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ARTICLE

Geographic variation in plumage coloration of Turquoise Tanager *Tangara mexicana* (Linnaeus, 1766)

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ABSTRACT: The Turquoise Tanager *Tangara mexicana* is largely distributed in northern South America, and has been considered a polytypic species comprising four or five subspecies. Our study on plumage coloration of 175 specimens, from localities covering the entire species' range, revealed the existence of two variable characters: color of underparts and color of lesser upper-wing coverts. Seven morphotypes were found that combine the different states presented by these two characters. Two morphotypes were very distinct, representing two of the most easily diagnosable subspecies (*T. m. mexicana*, having yellowish white underparts and a contrasting turquoise green humeral patch; and *T. m. boliviana*, having bright yellow underparts and the blue of lesser upper-wing coverts similar to that of the sides of head, throat, breast and rump). The other morphotypes (including those representing subspecies *T. m. media*, *T. m. vieilloti* and *T. m. lateralis*) are shared by birds with character states that are intermediate between those found in *T. m. mexicana* and *T. m. boliviana*, thus representing a polymorphic population ranging widely across central Amazonia, from northern Venezuela and Trinidad to the south of the lower Amazon. This large area may be considered as a hybrid zone of considerable phenotypic instability, more evident especially in the region between the lower Rio Madeira and east of the Tocantins in the Belém area. Based on the General Lineage Species Concept two species could be recognized based on plumage: *T. mexicana*, restricted to the Guyana center of endemism, and *T. boliviana*, which is widely distributed in western Amazonia and the eastern foothills of the Andes, an area corresponding to the centers of endemism Napo and Inambari. The taxonomic validity of *T. lateralis* is once more challenged.

KEY-WORDS: Amazonia, biodiversity, centers of endemism, hybrid zones, subspecies, taxonomy.

INTRODUCTION

Comprising about fifty species, *Tangara* is one of the richest genera of birds and one of the most representative of Neotropical birds (Peters 1970, Sibley 1996, Clements 2007, SACC 2015, Hilty 2011, Barker *et al.* 2013). Sedano & Burns (2010) produced a large phylogeny of tanagers based on mitochondrial genes, which lumps many morphologically distinctive groups into a few genera. Among the surprising results of this study is that *Thraupis* was found to be embedded in *Tangara.* The Turquoise Tanager is found in forest borders, varzea, second growth, plantations and gardens from southeastern Colombia and Ecuador to Guyanas, northern Brazil, Peru and northern Bolivia (Isler & Isler 1987, Ridgely & Tudor 1989). Five subspecies of the Turquoise Tanager *Tangara mexicana* (Linnaeus, 1766) have been proposed (Hellmayr 1936, Isler & Isler 1987, Hilty 2011). After the larger and paler White-bellied Tanager *Tangara brasiliensis* (Linnaeus, 1766) from southeastern Brazil had been treated as a separate species by Hellmayr (1936), it was considered a subspecies of *T. mexicana* (Zimmer 1943, Pinto 1944), but now it has been accepted as a valid and independent species again (Piacentini *et al.* 2015). *Tangara brasiliensis* shows a high level of genetic divergence (Burns & Naoki 2004), allopatric distribution (with no apparent gene flow) and consistent phenotypic differences (Isler & Isler 1987, Ridgely & Tudor 1989, Sick 1997), making it fully diagnosable from *T. mexicana*. However, *T. brasiliensis* is still considered a subspecies of *T. mexicana* by some authors (Clements 2007, Hilty 2011, SACC 2015). According to Hellmayr (1936), *T. m. mexicana* is known from the north of the lower Amazon (Guyanas and Brazil); *T. m. boliviana* (Bonaparte, 1851) is widely distributed in southeastern Colombia and Ecuador, Peru, northern Bolivia and Brazil from the Solimões to the lower Madeira; *T. m. vieilloti* (Sclater, 1857) is endemic to Trinidad, and *T. m. media* (Berlepsch & Hartert, 1902) is found in Venezuela and extreme northern Brazil. *Tangara m. lateralis* Todd, 1922, from southern Amazon (Todd 1922), was considered indistinct from *T. m. boliviana* by Hellmayr (1936) and treated as a hybrid between *T. m. mexicana* and *T. m.*

boliviana by Isler & Isler (1987). However, Griscom & Greenway (1941), Pinto (1944) and Gyldenstolpe (1945) recognized the validity of *T. m. lateralis*.

