



## Evidence of hybrid origin for *Tachyphonus nattereri* Pelzeln, 1870 (Aves: Thraupidae)

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### Abstract

*Tachyphonus nattereri* is one of the three “mystery birds” collected almost 200 years ago by J. Natterer in Brazil whose validity has been disputed in many publications over the last century. Known only from the male holotype and perhaps a female specimen without type status, it is currently treated as either a valid species, a subspecies or a doubtful taxon (an extreme of variation or an aberrant-colored individual). We reviewed the taxonomy of *T. nattereri* based on fieldwork near the type locality and a careful examination of the holotype and related museum specimens. Our extensive fieldwork revealed that no natural population found in the type locality matches the phenotype of *T. nattereri*. We found that the holotype is intermediate in plumage, morphometry and body shape between *Tachyphonus cristatus* and *T. luctuosus*, two sympatric species locally scarce and at their distributional edge around the type locality. We, therefore, suggest that *T. nattereri* is a hybrid. On the other hand, the purported female falls within the variation found in *Tachyphonus c. madeirae*, of which it probably represents an extreme phenotype.

**Key words:** birds, ecotone, hybrid, Neotropics, taxonomy

### Introduction

Johann Natterer was an Austrian naturalist and explorer who collected in Brazil from 1817 to 1835 (Vanzolini 1993), and is renowned worldwide as one of the most prolific and skilled field naturalists who ever travelled in South America (Mearns & Mearns 1998). Natterer collected 12,293 bird specimens, which resulted in the description of more than 200 new taxa of birds (Schiffner 1993). Among the avian taxa described from Natterer’s collection, three are known only from their type specimens, currently housed in the Naturhistorisches Museum Wien (NMW), Vienna, Austria: *Tityra leucura* Pelzeln, 1868; *Sporophila melanops* (Pelzeln, 1870); and *Tachyphonus nattereri* Pelzeln, 1870. These three taxa have been subject to taxonomic debates during the last century and a half, with different authors alternately considering them as valid species, subspecies, hybrids or aberrant specimens (see Mallet-Rodrigues 2008a,b for additional information about these taxa, including color photographs).

The validity of *Tityra leucura* has been advocated in a recent paper based on novel, though scarce, field data (Whittaker 2008), but a thorough analysis is needed (VQP, in prep.). The invalidity of *S. melanops* has been recently argued by VQP and co-authors (Areta *et al.* 2016). In this paper, we review the taxonomy of *Tachyphonus nattereri* based on critical examination of the type specimen and the purported female specimen, as well as on novel fieldwork near the collecting localities.

*Tachyphonus nattereri* is based on a male holotype (NMW 16338) collected on 18 August 1825 in forest on the right bank of the Rio Paraguay, in “Villa Maria” (now the municipality of Cáceres, ~16°04’S, 57°42’W), extreme western state of Mato Grosso, Brazil. Cáceres lies in a biogeographically interesting region because three semi-arid to arid ecoregions come into contact there: the Chiquitano Dry Forests, the Cerrado savannas and the Pantanal wetlands (Olson *et al.* 2001). Some Amazonian influence is also noted in the riparian forests along the Rio Paraguay (Pelzeln 1868–1870; Willis 1976).

A second specimen (NMW 16339) attributed to *T. nattereri* is a female collected on 16 October 1829 in “Salto Girao” [correctly spelled Salto do Jirau, ~09°16’S, 64°40’W], on the Rio Madeira, state of Rondônia, Brazil, in an area covered by Amazonian rain forest. Natterer did not specify on which bank of the Rio Madeira the purported female was collected, which is of significance since the Rio Madeira is one of the most important barriers to bird dispersal in Amazonia (Haffer 1974; Ribas *et al.* 2012).

The female specimen is usually regarded as a syntype, but there are reasons to consider only the male as the holotype of *T. nattereri*. Natterer himself was not convinced that both specimens belonged to the same species, as he named the male in his unpublished catalogue as “*Tanagra cristatella*” and the female as “*Tanagra* sp.” (Pelzeln 1870:214). Pelzeln (1870:329) also expressed his doubts about the identity of the female specimen, citing it after a question mark and stating that “whether the female described here actually belongs to the same species [of *T. nattereri*] remains questionable, but their agreement in dimensions and site of collection favor this assumption” [translated from German]. Such doubtful inclusion therefore excludes the female specimen from the type series (Article 72.4.1, International Code of Zoological Nomenclature; ICZN 1999).

