupreicauda*, *T. r. amazonicus* and the Alagoas population.

DIETARY PREFERENCES

The rate of insectivory relative to frugivory was much higher for *T. r. chrysochloros* (95%, $N = 20$) than in *T. r. rufus* (73%, $N = 22$), *T. r. tenellus* (53%, $N = 15$) and *T. r. cupreicauda* (42%, $N = 12$). In fact, we only found a single recorded instance of frugivory in *T. r. chrysochloros* (WA1211560 on wikiaves.com.br). We found both a caterpillar and fruits in the stomach of the only adult specimen from Alagoas.

PHYLOGENETIC STRUCTURE AND VARIATION

Maximum-likelihood and Bayesian analyses produced *ND2* gene trees with identical topologies and highly congruent bootstrap and posterior probability support values (Fig. 5). They recovered well-supported clades for *T. r. tenellus*, *T. r. cupreicauda*, the entire Atlantic forest metapopulation (*T. r. chrysochloros* + the Alagoas population), and the entire Amazonian metapopulation (*T. r. rufus* + *T. r. sulphureus* + *T. r. amazonicus*). A basal split exists between clades west and east of the Andes. For those to the west, there is a subsequent split between *T. r. tenellus* and *T. r. cupreicauda*. To the east, the metapopulations in the Atlantic Forest and Amazonia form distinct clades. In the Atlantic Forest, there is a further split between the well-supported clade represented by *T. r. chrysochloros* in the southern Atlantic Forest and the Alagoas population in the Pernambuco Centre of Endemism (uncorrected genetic distances: *ND2* 0.7–0.9% and *Cytb* 1.2%; Fig. 5) estimated to 0.79

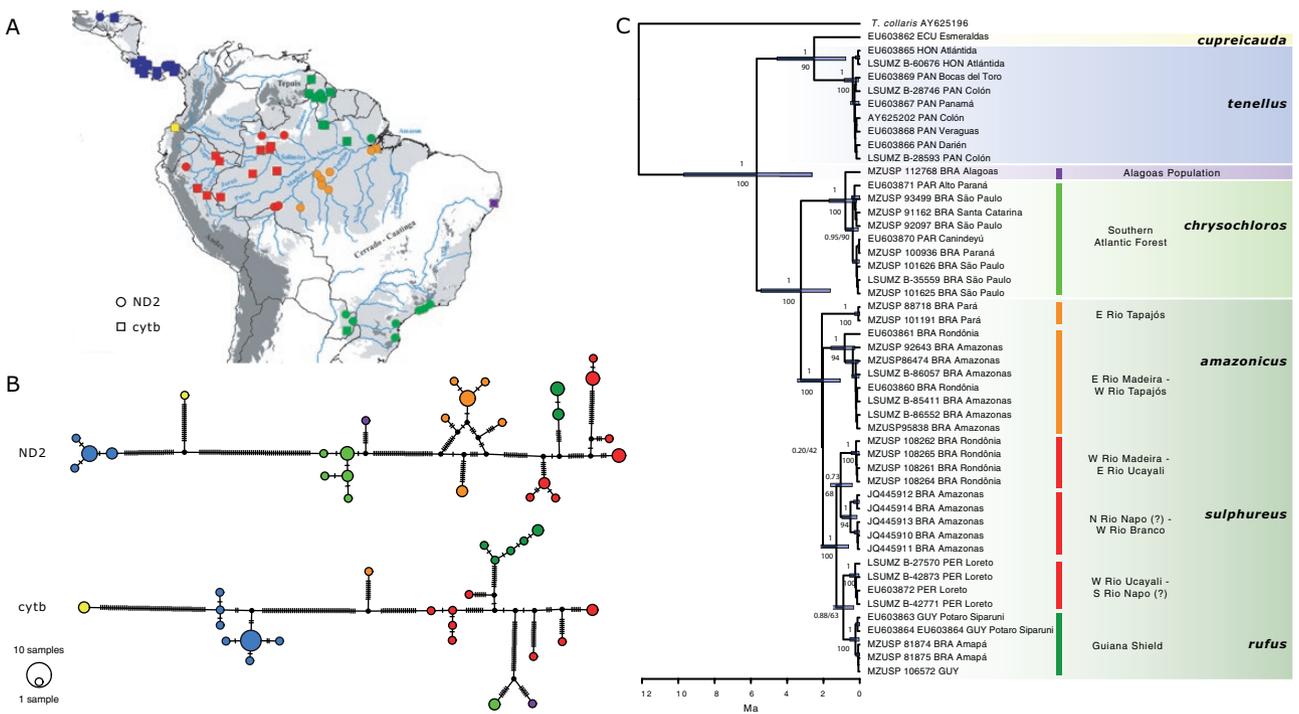


Figure 5. (A) Geographic localities of tissue samples considered in this study. Blue = *tenellus*, yellow = *cupreicauda*, dark green = *rufus*, red = *sulphureus*, orange = *amazonicus* and light green = *chrysochloros*. (B) TCS haplotype networks depicting relationships among the mitochondrial haplotypes (ND2 1,041 bp; cytb 1,011). The size of each circle is proportional to the corresponding haplotype frequency. Inferred intermediate haplotypes are shown as black circles on branches connecting observed haplotypes. Tick marks between haplotypes denote additional mutational steps. Colors follow the same scheme as Figure 5A. (C) 50% Maximum Clade Credibility time-calibrated gene-tree indicating phylogenetic relationships among clades in the *Trogon rufus* complex and outgroups derived from Bayesian inference based on ND2 sequences. A single unsupported and conflicting node between the Bayesian and maximum-likelihood topologies is collapsed (basal node of *amazonicus*). Numbers above nodes represent posterior probability values obtained for the Bayesian analysis. Numbers below nodes represent bootstrap support values for the maximum-likelihood gene tree. Node bars represent 95% confidence intervals for the highest posterior density (HPD) of divergence times.

Mya but with a 95% confidence interval of 0.18–1.69 Mya. Within Amazonia, each cluster corresponds to populations in river interfluves with shallow and unsupported structuring among them. As evidenced by estimated divergence times (2.4–5.5 Mya) and haplotype distances (uncorrected genetic distances: 3.9–9.4%; Fig. 5), genetic variation between the main clades is relatively high in comparison with other Neotropical intraspecific-level taxa (see: Smith *et al.*, 2014, 2017). The general topology obtained here is highly congruent with previous phylogenetic hypotheses estimated for *Trogon rufus* (Brumfield & Capparella, 1996; Smith *et al.*, 2014).

SPECIES LIMITS AND NOMENCLATURE

Based on congruence across datasets, we found five phenotypically and genetically distinct clusters with evidence of reproductive isolation (lack of interbreeding, levels of divergence, and divergence in traits involved in species-recognition, such as plumage, voice and behaviour) that we propose be considered as valid species (Fig. 6). Of these, four already possessed names with matching type specimens and localities. These are *Trogon rufus* Gmelin, 1788 in Amazonia, *T. chrysochloros* Pelzeln, 1856 in the southern Atlantic Forest, *T. tenellus* Cabanis, 1862 in Central America and *T. cupreicauda* (Chapman, 1914) in the Chocó-Magdalena. We recognized a fifth unnamed population in an isolated population inhabiting the mountain Atlantic Forest of Alagoas state, in the Pernambuco Centre of Endemism, north-east Brazil, by the unique combination of morphological, song and mitochondrial DNA features, despite the limited material available, and describe it as a new species below. The levels of diagnosability and mitochondrial DNA divergence of all these taxa meet the species-level criteria of the biological, phylogenetic and evolutionary species concepts.

Within Amazonia, we found three phenotypically distinct populations that lacked complete divergence in mitochondrial DNA and exhibited wide phenotypic intergradation, suggesting the existence of only a single valid species under the biological, phylogenetic and evolutionary species concepts. Therefore, despite their suggestive phenotypic differences and evidence of trait sorting, we conservatively considered them as subspecies of *T. rufus*. Those with green tails from the Guiana Shield match the type specimen and locality of *Trogon rufus rufus*, whilst the strongly coppery uppertails of specimens from western Amazonia (west of the Branco and Madeira Rivers) correspond to *Trogon rufus sulphureus* Spix, 1824. The barring differences and less coppery uppertail of specimens from south-eastern Amazonia (east of the Madeira River) match the type specimen and locality of *Trogon rufus amazonicus* Todd, 1943. Trait mixing on the

southern bank of the lower Amazon is indicative of an intergradation zone between *T. r. sulphureus* and *T. r. rufus*. Sharp clines of barring traits across the Madeira indicates a zone of intergradation between *T. r. sulphureus* and *T. r. amazonicus*.

We provide illustrations of all named taxa in Figures 6 and 7, and summarize male morphological characters in Table 1, female morphological characters in Table 2 and song characters in Table 3.

For common names, we propose retaining the compound name, ‘black-throated trogon’, to indicate the phylogenetic affinities of all the species involved. To differentiate between them, we propose using historical species names where available, namely the ‘graceful black-throated trogon’ for *T. tenellus* and ‘southern black-throated trogon’ for *T. chrysochloros*. Given the lack of historical common names for Amazonian taxa, we preferred naming each after the geographic region in which it is found, namely the ‘Amazonian black-throated trogon’ for *T. rufus*, ‘Guianan black-throated trogon’ for *T. r. rufus*, ‘western black-throated trogon’ for *T. r. sulphureus* and ‘eastern black-throated trogon’ for *T. r. amazonicus*. Given that ‘Chocó trogon’ is already the established common name for *T. comptus* Zimmer, 1948, we suggest naming *T. cupreicauda* ‘Chapman’s black-throated trogon’ after the discoverer of the species.

SPECIES DESCRIPTIONS

TROGON RUFUS GMELIN, 1788

Proposed English name: Amazonian black-throated trogon.

TROGON RUFUS RUFUS GMELIN, 1788

Proposed English name: Guianan black-throated trogon.

‘Yellow-bellied Green Cuckoo’ Edwards, 1764, Gleanings of Nat. Hist., III, p. 256, pl. 331 – *Trogon rufus* Gmelin, 1788, Syst. Nat., I, p. 404 [based on the illustration of ‘Le Courucou à queue rousse de Cayenne’, Buffon & d’Aubenton, 1765–81, Hist Nat des Ois. 6, p. 293, pl. 736, and the ‘Rufous Curucui’, Latham, 1782, Gen. Syn. 1(2), p. 490, pl. XXI], Cayenne – *Trogon atricollis* Vieillot, 1817, Nouv. Dict. D’Hist. Nat. VIII, p. 318 (based on ‘Le Couroucous aranga’ LeVaillant in Couroucous, pl. 8), Guyana, Suriname and Trinidad – *Trogon atricollis* Gould, 1838, a monograph of the Trogonidae or family of the Trogons, p. 39, pl. 8 (synonymising *rufus* with *atricollis*) – *Trogon lepturus* Swainson, 1838, Animals in Mengaries, part iii, p. 331 [composite species referring to Buffon & d’Aubenton’s ‘Le Courucou à queue rousse de Cayenne’ (= *T. r. rufus*]

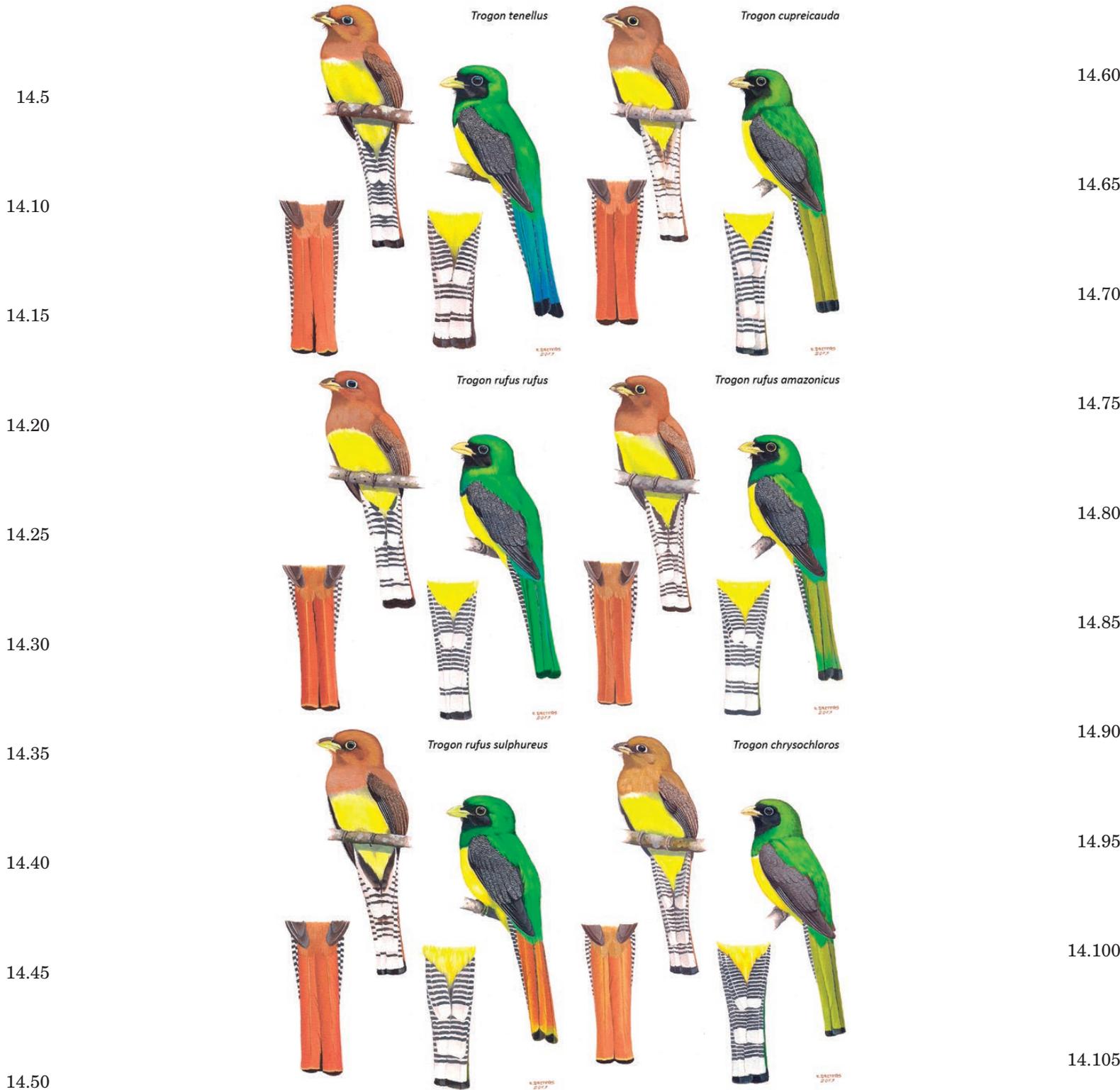


Figure 6. Illustrations of *Trogon tenellus* (male MCZ 119718, female UCLA 35211), *Trogon cupreicauda* (male CM66700, female ANSP 182341), *Trogon rufus rufus* (male CM 61200, female CM 61561), *Trogon rufus amazonicus* (male MZUSP 44171, female MZUSP 95839), *Trogon rufus sulphureus* (male LSUMZ 114718, female CM 96851), and *Trogon chrysochloros* (male MNRJ 35251, female MZUSP 54852).
 Illustrations by Eduardo Brettas. Not to scale.

female), pl. 736 and ‘Couroucou de Cayenne’, pl. 195 (= *T. viridis* Linnaeus, 1766 subadult male), Cayenne] – *Pothinus atricollis* Cabanis & Heine, 1862–63, Mus. Hein., part IV, no. 1, pp. 180–181 – *Trogon atricollis* Pelzeln J, 1868, Zur Orn. Bras., pp. 226–331: Borba (right bank Rio Madeira), Marabitanas Cucuí (upper Rio Negro) and Barra do Rio Negro (= Manaus) – *Trogon atricollis* (Race A) Grant, 1892, Cat. Birds. Brit. Mus., 17, pp. 455–458: Dutch Guiana (= Suriname) (Demerara), British Guiana (Bartica Grove) and Barra do Rio Negro (= Manaus) – *Trogon atricollis atricollis* Richmond, 1893, Proc. U.S. Nat. Mus., 16, p. 513 – *Trogon atricollis* Ihering & Ihering, 1907, Part. Catal. Fauna Brasil., I, Aves, p. 158, Rio Grande do Sul to Central America – *Trogon rufus* Berlepsch, 1908, Novitates Zoologicae 15, p. 277 – *Trogonurus curucui curucui* Ridgway, 1911, Bull. U.S. Nat. Mus. 50 (5), p. 764 – *Trogon rufus* Sneath, 1914, Part. Bol. Mus. Goeldi. 8, p. 208: Rio Guamá (Sta. Maria de S. Miguel), Obidos, Rio Jamundá (Faro) – *Trogonurus curucui curucui* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325 – *Trogonurus rufus rufus* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158 – *Trogonurus rufus rufus* Pinto, 1938, Rev. Mus. Paul. 22, p. 289 – *Trogon curucui curucui* Griscom and Greenway, 1941, Bull. Mus. Comp. Zool., 88, pp.180–181 – *Trogon rufus rufus*, Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11. Upper Arucaú and Obidos, Brazil, Tamanoir and Pied Saut, French Guiana, and Rio Mocho, Venezuela – *Trogon rufus rufus* Peters, 1945, Check-list of Birds of the World, Vol 5, p. 157 – *Trogon rufus rufus* Zimmer, 1948, American Museum Novitates (1380), pp. 26–31 – *Trogon rufus rufus* Pinto, 1950, Papeíes Avilso de Zoologia, 9(9), pp. 89–136 – *Trogon rufus rufus* Pinto, 1978, Novo Catal. das Aves do Brasil, 1ª Parte, p. 218. S Venezuela, the Guianas and north Brazil (east of the Rio Negro and Madeira).