According to several authors (Hellmayr 1936, Zimmer 1943, Gyldenstolpe 1945) subspecies of *T. mexicana* are distinguished by the tone of blue on the sides of head, throat, breast and rump, and by the color of underparts (belly, thighs and under-tail coverts) and lesser upper-wing coverts. While the underparts are yellowish white in the nominate form (*T. m. mexicana*) and bright yellow in *T. m. boliviana*, the other three nominal taxa *T. m. vieilloti*, *T. m. media* and *T. m. lateralis* are transitional forms showing intermediate shades of yellow on the underparts between those found in *T. m. mexicana* and *T. m. boliviana*. Birds from Trinidad (*T. m. vieilloti*) are usually distinguished from those in Venezuela (*T. m. media*) by the darker blue plumage and brighter yellow underparts, although some birds from Venezuela were very similar to *T. m. vieilloti* specimens (Hellmayr 1936). *Tangara m. boliviana* is diagnosed primarily by the bright yellow underparts and the blue of lesser upper-wing coverts similar to that of the sides of head, throat, breast and rump. While this phenotype predominates in western Amazonia, several specimens (especially towards the lower Amazon) have paler blue lesser upper-wing coverts (Hellmayr 1936, Zimmer 1943).

Understanding the geographic differentiation of plumage in *T. mexicana* has been considered a challenge by some authors (Hellmayr 1936, Zimmer 1943, Hilty 2011). Therefore, we present here a review of the complex pattern of geographical differentiation in plumage coloration of the Turquoise Tanager throughout its entire distribution and discuss taxonomic implications and interpretations that emerged from the obtained data.

METHODS

We examined 101 specimens of *T. mexicana* housed at the Museu Nacional do Rio de Janeiro (MNRJ), Museu Paraense Emílio Goeldi (MPEG), and Museu de Zoologia da Universidade de São Paulo (MZUSP) (Appendix I). Additionally, we examined photographs of 74 specimens pertaining to the ornithological collections of the American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Carnegie Museum of Natural History (CMNH), Colección Ornitológica Phelps (COP), Field Museum of Natural History (FMNH), Muséum National d'Histoire Naturelle (MNHN), and Yale Peabody Museum (YPM) (Appendix II). Photographs examined include those of the type specimens of *Tangara mexicana boliviana* [formerly *Callospiza boliviana*] (MNHN 7897), *Tangara mexicana media* [formerly *Calliste mexicana media*] (AMNH 513316) and *Tangara boliviana lateralis* (CMNH 78031). To obtain comparable color measurements, the photos were taken in a standardized fashion with the specimens photographed with the use of flashes in similar conditions. The color descriptions in the photos were taken by looking them in the same computer screen. Only adult birds were included in this study. Both sexes were included in the analysis because sexual dimorphism in plumage is not recognized in *Tangara mexicana* (Isler & Isler 1987, Hilty 2011).

We based our analyses on the following plumage color characters traditionally employed to diagnose taxa in *T. mexicana*: 1) the tone of blue on the sides of head, throat, breast and rump; 2) the color of underparts; and 3) the color of lesser upper-wing coverts. We used Smithe (1975, 1981) to determine the colors corresponding to different character states. These were referred to as italicized names (with corresponding numbers in the first citation). The color description of each specimen was made with no regard to its possible subspecies allocation or collection locality. Geographic coordinates of collecting localities of the specimens analyzed were obtained from Paynter (1982), Paynter Jr. & Traylor Jr. (1991) and Vanzolini (1992).

Plumage color character states obtained for each specimen were mapped separately to assess the degree and kind of geografic variation associated with each character. Subsequently, all character states variations were mapped together to assess overall trends of geographic variation. We gave special attention to the identification of localities that had one or more specimens with intermediate plumage characters because they could indicate the existence of hybrid zones. Localities with evidence of intermediate character states were classified as representing hybrid zones.

RESULTS

Variation of character states

We found no significant individual variation in the color of head, throat, breast and rump, which was *Ultramarine Blue* (Color 170A) in all specimens analyzed (including those examined through photographs).

Four states were recognized for the color of underparts, namely *Pale Horn* (Color 92), *Cream* (Color 54), *Straw Yellow* (Color 56) and *Spectrum Yellow* (Color 55) (Figure 1), while the color of wing coverts presented three states, namely *Ultramarine Blue* (Color 170A), *Sky Blue* (Color 168C) and *Turquoise Green* (Color 64) (Figure 2). *Ultramarine Blue* wing coverts always occurred together with *Spectrum Yellow* or *Straw Yellow* underparts, while *Turquoise Green* wing coverts were accompanied by *Pale Horn*, *Cream* and *Straw Yellow* underparts.

FIGURE 1. Color character states of underparts in *Tangara mexicana*. Colors from left to right: *Pale Horn* (MPEG 22995), *Cream* (MPEG 21553), *Straw Yellow* (MPEG 43353), and *Spectrum Yellow* (MPEG 23003).

FIGURE 2. Color character states of lesser upper-wing coverts in *Tangara mexicana*. From left to right: *Ultramarine Blue* (AMNH 513329), *Sky Blue* (AMNH 278331) and *Turquoise-Green* (AMNH 513315).