Both male and female specimens were examined by Sclater (1885, 1886), who concluded that *T. nattereri* is “an excellent species” similar in form to *T. delatrii* (Lafresnaye) but distinctive. Hellmayr (1936), one of the few authors to have examined the holotype and the female specimen after Sclater, concluded that *T. nattereri* is “a very distinct species, [which] bears a superficial resemblance to *T. l[uctuosus] nitidissimus* [Salvin], but is larger; the much more extensive vertical patch is uniform orange-rufous, the feathers of the crown being considerably lengthened so as to form a conspicuous crest as in *T. cristatus* [(Linnaeus)]; the rump is suffused with dull orange-rufous; the bill much more slender. The female is closely similar to that of *T. cristatus*, but smaller, more rufescent underneath, and has the rump and upper tail coverts much more rufous”. Several subsequent authors (Ihering & Ihering 1907; Berlepsch 1911; Brabourne & Chubb 1912; Naumburg 1930; Pinto 1944) also considered *T. nattereri* as a valid species, but they presented no additional observations and almost certainly did not examine the holotype and the female specimen.

Zimmer (1945) was the first to consider *nattereri* “at best” a subspecies of *T. cristatus*, based on insufficient available material, but he did not examine the specimens, instead relying on literature descriptions. Zimmer’s (1945) two main arguments were: 1) that the female may not belong to the same taxon as the male, instead probably belonging to *T. c. madeirae* Zimmer, with which its description and structure agreed; and 2) that the morphological differences between *T. nattereri* and *T. cristatus*, namely its smaller size, more orange crest, more restricted uropygial patch, and lack of pale gular area, were not convincing specific characters.

Several later authors nevertheless continued considering *nattereri* as a distinct species (Meyer de Schauensee 1966; Nørgaard-Olesen 1974; Sick 1997; Perlo 2009; Grantsau 2010), while others considered it as a subspecies of *T. cristatus* (Storer 1970; Isler & Isler 1987; Ridgely & Tudor 1989; Sibley & Monroe 1990; Stotz *et al.* 1996; Clements 2007; Hilty 2011; Dickinson & Christidis 2014). The Brazilian Ornithological Records Committee considers it a valid species (Piacentini *et al.* 2015), the International Ornithological Committee considers it a subspecies of *T. cristatus* (Gill & Donsker 2016) and the South American Classification Committee considers it as a dubious taxon (Remsen *et al.* 2016).

## Material and methods

We started our investigation on the taxonomy of *T. nattereri* in the field, trying to rediscover the species on its type locality. LEL joined two expeditions of nine days each to the Cáceres region, one in February 2008 and another in August 2008. During these expeditions, a party of five ornithologists led by J. B. de Pinho conducted a detailed inventory of the region, including observations with binoculars, mist-net captures and collecting of specimens with air rifles and shotguns. LEL visited all main habitat types found in the region, including marshes, savannas, deciduous and semideciduous forests, bamboo thickets and riparian forests. Results of this inventory have been published elsewhere (Lopes *et al.* 2011, 2012, 2016). Several other expeditions visited the region during the last two centuries (e.g. Francis de Castelnau, Gustav Garlepp, M. Moquerys, Roosevelt-Rondon Expedition, Museu de Zoologia da Universidade de São Paulo (MZUSP) Expedition, Colorado Museum Expedition, Marshall Field Expedition, Academy of Natural Sciences of Philadelphia Expedition). These expeditions made Cáceres one of the best-sampled regions in west-central Brazil, but no further specimen attributable to *T. nattereri* has ever been collected (Lopes *et al.* 2016).