Diagnosis: White, grey, blue or blue-grey eye-ring diagnostic against *T. r. sulphureus*, *T. r. amazonicus* and *T. cupreicauda*. Bill less serrated and body size smaller than in *T. chrysochloros*. *Males:* Compared to other Amazonian subspecies the uppertail is greener (≤ 587 nm), subterminal band of greener coloration absent and white breast band present or absent. Rump and chest also generally bluer-green. The undertail and wing panel have denser barring, narrower black bars and generally narrower white bars than *T. r. sulphureus*. Against *T. r. amazonicus*, wing panels have narrower white bars and greater density. Uppertail hue usually higher than *T. tenellus*, with narrower black bars and greater barring density on the undertail, and narrower white bars and higher density on the wing panel. Compared to *T. cupreicauda*, uppertail hue usually lower, undertail barring denser

with narrower white bars, whilst wing panel black bars are narrower than in southern individuals. Compared to *T. chrysochloros*, the undertail and wing-panel barring are less dense, the percentage area black lower and white bars narrower. *Females:* Only safely separable from *T. r. sulphureus* and *T. r. amazonicus* by blue eye ring in some individuals. Still, compared to *T. r. sulphureus* the undertail and wing panel are usually more densely barred with narrower light brown bars, whilst in northern specimens the head is a darker, more reddish brown, chest lighter but less saturated and uppertail less saturated. The same trends in coloration separate it from *T. r. amazonicus* but the barring is similar. Against *T. chrysochloros*, the wing panel barring is less dense and black bars broader, uppertail saturation lower, head darker, more saturated and redder, mantle less yellow but more saturated, and chest less yellow and lighter. Against *T. tenellus*, the wing panel has broader black bars, higher percentage area black and generally greater density, the head and mantle are warmer and less saturated, chest usually less saturated and southern individuals (close to the Amazon River) have more saturated uppertails. The lack of an extensive brown wash on the undertail, broad wing panel black bars, relatively high undertail barring density and narrow white bars, and more saturated uppertail colour differentiate it from *T. cupreicauda*. Southern individuals also generally have a less saturated heads but more saturated mantles and chests.

Song: The lowest note frequencies of all taxa. Fewer notes per phrase, slower pace, longer note and pause durations and lower note frequencies than *T. chrysochloros*. Lower frequencies than *T. tenellus*. Fewer notes, lower frequencies and longer note durations than *T. cupreicauda*. Not safely separable from other Amazonian subspecies, although introductory note frequencies, especially low frequency, generally lower than in *T. r. sulphureus*. Compared to *T. r. amazonicus*, it generally has fewer notes per phrase, faster pace and a lower frequency introductory note with slightly shorter duration.

Distribution and habitat: Primary and advanced secondary growth humid forests of the Guiana Shield, including the Tepuis, from the east bank of the upper Rio Negro south to the Lower Amazon, in French Guiana, Guyana, Suriname, Venezuela and Brazil. Up to an elevation of 1000 m. Absent from Marajó Island. Intergrades zone with *T. r. amazonicus* on the southern bank of the Lower Amazon.

Type material: *Holotype:* Plate of ‘Couroucou à queue rousse de Cayenne’ (= Russet-tailed Curucui) ex Buffon

Table 1. Comparison of male morphological characters between taxa in the *Trogon rufus* complex with mean, minimum and maximum measured values. Values for *T. muriciensis* sp. nov. are of the holotype, expect for morphometric measurements, for which the holotype is indicated with an *.

	<i>T. r. rufus</i>	<i>T. r. sulphureus</i>	<i>T. r. amazonicus</i>	<i>T. chrysochloros</i>	<i>T. muriciensis</i>	<i>T. tenellus</i>	<i>T. cupreicauda</i>
COLOUR PATTERNING							
Uppertail	Blue-green to shiny olive-green	Reddish-copper to slightly coppery-green	Reddish-copper to shiny olive-green	Green to slightly coppery-green	Green	Blue to green	Green to greenish-copper
Hue (nm)	562, 536–587	632, 607–657	608, 573–655	586, 558–624	563	531, 488–554	595, 568–619
Bright (%)	13, 8–14	13, 11–15	12, 7–15	13, 10–17	8	15, 10–18	14, 11–18
Head & Mantle	Coppery-green	Coppery-green	Coppery-green	Coppery-green	Coppery Green	Brighter	Less bright
Hue (nm)	573, 548–600	578, 551–618	574, 549–616	569, 540–600	586	coppery-green	coppery-green
Bright (%)	11, 8–16)	11, 8–13	11, 7–17	11, 7–16	10	12, 9–17	571, 552–598
Rump	More blue-green	More golden-green	More golden-green	More plain-green	More blue-green	More plain-green	More blue-green
Hue (nm)	544, 513–571	553, 524–586	555, 522–598	549, 527–575	551	550, 522–584	543, 518–563
Bright (%)	10, 7–14	10, 6–13	9, 8, 6–13	10, 7–14	9	11, 8–14	9, 6–12
Chest	More blue-green	Mostly more blue-green	Blue-green to golden-green	Less bright blue-green to golden-green	Blue-green to golden-green	Generally brighter	Bright blue-green to golden-green
Hue (nm)	541, 518–568	542, 518–596	547, 519–570	544, 521–584	553	555, 521–572	549, 517–580
Bright (%)	8, 5–12	8, 5–12	8, 5–13	8, 5–14	8	9, 7–14	9, 7–12
Subterminal	Absent	Present	Present	Absent	Absent	Absent	Present (50)
Tailband (%)	Moderate	Moderate	Moderate	Moderate	Moderate	Narrow	Absent (50)
Terminal	11.0, 8–16	11.5, 6–17	10.2, 6–15	11.5, 9–14	10.2	9.7, 5–14	Broad
Tailband (mm)	Complete (42), Incomplete (21), Absent (38)	Absent (92), Incomplete (3), Complete (5)	Absent (91), Incomplete (9)	Complete (49), Incomplete (47), Absent (6)	Absent (100)	Complete (82), Incomplete (14), Absent (4)	Incomplete (58), Absent (29), Complete (13)
Breast band (%)	Complete (42), Incomplete (21), Absent (38)	Absent (92), Incomplete (3), Complete (5)	Absent (91), Incomplete (9)	Complete (49), Incomplete (47), Absent (6)	Absent (100)	Complete (82), Incomplete (14), Absent (4)	Incomplete (58), Absent (29), Complete (13)
UNDERTAIL BARRING							
Black bars (mm)	Narrow	Moderate	Narrow	Relatively narrow	Narrow	Broad	Relatively narrow to relatively broad
White bars (mm)	1.75, 1.3–2.3	2.1, 1.4–2.7	1.68, 1.2–2.1	1.86, 1.4–2.3	1.46	2.34, 1.8–3.0	2.00, 1.0–2.6
Density (bars cm ⁻¹)	Moderate	Relatively broad	Moderate	Narrow	Relatively narrow	Relatively broad	Broad
Percentage area black	2.00, 1.6–2.6	2.22, 1.8–2.8	1.94, 1.6–2.6	1.22, 0.9–1.7	1.39	2.19, 1.6–2.8	2.45, 1.8–3.8
	Moderate	Relatively low	Moderate	High	High	Low	Low
	5.30, 4.2–6.3	4.63, 4.0–5.6	5.52, 4.4–6.5	6.47, 5.2–7.5	7.03	4.47, 3.7–5.3	4.38, 3.7–4.9
	Low	Relatively low	Low	High	Moderate	Moderate	Low to moderate
	46.8, 36–55	49.2, 38–66	46.6, 38–56	60.3, 50–70	50	51.6, 44–60	44.7, 31–60

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Table 1. Continued

	<i>T. r. rufus</i>	<i>T. r. sulphureus</i>	<i>T. r. amazonicus</i>	<i>T. chrysochloros</i>	<i>T. muriciensis</i>	<i>T. tenellus</i>	<i>T. cupreicauda</i>
WING COVERTS BARRING							
Black bars (mm)	Narrow 0.41, 0.3–0.7	Broad 0.60, 0.3–1.0	Narrow to moderate 0.45, 0.3–0.8	Narrow to moderate 0.45, 0.3–0.7	Narrow 0.4	Narrow 0.37, 0.2–0.6	Narrow to broad 0.54, 0.3–1.0
White bars (mm)	Moderate 0.38, 0.3–0.6	Relatively Broad 0.45, 0.3–0.7	Broad 0.49, 0.3–0.8	Narrow 0.33, 0.2–0.4	Narrow 0.3	Relatively Broad 0.45, 0.3–0.7	Relatively Broad 0.45, 0.3–0.7
Density (bars cm ⁻¹)	Moderate 12.59, 9.5–16.0	Low 10.19, 6.5–13.0	Low 10.40, 7.5–14.0	High 15.25, 12.5–17.5	High 14.5	Low 10.74, 7.0–15.5	Very low 9.6, 6.5–12.5
Percentage area black	Moderate 51.9, 42–60	High 56.9, 40–57	Relatively low 47.9, 40–56	High 57.2, 46–71	Moderate 54	Low 44.6, 33–55	Low to high 53.4, 41–69
MORPHOMETRICS							
Mass (g)	Moderate 54.3, 49–60.5	Moderate 53.4, 45.5–65	Small 48.4, 43–53	Large 59.7, 54.5–66	Moderate 54.5, 54–55*	Relatively small 52.1, 49.8–56	Unknown
Tail length (mm)	Moderately short 153.5, 142–162	Moderately short 154.2, 142–168	Moderately short 151.8, 142–165	Long 165.5, 142–184	Moderate 145*–159	Short 148.8, 138–163	Short 150.4, 143–158
Wing length (mm)	Short 113.8, 109–122	Short 115.5, 110–120	Short 113.9, 109–119	Long 123.7, 116–131	Moderate 115.5, 111*–120	Short 114.9, 107–124	Short 114.9, 108–121
Culmen length (mm)	Longer 16.61, 15.3–18.1	Longer 16.64, 15.0–18.2	Shorter 15.99, 14.7–17.1	Moderate 16.52, 15.5–18.0	Moderate 16.2, 15.5*–16.8	Longer 16.81, 15.0–18.4	Longer 16.72, 15.0–18.5
Bill width (mm)	Wider 13.89, 12.7–14.7	Wider 13.93, 12.8–14.6	Relatively narrow 13.52, 12.4–14.4	Narrow 13.44, 12.4–14.5	Wider 13.9–15.0*	Wider 13.70, 12.8–14.8	Wider 13.82, 13.0–14.9
Bill height (mm)	Higher 9.64, 8.9–10.6	Higher 9.61, 8.8–10.8	Moderate 9.41, 8.2–10.9	Narrower 9.20, 8.2–10.5	Moderate 9.3–11.4*	Moderate 9.47, 8.4–10.7	Moderate 9.28, 8.5–10.1
Serrations (per side of upper bill)	Few 2.6, 2.0–5.0	Few 3.6, 2.0–8.0	Few 2.5, 1.5–4.5	Many 6.3, 2.0–9.0	Few to many 5.3, 2*–7	Few 2.0, 0.0–3.0	Few 2.5, 1.5–7.0
BARE PARTS COLOURATION							
Eye-ring (%)	White (45), Blue (27), Grey (18), Blue-grey (9), Green (9) [<i>n</i> = 11]	Yellow-green (44), Yellow (39), Green (6), Blue-grey (6), White (6) [<i>n</i> = 18]	Yellow-green (43), Yellow (39), Green (9), Blue-grey (4), Blue (4) [<i>n</i> = 23]	Blue (93), Blue-grey (4), White (2) [<i>n</i> = 267]	Blue (100) [<i>n</i> = 4]	Blue (81), Blue-grey (13), Grey (3), Green (3) [<i>n</i> = 72]	Yellow (80), Yellow-green (2) [<i>n</i> = 10]
Tarsus (%)	Grey (50), Olive (38), Pink-grey (13) [<i>n</i> = 16]	Olive (61), Grey (36), Blue-grey (3) [<i>n</i> = 33]	Olive (52), Grey (43), Pink-grey (4) [<i>n</i> = 23]	Blue-grey (43), Grey (34), Pink-grey (14), Olive (9) [<i>n</i> = 104]	Grey (100) [<i>n</i> = 3]	Grey (55), Blue-grey (43), Olive (2) [<i>n</i> = 51]	Olive (88), Grey (13) [<i>n</i> = 16]

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Table 2. Comparison of female morphological characters between taxa in the *Trogon rufus* complex with mean, minimum and maximum measured values. The female of *Trogon muriciensis* sp. nov. is unknown. Abbreviations correspond to Munsell hues: Y = Yellow, R = Red, YR = halfway between Yellow and Red.