Geographic distribution of character states

Specimens with *Pale Horn* underparts were recorded exclusively from the north of the lower Amazon (Guyanas and adjacent parts of Brazil). Specimens with *Cream* underparts were recorded from the upper Rio Branco to the Rio Orinoco in Venezuela. Several birds with *Straw Yellow* underparts were from the southern bank of middle and lower Amazon (lower Rio Madeira, Rio Tapajós, Rio Xingu and Rio Tocantins) but also from the upper Rio Negro, northern Guyana and all specimens from Trinidad. Specimens with *Spectrum Yellow* underparts were widely distributed across western Amazonian Brazil, southern Colombia, eastern Peru and northern Bolivia (Figure 3).

Ultramarine Blue wing coverts were predominant in the upper Amazon, with some specimens occurring on the southern bank of middle and lower Amazon. Birds with *Turquoise Green* humeral patches were restricted to the north of the lower Amazon, Guyanas, upper Rio Branco, Venezuela and Trinidad. Specimens with *Sky Blue* humeral patches were found mainly in the southern bank of the lower and middle Amazon, but also in the upper Rio Negro (Figure 4).

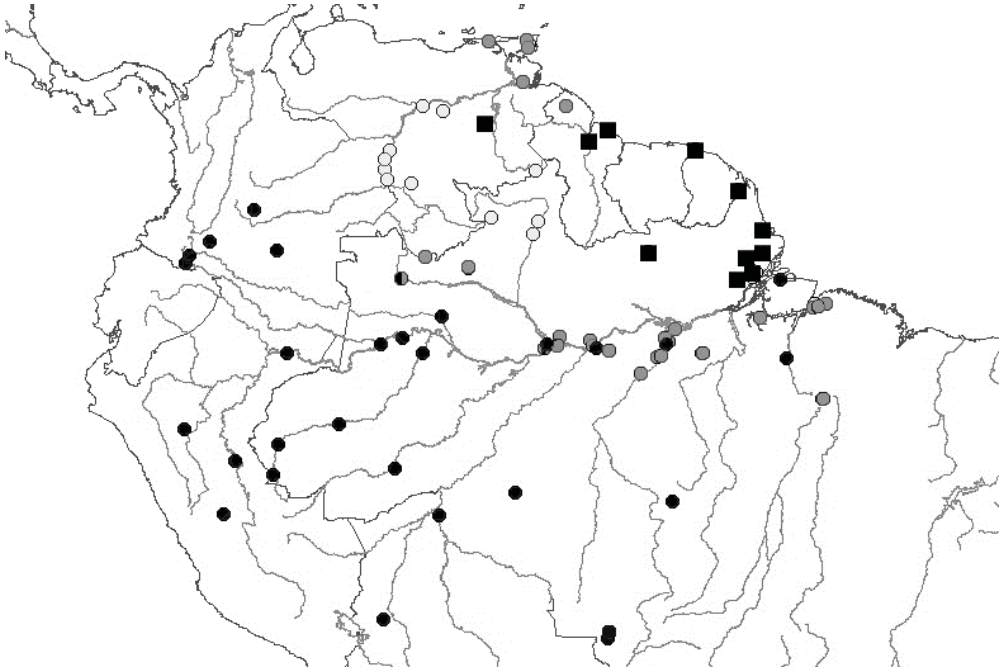

FIGURE 3. Geographic distribution of underparts color character states in *Tangara mexicana* (black circles – *Spectrum Yellow*, gray circles – *Straw Yellow*, light gray circles – *Cream*, black squares – *Pale Horn*).