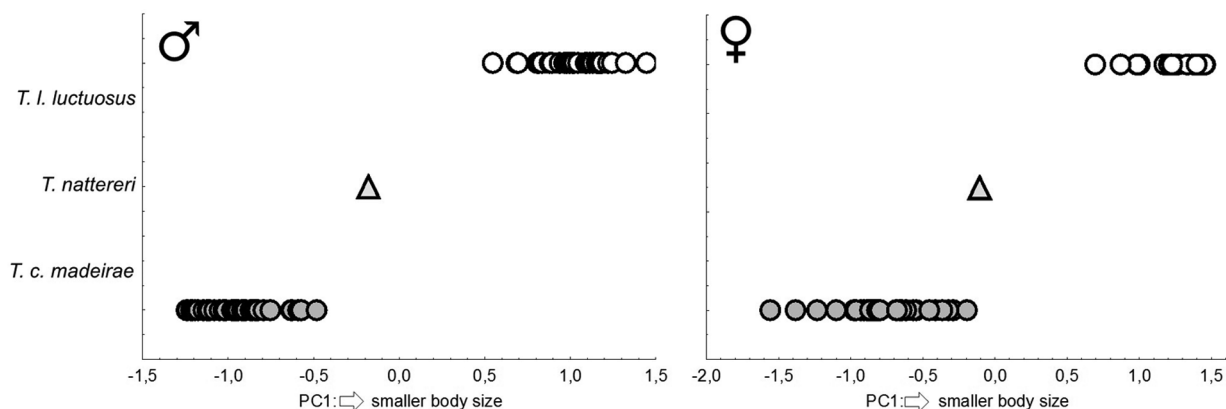
Since 2011, VQP took part on five field expeditions together with MZUSP personnel to Salto do Jirau and surroundings, as well as two field trips to the nearby Rio Ji-Paraná (or Machado), in eastern Rondônia. The fieldwork included observations with binoculars, mist-net captures, voice recording, and collecting of specimens with air rifles and shotguns. Details of these expeditions will be presented elsewhere (L. F. Silveira *et al.*, in prep.).

After our failure to rediscover *T. nattereri* in the field, we decided to seek an answer in museum collections. To explore alternative explanations, such as the type being an extreme individual variant or a hybrid, LEL examined the entire series of *Tachyphonus cristatus* and *T. luctuosus* d'Orbigny & Lafresnaye, housed in the following collections: American Museum of Natural History, New York, USA (AMNH); Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (DZUFMG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Naturhistorisches Museum Wien, Vienna, Austria (NMW), and Universidade Federal de Mato Grosso, Cuiabá, Brazil (UFMT). LEL also briefly inspected the series of *T. cristatus* in the Museu Nacional, Rio de Janeiro, Brazil (MNRJ). VQP independently studied the collections of MZUSP and NMW, and further examined specimens in the Academy of Natural Sciences of Drexel University, Philadelphia, USA (ANSP). Geographical coordinates were obtained directly from the original sources or from ornithological gazetteers (Paynter & Traylor 1991; Vanzolini 1992).

LEL used a dial caliper to measure, to the nearest 0.1 mm, the length of total culmen, closed wing (chord), tail and tarsus (Baldwin *et al.* 1931). We only measured specimens in definitive basic plumage, for a total of 33 males and 31 females of *T. c. madeirae*, and 31 males and 20 females of *T. l. luctuosus*. We conducted a Principal Component Analysis (PCA) (Tabachnick & Fidell 2007) with the aid of the software STATISTICA 8.0 (StatSoft 2007). Plumage comparisons and descriptions were made with the aid of color catalogues (Smithe 1975; Munsell 2000).

## Results

**Body size and shape.** All four body measurements taken were highly correlated in the three taxa studied. Therefore, only one component was sufficient to explain 95% and 88% of the variation observed in males and females, respectively, with all four morphometric variables presenting a factor loading > 0.90. The male of *T. nattereri* falls in an intermediate position between *T. c. madeirae* and *T. l. luctuosus* (Figure 1). On the other hand, the purported female of *T. nattereri* falls in the lower end of the spectrum of body size variation observed in *T. c. madeirae*.



**FIGURE 1.** Graphic representation of PC1 scores of a Principal Component Analysis of morphometric variables measured from specimens of *Tachyphonus l. luctuosus* (white circles) *T. c. madeirae* (gray circles), and the holotype and putative female of *T. nattereri* (triangles). Each symbol represents one specimen.

Even though we have not formally measured the feathers of the crest, it is noticeable that the holotype of *T. nattereri* has shorter crest feathers than *T. c. madeirae*. *Tachyphonus luctuosus* does not show elongated crest feathers (Figure 2).