<i>Trogon</i>	<i>T. r. rufus</i>	<i>T. r. sulphureus</i>	<i>T. r. amazonicus</i>	<i>T. chrysochloros</i>	<i>T. tenellus</i>	<i>T. cupreicauda</i>
COLOUR PATTERNING						
Head colour	Redder, less saturated, generally darker Dark to Very Dark Brown	Generally yellower, less saturated & lighter Dark Yellowish Brown to Very Dark Brown	Yellowish to reddish, generally less saturated & lighter Dark Yellowish Brown to Very Dark Brown	Yellower, poorly saturated, lighter Dark to Dark Yellowish Brown	Yellower, more saturated, lighter Dark Yellowish to Dark Olive Brown	Reddish to yellowish, poorly saturated, dark to light Dark to Very Dark Brown
Hue:	8.45YR, 7.5–10	8.98YR, 7.5–10	8.80YR, 7.5–10	9.93YR, 7.5–10	9.95YR, 7.5YR–2.5Y	8.75, 7.5YR–2.5Y
Chroma:	3.2, 3–5	3.3, 3–6	3.3, 3–4	3.1, 2–4	3.9, 3–6	3.1, 2–5
Value:	2.84, 2.75–3.0	2.89, 2.5–3.0	2.89, 2.8–3.0	2.97, 2.0–3.0	2.99, 2.5–3.0	2.87, 2.0–3.0
Mantle colour	Generally less yellow, poorly to highly saturated Dark Olive to Dark Yellowish Brown	Generally less yellow, poorly to moderately saturated Dark Olive to Dark Yellowish Brown	Generally more yellow, poorly to highly saturated Dark Olive to Dark Yellowish Brown	Yellowish, poorly saturated Dark Olive to Dark Yellowish Brown	Generally more yellow, poorly saturated to Dark Olive to Dark Yellowish Brown	More to less yellow, poorly saturated Dark Olive to Dark Yellowish Brown
Hue:	0.42Y, 7.7YR–2.5Y	0.92Y, 7.5YR–2.5Y	1.71Y, 10YR–2.5Y	1.99Y, 10YR–2.5Y	1.75Y, 10YR–2.5Y	1.42Y, 10YR–2.5Y
Chroma:	3.3, 3–4	3.2, 2.5–4	3.4, 3–4	3.1, 3–4	3.1, 3–4	3.0, 3–3
Value:	3	3	3	3	3	3
Chest colour	Generally yellower & lighter, moderately saturated Olive to Dark Yellowish Brown	Generally yellower, more saturated, relatively light Olive to Dark Yellowish Brown	Yellower, generally more saturated, & lighter Olive to Dark Yellowish Brown	Yellower, moderately saturated & light to dark Olive to Dark Yellowish Brown	Moderately yellow, more saturated, light to dark Olive to Dark Yellowish Brown	More to less yellow, poorly saturated, generally darker Olive to Dark Yellowish Brown
Hue:	1.84Y, 8.75YR–2.5Y	1.74Y, 8.75YR–2.5Y	2.2Y, 10YR–2.5Y	2.2Y, 10YR–2.5Y	1.66Y, 10YR–2.5Y	1.62Y, 10YR–2.5Y
Chroma:	3.6, 3–4	3.9, 3–5	3.5, 2–4.5	3.4, 3–4.5	4.0, 3–5	3.4, 3–4.5
Value	3.82, 3.0–5.0	3.72, 3.0–5.0	3.84, 3.0–5.0	3.47, 3.0–4.0	3.45, 3.0–4.0	3.31, 3.0–4.0
Uppertail colour	More to less saturated Dark Reddish Brown	Generally more saturated Dark Reddish Brown	More saturated, sometimes darker, Dark Reddish Brown to Very Dark Brown	More saturated Dark Reddish Brown to Dark Brown	Moderately saturated Dark Reddish Brown	Poorly saturated Dark Reddish Brown to Very Dark Brown & Dusky Red
Hue:	5YR	5YR	5.1YR, 5–7.5YR	5.15YR, 5–7.5YR	5YR	5YR, 2.5–5YR
Chroma:	3.7, 3–4	3.7, 3–4	3.9, 3–4	3.9, 3–4	3.6, 3–4	3.0, 2.0–3.5
Value	3	3	2.98, 2.5–3.0	3	3	2.94, 2.5–3.0
Brown undertail wash (%)	Edging (71), Absent (14), Base (14) [n = 28]	Edging (87), Base (13) [n = 15]	Edging (67), Absent (20), Base (13) [n = 15]	Absent (52), Base (24), Edging (24) [n = 34]	Base (63), Absent (30), Edging (7) [n = 73]	Extensive (100) [n = 21]
Terminal tailband (mm)	Wider 5.0, 1–8	Narrower 3.5, 2–5	Narrower 3.6, 2–5	Narrower 3.8, 1–7	Wider 4.4, 2–7	Narrower 3.8, 2–6

Table 2. Continued

<i>Trogon</i>	<i>T. r. rufus</i>	<i>T. r. sulphureus</i>	<i>T. r. amazonicus</i>	<i>T. chrysochloros</i>	<i>T. tenellus</i>	<i>T. cupreicauda</i>
UNDERTAIL BARRING						
Black bars (mm)	Narrow 1.63, 1.1–2.6	Broad 1.84, 1.3–2.4	Narrow 1.47, 1.1–1.9	Narrow 1.57, 1.1–2.2	Broad 2.01, 1.0–3.1	Narrow 1.59, 1.1–2.2
White bars (mm)	Narrow 2.93, 2.2–5.7	Broad 4.18, 2.6–7.2	Generally narrow 3.04, 2.2–4.3	Narrow 2.79, 1.3–3.95	Narrow 2.99, 1.7–4.6	Broad 3.56, 2.6–4.5
Density (bars cm ⁻¹)	Relatively high 4.47, 2.4–5.9	Low 3.45, 2.2–4.3	Relatively high 4.45, 3.6–5.5	High 4.72, 3.8–5.9	Moderate 4.05, 3.1–5.6	Moderate 4.01, 3.2–5.1
Percentage area black	Moderate 35.7, 27–44	Low to relatively high 31.8, 17–47	Low 32.9, 23–41	Moderate 35.8, 25–46	High 39.9, 20–55	Low 31.5, 22–46
WING COVERTS BARRING						
Black bars (mm)	Moderate 0.36, 0.25–0.48	Moderate to broad 0.39, 0.28–0.65	Generally narrow 0.36, 0.22–0.55	Narrow 0.33, 0.18–0.50	Narrow 0.30, 0.20–0.43	Moderate to broad 0.40, 0.28–0.60
Light brown bars (mm)	Narrow 0.45, 0.33–0.6	Moderate to broad 0.58, 0.30–0.94	Relatively narrow 0.48, 0.30–0.60	Narrow 0.44, 0.25–0.55	Moderate 0.51, 0.38–0.85	Narrow to broad 0.53, 0.38–0.70
Density (bars cm ⁻¹)	Moderate to high 12.0, 9–16.5	Moderate to low 10.0, 7.0–12.5	Moderate 11.4, 9.5–13.5	High 12.9, 11–15	Moderate 11.3, 7.5–14.5	Low 9.1, 7.5–12
Percentage area black	Generally high 44.9, 35–52	Generally high 41.6, 33–49	Generally high 43.4, 36–51	Generally high 42.6, 33–57	Generally low 37.2, 23–45	Generally high 43.5, 34–52
MORPHOMETRICS						
Mass (g)	Generally small 50.0, 45–57	Large 59.0, 50–71	Small 49.2, 42–58	Large 58.4, 49–65	Moderate 54.2, 50–59	Moderately large 56.3, 53–59
Tail length (mm)	Relatively short 140–167	Relatively short 145–170	Relatively short 155.4, 148–164	Long 171.9, 151–191	Short 151.9, 137–166	Short 150.3, 141–159
Wing length (mm)	Relatively short 116.5, 110–124	Relatively short 116.6, 112–125	Short 115.3, 113–118	Long 126.4, 121–132	Relatively short 116.0, 109–123	Short 113.9, 109–119
Culmen length (mm)	Generally short 15.98, 15.2–17.2	Moderate to long 16.46, 14.9–17.7	Generally short 15.96, 14.5–17.2	Generally short 15.94, 14.8–16.8	Generally long 16.63, 15.2–18.2	Moderate 16.54, 15.3–18.2
Bill width (mm)	Moderate 13.64, 12.7–14.6	Narrow 13.48, 13.0–14.1	Narrow 13.50, 13.0–13.9	Narrow 13.41, 12.7–14.0	Narrow to wide 13.44, 11.8–14.8	Wide 13.82, 12.8–14.9
Bill height (mm)	Moderate 9.33, 8.7–0.2	Generally wider 9.37, 8.2–10.2	Generally narrower 9.05, 8.0–10.0	Generally narrower 9.04, 8.4–9.7	Generally wider 9.25, 8.4–0.2	Generally wider 9.30, 8.8–9.9
Serrations (per side of upper bill)	Few 2.2, 2–3	Generally few 3.0, 2–5.5	Few 2.1, 1.5–3	Many 6.4, 3.5–9	Few 2.0, 1–3.5	Few 2.1, 2–3
BAREPARTS						
Eye-ring (%)	Blue–grey (33), Blue (25), Grey (25), White (17) [n = 11]	Yellow–green (50), Green (50) [n = 2]	Yellow (62), Yellow–green (8), Green (8), Blue–grey (8), Blue (15) [n = 13]	Blue–grey (78), Blue (17), Grey (5) [n = 128]	Blue–grey (63), Blue (36) [n = 55]	Yellow (100) [n = 7]
Tarsus (%)	Grey (73), Olive (18), Pink–grey (9) [n = 22]	Olive (82), Grey (18) [n = 11]	Grey (73), Olive (20), Pink–grey (7) [n = 15]	Blue–grey (33), Pink–grey (30), Grey (28), Olive (10) [n = 60]	Blue–grey (51), Grey (43), Pink–grey (6) [n = 47]	Olive (67), Grey (25), Blue–grey (8) [n = 12]

Table 3. Comparison of song characters between taxa in the *Trogon rufus* complex with mean, minimum and maximum measured values.

	T. r. rufus	T. r. sulphureus	T. r. amazonicus	T. chrysochloros	T. tenellus	T. cupreicauda	T. muricicensis
Notes per phrase	Few 3.2, 2-6	Few 3.8, 2-6	Moderate 4.4, 3-6	Many 6.5, 4-11	Few 3.1, 2-6	Many 7.0, 4-10	Moderate 4.5, 3-5
Pace (notes s ⁻¹)	Moderate 2.10, 1.8-2.4	Moderately slow 2.01, 1.8-2.3	Slow 1.85, 1.8-2.1	Fast 2.36, 1.8-2.8	Moderately slow 1.98, 1.8-2.3	Slow 1.87, 1.6-2.2	Moderately slow 2.00, 1.9-2.1
Intro note duration(s)	Relatively long 0.27, 0.19-0.33	Relatively long 0.27, 0.20-0.36	Long 0.30, 0.20-0.37	Moderate 0.23, 0.16-0.19	Relatively long 0.29, 0.21-0.37	Short 0.17, 0.13-0.25	Relatively long 0.26, 0.18-0.33
Pause duration (s)	Moderate 0.37, 0.28-0.47	Moderate 0.36, 0.26-0.45	Moderate 0.35, 0.30-0.40	Short 0.27, 0.18-0.36	Moderately long 0.42, 0.34-0.51	Long 0.47, 0.37-0.53	Moderate 0.34, 0.26-0.40
Loudsong note duration (s)	Moderate 0.28, 0.23-0.34	Relatively long 0.30, 0.24-0.37	Long 0.31, 0.26-0.36	Relatively short 0.24, 0.18-0.33	Relatively long 0.30, 0.23-0.36	Short 0.20, 0.14-0.27	Moderate 0.28, 0.25-0.35
Intro note peak freq. (kHz)	Low 1.33, 1.12-1.57	Moderately low 1.43, 1.15-1.61	Moderately low 1.36, 1.24-1.44	High 1.57, 1.30-1.74	Moderately high 1.52, 1.31-1.75	Moderately high 1.49, 1.29-1.78	Moderately high 1.49, 1.43-1.55
Intro note high freq. (kHz)	Low 1.44, 1.21-1.68	Moderately low 1.55, 1.23-1.77	Moderately low 1.50, 1.34-1.75	High 1.76, 1.44-2.05	High 1.75, 1.50-1.95	Moderate 1.61, 1.37-1.94	Moderate 1.64, 1.55-1.76
Intro note low freq. (kHz)	Low 0.94, 0.75-1.31	Moderate 1.10, 0.80-1.38	Moderate 1.09, 0.91-1.34	High 1.26, 0.97-1.51	Relatively high 1.25, 1.04-1.58	Relatively high 1.15, 1.01-1.36	Relatively high 1.20, 1.02-1.40
Intro note BW freq. (kHz)	Narrow 0.15, 0.10-0.25	Narrow 0.16, 0.09-0.24	Narrow 0.16, 0.07-0.30	Moderately wide 0.21, 0.10-0.35	Narrow 0.15, 0.09-0.11	Moderate 0.17, 0.07-0.26	Wide 0.23, 0.11-0.30
Loudsong note peak freq. (kHz)	Low 1.34, 1.15-1.57	Moderately low 1.40, 1.12-1.58	Moderately low 1.40, 1.21-1.50	High 1.50, 1.26-1.66	Moderate to high 1.47, 1.22-1.62	Moderate 1.44, 1.19-1.60	Moderately low 1.40, 1.36-1.45
Loudsong note high freq. (kHz)	Low 1.47, 1.20-1.68	Moderately low 1.54, 1.22-1.70	Moderately low 1.51, 1.34-1.70	High 1.63, 1.37-1.81	High 1.61, 1.49-1.77	Moderate 1.55, 1.28-1.70	Moderately low 1.53, 1.48-1.65
Loudsong note low freq. (kHz)	Low 0.88, 0.70-0.86	Moderate 0.96, 0.71-1.16	Moderate 1.0, 0.82-1.20	High 1.11, 0.92-1.37	Relatively high 1.05, 0.82-1.21	Moderate 0.99, 0.82-1.23	Moderate 0.99, 0.85-1.10
Loudsong note Bandwidth freq. (kHz)	Narrow 0.17, 0.10-0.27	Narrow 0.17, 0.10-0.26	Narrow 0.18, 0.14-0.26	Narrow 0.19, 0.10-0.30	Narrow 0.20, 0.12-0.28	Narrow 0.20, 0.11-0.33	Wide 0.24, 0.18-0.27

Abbreviations correspond to Munsell hues: Y = Yellow, R = Red, YR = halfway between Yellow and Red.

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& Daubenton 1765–81, pl. enl 736, from ‘Cayenne’ (= French Guiana).

Description: Both sexes are small compared to *T. chrysochloros* but generally larger than *T. tenellus*, *T. cupreicauda* and *T. r. amazonicus*. *Males:* Uppertail typically plain-green but varying from bottle-green (rarely more bluish) to shiny olive-green. Subterminal band of greener coloration absent. Head and mantle coppery green. Rump and chest generally more blue-green. Belly yellow. Breast band usually present and complete, less often absent or incomplete. The wing-panel barring is moderately dense with narrow black bars, moderate white bars and low percentage area black. The white bars become narrower and barring denser on a northerly gradient so northern specimens have a more pronounced difference from Amazonian subspecies than those from closer to the Amazon River. Moderate terminal tailband width. *Females:* Brown coloration generally warmer, darker and less saturated than other taxa. Head is mostly warmer, less saturated and generally darker Dark to Very Dark Brown. The mantle varies from more to less yellow and less to more saturated Dark Yellowish Brown to Dark Olive Brown in a southerly direction towards the Amazon River. Chest is generally more-yellow, moderately saturated and generally lighter Olive Brown, sometimes with warmer Dark Yellowish Brown hues. Belly yellow. Uppertail Dark Reddish Brown, varying from poorly to highly saturated in a southerly direction. Brown wash on undertail usually restricted to the area surrounding the black patch at the base of the rectrices (not visible in natural position), less often restricted to the base or absent. Undertail with narrow black and white bars, high barring density and a moderate percentage area black. Wing panel with moderate black bars widths, narrow light brown bars, moderate to high barring density and generally high percentage area black. *Bareparts:* Male eye-ring usually white or blue, less often grey, blue-grey or green. Female eye-ring usually blue-grey, blue or grey, sometimes white. Tarsi mostly grey, less often olive, uncommonly pink to purplish-grey. Bill yellow-green to yellow, occasionally grey, less vivid in females with black along culmen ridge until just posterior to the tip of the bill. Iris brown to black.

Song: A simple phrase of around three repeated notes, moderate pace, relatively long introductory note and moderate loudsong note durations, moderate pause following introductory note, low introductory note frequencies, low loudsong note frequencies and narrow introductory and loudsong note bandwidths. Twenty-one per cent of songs contained two-note phrases. The similar frequencies of the introductory note compared to the loudsong notes gives it a less ‘introductory’ quality than in other taxa.

TROGON RUFUS SULPHUREUS (SPIX, 1824)

Proposed English name: Western black-throated trogon.