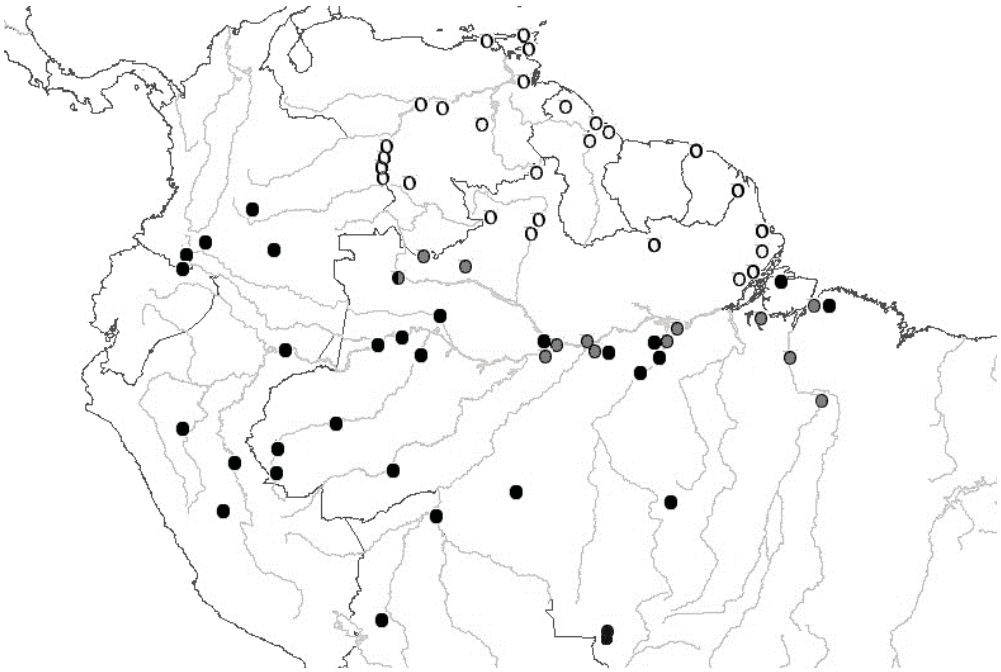

FIGURE 4. Geographic distribution of lesser upper-wing coverts color character states in *Tangara mexicana* (black circles – *Ultramarine Blue*, gray circles – *Sky Blue*, white circles – *Turquoise-Green*).

Morphotypes and their geographic distribution

We found seven morphotypes that combine the different character states (Figure 5). Five of these morphotypes correspond to described taxa that have been considered subspecies of *T. mexicana*.

Morphotype 1 is characterized by having the head, throat, breast, rump and lesser upper-wing coverts *Ultramarine Blue* and *Spectrum Yellow* underparts (Figure 5). Specimens of this morphotype were found from the eastern foothills of the Andes (Colombia, Peru and Bolivia), to lower Rio Negro and southern bank of the lower Amazon (from the middle Rio Tocantins to the Marajó island). This morphotype was very poorly represented in the lower Amazon (Figure 6). It includes the holotype of *Callospiza boliviana*.

Morphotype 2 differs from morphotype 1 only by the underparts, which are *Straw Yellow* (Figure 5). It was found on the southern bank of the middle and lower Amazon, between the right bank of the lower Rio Madeira and the region of Belém (Figure 6). It includes the holotype of *Tangara boliviana lateralis*.

Morphotype 3 is similar to morphotype 1 with respect to the color of underparts, but it has *Sky Blue* humeral patch (Figure 5). The distribution of morphotype 3 coincides with that of morphotype 2, ranging from the left bank of the Rio Madeira to the lower Rio Tocantins (Figure 6).

Morphotype 4 is characterized by the combination of a *Sky Blue* humeral patch and *Straw Yellow* underparts (Figure 5). It occurs from Belém to Manaus, and in upper Rio Negro (Figure 6).

Morphotype 5 is characterized by having *Straw Yellow* underparts and *Turquoise Green* humeral patches (Figure 5). It was found in lower Rio Orinoco (Venezuela), northern Guyana and Trinidad (Figure 6). The holotype of *Calliste vieilloti*, from Trinidad, was not examined, but supposedly would belong to this morphotype.

Morphotype 6 has *Cream* underparts and *Turquoise Green* humeral patches (Figure 5). It is widely distributed in central Venezuela and upper Rio Branco in Brazil (Figure 6). It includes the holotype of *Calliste mexicana media*.

Morphotype 7 differs from all other morphotypes by having *Pale Horn* underparts and *Turquoise Green* humeral patches (Figure 5). Specimens of this morphotype were from the Guyanas and north of the lower Amazon (Figure 6). It corresponds to the nominate *T. m. mexicana*.