Bill shape is also distinct between *T. nattereri* and *T. c. madeirae*. The holotype of *T. nattereri* has a somewhat slender bill with attenuated tip of the maxilla compared to the more robust and “toothed” bill of *T. cristatus* (and of the purported female; Figure 3).



**FIGURE 2.** Comparison between the crest of *T. c. madeirae* (left; NMW 69243—Borba, Rio Madeira, Amazonas, Brazil) and the holotype of *T. nattereri* (right, NMW 16338—Villa Maria [= Cáceres], Mato Grosso, Brazil). Note the holotype’s shorter and yellower crest feathers.



**FIGURE 3.** Comparison between the bill shape of the holotype of *Tachyphonus nattereri* (above in both pictures; NMW 16338—Villa Maria [= Cáceres], Mato Grosso, Brazil) and a male *T. c. madeirae* (below, left; NMW 69243—Borba, Rio Madeira, Amazonas, Brazil) and the purported female of *T. nattereri* (below, right; NMW 16339—Salto do Jirau, Rondônia, Brazil).



**FIGURE 4.** From left to right, males of *Tachyphonus luctuosus nitidissimus* (NMW 2832—Bugaba, Chiriquí, Panamá), *Tachyphonus l. luctuosus* (NMW 69215—Villa Maria [= Cáceres], Mato Grosso, Brazil), *Tachyphonus nattereri* (Holotype, NMW 16338—Villa Maria [= Cáceres], Mato Grosso, Brazil), *Tachyphonus cristatus madeirae* (NMW 69243—Borba, Rio Madeira, Amazonas, Brazil), and *Tachyphonus c. brunneus* (NMW 86987—“Bahia”, Brazil).

**Plumage coloration.** The male of *T. nattereri* presents several distinctive characters compared to male *T. c. madeirae* (Figure 4). The main differences observed are summarized in Table 1 and are described below. First, the upperparts and underparts of *T. nattereri* are darker than those of *T. c. madeirae*, approaching *T. l. luctuosus*. The difference is exaggerated by the age of the specimens being compared. This is because body coloration of *T. l. luctuosus*, and probably of *T. nattereri*, does not change noticeably over time, while distinct changes in coloration can occur in old specimens of *T. c. madeirae*, which are not as dark as freshly collected ones, which approach the coloration of *T. l. luctuosus*.

The pale throat patch is lacking in *T. nattereri*, thus agreeing with *T. l. luctuosus*. In contrast, the throat patch was present in all ~350 male specimens of *T. cristatus* examined by us, including all known subspecies, even in first basic (female-like) plumage molting into the definitive plumage. The extent of the throat patch seems to vary geographically, with males from north of the Rio Amazonas (especially *T. c. huarandosae* Chapman) showing a more restricted throat patch than those from south of the river.

The crest is more heavily pigmented in *T. c. madeirae* than in *T. nattereri*. On the other hand, *T. l. luctuosus* (which has no crest) presents a black crown, with some rare specimens (e.g. MZUSP 19392) presenting a few feathers tipped flame scarlet (color 15), forming an indistinct, concealed crown patch. Nevertheless, the subspecies *T. l. nitidissimus* (Caribbean coast from Honduras to Panama) presents a distinct but concealed crown patch, with color extremes ranging from Spectrum Orange (color 17) to Spectrum Yellow (color 55). Thus, the color of the crest in the holotype of *T. nattereri* is intermediate between both species if we consider the taxon *T. l. nitidissimus*, which expresses brightly colored crown feathers.

The holotype of *T. nattereri* further differs from *T. c. madeirae* by the darker and more restricted rump patch, approaching the features exhibited by *T. l. luctuosus*, which has no rump patch. In fact, in the holotype of *T. nattereri* the rump patch is reduced, irregularly shaped and with diluted colors (especially on its borders; Figure 5).



**FIGURE 5.** Comparison of the rump patch between *T. c. madeirae* (left; NMW 69243—Borba, Rio Madeira, Amazonas, Brazil) and the holotype of *T. nattereri* (right, NMW 16338—Villa Maria [= Cáceres], Mato Grosso, Brazil).