Trogon sulphureus Spix, 1824, Av. Sp. Nov. Brasil. 1, p. 48 pl. 38 g.1 – Tabatinga, Brazil. – *Aganus devillei* Cabanis & Heine 1862–1863, Mus. Hein., part IV, no. 1, p. 191, footnote: Santa Maria (= South of Pebas, Perú), Peru [based on *Trogon meridionalis* Deville & Desmurs, 1849, (nec Swainson), Rev. Mag. Zool., (2), 1, p. 333]. – *Pothinus sulphureus* Cabanis & Heine, 1862–63, Mus. Hein., part IV, no. 1, p. 184. – *Trogon atricollis* Pelzeln J, 1868, Zur Orn. Bras., pp. 226–331: Borba (right bank Rio Madeira), Marabitanas Cucuí (upper Rio Negro) and Barra do Rio Negro (= Manaus). – *Trogon atricollis* (Race A) Grant, 1892, Cat. Birds. Brit. Mus., 17, pp. 455–458: Borba (Rio Madeira), Eastern Peru and Ecuador. – *Trogon atricollis atricollis* Richmond, 1893, Proc. U.S. Nat. Mus., 16, p. 513. – *Trogon atricollis* Ihering, 1904, Rev. Mus. Paul. VI, p. 444: Rio Juruá. – *Trogon atricollis Hellmayr*, 1906, Abhandl. K. Bayer. akad. Wissens. II KI., XXII, p. 596 (in reference to *sulphureus* Spix) – *Trogon atricollis atricollis* Hellmayr, 1906, Novit. Zool., 13, p. 380, Prata (near Belém). – *Trogon atricollis* Ihering & Ihering, 1907, Part. Catal. Fauna Brasil., I, Aves, p. 158, from Rio Grande do Sul to Central America. – *Trogon rufus rufus* Hellmayr, 1910, Novit. Zool., 17, p. 387, Borba and Humayta (= Humaita), Rio Madeira. – *Trogonurus curucui curucui* Ridgway, 1911, Bull. U.S. Nat. Mus. 50 (5), p. 764. – *Trogon rufus* Snethlage, 1914, Part. Bol. Mus. Goeldi. 8, p. 208, Rio Guamá (Sta. Maria de S. Miguel), Rio Tapajos (Villa Braga), Rio Purús, Rio Jamundá (Faro). – *Trogonurus curucui curucui* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325. – *Trogonurus rufus rufus* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158. – *Trogonurus rufus devillei* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158 (in reference to *Aganus devillei* Cabanis & Heine 1862–63). – *Trogonurus rufus devillei* Zimmer, 1930, Field Mus. Nat. Hist. Zool. Ser., 17, p. 295, Puerto Bermudez, Peru (in reference to *Aganus devillei* Cabanis & Heine 1863). – *Trogonurus rufus rufus* Pinto 1938, Rev. Mus. Paul. 22, p. 289. – *Trogon curucui sulphureus* Griscom & Greenway, 1941, Bull. Mus. Comp. Zool., 88, pp. 180–181. – *Trogon rufus sulphureus* Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11. Hyutanahan, Tonantins and Manacapurú, Brazil. – *Trogon rufus devillei* Gyldenstolpe, 1945, Kungl. Sv. Vet. Akad. Handl., 22 (3), pp. 85–87 (not in reference to *sulphureus* Spix): Igarapé Grande, Rio Juruá. – *Trogon rufus sulphureus* Peters, 1945, Checklist of Birds of the World, Vol. 5, p. 157. – *Trogon rufus rufus* Friedman, 1948, Proc. U.S. Nat. Mus., 97, p. 425, Salto do Huá and Rio Maturacá (upper Rio Negro, Brazil) and Braço Cassiquiare plus Cerro Japacana

- (upper Orinoco, Venezuela). – *Trogon rufus sulphureus* Zimmer, 1948, American Museum Novitates (1380), pp. 26–31. – *Trogon rufus sulphureus* Pinto, 1950, Papeíes Avilso de Zoologia, 9(9), pp. 89–136. – *Trogon rufus sulphureus* Gyldenstolpe, 1951, Ark. F. Zool., Kungl. Sv. Vet. Akad. Handl., 22 (3), pp. 85–87, female from Igarapé Castanha, Amazonas, Brazil. [He also refers to his earlier identification of *Trogon rufus devillei* (Gyldenstolpe, 1945) from the Rio Juruá as erroneous renaming it *T. r. sulphureus*.] – *Trogon rufus sulphureus* Pinto, 1978, Novo Catal. das Aves do Brasil, 1a Parte, p. 218, Western Amazonia, including S Venezuela (Cassiquaire), E Ecuador, NE Peru and Brazil west of the Negro and Madeira rivers.
- Diagnosis:* Yellow to greenish-yellow eye-ring diagnostic against *T. r. rufus*, *T. chrysochloros* and *T. tenellus*. Usually smaller with less serrated bill than *T. chrysochloros*. *Males:* The coppery-green to reddish uppertail with a subterminal band of greener coloration and breast band absence are diagnostic against *T. tenellus*, *T. cupreicauda* and *T. r. rufus*. Compared to *T. r. rufus* and *T. r. amazonicus*, the undertail barring is less dense with broader black bars. Furthermore, the wing panel has lower barring density, broader black and white bars and higher percentage area black than *T. r. rufus*, whilst the percentage area black is distinctly higher, and black bars broader in *T. r. amazonicus*, which also usually has a lower uppertail hue. Compared to *T. chrysochloros*, the undertail and wing panel barring have much broader white bars and lower barring densities. From *T. tenellus*, they may be further distinguished by having broader black bars and higher percentage area black on the wing panel. From *T. cupreicauda*, they differ by usually possessing a warmer uppertail hue (> 619 nm), absent breast band, and broader black bars and higher percentage areas black on the undertail and wing panel. *Females:* Not completely separable from other Amazonian subspecies. Usually diagnosable from northern specimens of *T. r. rufus* by their generally brighter, more yellow-brown head and more saturated uppertail. The undertail and wing-panel barring are less dense with broader black and light brown bars than *T. chrysochloros* and usually also *T. r. rufus* and *T. r. amazonicus*. The head is generally also less yellow, more saturated and darker, mantle less yellow, and chest less yellow and more saturated compared to *T. chrysochloros*. Mantle and chest often less yellow than *T. r. amazonicus*. Compared to *T. cupreicauda*, they lack the extensive brown undertail wash, have a more saturated uppertail colour, generally more saturated and yellower brown head, and brighter and more saturated chest. Also, the undertail barring is less dense with generally broader black and white bars and wing panel barring denser. Compared to *T. tenellus*, the wing panel has broader black bars, a higher percentage area black and sometimes lower density, whilst the undertail has broader white bars, lower barring density and sometimes lower percentage area black. Furthermore, the head is not as yellow, saturated or bright and the mantle less yellow, whilst the chest is usually brighter and yellower and uppertail more saturated.
- Song:* Fewer notes per phrase, slower pace, longer note and pause durations, lower note frequencies and narrower note bandwidths than *T. chrysochloros*. Lower note frequencies than *T. tenellus*. Fewer notes and longer note durations than *T. cupreicauda*. Not safely separable from other Amazonian subspecies, although generally has higher note frequencies, particularly of the first note, giving it a more ‘introductory’ quality compared to *T. r. rufus*. From *T. r. amazonicus*, it differs by having generally fewer notes per phrase and faster pace.
- Distribution and habitat:* Terra firme forests of western Amazonia, west of the Branco-Negro and Madeira Rivers and south of the Tepuis, in Venezuela, Colombia, Ecuador, Peru, extreme NE Bolivia and Brazil. Rare in SE Peru and NE Bolivia. Up to an elevation of ~1200 m. An intergradation zone with *T. r. amazonicus* stretches along both banks of the Madeira River.
- Type material:* Lectotype: ZSM-B35 (adult male), Tabatinga (*in sylvis Tabatingae*), Rio Solimões, Brazil, collected by Spix. Female syntype long known to be a female *T. ramonianus* Gmelin, 1788.
- Description:* Although relatively small, this is the only taxon that occasionally overlaps in size and bill serration with *T. chrysochloros* but is generally larger than *T. tenellus*, *T. cupreicauda* and *T. r. amazonicus*. *Males:* Uppertail notably coppery but varying from deep reddish-copper to slightly coppery-green. Subterminal band of greener coloration present. Head and mantle coppery green. Rump usually more golden-green. Chest usually more blue-green. Belly yellow. Breast band absent but occasionally present in individuals from the base of the Andes. Undertail with moderate barring density and black bar widths, relatively broad white bars and moderately low percentage area black. The wing-panel barring has the broadest black bars of all taxa, relatively broad white bars, low barring density and high percentage area black. Moderate terminal tailband width. *Females:* Head generally yellower, less saturated and lighter Dark Brown to Dark Yellowish Brown. Mantle, relatively less yellow and poorly to moderately saturated Dark Yellowish Brown to Dark Olive Brown. Chest yellower, more saturated and relatively light Olive Brown to Dark

Yellowish Brown. Belly yellow. Uppertail generally more saturated Dark Reddish Brown. Brown wash on undertail usually only edging to basal black patch or less often restricted to base of outer rectrices (not visible in natural position). Undertail barring with broad black and white bars, low density and low to relatively high percentage area black. Wing panel with moderate to broad black and light brown bars, moderate to low barring density and generally high percentage area black. *Bareparts*: In both sexes, eye-rings yellow or greenish-yellow with occasional records of individuals with green or blue-grey eye-rings from the base of the Andes. Tarsi olive throughout most of range with a minority grey, particularly along the base of the Andes, where a single specimen with blue-grey tarsi was also recorded.

Song: Few notes per phrase, moderately slow pace, relatively long introductory and loudsong note durations, moderate duration pause following the introductory note, introductory note with moderately low peak and high frequencies and low low-frequency, loudsong notes with moderately low peak and high frequencies and low low-frequency. Narrow introductory note and loudsong note bandwidths. Similar to *T. r. rufus* but with a higher first note, giving it a more ‘introductory’ quality. Ten per cent of songs contained two-note phrases.

TROGON RUFUS AMAZONICUS TODD, 1943

Proposed English name: Eastern black-throated trogon.

Trogon atricollis Pelzeln J, 1868, Zur Orn. Bras., pp. 226–331, Borba (right bank Rio Madeira), Barra do Rio Negro (= Manaus), and Marabitanas Cucuí (upper Rio Negro). – *Trogon atricollis* (Race A) Grant, 1892, Cat. Birds. Brit. Mus., 17, pp. 455–458, Borba (Rio Madeira), Eastern Peru and Ecuador. – *Trogon atricollis atricollis* Hellmayr, 1906, Novit. Zool., 13, p. 380: Prata (near Belém). – *Trogon rufus rufus* Hellmayr, 1910, Novit. Zool., 17 p. 387 [Borba and Humayta (= Humaita)], Rio Madeira. – *Trogonurus curucui curucui* Ridgway, 1911, Bull. U.S. Nat. Mus. 50 (5), p. 764 – *Trogon rufus* Sneath, 1914, Part. Bol. Mus. Goeldi. 8, p. 208: Rio Guamá (Sta. Maria de S. Miguel), Rio Tapajos (Villa Braga), Rio Purús, Rio Jamundá (Faro). – *Trogonurus curucui curucui* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325. – *Trogonurus rufus rufus* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158. – *Trogonurus rufus rufus* Pinto, 1938, Rev. Mus. Paul. 22, p. 289. – *Trogon curucui sulphureus* Griscom & Greenway, 1941, Bull. Mus. Comp. Zool., 88, pp. 180–181. – *Trogon rufus amazonicus* Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11, Villa Braga (left bank Rio Tapajos), Brazil. – *Trogon rufus amazonicus* Pinto, 1947, Arquiv. de Zool. do Est. de São Paulo, 5,

p. 371, Rio Arapiuns. – *Trogon rufus amazonicus* Zimmer, 1948, American Museum Novitates no. 1380, pp. 26–31. – *Trogon rufus rufus* Pinto, 1950, Papeéis Avulsos de Zoologia, 9(9), pp. 89–136. – *Trogon rufus sulphureus* Gyldenstolpe, 1951, Ark. F. Zool., Kungl. Sv. Vet. Akad. Handl., 22 (3), pp. 85–87: female from Igarapé Castanha, Amazonas, Brazil. – *Trogon rufus rufus* Pinto, 1978, Novo Catal. das Aves do Brasil, 1a Parte, p. 218, S Venezuela, the Guianas and north Brazil, east of the Rio Negro and Madeira.

Diagnosis: Yellow or greenish-yellow eye-rings diagnostic against *T. r. rufus*, *T. chrysochloros* and *T. tenellus*. Smaller, with less serrated bill than *T. chrysochloros*. *Males*: Uppertail hue warmer (more coppery) than *T. r. rufus* (> 587 nm) but generally cooler (greener) than *T. r. sulphureus*. Subterminal band of greener coloration present and breast band usually absent, unlike in *T. r. rufus*, *T. chrysochloros*, *T. tenellus* and sometimes *T. cupreicauda*. Compared to *T. r. rufus*, the wing panel barring is less dense and percentage area black lower due to the broader white wing bars. Compared to *T. r. sulphureus*, the undertail barring is denser with narrower black and white bars, whilst the wing panel has a distinctly lower percentage area black and generally narrower black bars. Differs from *T. tenellus* by the more coppery uppertail, breast band absence, and denser undertail barring with narrower black bars. Compared to *T. cupreicauda*, the undertail barring is denser with narrower black and white bars. *Females*: Not safely separable from other Amazonian subspecies but the brown coloration generally more yellow-brown, and the uppertail, head and chest more saturated than in *T. r. rufus*. Compared to *T. r. sulphureus*, the undertail barring is denser with narrower black and white bars and lower percentage area black, whilst the wing-panel barring is generally denser with narrower light brown bars. In terms of coloration, the mantle is often yellower and sometimes more saturated, and the chest often yellower and brighter. Against *T. chrysochloros*, the undertail barring generally has a lower percentage area black and slightly lower density, the wing panel barring is generally less dense with slightly broader bar widths, the head is generally less yellow, mantle more saturated, and chest generally more saturated, and lighter. Compared to *T. tenellus*, the undertail barring is generally denser with narrower black bars and a lower percentage area black. The wing panel barring generally has slightly broader black bars, narrower light brown bars and greater percentage area black. The head colour is less yellow and less saturated, mantle more saturated, chest yellower, lighter and generally less saturated, and uppertail more saturated. They differ from *T. cupreicauda* by the lack of an extensive brown wash on the undertail, whilst the

undertail and wing-panel barring are generally denser with narrower light brown bars, the brown coloration is generally more saturated, and chest lighter.

- 24.5 *Song*: Fewer notes per phrase, slower pace, longer note and pause durations, lower note frequencies and narrower note bandwidths than *T. chrysochloros*. Lower note frequencies than *T. tenellus*. Fewer notes and longer note durations than *T. cupreicauda*. Not safely separable from other Amazonian subspecies but generally has more notes per phrase (no two-note phrases), slower pace and sometimes longer note durations. Generally higher frequencies, particularly of the first note, which give it an ‘introductory’ nature, compared to *T. rufus*.
- 24.10
- 24.15
- 24.20 *Distribution and habitat*: *Terra firme* forests of south-eastern Amazonia, south of the Amazon and east of the Madeira Rivers in Brazil. An intergradation zone with *T. r. rufus* stretches along the southern bank of the Amazon and with *T. r. sulphureus* along both margins of the Madeira River. Absent from Marajó Island.
- 24.25 *Type material*: *Holotype*: CM 75224 (Adult Male). Villa Braga, Tapajos R., Brazil, 01.xii.1919, S. M. Klages.
- 24.30 *Description*: Smallest body mass of all taxa, although the relatively short wing and tail lengths are generally longer than for *T. tenellus* and *T. cupreicauda* but much shorter than *T. chrysochloros*. *Males*: The uppertail hue is generally slightly coppery-green but varies from deep reddish-copper to shiny olive-green. Subterminal tailband of greener coloration present but often indistinct. Head and mantle coppery green. Rump usually more golden-green. Chest blue-green to golden-green. Belly yellow. Breast band typically absent, although sometimes inconspicuous in intergradation zone with *T. r. rufus*. Undertail barring like *T. r. rufus* with narrow black bars, moderate white bars, moderate density and low percentage area black. Wing panel barring with narrow to moderate black bars, broad white bars, low density and relatively low percentage area black. Moderate terminal tailband width. *Females*: Head colour generally less saturated and darker Dark Brown to Dark Yellow Brown. Mantle, generally yellower, poorly to highly saturated Dark Yellowish Brown to Dark Olive Brown. Overall, chest slightly more saturated, lighter Olive Brown to Dark Yellowish Brown. Uppertail highly saturated Dark Reddish Brown. Extent of brown on undertail usually as edging around black patch, absent or sometimes restricted to base of outer rectrices. Undertail barring with high bar density, narrow black bars, generally narrow white bars and low percentage area black.
- 24.45
- 24.50
- 24.55
- 24.56

to broad black and light brown bars and generally high percentage area black. *Bareparts*: Eye-rings typically yellow or yellow-green but with a moderate number green and small numbers blue-grey, blue and white in the intergradation zone with *T. r. rufus* and further south in the Madeira–Tapajos interfluve. Tarsi usually grey – especially in the intergradation zones and Madeira–Tapajos interfluve – or olive and occasionally pink to purplish-grey (single female).