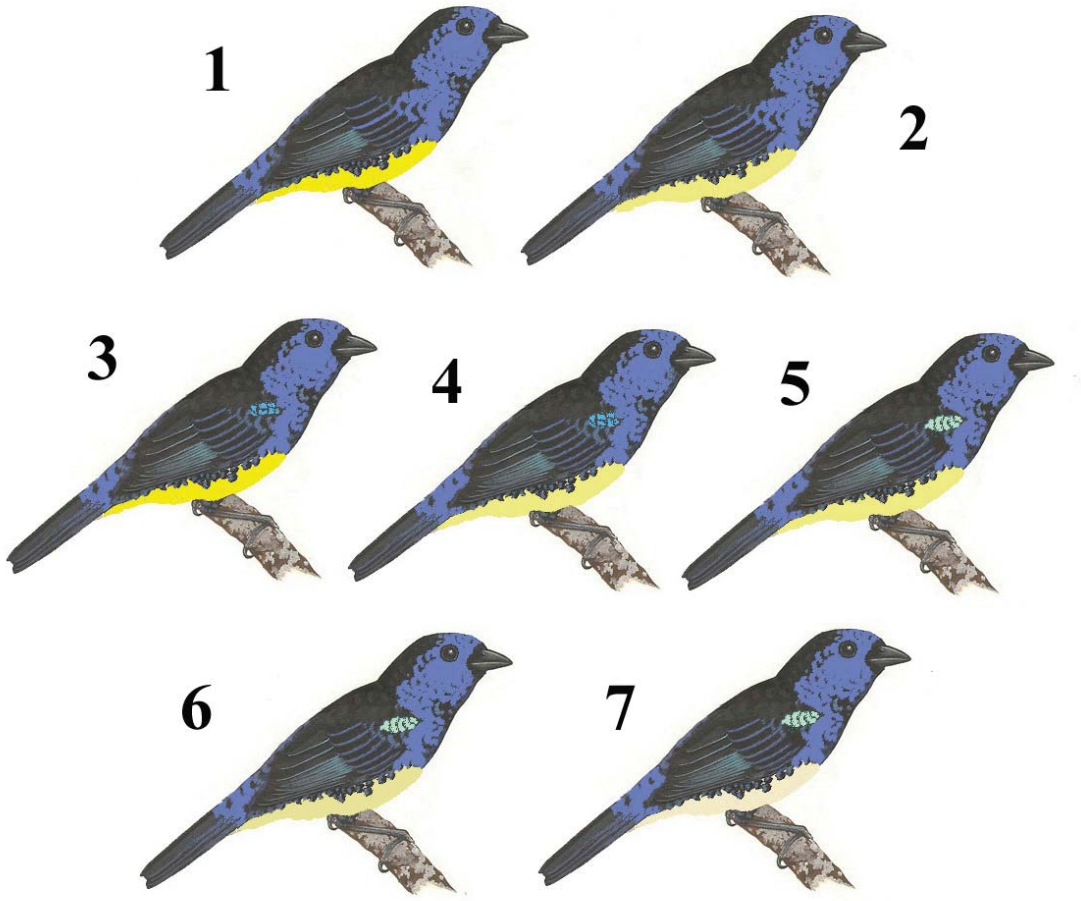

FIGURE 5. Morphotypes of *Tangara mexicana* based on the combined coloration of underparts and lesser upper-wing coverts (drawing: Raphael Dutra). See text for details.