**FIGURE 6.** Comparison between the female of *Tachyphonus nattereri* (in the center, NMW 16339—Salto do Jirau, Rondônia, Brazil) and two females of *T. cristatus madeirae* (left, NMW 69245—Borba, Rio Madeira, Amazonas, Brazil; right NMW 69247—Engenho do Gama, Mato Grosso, Brazil).

Lastly, the holotype of *T. nattereri* shows a large white patch on the wing coverts, extending to the greater coverts and thus differing markedly from *T. c. madeirae* and again approaching *T. l. luctuosus*. It is slightly more restricted in *T. nattereri* than in *T. l. luctuosus*, since it shows black tips on the secondary coverts. Therefore, we consider the white patch in *T. nattereri* as intermediate between *T. c. madeirae* and *T. l. luctuosus*.

The purported female of *T. nattereri* differs from the few females of *T. c. madeirae* collected by Natterer and housed in the NMW in being somewhat more rufescent (Figure 6). Nevertheless, analysis of a large series of females housed in AMNH and MZUSP revealed large chromatic variation in this subspecies, with some approaching the color of the purported female of *T. nattereri* (Figure 7).



**FIGURE 7.** Chromatic variation exhibited by females of *Tachyphonus cristatus madeirae* collected in the state of Pará, Brazil. From left to right, AMNH 430116—Tapará, Rio Xingu; AMNH 288031—Caxiricatuba, Rio Tapajós, and AMNH 288025—Aramaná, Rio Tapajós.

A brief description of the purported female is presented here: forehead dark yellowish brown (10YR 4/4); crown and crest dark brown (7.5YR 3/4); nape, back and scapulars dark brown (10YR 3/3); rump strong brown (7.5YR 5/8); upper tail coverts strong brown (7.5YR 4/6); rectrices dark brown (10YR 3/3), with the outer vanes edged yellowish red (5YR 4/6); chin, throat, breast, belly, underwing coverts and axillaries approaching reddish yellow (~7.5YR 6/8); wing coverts approaching dark brown (~7.5YR 3/3); tertials dark brown (10YR 3/3);



secondaries very dark grayish brown (10YR3/2), edged yellowish red (5YR 4/6) on the outer vane; primaries very dark grayish brown (10YR 3/2), edged strong brown (7.5YR 4/6) on the outer vanes, with tips very dark brown (10YR 2/2).

**TABLE 1.** Comparison between plumage coloration of the male holotype of *Tachyphonus nattereri* and definitively plumaged males of *T. cristatus madeirae* and *T. l. luctuosus*. Given that the holotype is almost 200 years old, and, consequently, has probably suffered changes in coloration due to fading and/or foxing, we compare it with specimens of approximately the same age. Color names and notation follow Smithe (1975) and Munsell (2000) and are for comparative purposes only, not intending to represent exact coloration. Color of freshly collected specimens, especially of *T. c. madeirae*, differs considerably from what is presented here.

Topographic region	<i>T. c. madeirae</i>	<i>T. nattereri</i>	<i>T. l. luctuosus</i>
Upperparts	Very dark brown (10YR 2/2)	Jet black (color 89)	Jet black (color 89)
Underparts	Very dark brown (7.5YR 2.5/2)	Jet black (color 89)	Jet black (color 89)
Throat patch	Yellow (10YR 8/8)	Jet black (color 89)	Jet black (color 89)
Crest	Flame scarlet (color 15), with the anterior portion narrowly tinged yellow (10YR 8/6)	Yellowish red (5YR 5/8)	Jet black (color 89)
Rump	Yellow (10YR 8/8)	Black, with tips washed yellowish red (5YR 5/6)	Jet black (color 89)
Marginal coverts	White, with black feathers near wrist	White	White
Lesser secondary coverts	Black	White	White
Median secondary coverts	Black	White	White
Greater secondary coverts	Black	White, tipped black, especially on outer vane	White