Song: Moderate number of notes per phrase, slow pace, long introductory and loudsong note durations, moderate pause following the introductory note, introductory note with moderately low peak and high frequencies and low low-frequency, loudsong with moderately low peak and high frequencies and low low-frequency. Narrow introductory note and loudsong note bandwidths. Similar to *T. r. rufus* but with a generally higher first note, giving it a more ‘introductory’ quality. Two-note phrases not known from recorded songs.

TROGON CHRYSOCHLOROS PELZELN, 1856

Proposed English name: Southern black-throated trogon.

Trogon chrysochloros Pelzeln J., 1856, Sitz. K. Akad. Wiss. Wien, XX, Heft 2, pp. 496–498, 505–506, Ypanema (= Ipanema), São Paulo, Brazil. – *Pothinus atricollis* Cabanis & Heine, 1862–1863, Mus. Hein., part IV, pp. 180–181. – *Trogon chrysochloros* Pelzeln J, 1868, Zur Orn. Bras., pp. 226–331 (reiteration of species description with additional specimens from Nas Lagos, São Paulo). – *Trogon atricollis chrysochloros* Berlepsch & Ihering, 1885, Zeitschr. ges. Ornithol., 2, p. 160, Taquara (Rio Grande do Sul). – *Trogon atricollis* (Race A) Grant, 1892, Cat. Birds Brit. Mus., 17, pp. 455–458, Nova Friburgo (Rio de Janeiro), Ipanema (São Paulo) and Rio Grande do Sul. – *Trogon atricollis* Ihering, 1898, Rev. Mus. Paul. III, p. 294, São Sebastião and Iquape (São Paulo). – *Trogon splendidus* Bertoni 1901, Av. Nuev. Paraguay, 1901, p. 35, Alto Paraná, Paraguay. – *Trogon atricollis chrysochloros* Hellmayr, 1906, Novit. Zool., 13, p. 380. – *Trogon atricollis* Ihering & Ihering, 1907, Part. Catal. Fauna Brasil., I, Aves, p. 158, from Rio Grande do Sul to Central America, including specimens from Espirito Santo (Rio Doce). – *Trogonurus curucui curucui* Ridgway, 1911, Bull. Un. St. Nat. Mus. 50 (5), p. 764. – *Trogon rufus* Sneath, 1914, Part. Bol. Mus. Goeldi, 8, p. 208. – *Trogonurus curucui curucui* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325. – *Trogon curucui curucui* Sztolcman, 1926, Annal. Zool. Mus. Polon. Hist. Natur., 5, p. 133, Vermelho and Terezina (Paraná). – *Trogonurus rufus chrysochloros* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158. – *Trogon curucui curucui* Pinto, 1932, Rev.

Mus. Paul. 17, p. 50, Valparaíso (western São Paulo). – *Trogon curucui curucui* Pinto, 1935, Rev. Mus. Paul. 19, p. 144, Rio Jucurucú (S Bahia). – *Trogon curucui chrysochloros* Pinto, 1935, Rev. Mus. Paul. 19, p. 144, São Paulo. – *Trogonurus rufus rufus* Pinto, 1938, Rev. Mus. Paul. 22, p. 289. – *Trogon curucui chrysochloros* Griscom & Greenway, 1941, Bull. Mus. Comp. Zool., 88, pp. 180–181. – *Trogon rufus chrysochloros* Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11. – *Trogon rufus chrysochloros* Peters, 1945, Check-list of Birds of the World, Vol 5, p. 157, Southern Brazil from Bahia to São Paulo and east to Mato Grosso; Paraguay and Misiones (Argentina). – *Trogonurus rufus rufus* Camargo, 1946, Papéis Avulsos do Dept. de Zool. 7 (5), pp. 147, 157, Boracéia (S. Paulo). – *Trogon rufus chrysochloros* Zimmer, 1948, American Museum Novitates (1380), pp. 26–31. – *Trogon rufus chrysochloros* Pinto, 1950, Papeéis Avulsos de Zoologia, 9(9), pp. 89–136. – *Trogon rufus chrysochloros* Pinto 1978, Novo Catal. das Aves do Brasil, 1a Parte, p. 218, Paraguay, Misiones (Argentina) and Brazil from S Bahia to Rio Grande do Sul, including Minas Gerais.

Diagnosis: Both sexes are markedly larger with a relatively smaller and more highly serrated bill than all other taxa. The blue, blue-grey, grey or white eye-ring is diagnostic against *T. sulphureus*, *T. r. amazonicus* and *T. cupreicauda*. *Males:* The undertail and wing panel barring are diagnostic against all other taxa due to their distinctly high density and narrow white bars, whilst the undertail barring also has a higher percentage area black. Compared to *T. r. rufus* and *T. r. amazonicus*, the undertail black bars are also slightly broader overall. The uppertail hue is generally higher than in *T. r. rufus* but lower than in *amazonicus*. Compared to *T. r. sulphureus*, the uppertail is less coppery, whilst the black bar widths on the wing panel and, to a lesser extent, undertail are narrower. Possession of a breast band also distinguishes *T. chrysochloros* from *T. r. sulphureus* and *T. r. amazonicus*. Against *T. tenellus*, the undertail barring has narrower black bars, whilst the wing panel barring has broader black bars and a higher percentage area black. Compared to *T. cupreicauda*, the uppertail is generally less coppery, undertail and wing panel black bars generally narrower and wing panel percentage area black greater. In mountainous and southern regions the chest is also usually less bright than other taxa and generally bluer than *T. tenellus*, *T. cupreicauda* and *T. r. amazonicus*. *Females:* Wing coverts more densely barred than all other taxa. However, this is only generally the case against *T. r. rufus*, from which they differ further by generally possessing narrower black bars on the wing panel, denser undertail barring, a yellower and lighter head, yellower and less saturated mantle, and yellower and duller chest. The uppertail is

also more saturated compared to northern individuals of *T. r. rufus*. Compared to *T. r. sulphureus*, they have narrower black bars, often a yellower and brighter head, yellower but less saturated mantle, and generally more saturated and lighter chest, which is also slightly more often yellower. Against *T. r. amazonicus*, they have a greater percentage area black and narrower black bars on the wing panel, less saturated and more frequently yellower-brown and lighter head, more frequently less saturated and yellower mantle, and duller chest. Compared to *T. r. tenellus*, the undertail and wing panel barring have a greater percentage area black and broader black bars, the head is usually less saturated, and chest usually yellower and less saturated. Against *T. r. cupreicauda*, they lack the extensive brown undertail wash, possess a greater percentage area black on the undertail barring, and usually has a brighter, more yellow head, yellower mantle, and yellower, often more saturated and slightly brighter chest.

Song: More notes per phrase, faster pace, shorter note durations and pause following introductory note, as well as higher note frequencies and wider introductory note bandwidth than *T. rufus* subspecies. The greater number of notes per phrase, faster pace and shorter durations are also diagnostic against *T. tenellus*. Compared to *T. cupreicauda*, the pace is faster, the pause duration shorter and frequencies usually higher.

Habitat and distribution: Primary and secondary Atlantic Forest from Bahia state (south of the Rio São Francisco) to Rio Grande do Sul in Brazil, Misiones province (and likely also north-eastern Corrientes), Argentina, and eastern Paraguay. Up to an elevation of 1600 m.

Type material: *Syntypes:* NMW 40731 (adult male) and NMW 54701 (subadult female), collected by Natterer at Ypanema (now Fazenda Ipanema), Iperó, São Paulo, Brazil.

Description: Both sexes distinctly larger than all other taxa, with highly serrated bill. Although the bill is also generally narrower than all other taxa, besides males of *T. r. amazonicus*, it appears smaller relative to the larger body. *Males:* The uppertail is mostly shiny olive-green but varies between plain green to slightly coppery-green. Head and mantle coppery-green. Rump usually plain-green. Upperchest distinctly less brilliant than in other taxa. However, the hue of the iridescent plumage decreases overall with increasing elevation (Supporting Information, Fig. S2), varying from more coppery heads and mantles and golden-green rumps and chests at lower elevations (*c.* < 550 m above sea level) to plainer-green heads and mantles

- and blue-green rumps and chests in mountainous regions (*c.* > 550 m above sea levels). This is somewhat also linked to latitude, with northern birds having the warmest coloration and those from mountainous areas in the south, the bluest. Belly yellow. Breast band usually present, often inconspicuous and difficult to detect, sometimes consisting of only a few white flecks, but uncommonly completely absent. Undertail and wing panels with exceptionally dense barring and narrow white bars, relatively narrow black bars and high percentage areas black. Moderately wide terminal tailband. *Females*: Head is usually poorly saturated, lighter and yellower Dark Brown to Dark Yellowish Brown. Mantle usually poorly saturated, yellowish Dark Olive Brown. Chest usually moderately saturated, lighter to darker Olive Brown to Dark Olive Brown. Belly yellow. Uppertail typically saturated Dark Reddish Brown, occasionally with yellower or redder hues. The brown wash on the undertail is mostly absent and less often restricted to the base of the rectrices or edging the black patch at the base of the rectrices (not visible in natural position). Undertail and wing-panel barring densities high with narrow black and light brown bars. Percentage area black moderate on undertail and generally high on wing panel. *Bareparts*: In males, eye-rings typically blue with minorities blue-grey or white. Tarsi, usually blue-grey, less often grey or sometimes pink to purplish-grey or olive. In females, eye-rings typically blue-grey, sometimes blue and rarely grey. Tarsi blue-grey, pink to purplish-grey or grey, less often olive.
- Song*: Distinctive song with a high number of notes per phrase, fast pace, moderate introductory note and relatively short loudsong note durations, short pause after the introductory note, high introductory note frequencies, low loudsong note frequencies, moderately wide introductory note bandwidth and wide loudsong note bandwidths.
- TROGON TENELLUS* CABANIS, 1862
- Proposed English name*: Graceful black-throated trogon.
- Trogon tenellus* Cabanis, 1862, Journ. für Ornith., 10 no.57, p. 173, Costa Rica. – *Pothinus tenellus* Cabanis & Heine, 1862–63, Mus. Hein., part IV, p. 181. – *Trogon atricollis* (Race B) Grant, 1892, Cat. Birds Brit. Mus., 17, pp. 455–458. – *Trogon atricollis tenellus* Richmond, 1893, Proc. U.S. Nat. Mus., 16, p. 513. – *Trogon chrysomelas* Richmond, 1893, Proc. U.S. Nat. Mus., 16, p. 513: Escondo River, Nicaragua (melaniscite adult male) – *Trogon atricollis* Salvin and Godman, 1888, Biol. Centr. Am., Aves, II, p. 458. – *Trogon atricollis* Ihering & Ihering, 1907, Part. Catal. Fauna Brasil., I, Aves, p. 158, from Rio Grande do Sul to Central America. – *Trogonurus curucui tenellus* Ridgway, 1911, Bull. U.S. Nat. Mus. 50 (5), p. 764. – *Trogon rufus* Sneathlage, 1914, Part. Bol. Mus. Goeldi. 8, p. 208. – *Trogonurus curucui tenellus* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325. – *Trogonurus rufus tenellus* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158. – *Trogon rufus tenellus* Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11. – *Trogon rufus tenellus* Peters, 1945, Checklist of Birds of the World, Vol. 5, p. 157
- Diagnosis*: Blue, blue-grey, grey or white eye-rings differentiate it from *T. cupreicauda*, *T. r. sulphureus* and *T. r. amazonicus*. Blue-grey tarsi usually distinct against *T. cupreicauda*, *T. r. sulphureus* and *T. r. amazonicus*. Small size and poorly serrated bill compared to *T. chrysochloros*. *Males*: The uppertail is bluer than all others in the complex besides some individuals of *T. r. rufus*. The rest of the iridescent plumage is generally brighter than all other species, besides the upperchest and uppertail of *T. cupreicauda*. The chest is also warmer than all besides *T. cupreicauda*. Breast band presence diagnostic against *T. r. sulphureus* and *T. r. amazonicus*. The undertail black bar widths and intermediate percentage area black are generally greater than individuals of *T. cupreicauda*, particularly those near the contact zone but may be similar to more southerly individuals. Wing coverts usually have narrower black bars and lower percentage area black, particularly compared to southerly specimens of *T. cupreicauda* but may be similar to those nearer the contact zone. They also generally have a narrower black band at the tip of the uppertail compared to *T. cupreicauda*. Compared to *T. r. rufus* and *T. r. amazonicus*, the undertail has broader black bars, lower barring density and generally broader white bars and higher percentage area black, whilst the wing panel barring is less dense and has a lower percentage area black with generally broader white bars than *T. r. rufus*. From *T. r. sulphureus*, they differ by having wing panel barring with much narrower black bars and lower percentage area black. However, the undertail barring is similar but differs overall by having slightly broader black bars, lower density and higher percentage areas black. In relation to *T. chrysochloros*, the barring densities and percentage areas black of the undertail and wing panel are much lower, undertail bar widths are much broader, white wing panel bars broader but black bars generally narrower. *Females*: The head is generally yellower, more saturated and brighter than all other taxa. In contrast the chest is usually less yellowish but more saturated. The undertail generally has broader black bars and a higher percentage area black than all besides *T. r. sulphureus*, whilst the wing panel generally has a lower percentage area black

27.5	than all other taxa and narrower black bars than all besides <i>T. chrysochloros</i> . Compared to <i>T. cupreicauda</i> , the plumage is generally yellower, more saturated and brighter, except against a handful of individuals near the contact zone, and lacks an extensive brown undertail wash. Compared to <i>T. r. rufus</i> and <i>T. r. sulphureus</i> , the mantle is yellower and less saturated overall, and the chest generally yellower, more saturated and less bright. The uppertail is also generally less saturated	with only a single record (UCLA 22738) from Costa Rica, far from the contact zone with <i>T. cupreicauda</i> . Subterminal band absent. Head and mantle coppery-green. Rump typically plain-green. Chest usually bright golden-green. Belly yellow. The breast band is usually complete, sometimes inconspicuous and rarely absent. The undertail barring has broad black bars, relatively broad white bars, low density and moderate percentage area black, whilst the terminal tailband is generally narrow. The wing panel barring has narrow black bars, relatively broad white bars, low density and low percentage area black. <i>Females</i> : Head generally yellower, more saturated and bright Dark Brown to Dark Yellowish Brown, occasionally even Dark Olive Brown or rarely Very Dark Brown. Mantle generally yellower, poorly saturated Dark Olive Brown to Dark Yellowish Brown. Chest moderately to more yellow, more saturated, light to dark Olive Brown, Dark Olive Brown to Dark Yellowish Brown. Belly yellow. Uppertail moderately saturated Dark Reddish Brown. Undertail wash limited to the base of the rectrices, or completely absent, with only a small fraction present in which it edges the black at the base of the rectrices (not visible in natural position). Undertail barring with broad black bars, narrow white bars, moderate density and high percentage area black. Wing panel barring with narrow black bars, moderate light brown bars, moderate density and generally low percentage area black. <i>Bareparts</i> : Eye-ring, in males, usually blue, sometimes blue-grey with small minorities grey or green. In females, the eye-ring is usually blue-grey and less often blue. Tarsi usually grey or blue-grey in both sexes, the later usually distinctive against <i>T. cupreicauda</i> , with small minorities pink to purplish-grey in females and a single male recorded with olive.	27.60
27.10	than <i>T. r. sulphureus</i> and southern specimens of <i>T. r. rufus</i> . The barring is usually less dense overall and wing panel light brown bars are generally broader than in <i>T. r. rufus</i> , whilst undertail and wing panel light brown bars are narrower and density higher than in <i>T. r. sulphureus</i> . Against <i>T. r. amazonicus</i> , the uppertail saturation is lower, whilst there are also subtle differences in coloration, namely a slightly less saturated mantle, and less yellow, saturated and bright chest. The undertail barring density is also slightly lower and wing panel light brown bars slightly broader. Compared to <i>T. chrysochloros</i> , the uppertail saturation is lower, chest less yellow and generally less saturated, barring densities lower, and wing panel light brown bars broader.	27.65	
27.15		27.70	
27.20		27.75	
27.25	<i>Song</i> : Diagnosed from neighbouring <i>T. cupreicauda</i> by fewer notes per phrase, longer note durations and generally higher note frequencies, particularly the introductory note high frequency. Note frequencies, particularly the introductory note high frequency, are higher than for <i>T. rufus</i> subspecies. Fewer notes per phrase, slower pace and longer durations of notes and pause following introductory note than <i>T. chrysochloros</i> .	27.80	
27.30		27.85	
27.35	<i>Distribution and habitat</i> : Primary and secondary humid forests (often with bamboo) in Central America; from southern Guatemala and northern Honduras south to the extreme north-western portion of Chocó Department, Colombia. Unrecorded but presumably present in El Salvador given faunal similarities with neighbouring countries. Up to an elevation of 1300 m.	27.90	
27.40		27.95	
27.45	<i>Type material</i> : <i>Holotype</i> : (missing) ZMB 16402 (subadult male) collected by Frantzius, V from ‘Costa Rica’. Last recorded in the Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin (MfN).	27.100	
27.50	<i>Description</i> : Small body size, similar to <i>T. cupreicauda</i> , but overlapping substantially with <i>T. rufus</i> . Shortest tail length of all taxa. Bill poorly serrated. <i>Males</i> : Uppertail mostly blue green but varying from deep blue to plain green. Individuals with shiny olive-green uppertails (> 554 nm) are rare	27.105	
27.55		27.110	
27.56		27.111 27.112	

TROGON CUPREICAUDA (CHAPMAN, 1914)

Proposed English name: Chapman’s black-throated trogon.