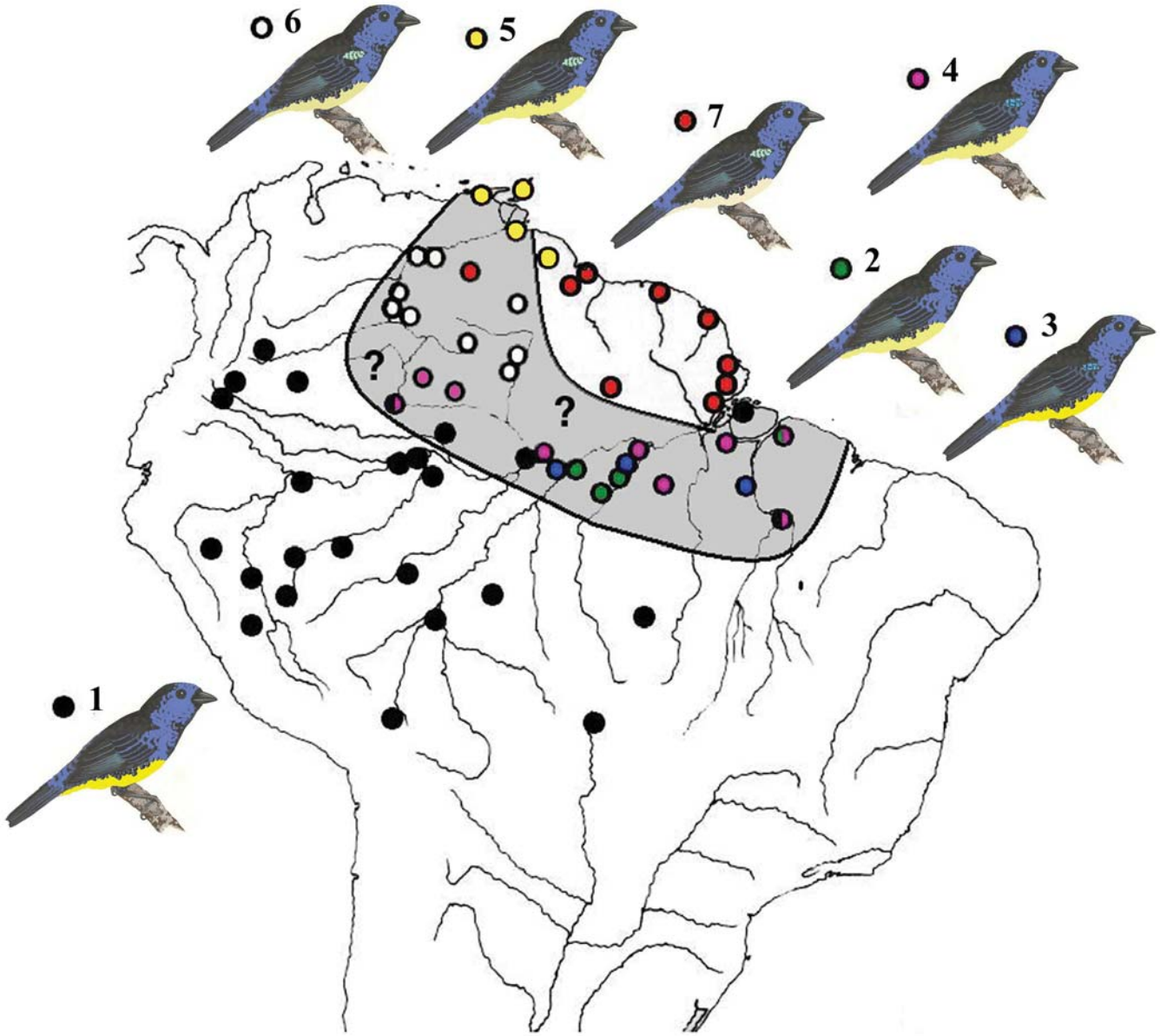

FIGURE 6. Geographic distribution of morphotypes of *Tangara mexicana* recognized in this study, showing a possible hybrid zone highlighted in gray.

DISCUSSION

Our analyses revealed the existence of at least two main areas of plumage color character state stability in the Turquoise Tanager (corresponding to morphotypes 1 and 7), separated by a smaller geographic area where intermediate phenotypes are present, sometimes even at the same locality (corresponding to morphotypes 2-6) (Figures 5 and 6). Two alternative interpretations of this overall pattern are: 1) morphotypes 1 and 7 represent evolutionary independent lineages / taxa that intergrade along a wide northwestern-southeastern trend hybrid zone across Central Amazonia; or 2) morphotypes 1 and 7 are extremes of a cline, with a corresponding wide intergradation zone in Central Amazonia. Below, we discuss these two alternatives with respect to the plumage color data but stress that distinguishing between them is difficult, and could be more easily accomplished by a phylogeographic study. Therefore, our data can be viewed as evidence supporting alternative scenarios of Turquoise Tanager diversification to be tested by future genetic studies.

Based on the General Lineage Species Concept (de Queiroz 1998), in which the only necessary property of a species is existence as a separately evolving metapopulation lineage (de Queiroz 2005), we propose that morphotypes 1 and 2 of *T. mexicana* found in this study would deserve the status of separate species. These two morphotypes have been traditionally recognized as the most distinct subspecies of the Turquoise Tanager (Zimmer 1943).

One of these (*T. m. mexicana*) occurs on the Guiana shield, being diagnosed by having *Pale Horn* underparts and a contrasting *Turquoise-Green* humeral patch, while the other (*T. m. boliviana*) is found from the base of the

Andes (below 500 m, following Hilty & Brown 1986) to the southern bank of the middle and lower Amazon, being diagnosed by having *Spectrum Yellow* underparts and the wing coverts indistinguishable from the blue of the rest of the plumage.

According to Hellmayr (1936) and Zimmer (1943), however, the challenge for understanding the complex pattern of geographical differentiation in *T. mexicana* is in the regions of the middle Amazon and southern bank of the lower Amazon. In this area we have found a significant individual variation in the color of underparts, with birds at times showing them *Spectrum Yellow* and *Straw Yellow* in the same locality. In the northern Amazon (upper Negro, Branco and Orinoco rivers) and Trinidad, although individual variation in the tone of yellow is less evident, some specimens are clearly distinct from others with respect to this character, as stated by Hellmayr (1936). The apparent phenotypic stability of the birds from Trinidad could result from the founder effect due to ca. 11,000 years of isolation from the continent (Snow 1985). However, some birds from the coast of Venezuela are barely distinct from those of Trinidad.

The color of lesser upper-wing coverts is another important variable character among populations of *T. mexicana*. While specimens from the Guyanas and north of the lower Amazon, upper Rio Branco, Venezuela and Trinidad have the wing coverts forming a bright *Turquoise-Green* humeral patch, birds from the southern bank of the middle and lower Amazon and upper Rio Negro have a *Sky Blue* or *Ultramarine Blue* humeral patch. All specimens from western Amazonia have dark blue (*Ultramarine Blue*) wing coverts. There is a trend to the occurrence of a lighter blue humeral patch in birds of the lower Amazon, as stated by Hellmayr (1936) and Zimmer (1943). However, birds with dark blue wing coverts also occur in the southern bank of the lower Amazon, and are indistinguishable from specimens from the upper Amazon, which reveals the instability of this character in the lower Amazon.