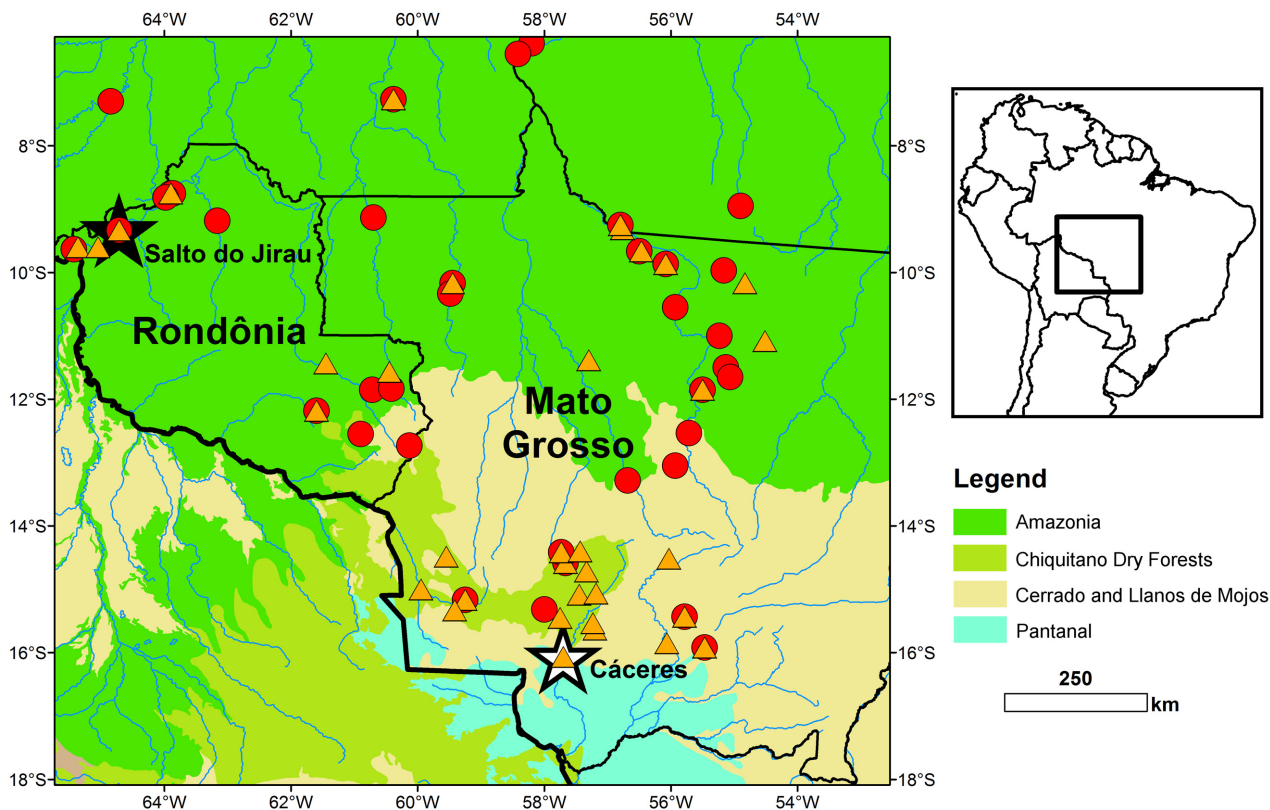
## Discussion

Despite much effort by us as well as other ornithologists (Cáceres and Salto do Jirau are two of the best-sampled sites for birds in the Pantanal and in the Amazonia, respectively), no natural population matching the phenotype of the holotype of *T. nattereri* has ever been found either around the type locality or anywhere else. Given that the habitat at both these sites is relatively well-preserved almost two centuries after Natterer's visit, the possibility that *T. nattereri* is an already extinct species that inhabited a specific habitat type in a small distribution range in highly improbable. Furthermore, all known members of *Tachyphonus* are common and tolerant of habitat disturbance (Stotz *et al.* 1996). Therefore, the lack of modern records casts strong doubts on the validity of the taxon. This conclusion matches the fact that the holotype of *T. nattereri* exhibits many morphometric and chromatic characters that are intermediate between *T. c. madeirae* and *T. l. luctuosus*, strongly suggesting that it represents a hybrid between these species. The irregular rump patch may also be indicative of hybridization, given that such irregular coloring of feathers is commonly seen in other hybrid birds (pers. obs.; see e.g. hybrid manakins; Vasconcelos *et al.* 2005; Guaraldo *et al.* 2008). Although *T. cristatus* and *T. luctuosus* are not sister species, they are closely related, with *T. luctuosus* sister to *T. rufiventer*, and *T. cristatus* sister to both of these (Burns *et al.* 2014). Even though frequency of hybridization within sister species is higher than within non-sister species (Gholamhosseini *et al.* 2013), non-sister hybridization is not rare in tanagers (Olson & Violani 1995; McCarthy 2006; Lopes & Gonzaga 2013).