Trogonurus curucui cupreicauda Chapman, 1914, Bull. Am. Mus. Nat. Hist. 33 p. 606, Bagado, Chocó,

- Colombia. – *Trogon rufus* Snethlage, 1914, Part. Bol. Mus. Goeldi. 8, p. 208. – *Trogonurus curucui cupreicauda* Cory, 1919, Field Mus. Nat. Hist. Zool. Ser., 13, p. 325. – *Trogonurus rufus cupreicauda* Stone, 1928, Proc. Acad. Nat. Sci. Philadelphia, 80, p. 158. – *Trogon rufus cupreicauda* Todd, 1943, Proc. Biol. Soc. Wash. 56, p. 11. – *Trogon rufus cupreicauda* Peters 1945. Check-list of Birds of the World, Vol 5, p. 157.
- 28.5
- 28.10 *Diagnosis:* Yellow eye-ring diagnostic against *T. chrysochloros*, *T. rufus* and *T. tenellus*. Olive tarsi usually distinct against *T. tenellus*. Small size and poorly serrated bill compared to *T. chrysochloros*. *Males:*
- 28.15 The coppery-green uppertail is diagnostic against *T. tenellus*, from which they differ further in undertail barring, which, particularly for northern specimens, has generally narrower black bars, broader white bars and a lower percentage area black, whilst the wing-panel barring, particularly of southern specimens,
- 28.20 has broader black bars, greater percentage area black and lower density. The head, mantle, and rump plumage are generally less bright, and the uppertail and upperchest brighter than all other taxa, besides *T. tenellus*. They differ from *T. r. rufus* by their usually warmer uppertail hue and sometimes by possessing a subterminal band of greener coloration. If in doubt, the undertail barring density is lower with broader black and, especially, white bars, and the wing panel barring less dense with broader white bars, whilst southern specimens also have broader black bars and a greater percentage area black. Compared to *T. r. sulphureus*, the uppertail hue is rarely as coppery and the subterminal band of greener coloration often absent (especially in southern specimens),
- 28.25 whilst the white breast band is sometimes present. Northern specimens also have undertails with a lower percentage area black, generally narrower black bars, broader white bars and wing panels with lower percentage area black, narrower black bars, generally broader white bars and lower density. They differ from *T. r. amazonicus* in their lower undertail and wing panel barring densities and broader bar widths, as well as by sometimes possessing a breast band or lacking a subterminal tailband of greener coloration.
- 28.30 For southern individuals, the wing panel also has a higher percentage area black, broader black bars and lower density. Compared to *T. chrysochloros*, the barred patterning is very different with broader black and white bars, lower density and lower percentage area black on the undertail, and much lower density, percentage area black and broader white bars, along with sometimes broader black bars (particularly in southern specimens) on the wing panel. A subterminal band is also sometimes present. The black terminal tailband is generally wider than other taxa, particularly
- 28.35
- 28.40
- 28.45
- 28.50
- 28.55
- 28.56
- T. tenellus. Females:* The extensive tan-brown wash on the undertail is diagnostic. Brown plumage coloration, particularly in the south, is generally also warmer-brown, less saturated and darker than most other taxa. In particular, the head is generally darker and redder brown and the uppertail less saturated against all other taxa, except some individuals of *T. r. rufus*. Wing panel barring density low compared to all, besides some *T. r. sulphureus*. Compared to *T. tenellus*, the undertail barring has narrower black bars, broader white bars and lower percentage area black, the wing panel generally has broader black bars, lower density and higher percentage area black, and the chest coloration is less saturated. Head and uppertail are only occasionally similarly coloured to *T. tenellus* in north. They differ from *T. r. rufus* by having undertail barring with broader white bars, lower percentage area black, and slightly lower density, wing coverts with lower density, higher percentage area black and generally broader light and black bars, and chest coloration that is duller, less saturated and generally less yellow-brown. Compared to *T. r. sulphureus*, the undertail barring generally has narrower black bars and higher density, and the chest is usually duller, less saturated and less yellow. Compared to *T. r. amazonicus*, the undertail barring is generally less dense with broader white bars, the wing coverts are generally less densely barred with broader black bars, whilst the chest is duller, less saturated and less yellow. In relation to *T. chrysochloros*, the undertail is generally less densely barred with broader black bars and lower percentage area black, the wing panels are also less densely barred with generally broader black and sometimes light brown bars, whilst the chest colour is less-yellow, less saturated and duller.
- Song:* Compared to *T. tenellus*, the song has more notes per phrase, shorter note durations and generally lower note frequencies. It also has more notes per phrase, shorter note durations but a longer pause after introductory note, and generally higher note frequencies, especially for the introductory note, than in *T. rufus* subspecies. Compared to *T. chrysochloros*, the song has a slower pace, longer pause following the introductory note, generally longer note durations and generally lower note frequencies.
- Distribution and habitat:* Primary or advanced secondary growth humid forests in the Chocó-Magdalena ecoregion, from Bolivar State and the Magdalena Valley in Colombia, south to Pichincha, Ecuador. Up to an elevation of 1500 m.
- Type material:* Holotype: AMNH 123271 (adult male) collected by Mrs E. L. Kerr. from Bagado, Chocó,

Colombia (5° 25' 0.12" N 76° 24' 0" W) on 25 September 1912.

Description: Small body size, similar to *T. tenellus*, but overlapping substantially with *T. rufus*. Bill poorly serrated. *Males:* Uppertail varying from plain green to greenish-copper. All plumage patches vary from cooler to warmer hues along a northwards gradient from NW Ecuador to the contact zone with *T. tenellus* in the NW Chocó and extending into the Magdalena Valley. Mantle less-bright coppery-green. Rump generally more blue-green and less bright. Chest bright blue-green to golden-green. The white breast band is usually present but mostly inconspicuous. Subterminal tailband of greener coloration mostly absent, sometimes present. Terminal tailband widest of all taxa. Undertail barring varies from relatively broad to relatively narrow black bar widths and moderate to low percentage areas black on a northwards gradient (Supporting Information, Fig. S3). Some individuals from the northern part of this species range possess a combination of exceptionally broad white bars and narrow black bars on the undertail that is unique compared to all other taxa. In contrast, the wing panel barring varies from having narrow to broad black bars and low to high percentage area black along this same gradient (Supporting Information, Fig. S4), whilst the barring density is low and white bars relatively broad. *Females:* Head colour poorly saturated, varying from darker, redder Dark Brown to Very Dark Brown to yellower, lighter Dark Brown to Dark Yellowish Brown, sometimes even Dark Olive Brown, along a northerly gradient. Mantle more to less yellow and poorly saturated Dark Olive Brown. Chest usually duller and darker Olive Brown to Dark Olive Brown, sometimes with Dark Yellowish Brown hues in the north. Belly yellow. The uppertail is poorly saturated and sometimes even darker, more reddish Dark Reddish Brown, occasionally as saturated as in *T. tenellus* in the north. Undertail always with extensive brown wash. Undertail barring with generally narrow black bars, broad white bars, moderate density and low percentage area black. Wing panel with moderate to broad black bars, narrow to broad light brown bars, low density and high percentage area black. *Bareparts:* Eye-rings yellow, sometimes greenish-yellow in males. Tarsi mostly olive, or grey in about a quarter of females and a minority of males, and rarely blue-grey.

Song: A drawn-out song with many notes per phrase, slow pace, short introductory note and loudsong note durations, long pause following the introductory note, moderately high peak and low introductory note frequencies, moderate introductory note high frequency, moderate loudsong note frequencies,

moderate introductory note bandwidth and narrow loudsong note bandwidth.

TROGON MURICIENSIS SP. NOV.

(FIG. 7)

Proposed English name: Alagoas black-throated trogon.

Proposed Portuguese name: Surucuá-de-Murici.

Zoobank registration: urn:lsid:zoobank.org:act:8D5FDDA6-D3F0-41CF-8E09-F1C8B77CEBC5

Type material: *Holotype:* MZUSP 112768 (Fig. 7), adult male (testes 2.0 × 2.0 mm, no bursa fabricii, skull 100% ossified, no moult). Voice-recorded and collected in the montane forest of the Estação Ecológica de Murici, Alagoas, Brazil (090 12'46"S/350 52'37"W, 583



Figure 7. Illustration of *Trogon muriciensis* holotype (MZUSP 112768) from Estação Ecológica de Murici, Alagoas state, Brazil. Illustrated by Eduardo Brettas.

m a.s.l.) by Luís Fábio Silveira on 05.x.2019. Prepared by Luís Fábio Silveira.

Paratype: MN 33853, subadult male (testes subequal in size, skull 100% ossified, second prebasic molt). Collected in forest midstory of the Estação Ecológica de Murici, Alagoas, Brazil (09° 15'S/35° 50'W, 550 m a.s.l.) by Dante Martins Teixeira on 19.ix.1983.

Diagnosis: We had little material available for the diagnosis of the new species *Trogon muriciensis*, particularly regarding external morphology, so caution must be taken until more information is collected. For comparison of plumage coloration and barred patterning, only the holotype was available. For morphometric traits, in addition to the holotype, we had measurements from the paratype and a ringed individual. For other discrete traits, we had photos from online depositories, in addition to those of the holotype (Supporting Information, Fig. S8) and ringed individual. For the song, we had slightly more material, with recordings from five separate individuals (including the holotype).

Males: *Trogon muriciensis* can be distinguished from all other species of trogons, besides *T. rufus*, *T. chrysochloros*, *T. tenellus* and *T. cupreicauda*, by the combination of the green head and citrus-yellow belly. Light-blue eye-ring is diagnostic against *T. r. sulphureus*, *T. r. amazonicus* and *T. cupreicauda*. Breast band absent, unlike most *T. chrysochloros*, *T. rufus*, *T. tenellus* and *T. cupreicauda*. The dense barring and narrow white bars on the undertail of the holotype are diagnostic against individuals of all taxa besides *T. chrysochloros*, whilst the dense barring and narrow white bars on the wing panel are diagnostic against all besides *T. chrysochloros* and *T. r. rufus*. Nevertheless, compared to *T. chrysochloros*, several subtle differences are present. Morphometrically, it has a smaller body size and variably serrated bill (vs. highly serrated), whilst the holotype has a greener uppertail hue and undertail with narrower black bars and lower percentage area black compared to almost all specimens of *T. chrysochloros* examined. Compared to *T. r. rufus*, the body mass appears slightly greater, whilst the holotype had denser undertail barring with narrower white bars than all individuals of *T. r. rufus* examined. Against *T. r. sulphureus* and *T. r. amazonicus*, the holotype had a consistently greener uppertail hue, greater barring density and narrower white bars on the undertail and wing panel barring, and greater body mass. Compared to *T. cupreicauda*, the undertail barring is also much denser with narrower white bars, the wing panel barring is denser and uppertail hue lower. Compared

to *T. tenellus*, the uppertail hue is greener and the undertail barring much denser with narrower black and white bars. Female: unknown.

Song: Compared to *T. chrysochloros*, the song of *T. muriciensis* has fewer notes per phrase, slower pace, longer note durations, longer pause following introductory note and generally lower note frequencies. It is similar to *T. r. rufus* but with generally more notes per phrase, higher introductory note frequencies and higher loudsong note low frequencies. Compared to *T. r. sulphureus*, it has wider bandwidth frequencies and generally more notes per phrase, whilst against *T. r. amazonicus*, it has faster pace, shorter note durations and a higher frequency introductory note. In relation to *T. tenellus*, it has a greater number of notes per phrase, shorter pause after the introductory note a generally lower introductory note high frequency, and generally lower peak and high loudsong note frequencies. It differs from *T. cupreicauda* by having fewer notes per phrase, longer note durations but a shorter pause after the introductory note. The bandwidth frequencies of the introductory and loudsong notes are generally wider than all other taxa, except *T. chrysochloros*.

Distribution and habitat: Only known from Estação Ecológica de Murici, Alagoas, Brazil, at just over 500 m elevation, where it occurs in mid-levels of the montane Atlantic Forest. It was presumably once more widespread throughout this habitat in the Pernambuco Centre of Endemism before the deforestation of the region.

Description of the holotype: Uppertail plain green, head and mantle green with coppery sheen, rump and upperchest green with blue sheen. Black facial mask extending from in line with dorsal edge of bill to the eye, across ear coverts to throat. Bright citrine-yellow from lower chest to vent. Undertail barred patterning (outer three rectrices) with narrow black bars (1.46 mm wide), relatively narrow white bars (1.39 mm wide), high bar density (6.7 bars/cm) and moderate percentage area black (50%). Wing coverts barred patterning with narrow black bars (0.4 mm), narrow white bars (0.3 mm), high bar density (14.5 bars/cm) and moderate percentage area black (54%). Flight feathers black with basal-third white (only visible ventrally), except for final primary, which is entirely black, and black and white barring on anterior margin. Eye-ring light blue, tarsi grey and bill greenish yellow. Measurements – total length: 251 mm, wing chord: 108 mm, tail: 154 mm, bill width: 14.8 mm, bill height: 11 mm, tarsi: 3.6 mm, number of bill serrations (per side of upper bill): 2, body mass:

30.60

30.65

30.70

30.75

30.80

30.85

30.90

30.95

30.100

30.105

30.110

30.111

30.112

55 g. Tissue sample MZUSP 112.768. Stomach content: remains of caterpillar and fruit.

Song: 4.1 ± 0.27 notes per phrase, duration of introductory note 0.28 ± 0.02 s, interval between introductory note and loudsong 0.31 ± 0.02 s, mean loudsong note duration 0.26 ± 0.03 s, loudsong pace 2.18 ± 0.05 notes per second, introductory note peak frequency 1.34 ± 0.04 kHz, low frequency 1.06 ± 0.03 kHz, high frequency 1.45 ± 0.02 kHz and 90% bandwidth 0.20 ± 0.06 kHz, loudsong note peak frequency 1.37 ± 0.03 kHz, low frequency 0.95 ± 0.04 kHz, high frequency 1.48 ± 0.02 kHz and 90% bandwidth 0.25 ± 0.04 kHz.