Our analysis of geographical variation in plumage characters, thus, revealed the existence of at least two major and up to four nuclear areas (with phenotypic stability) in *T. mexicana*. One of these coincides with the Guyana Center of Endemism (Cracraft 1985), including birds corresponding to morphotype 7 or *T. m. mexicana*. Another nuclear area is located in western Amazonia, encompassing the Napo and Inambari centers of endemism (Cracraft 1985), and including birds corresponding to morphotype 1 or *T. m. boliviana*. According to Zimmer (1943), these two forms have evolved separately when "an arm of the sea occupied the Amazon valley", *T. m. mexicana* in the Guiana shield and *T. m. boliviana* in western Amazonia. Two additional smaller areas of apparent phenotypic stability occur between those two, one in central Venezuela and upper Rio Branco in Brazil, including birds corresponding to morphotype 6 or *T. m. media*, with *Cream* underparts and a *Turquoise-Green* humeral patch, and the other in Trinidad and northern Venezuela, including birds corresponding to morphotype 5 or *T. m. vieilloti*, with *Straw Yellow* underparts and a *Turquoise-Green* humeral patch. However, the diagnose of these two morphotypes may be subtle in practice, so that both could alternatively be regarded as part of a larger polymorphic population ranging widely across central Amazonia, from northern Venezuela and Trinidad to the south of the lower Amazon (lower Rio Madeira to Belém). This includes forms described as *T. m. vieilloti*, *T. m. media* and *T. m. lateralis*, consisting of birds with character states that are intermediate between those found in *T. m. mexicana* and *T. m. boliviana*. As pointed out by Price (2008), subspecies rank has been often mistakenly assigned considering populations with different levels of character intergradation between distinct species. However, more studies on birds of Venezuela and Trinidad are needed to improve understanding of the taxonomic status of *T.m. media* and *T.m. vieilloti*.

The existence of a rather large area of polymorphism linking areas of phenotypic stability seems to preclude interpretation of morphotypes 1 and 7 as extremes of a clinal pattern of variation in the Turquoise Tanager. This whole range occupied by intermediate birds could be better considered as a hybrid zone because of the considerable phenotypic instability detected (distinct phenotypes coexisting in the same regions), which is more evident especially in the region between the lower Madeira River east across the Tocantins River in the Belém area. A relatively narrow hybrid zone along the Amazon valley has also been found between two purported phylogenetic species (*Icterus chrysocephalus* and *Icterus cayanensis*)(D'Horta *et al.* 2008). As advocated by Hellmayr (1936), who nevertheless recognized the taxonomic validity of *T. m. media* and *T. m. vieilloti*, this phenotypic instability does not allow a diagnosis of *T. m. lateralis*, described by Todd (1922) from the region of the Rio Tapajos and recognized by Gyldenstolpe (1945). Zimmer (1943), in turn, also preferred to consider populations from the lower Amazon as an unstable and intermediate *T. m. mexicana*/*T. m. boliviana* population, in which the recognition of a taxon is rather questionable.

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APPENDIX I.

Material examined (Specimens from each locality in parenthesis).

TRINIDAD. Trinidad (MZUSP 3706); VENEZUELA. *Monagas:* Maturin (MZUSP 2476); COLÔMBIA. Bogotá (MNRJ 6808); BRAZIL. ***Roraima:*** Alto Mucajaí (MPEG 21553; MZUSP 56239); Caracaraí (MPEG 56485); ***Amapá:*** Serra do Navio (MNRJ 29248); Fazenda Prosperidade, Rio Maracá, Mazagão (MPEG 22990; MPEG 22995); Rio Vila Nova, Macapá (MPEG 22991); Estrada do Curiaú km 01, Ilha Curuçá, Macapá (MPEG 28873); Igarapé Ariramba, afluente direito do Rio Tartarugal, Acampamento 4, Amapá (MPEG 28874); Rio Maruanum, Macapá (MPEG 28388); Fazenda Nova Califórnia, Rio Araguari (MPEG 22994); Fazenda Itauqueira, Tartarugalzinho (MPEG 53651; MPEG 53652); Oiapoque (MPEG 22996); ***Acre:*** Cruzeiro do Sul, Rio Juruá (MPEG 22997; MPEG 22998); Vila Taumaturgo, Seringal Oriente, Rio Juruá (MPEG 23000; MPEG 23001); ***Amazonas:*** São Gabriel da Cachoeira (MZUSP 16979); Acajutuba, Rio Negro (MPEG 12106); Maraã, margem esquerda do Rio Japurá, Maguari (MPEG 42934; MPEG 43352; MPEG 43353); Caitaú, margem direita do Rio Solimões, Uará (MPEG 50197; MPEG 50198); Santa Cruz, Rio Eirú, Juruá (MZUSP 18498; MZUSP 18504); Santo Antônio do Içá (MZUSP 69910); Bom Lugar, Rio Purus (MPEG 3499); Rio Jutaí (MZUSP 69909); Manacapuru (MNRJ 6816; MZUSP 16977; MZUSP 16978); Reserva Ducke, Manaus (MPEG 30079; MPEG 30370; MPEG 30371); Itacoatiara (MNRJ 32790; MNRJ 32791; MZUSP 17798; MZUSP 18499; MZUSP 18500; MZUSP 18501; MZUSP 18502; MZUSP 18505; MZUSP 18506); Igarapé Anibá (MZUSP 18496; MZUSP 18508); Rio Maraú (MZUSP 62116); Lago Baptista (MPEG 18493; MZUSP 17797; MZUSP 18494; MZUSP 18495; MZUSP 18497); ***Pará:*** Rio Paru (MNRJ 27369; MNRJ 27370; MNRJ 27371); Ilha de Marajó, cerca de 4km ao sul de Chaves (MPEG 58095); Santa Bárbara, Benevides (MPEG 22190); Portel, Rio Anapu (MPEG 23012; MPEG 23014); Val-de-Cans (MPEG 23672); Utinga, Belém (MZUSP 36041; MZUSP 36098; MZUSP 36100; MZUSP 36101); Providência, Belém (MPEG 5543; MPEG 7741); Vila do Outeiro, Ilha de Caratateua, Belém (MPEG 29883; MPEG 29884); Murutucu (MZUSP 36099); Igarapé Pucuruzinho, BR-422, km 67, Tucuruí/Novo Repartimento (MPEG 35346; MPEG 47957); Santarém (MZUSP 3359; MZUSP 3360); Fordlândia, Rio Tapajós (MZUSP 47352; MZUSP 47353); Aramanaí, Rio Tapajós (MZUSP 32773); Sumaúma, Rio Tapajós (MZUSP 47354); Villa Braga, Rio Tapajós (MNRJ 6815; MPEG 13126); Boim, Rio Tapajós (MPEG 8581); Alcobaça, Rio Tocantins (MPEG 5373); ***Tocantins:*** Araguatins (MPEG 20682; MZUSP 53054; MZUSP 65820; MZUSP 66095; MZUSP 66096); ***Rondônia:*** Guajará-Mirim, Rio Mamoré (MPEG 23002; MPEG 23003; MPEG 23005; MPEG 23006; MPEG 23008; MPEG 23010); Cachoeira Nazaré, margem oeste do Rio Jiparaná (MPEG 40290); ***Mato Grosso:*** Salto de Sepotuba (MNRJ 6809); Salto do Rio Jauru (MNRJ 6810); Fazenda São José, Rio Peixoto de Azevedo (MPEG 33846); PERU. ***Ucayali:*** Pucallpa (MZUSP 68248).

