

Vocal variation and species limits in the genus *Sirystes* (Tyrannidae)

Variación en vocalizaciones y límites de especies en el género Sirystes (Tyrannidae)

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Abstract

Sirystes was for a long time treated as a monotypic genus with several subspecies, one of which was recently proposed for species rank. Vocal differentiation in the genus was studied using quantitative methods and the determination of primary, secondary and other kinds of vocalizations for different populations. The widely recognized split of Western *Sirystes* *S. albogriseus* of the Chocó (Panama, Colombia and Ecuador) from the more widespread Eastern *Sirystes* *S. sibilator* is strongly supported by differences in vocal repertoire and quantitative vocal differentiation. Eastern *Sirystes* is itself a superspecies comprised of three allopatric species which are vocally differentiated (quantitatively and in repertoire) to such an extent that species rank would be afforded under a modern biological species concept for: (i) White-rumped *Sirystes* *S. albocinereus* of Western Amazonia (in Venezuela, Colombia, Ecuador, Peru, Bolivia and western Amazonas and Acre states, Brazil); (ii) Todd's *Sirystes* *S. subcanescens* of North Amazonia (in northern Amazonas, northern Pará and Amapá states in Brazil, French Guiana and Guyana); and (iii) Sibilant *Sirystes* *S. sibilator* (including subspecies *atimastus*) of the Atlantic and Cerrado regions (in southern Pará state South through most of the rest of Brazil to northern Argentina and eastern Paraguay). Considerable variation in the kind of primary and secondary vocalizations are evident between these four proposed species, with primary vocalizations of particular taxa appearing as rare or secondary vocalizations or not being given at all by others. The four proposed species also show considerable morphological differences in the context of Tyrannidae. Vocal and morphological differences for the four proposed species exceed requirements for proposed "species scoring" tests. "Eastern *Sirystes*" is not as widespread as was previously thought. Because *Sirystes* populations are primary forest dependent, the threat status of species recognized here should be re-evaluated. *S. albogriseus* in particular may be threatened or near-threatened.

Key words *Sirystes* Tyrannidae, vocalizations, species, subspecies, distribution.

Resumen

Sirystes por mucho tiempo ha sido tratado como un género monotípico con varias subspecies, una de las cuales recientemente fue propuesta para estatus de especie. Se realizó un estudio de diferenciación en las vocalizaciones del género, utilizando métodos cuantitativos y la determinación de las clases de vocalizaciones de las diferentes poblaciones como vocalización principal, secundaria u otra. La separación (ampliamente reconocida) de *S. albogriseus* del

Chocó (Panamá, Colombia y Ecuador), de poblaciones orientales (*S. sibilator*), es fuertemente apoyada por las diferencias en clase de vocalizaciones principales y diferencias cuantitativas en vocalizaciones. Las poblaciones orientales representan una super-especie compuesta por tres especies alopátricas que se diferencian vocalmente (cuantitativamente y en clases de vocalizaciones) hasta tal punto que el estatus de especie se recomienda, bajo conceptos biológicos: (i) *S. albocinereus* de la Amazonia Occidental (en Venezuela, Colombia, Ecuador, Perú, Bolivia, estados Brasileños de Amazonas (parte occidental) y Acre), (ii) *S. subcanescens* (Todd, 1920), (norte del Amazonas de Brasil (Pará y Amapá), Guayana Francesa y Guyana), y (iii) *S. sibilator* (incluyendo la subespecie *atimastus*) de las regiones Atlántico y Cerrado (en el sur del estado de Pará hacia el sur a través de la mayor parte de Brasil hasta el norte de Argentina y el este de Paraguay). Variaciones notables en las clases de vocalizaciones principales y secundarias, son evidentes entre las cuatro especies propuestas, con vocalizaciones que son primarias en ciertas especies siendo vocalizaciones secundarias, raras o ausentes en otras. Las cuatro especies propuestas también demuestran considerables diferencias morfológicas en el contexto de la familia Tyrannidae. Diferencias vocales y morfológicas de las cuatro especies propuestas, exceden los requisitos propuestos para "puntuación de especies". Poblaciones al oriente de los Andes, no son tan extensas en sus distribuciones como se pensaba antes. Debido a que las poblaciones de *Sirystes*, son dependientes de bosques primarios, el estado de amenaza de las especies reconocidas aquí deben ser re-evaluados. *S. albogriseus* en particular podía ser amenazada o casi-amenazada.

Palabras clave *Sirystes*, Tyrannidae, vocalizaciones, especie, subespecie, distribución.