Variation in type material: The immature nature of the paratype makes it difficult to determine whether variation between it and the holotype are due to age or intrapopulation variation. The upperparts of the paratype present a strongly coppery head and mantle, golden-green rump, predominantly brown upperchest with golden-green feathers, and reddish-brown uppertail (central rectrices). The brown rectrices and chest feathers represent an individual that has undergone second prebasic molt and not yet obtained fully formative plumage (Ryder & Wolfe, 2009). Therefore, whether the warmer hues of the upperparts, compared to the holotype, are related to its age is unclear, although past research has not found changes in the tonality of structural colours with age (Prum, 2006). It is similar to the warmer hued upperparts of *T. chrysochloros* individuals found below 500 m a.s.l., which are likely controlled by humidity, but this is unlikely the case in this instance since both type specimens originate from the same area, just above 500 m a.s.l. and the holotype has plumage with cooler hues, consistent with the higher elevation and humidity of Murici. In terms of the barred patterning, the paratype differs from the holotype in undertail barring by having substantially broader black (2.23 mm) and white bars (2.17 mm) and lower bar density (4.65 bars/cm), but a similar percentage area black (50%). This is much more akin to *T. r. sulphureus*. However, the more pointed tips of these rectrices suggest they are immature, whilst the similarly lower density of the undertail barring on immatures of other species in the complex suggest this is also the result of age. In terms of the wing panel barring, compared to the holotype, the paratype had narrower black bars (0.23 mm) and white bars (0.33 mm) and a lower percentage area black (41%) but similar bar density (14.5 bars/cm). This is more similar to *T. chrysochloros* and may represent the affinity between the two species. However, the brown in the wing coverts feathers suggest they are not mature, so this variation may also be due to age. In terms of morphometrics, although body mass provides

a consistent means of comparison, the variability of other measurements between type specimens is likely the result of observer bias. For discrete characters, the faded underparts of the paratype make it difficult to ascertain the presence of a breast band but the absence of pure white feathers in the area, adjacent the upperchest, suggest it is absent, as in the holotype. The bareparts' colours are also consistent with the holotype, with the eye ring noted as blue and the tarsus grey.

Etymology: The name refers to the only remaining locality where this taxon is known to occur (Estação Ecológica de Murici, Alagoas state, Brazil), to draw attention to the critical level of biodiversity loss in the region and dire need for conservation.

Remarks: Despite the scarcity of material, we were able to diagnose *Trogon muriciensis* as exhibiting a unique combination of features typical of, or intermediate to, either *T. chrysochloros* in the southern Atlantic Forest or one of the *T. rufus* subspecies in Amazonia. The plumage patterning most resembled *T. chrysochloros* with a shiny green uppertail towards the end of the range for *T. chrysochloros*, blue eye-ring and dense undertail and wing panel barring with similarly narrow white bars, which is unsurprising given that they are sister-species, according to the mtDNA. Nevertheless, subtle differences are present between the holotype and all examined specimens of *T. chrysochloros*, namely, in the slightly narrower black bar widths and lower percentage area black on the undertail. Unlike most *T. chrysochloros*, however, it lacked a breast band, which is more typical of *T. r. sulphureus* and *T. r. amazonicus*. On the other hand, the body mass is intermediate between *T. chrysochloros* and *T. rufus* subspecies, whilst tail and wing lengths are shorter than *T. chrysochloros* but consistent with *T. rufus* subspecies. The degree of bill serration is also intermediate between these taxa and may indicate an omnivorous diet, as is typical of all taxa besides *T. chrysochloros*, which prefers large arthropods and seems likely the reason for its more serrated bill. This is further supported by the presence of both fruit and insect remains in the stomach contents of the holotype and suggest that the ecological niche it occupies is different to that occupied by *T. chrysochloros*. In contrast, the song is different from *T. chrysochloros*, with fewer notes per phrase, slower pace, longer note durations, longer pause following introductory note and generally lower note frequencies. However, it was similar to *T. rufus* subspecies, especially *T. r. sulphureus*, with only slightly more notes per phrase overall. The introductory note and loudsong bandwidths also appear to be generally wider than in all other taxa, besides *T. chrysochloros*. Nevertheless,

these differences require confirmation with further sampling.

This combination of characters, typical of related Atlantic Forest and Amazonian species, is unsurprising when one considers that the Pernambuco Centre of Endemism was once at the centre of biotic interchange between these regions during the Plio-Pleistocene (Costa, 2003; Batalha-Filho *et al.*, 2013). In fact, there are 42 other cryptic endemic species and subspecies known from this region with affinities to either the Atlantic Forest or Amazonia (Teixeira & Gonzaga, 1983, 1985; Da Silva *et al.*, 2002; Silveira *et al.*, 2003; Barnett & Buzzetti, 2014; Tello *et al.*, 2014; Thom & Aleixo, 2015; Bocalini *et al.*, 2020).

The conservation status of this population is worrisome with all records originating from only a single locality. During our fieldwork in 2019, we were able to detect only about 20 individuals, and explicitly avoided collecting more than one specimen. We, therefore, recommend that it be listed as Critically Endangered (IUCN, 2012) as < 30 km² of the forest remains at this site (criterion B1), mostly in small fragments and not all suitable for this species. It can also be inferred to have suffered a population reduction of ≥ 90% (criterion A1) given the > 98% loss of forest cover in NE Brazil, which still continues (Silveira *et al.*, 2003; Trindade *et al.*, 2008). In fact, based on the population density of *T. r. rufus* – three pairs/km² (Thiollay, 1994) – and the remaining forest area, an optimistic estimation of the maximum population size is around 90 pairs (criterion C). However, given the continued reduction in forest cover, fragmentation, edge effect and secundarization of the old growth forest (Ranta *et al.*, 1998; Silveira *et al.*, 2003; Trindade *et al.*, 2008; Pereira *et al.*, 2014), the actual figure is likely much lower with recent searches having repeatedly failed to locate it at any other fragments in the region (LFS per. obs.). It is, therefore, the most threatened trogon in the world, followed by the vulnerable (VU) Javan trogon, *Apalharpactes reinwardtii* (Temminck, 1822), with eight other species currently considered globally near-threatened (IUCN, 2018).

The conservation importance of this region is well known as it contains more globally threatened species than anywhere else in the Americas (Wege & Adrian, 1995; Stattersfield *et al.* 1998; Silveira *et al.*, 2003; Pereira *et al.*, 2014). This is primarily the direct result of pervasive habitat loss and degradation within the Pernambuco Centre of Endemism (Pereira *et al.*, 2014), which have already led to the recent extinction of other PCE endemics, namely *Cichlocolaptes mazarbarnetti* Mazar Barnett & Buzzetti, 2014, *Glaucidium mooreorum* da Silva, Coelho & Pedreira, 2002 and *Philydor novaesi* Teixeira & Gonzaga, 1983, representing the first modern bird extinctions

for Brazil (Pereira *et al.*, 2014; Butchart *et al.*, 2018; ICMBio, 2018). Urgent actions are, therefore, required to prevent further losses in the region. Namely, the consolidation of existing forest fragments into larger continuous blocks and conferring legal protection to large, existing patches of forest that remain unprotected, including Murici, as recommended by Pereira *et al.* (2014). Furthermore, we recommend a captive breeding programme based on the knowledge and experience acquired from successfully hatching and raising other species of Trogons in captivity to save the last remaining individuals of *Trogon muriciensis*.

DISCUSSION

We propose that *Trogon tenellus*, *T. cupreicauda*, *T. chrysochloros* and *T. rufus* be elevated to species-level status, whilst Amazonian populations be maintained as separate subspecies. Also, we describe a new species from the Pernambuco Centre of Endemism.

The lack of geographic overlap or intermediates between *T. tenellus* and *T. cupreicauda* provides a classic case of biological sister-species (Mayr, 1942) coming into contact in the far north-western portion of the Chocó Department, Colombia, in a region known as the Darién Gap. From the distribution of voucher specimens in this region there appears to be a suture zone running from east of the Atrato River mouth to between the Juradó and Jurubidá Rivers on the Pacific. From the lower Atrato, we have three specimens of *T. tenellus* from west of the river, at Unguía, and three from the east, at Sautatá. This is only about 30 km from the closest (two) vouchers of *T. cupreicauda* from the Upper Rio Chigorodó, north-western Antioquia, whilst a third comes from the west bank of the Atrato from further upstream at ‘Truando Falls’ (Paynter, 1997). On the Pacific slope, we have a single specimen of *T. tenellus* from the Rio Juradó and several *T. cupreicauda* from the near the Rio Jurubidá. Unfortunately, there are no accounts of how these birds behave towards each other in the wild or any more recent records, given the inaccessibility of the region in recent decades due to civil unrest. Nevertheless, the entire region is characterized by low mountains covered by thick humid forests with no obvious barrier for lowland populations, so they likely do interact. This pattern of Central and South American sister-species coming into contact in the Darién Gap has been recognized between several other lowland species-level taxa, such as *Sipia laemosticta* Salvin, 1865 and *S. nigricauda* (Salvin & Godman, 1892)/*S. palliata* (Todd, 1917) (Chaves *et al.*, 2010), populations of *Sclerurus mexicanus* Sclater, 1857 (D’Horta *et al.*, 2013) and a wealth of other

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groups (Haffer, 1967; Brumfield & Capparella, 1996). Mechanisms for the original divergence and posterior secondary contact of these populations are likely associated with the complex climatic and geological dynamics around the closure of the Isthmus of Panama (Bacon *et al.*, 2016). Within the trogons, DaCosta & Klicka (2008) suggested that species endemic to the Chocó-Magdalena, namely *Trogon caligatus* Gould, 1838, *T. chionurus* Sclater & Salvin, 1871 and *T. comptus*, are the result of secondary dispersal events to the South American mainland from Panama around 3 Mya, after the formation of the Andes, which prevented dispersal further south. The split between *T. tenellus* and *T. cupreicauda* corresponds to precisely this period. Hence, we hypothesize that *T. cupreicauda* is the result of such a secondary dispersal event from Panama to South America during the formation of the isthmus and that the reproductive isolation between *T. tenellus* and *T. cupreicauda* is maintained by biotic pressures after secondary contact.

The earliest divergence in the complex, however, is between species west and east of the Andes, and corresponds to the rise of these mountains around 5–6 Mya, which present a formidable barrier to lowland forest species and are well known to have caused speciation in a wide variety of lowland forest bird lineages (Smith *et al.*, 2014). This includes other clades of lowland trogons, namely *T. caligatus*–*T. violaceus/ramonianus/curucui/surrucua* and *T. chionurus/bairdii*–*T. viridis* (DaCosta & Klicka, 2008).

East of the Andes, metapopulations in the Atlantic Forest (*Trogon chrysochloros* and *T. muriciensis*) and Amazonia (*Trogon rufus*) are reciprocally monophyletic with the divergence between them dated to ~3 Mya, coinciding with the separation between the Amazon and Atlantic forests (Costa, 2003; Batalha-Filho *et al.*, 2013). Numerous other speciation events are congruent with this separation, including between species of *Dendrocincla* G. R. Gray, 1840, *Dendrocolaptes* Hermann, 1804 and *Xiphorhynchus* Swainson, 1827 woodcreepers (Cabanne *et al.*, 2008; Weir & Price, 2011; Batalha-Filho *et al.*, 2013), *Mitu* Lesson, 1831 and *Pauxi* Temminck, 1813 curassows (Pereira & Baker, 2004) and several lineages of forest-dwelling small mammals (Costa, 2003). This split is also of similar age to that between *T. tenellus* and *T. cupreicauda*, which show strong pre-mating isolation. Although *T. chrysochloros*, *T. muriciensis* and *T. rufus* are allopatric, making it difficult to assess the degree of reproductive isolation between them, all have distinct barred patterning, which Bitton & Doucet, (2014, 2016) showed to be linked to species recognition. They also have prominent differences in song, which are well known to mediate species recognition and are heavily involved in sexual selection in birds

(Catchpole & Slater, 2003), supporting their species-level distinction (Paterson, 1985; Masters *et al.*, 1987). Furthermore, the sister-relationship with shallow divergence between *T. chrysochloros* in the southern Atlantic Forest and *T. muriciensis* in the Pernambuco Centre of Endemism fits an increasingly common pattern of species from the Pernambuco Centre of Endemism being more closely related to species in the southern Atlantic Forest (Bocalini *et al.*, 2020) than they are to those in Amazonia (e.g. Tello *et al.*, 2014; Thom & Aleixo, 2015).

We can also observe the distinctiveness of *T. chrysochloros* in its dietary preferences, which are almost entirely insectivorous, differing substantially from all other species in the complex, which are more omnivorous. In fact, the recorded rate of insectivory of 95% makes *T. chrysochloros* the most insectivorous species of *Trogon*, followed by *T. rufus* and *T. personatus* Gould, 1842 (Remsen *et al.*, 1993) at 73%. Furthermore, prey items consisted entirely of large arthropods (large caterpillars, Phasmatodea, Mantodea, Orthoptera, Cicadoidea and large moths), explaining the possession of bill serrations, which are known to be an adaptation to prevent the escape of strong or slippery prey (Gosner, 1993). This specialization may also explain the greater rarity of *T. chrysochloros* compared to the more generalist *T. viridis* and *T. surrucura* Vieillot, 1817, with which it is sympatric (Remsen *et al.*, 1993; Pizo, 2007). It also explains their unique behaviour among trogons of following ant-swarms, monkeys and coatis (Beisiegel, 2007), as they may flush such prey species, providing easy meals for the trogons. Above all, however, the occupation of a different ecological niche by *T. chrysochloros* is good evidence of species-level differentiation (Andersson, 1990).

In all the above-mentioned taxa, differences are particularly evident in the barred patterning, which is unsurprising given the role it plays in species recognition (Bitton & Doucet, 2014, 2016). However, the similarly large variations in wing panel barring, uppertail colour, eye-ring colour, tarsus colour and breast band presence/absence suggest they are just as important. On the other hand, the high variability and lack of strong interspecific differences in the iridescent coloration of the head, mantle, rump and chest caution against its use in delimiting species. In *T. chrysochloros*, the variation of the upperparts from coppery- to blue-green with increasing elevation suggests environmental control. Indeed, Eliason & Shawkey (2010) showed experimentally that iridescent feather coloration changed rapidly (and reversibly) in response to ambient humidity due to the swelling of the melanosomes caused by water absorption. Therefore, *Trogon chrysochloros* may provide the first known case of a naturally occurring environmentally