APPENDIX II.

Specimens examined through color photographs (Specimens from each locality in parenthesis).

TRINIDAD. Santa Cruz (YPM 26422); Brasso, Caroni (YPM 26427); Caroni Swamp, Caroni (YPM 26428); VENEZUELA. *Delta Amacuro* (COP 48307); *Sucre* (COP 56715; COP 56715; COP 56715; COP 56715; COP 56715; COP 56715; COP 56715) *Amazonas* (COP 21207; COP 21208; COP 21209; COP 21391; COP 22153; COP 22154; COP 22155; COP 38788; COP 69709; COP 69710; COP 69711; COP 69712); *Bolívar* (COP 16591; COP 16592; COP 17977; COP 17978; COP 17979; COP 26062; COP 26063; COP 26064; COP 26065; COP 45212); GUYANA. Georgetown (FMNH 32389; FMNH 32390); *North West District*: Koriabo (FMNH 190651; YPM 26429); *Demerara-Berbice*: Rio Essequibo, Rockstone (FMNH 108649); *Potaro-Siparuni*: Rio Essequibo, Iwokrama Reserve (ANSP 189019); Rio Abary (ANSP 189015; ANSP 189016; ANSP 189018); *Mahaica-Berbice*: Onverwagt (ANSP 189020); FRENCH GUYANA. *Mana*: Mana (YPM 31203; YPM 31204; YPM 31205); COLOMBIA. *Vichada*: Maipures (AMNH 513316) [type specimen of *T. m. media*]; *Meta*: Serrania de Macarena, Rio Guapaya (FMNH 249262; FMNH 249263); *Caquetá*: Morelia (ANSP 152949); *Putumayo*: Guascayaco (FMNH 282349); Mocoa (FMNH 282350); Santo Antonio Guamez (FMNH 287583); Umbria (ANSP 160131); Rio San Miguel (ANSP 165547); Rio Rumyiaco (ANSP 165546);; BRAZIL. *Amazonas*: Padauari (COP 35056; COP 35057; COP 35059; COP 35060; COP 35061); Manacapuru, Solimões (ANSP 67172; ANSP 67173); *Pará*: Castanhal (ANSP 80760; ANSP 80761); Apacy, Rio Tapajós (CMNH 78031) [type specimen of *T. m. lateralis*]; Pinhy, Rio Tapajós (ANSP 108373); PERU. *Napo*: Apayucu (ANSP 83750); *San Martin*: San Martin (ANSP 116134); Yurinaqui (ANSP 176557); BOLÍVIA. *Huanay*: Rio Mapiri (ANSP 119228; ANSP 119229; ANSP 119230); *Santa Cruz*: Guarayos (MNHN 7897) [type specimen of *T. m. boliviana*].