The hypothesis that the purported female of *T. nattereri* might also represent a hybrid is improbable and unsupported by the phenotypic characters observed. This is because females of *T. l. luctuosus* differ greatly from those of *T. c. madeirae*, being much smaller and presenting bright olive-green upperparts, yellow underparts, gray head and greyish-white throat (Hilty 2011). Hybridization with another species of tanager found within its range is unlikely. As discussed above, the purported female of *T. nattereri* falls within the lower extreme of variation in size of *T. c. madeirae*, and its color also fits within the extremes of variation observed in this taxon. The nature of such variation (e.g. due to age, feather wear, individual and/or geography) is still unclear.

*Tachyphonus l. luctuosus* and *T. c. madeirae* are largely sympatric (Figure 8). These Amazonian taxa only reach the borders of the Cerrado (Ridgely & Tudor 1989; Hilty 2011), where they inhabit forests with some Amazonian influence (Naumburg 1930; Willis 1976; Willis & Oniki 1990). *Tachyphonus l. luctuosus* is rare and local in Cáceres (Pelzeln 1868–1870, pers. obs.). There are no records of *T. c. madeirae* from the Cáceres region (Lopes *et al.* 2016), but there are scattered nearby records, so it might occur at least as a vagrant in the region.

The fact that the two species of *Tachyphonus* studied here occur in small numbers in southwestern Mato Grosso, at the extremes of their geographic ranges, and possibly in suboptimal habitats, makes hybridization more likely due to the difficulty of finding conspecific mates, as suggested for some Pipridae and *Sporophila* seedeaters (Sick 1979, 1997; see also Mayr & Diamond 2001).



**FIGURE 8.** Range of *Tachyphonus cristatus* (circles) and *T. luctuosus* (triangles) in southwestern Brazil. Type locality of *T. nattereri* (Cáceres) is indicated by the white star. The place of collection of the purported female of *T. nattereri* (Salto do Jirau) is indicated by the black star. Limits of the ecoregions follow Olson *et al.* (2001). Occurrences of the taxa studied are based on the specimens examined, records in the Wikiaves Portal ([www.wikiaves.com.br](http://www.wikiaves.com.br)) and key references (Naumburg 1930; Willis 1976; Lopes *et al.* 2009).

Given the above, we propose that *T. nattereri* is an invalid taxon, described from a hybrid male, the product of a pairing between *T. c. madeirae* and *T. l. luctuosus*. We also propose that the purported female, which has no type status, is an extreme phenotypic variant of *T. c. madeirae*. A hint of this conclusion exists in Hellmayr (1936), who mentioned the similarity between the males of *T. nattereri* and *T. l. nitidissimus*, and in Zimmer (1945), who observed high morphological variation in females of *T. cristatus madeirae*. Variation observed between subspecies of these two species of *Tachyphonus* also suggests that more than two biological species are involved, and Burns & Racicot (2009) found higher levels of intraspecific sequence divergence within each of these two species than that found within many recognized bird species.

The hypothesis of a hybrid origin for *T. nattereri* has never been formally discussed before and should be tested with a DNA-based study, including mitochondrial and nuclear genes. Beyond being a taxonomic explanation, it can foster future research on the expression of phenotypic traits. For example, the apparent intermediate state of the color of the crest feathers in *T. nattereri* would hold true only if the black-crowned *T. l. luctuosus* carry inactive genes for a yellow crown patch, as seen in its sister taxon *T. l. nitidissimus*. The speculative nature of this hypothesis can be formally tested in future molecular studies.

No author since Hellmayr (1936) had examined the holotype and the purported female. Fortunately, the holotype and the purported female specimen of *T. nattereri* are still extant and housed in one of the most renowned and accessible museums in Europe (Roselaar 2003). Examination of these specimens could have precluded decades of taxonomic uncertainty.

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