- controlled cline in structural coloration. Differences in the hue of iridescent plumage between populations are, therefore, poor indicators of taxonomic differences. Instead, they provide a strong impetus to question the validity of other *Trogon* species and subspecies distinguished by the tonality of their iridescent plumage, especially those that inhabit areas with different levels of humidity, particularly altitudinal zones. However, the uppertail colour does not follow this trend since specimens in close proximity between neighbouring taxa, namely *T. tenellus* and *T. cupreicauda*, and Amazonian subspecies (see below), have greatly differentiated uppertail colours but live under similar climatic conditions. This means that it is subject to selection rather than environmental control and the fact that these differences are present between neighbouring taxa suggest they are the result of character displacement. Accordingly, differences in traits subject to selection between neighbouring taxa, such as uppertail colour, are augmented due to the costs incurred by individuals with intermediary trait values (i.e. similarly coloured tails), such as hybridization, interspecific aggression, and competition for signalling space or ecological interactions that secondarily influence colour patterns (Martin *et al.*, 2015). Therefore, differences in uppertail colour likely play a key role in species recognition in the complex, acting as a pre-mating barrier and leading to speciation, which is unsurprising given its involvement in the tail-raising display.
- Ring-shaped intergradation between Amazonian subspecies:* Within Amazonia, *Trogon r. rufus*, *T. r. sulphureus* and *T. r. amazonicus* are phenotypically distinct in uppertail colour, eye-ring colour, breast band presence/absence and barring. However, the more phenotypically distinct *T. r. rufus* and *T. r. sulphureus* were paraphyletic in *Cytb* and *ND2* sequences. Still, the fact that there is displacement or sorting in the above-mentioned traits between these subspecies is highly suggestive of mutually occurring mate recognition. Indeed, these are the same traits sorted or displaced between *T. tenellus* and *T. cupreicauda*, which are clear biological species. Differences in eye-ring colour, possession of a breast band and tail patterning are also among the traits known to undergo trait sorting between sympatric species of *Trogon* (Bitton, 2015). In addition, as mentioned above, the stark differences in uppertail colour of specimens in close proximity between neighbouring taxa, namely *T. r. rufus*–*T. r. sulphureus* across the Negro-Branco and *T. r. rufus*–*T. r. amazonicus* across the Lower Amazon, suggest that they cannot be suggested to environmental control, but are subject to displacement and trait sorting. Thus, it seems likely that mate recognition acts as a pre-mating barrier between Amazonian subspecies and explains the differences between them.
- However, there is clearly also intergradation between *T. r. rufus*–*T. r. amazonicus* and *T. r. amazonicus*–*T. r. sulphureus*. Between *T. r. rufus* and *T. r. amazonicus*, this is limited to the southern bank of the Amazon River, from the Madeira–Tapajos interfluvium east to the Belém Centre of Endemism with a particularly large number of intermediates around the lower Tapajos. It is especially evident in the intrusion of *T. r. rufus*-like blue (and intermediate green) eye-rings (Fig. 3B), breast band presence (Supporting Information, Fig. S6) and greener uppertail hues (Fig. 3A) into the distribution of *T. r. amazonicus*. The specimen from the Rio Arapiuns on the southern bank of the Amazon is particularly *T. r. rufus*-like in morphology. Between *T. r. sulphureus* and *T. r. amazonicus*, the distinction is subtler with a steep cline in the dimensions of the undertail barring occurring between the Madeira and west bank of the Rio Purus.
- Despite shallow levels of geographic structuring, with clustering of private mitochondrial alleles in all interfluvia, our genetic and geographic sampling does not allow an accurate assessment of the current degree of reproductive isolation in Amazonian populations. Unsourced nuclear genomic regions, particularly those evolving at slower rates than mtDNA, can exhibit higher levels of admixture reflecting either on-going gene flow (Weir *et al.*, 2015) or the existence of ancestral polymorphisms (Charlesworth, 2010). On the contrary, if there is strong selection for genes associated with specific phenotypic traits, as trait sorting would indicate, they will reach fixation more rapidly relative to mtDNA and mask divergence (Campagna *et al.*, 2015, 2017). Either way, we are presented with taxa in De Queiroz's (2007) 'grey zone', where, depending on the criteria used for species delimitation, one, two or three species may be defined. According to the biological species concept, the presence of extensive interbreeding, especially between *T. r. sulphureus* and *T. r. amazonicus*, indicates a single Amazonian species. The lack of reciprocal monophyly or complete diagnosability would also suggest a single Amazonian species under the phylogenetic (Cracraft, 1983; Donoghue, 2016) and evolutionary (Wiley, 1978) species concepts. Consequently, in spite of observing phenotypical differentiation and trait sorting between populations, we conservatively propose the treatment of these populations as subspecies due to the presence of extensive zones of phenotypic intergradation. Thorough analyses with increased phenotypic, genomic and geographic sampling, particularly around the intergradation zones and in river headwaters, will be critical to assess the existence and the extent of on-going gene flow between

Amazonian populations. Furthermore, the discordance between differences in the phenotype and mtDNA sequences between populations in separate interfluves calls into question the validity of other trogons recently elevated to species level based mostly on differences at these same gene loci, namely *T. caligatus*, *T. chionurus* and *T. ramonianus* (Remsen, 2008a, b, c).

The location of intergradation between *T. rufus* subspecies is consistent with contact zones found between numerous other taxa. At least eight other Guiana Shield taxa cross the lower Amazon and make contact with their southern counterparts (Haffer, 1997a), like *T. r. rufus*, and at least three taxon-pairs have contact zones west of the Madeira (Haffer, 1997a), like *T. r. amazonicus*–*T. r. sulphureus*. To the north of the Amazon River, however, discrepancies in the barring dimensions in several specimens from between the upper Rio Negro and Central Venezuela (Supporting Information, Figs S3, S4), suggest that there may be intergradation between *T. r. rufus* and *T. r. sulphureus*, but the scarcity of specimens from the region prevents us from making a robust assessment. This area is well-known for possessing contact zones of at least 78 taxon-pairs that are acutely clustered in pockets of suitable habitat produced by the pronounced changes in elevation and forest–non-forest habitat typical of the region (Naka *et al.*, 2012).

The scenarios used to explain these patterns differ according to the different hypotheses for the major causes of speciation in Amazonia. Under the river barriers hypothesis, which suggests that the vicariant effect of major rivers is the driving force of speciation, changes in the course of rivers are linked to contact between closely related taxa in adjacent interfluves (Ayres, 1986; Capparella, 1991; Ayres & Clutton-Brock, 1992). Such shifts in river courses are well established (Gascon *et al.*, 2000; Ruokolainen *et al.*, 2018) and linked to hybrid zones (Somenzari & Silveira, 2015). There is no evidence for changes in the courses of the lower Amazon and Branco but there have been repeated shifts between the Madeira, Purus and Juruá (Ruokolainen *et al.*, 2018), corresponding to the location of intergradation between *T. r. amazonicus* and *T. r. sulphureus*. Alternatively, the forest refuge hypothesis asserts that speciation of forest species is the result of their divergence in isolated blocks of forest that remained during glacial dry periods, especially during the Quaternary (Haffer, 1969, 1997b, 2008). In this case, the re-expansion of forests during interglacial wet periods enabled contact between populations, regardless of the presence of rivers. This is now regularly observed in modern taxonomic and biogeographical works (Weir *et al.*, 2015; Pulido-Santacruz *et al.*, 2018), with many more species than previously thought now known to have distributions that cross large rivers (Oliveira *et al.*, 2017), calling into

question the validity of Cracraft's Areas of Endemism (Cracraft, 1985). In fact, the contact between taxa originating in the Guiana refuge with their southern counterpart on the southern bank of the lower Amazon was a specific prediction of the forest refuge hypothesis (Haffer, 1997a). In cases where the divergence between these taxa was incomplete, it would also result in hybridization, as is observed between *T. r. rufus* and *T. r. amazonicus*. Either way, it seems likely that the intergradation observed between subspecies of *T. rufus* is the result of ingressive hybridization.

This pattern of intergradation between subspecies in a circle pivoted around the confluences of the three largest rivers (Amazonas, Negro and Madeira) in central Amazonia is reminiscent of a ring species (Mayr, 1942; Martins *et al.*, 2013). Accordingly, separate populations of widespread species become isolated by distance, often in association with semipermeable barriers, but are linked through a series of contact zones with the terminal populations becoming reproductively isolated before later coming into contact (Mayr, 1942; Martins *et al.*, 2013). It is best known in organisms inhabiting bands of lower elevation around mountain ranges (Wake *et al.*, 1986; Irwin, 2000) but may be more prevalent in Amazonia of contact zones between populations in adjacent interfluves (Weir *et al.*, 2015; Pulido-Santacruz *et al.*, 2018). Accordingly, taxa occupying the interfluvia separated by the largest Central Amazonian rivers (whether originating due to the river barrier or forest refuge hypotheses) come into contact in river headwaters or regions where the river has shifted course, resulting in introgressive hybridization in these places, creating a ring of interlinking taxa. Such patterns are noted in the examples of *Pteroglossus* Illiger, 1811 and *Ramphastos* Linnaeus, 1758 toucans (Eberhard & Bermingham, 2005; Patané *et al.*, 2009), *Pionopsitta* Bonaparte, 1854 parrots (Eberhard & Bermingham, 2005), *Xiphorhynchus* woodcreepers (Aleixo, 2004; Pulido-Santacruz *et al.*, 2018), wedge-billed woodcreeper *Glyphorhynchus spirurus* (Vieillot, 1819), scale-backed antbird *Willisornis poecilinotus* (Cabanis, 1847) (Weir *et al.*, 2015; Pulido-Santacruz *et al.*, 2018) and white-crowned manakin *Dixiphia pipra* (Linnaeus, 1758) (Castro-Astor, 2014).

Although the species-level validity of *T. tenellus*, *T. cupreicauda*, *T. chrysochloros* and *T. rufus* is clear, further investigation is required to resolve the patterns of contact and reproductive isolation between *T. rufus* populations, which we have conservatively retained as subspecies. Finally, although the isolated population in the Pernambuco Centre of Endemism is fully diagnosable as the species *T. muriciensis*, additional information is required to describe the variation within the population, but we caution against the collection of

further specimens given its threatened status and call for urgent conservation action to be taken to save this new species from extinction.

ACKNOWLEDGEMENTS

We thank the curatorial staff of the museums that provided specimens and tissue samples, namely Nate Rice (ANSP), Brian Schmidt (USNM), Steve Rogers (CM), Ben Marks (FMNH), Jeremiah Trimble (MCZ), Paul Sweet & Lydia Garetano (American Museum of Natural History [AMNH]), J. V. Van Remsen Jr., Steve Cardiff, Robb Brumfield and Donna Dittmann (LSUMZ), Kathy Molina (UCLA), Kristof Zyskowski (YPM), John Demboski (DMNS), James Maley (MLZ), Kimbal Garret (LACM), Marcos Raposo (MN) and Alexandre Aleixo (MPEG). Tammy Bishop (ML) and Paula Caicedo (IVAH) for providing sound recordings. Berg Hans-Martin (NMW), Markus Unsöld (ZSM), Sylke Frahnert (MFN-Berlin) for photographs and information on type specimens. An exceptional thank you goes to Ms Janet Hinshaw (UMMZ) for receiving me for nearly a month. We are indebted to Eduardo Parentoni Brettas for illustrating the species plates. Bruno Rennó, Felipe Arantes, André Grassi Corrêa, Bret Whitney, Roberto Guido, Vítor Piacentini, Fábio Schunk, Fábio Maffei, Robson Czaban, Sara Miranda Almeida, Claudia Brasileira, Rafael Marcondes, Vagner Cavarzere, Andre de Luca and Marcio Efe for sharing their private photographs and song recordings. Thank you to Eric Lira for help with DCRAW, Tiago Montanher (IME-IB, USP) for help converting PROSPEC files. Bruno Ehlers (UPS), Marcello Brito (Agropalma), Wilson Lemos de Moraes Neto (Fazenda Fatura), Alberto Fonseca (MPE/AL), Fernando Pinto (IPMA), Marco Antônio de Freitas (ESEC Murici), Arthur Andrade (UFAL), Mercival Francisco and Luiza Prado (UFSCar) and Marjory Spina (MZUSP) for support in the field and laboratory. Scott Herke (LSU Genomics Facility), Jaqueline Battilana, and Renata Beco (MZUSP) assisted with the molecular work. JKD received funding from CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for Masters Research and a Collection Study Grant from the AMNH. Molecular work was funded by a grant from the São Paulo Research Foundation – FAPESP to GAB (2012-23852-0). LFS receives grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 457455/2012-8 and 308337/2019-0), and FAPESP (2017/23548-2 and 2018/20249-7). Specimens were collected under permits SISBIO 10013-2 and 21405-10, and under the approval of the ethics' committee (001/2016 and 227/2015). We, the authors, declare that we have no financial interests or

connections, direct or indirect, or other situations that might raise the question of bias in the work reported or the conclusions, implications or opinions stated – including pertinent commercial or other sources of funding for the individual author(s) or for the associated department(s) or organization(s), personal relationships, or direct academic competition.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

File S1. Museum Skins Analyzed. 41.60

41.5 **File S2.** Voice Recordings Analyzed.

File S3. Tissue Samples Analyzed.

Figure S1. Uppertail hue variation in the *Trogon rufus* complex: *Trogon tenellus* (Bocas del Toro, and El Llano, Panama), *Trogon r. rufus* (Potaro, Guyana), *Trogon chrysochloros* (Rio de Janeiro, Brazil), *Trogon cupreicauda* (Bolívar, Colombia), *Trogon r. amazonicus* (Rod. Belém-Brasília, Pará and Rio Madeira, Rondônia), *Trogon r. sulphureus* (Rio Tonantins, southern tributary of Solimões, Amazonas, Brazil) and *Trogon muriciensis* sp. nov. (Murici, Alagoas, Brazil). 41.65

Figure S2. (a) Decrease in interpolated hue (from more coppery to more blue-green) of mantle, rump and chest with increasing elevation in *Trogon chrysochloros*. (b) Specimens ordered according to increasing elevation (bottom to top). 41.70

Figure S3. (a) Undertail barring in the *Trogon rufus* complex: *Trogon chrysochloros* (São Paulo, Brazil), *Trogon tenellus* (Unguia, west of Rio Atrato, Chocó, Colombia), *Trogon cupreicauda* (Rio Jurubidá, Chocó, Colombia), *Trogon r. sulphureus* (Loreto, Peru), *Trogon r. amazonicus* (Rod. Belém-Brasília km 86, Para, Brazil), *Trogon r. rufus* (Amapá, Brazil) and *Trogon muriciensis* sp. nov. (Murici, Alagoas, Brazil). Interpolation by distance of undertail (b) black bar widths, (c) white bar widths, (d) barring density and (e) percentage area black. 41.75

Figure S4. (a) Wing panel barring in the *Trogon rufus* complex: *T. chrysochloros* (São Paulo, Brazil), *T. tenellus* (Costa Rica), *T. cupreicauda* (Santander, Colombia), *T. r. rufus* (French Guiana), *T. r. sulphureus* (Jirau, Rondônia, Brazil), *T. r. amazonicus* (Rod. Belém-Brasília, Pará, Brazil) and *T. muriciensis* sp. nov. (Murici, Alagoas, Brazil). Interpolation by distance of wing panel (b) black bar widths, (c) white bar widths, (d) barring density and (e) percentage area black. 41.80

Figure S5. Unique brown wash to the undertail of female *Trogon cupreicauda* (four right, from left to right: two from Valle Del Cauca, Baudo Mountains (Chocó) and Antioquia, Colombia) compared to the typically pure white background colour of *Trogon tenellus* (four left, from left to right: Rio Indio, Cana, Chiriqui and Rio Indio, Panama). Figure S6. Distribution of complete, inconspicuous or absent breast band in the *Trogon rufus* complex. 41.85

Figure S7. Distribution of tarsus colours in the *Trogon rufus* complex (circle = male, squares = female, large shapes = museum specimens, small shapes = digital photographs). 41.85

Figure S8. Ventral, lateral and dorsal views and close-up of head shortly after death of *Trogon muriciensis* sp. nov. holotype (MZUSP 112768). Voucher specimen photographs taken by Juan Ríos-Orjuela and head by Luis Fábio Silveira. 41.90

Table S1. Loadings of discriminant factors in the linear discriminant function analysis of male extremal morphology of putative taxa in the *Trogon rufus* complex. 41.90

Table S2. Differences in male coloration (*P*-values) between putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. 41.95

Table S3. Differences in barring characters (*P*-values) between adult males of putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. 41.100

Table S4. Differences in morphometric characters (*P*-values) between males of putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. 41.100

Table S5. Loadings of discriminant factors in the linear discriminant function analysis of female extremal morphology of putative taxa in the *Trogon rufus* complex. 41.105

Table S6. Differences in female coloration (*P*-values) between putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. The Mantle z-value was constant across groups. 41.105

Table S7. Differences in barring characters (*P*-values) between adult females of putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. 41.110

Table S8. Differences in morphometric characters (*P*-values) between females of putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus*. 41.111

41.55 41.111

41.56 41.112

Table S9. Loading values of song characters in the linear discriminant analysis of putative taxa in the *Trogon rufus* complex.

Table S10. Loading values of song characters in the linear discriminant analysis of putative taxa in the *Trogon rufus* complex occurring east of the Andes.

Table S11. Differences of song characters (*P*-values) between putative taxa in the *Trogon rufus* complex determined by the Student–Newman–Keuls test. The number of notes, pace, durations and bandwidths were log-transformed. Abbreviations are as follows: AM = *amazonicus*, CH = *chrysochloros*, CU = *cupreicauda*, RU = *rufus*, SU = *sulphureus*, TE = *tenellus* and TN = Alagoas population. The mean frequency range of the intro note or loudsong notes did not differ between taxa.

42.60

42.65

42.70

42.75

42.80

42.85

42.90

42.95

42.100

42.105

42.110

42.111

42.112