Introduction

Taxonomic History

The tyrant-flycatchers (Tyrannidae) of the genus *Sirystes* are related to *Myiarchus* and *Casiornis* (Lanyon & Fitzpatrick 1983, Birdsley 20002, Joseph *et al.* 2004, Chaves *et al.* 2008, Tello *et al.* 2009) and found principally in the lowland forests of South America. The genus was described by Cabanis & Heine (1859-1860) based on the type species *Muscicapa sibilator* Vieillot, 1818 (type locality: Paraguay). Vieillot (1818)'s description was itself based on Azara (1802-5)'s "*suiriri pitador*". The name *pitador* was treated by most subsequent authors, including Hartlaub (1847), as a vernacular name (not using Linnean nomenclature) and thus unavailable, with the genus *Suiriri* likewise not generally considered formally described by Azara (1802-5) and

attributed to d'Orbigny (1840) (e.g. Dickinson 2003). Five subspecies have been traditionally recognized, in addition to the nominate: *albogriseus* (Lawrence, 1867) (type locality: Lion Hill, Panama), *albocinereus* (Sclater & Salvin, 1880) (type locality: Bogotá, but the BMNH cotype is a specimen of the Western Amazonian population: Fig. 3(iii)), *atimastus* Oberholser, 1902 (type locality: Chapada, Mato Grosso, Brazil) and *subcanescens* Todd, 1920 (type locality: Upper Rocana, northern Pará, Brazil).

Another name, *sibilans*, was described by Lichtenstein (1823), also based on Azara (1802-5) and a specimen from São Paulo. The reason for Lichtenstein (1823)'s second description is not clear, but could have been influenced by the then ongoing nomenclatural controversies between Vieillot and other ornithologists of the era such as Temminck (see e.g. Miracle 2011). Hartlaub (1847) and Burmeister (1856) also used *sibilans* Lichtenstein, 1823, but it is a junior synonym of *sibilator* Vieillot, 1818 (Hellmayr 1927). Because Lichtenstein (1823) is based on a São Paulo syntype as well as birds studied by Azara (1802-5) used in Vieillot (1818)'s description, the two names are subjective and not objective synonyms.

Sirystes was chosen as the subject of this study for two reasons. First, as part of work on updating the Colombian checklist (Salaman *et al.* 2008, 2010, Donegan *et al.* 2009, 2010, 2011, 2012), an initial study of sonagrams in www.xeno-canto.org of species split by Gill & Wright (2006) identified *Sirystes* as a strong candidate for taxonomic revision based on clear vocal differences. Second, although its present taxonomy results in a widespread distribution (Ridgely & Tudor 1994) and an IUCN status of Least Concern, the species is considered primary forest-dependent (Stotz *et al.* 1996). *Sirystes* are canopy-dwelling birds and some populations have been found to require large territories to persist compared to other tyrant-flycatchers (Lopes & Marini 2006), and they are nuclear flock leaders in southern Brazil (A. Lees *in litt.* 2013). Local extinctions of *Sirystes* have been reported in Panama (Karr 1982) and Brazil (Christiansen & Pitter 1997) following forest loss and fragmentation. The species is particularly sensitive to forest fragmentation (Dos Anjos *et al.* 2011) and was reported not to persist following a forest fire in Brazil (Willis 2003). *Sirystes* has been considered "rare", "local" or "uncommon" throughout its range (Ridgely & Gwynne 1989, Ridgely & Greenfield 2001, Schulenberg *et al.* 2007, Honkala & Niiranen 2010, McMullan *et al.* 2011, Lees *et al.* 2013). There are only a few known modern localities for Western *Sirystes* in Colombia, including in Chocó (N. Athanas: see Appendix 1 and cover) and along the RNA Las Tangaras to Santana road in Valle del Cauca (J. C. Luna pers. comm. 2013). As taxonomic revisions of over-lumped taxa can reveal smaller populations of conservation concern, and given that this species is sensitive to habitat loss and fragmentation, *Sirystes* emerged as a priority for a detailed taxonomic revision.

Morphological variation

S. sibilator is today often considered a widely distributed species (Ridgely & Tudor 1994, 2009, Fitzpatrick 2004, Restall *et al.* 2006), although this study suggests its range has been widely over-reported (Fig. 5). The nominate subspecies occurs in the Atlantic region of Brazil and into Paraguay and Argentina. Subspecies *atimastus* is little studied and often overlooked in modern literature, having been treated as conspecific with *sibilator* since its original description. Hellmayr (1927) restricted *atimastus* to the type locality in Mato Grosso. It differs from geographically proximate *sibilator* in having paler lower underparts and a more extensively white rump (Fig. 3(v)). Hellmayr (1927) also referred to a "clearer" foreneck, whilst Oberholser (1902) and Ridgway (1907) cited its smaller size (Ridgway 1907 noting shorter tail length), lighter and more greyish upperparts; these other differences are slight. Photographs of birds showing paler lower underparts in WikiAves Brazil hail from various localities in the cerrado region. The geographic segregation between this form and *sibilator*, which can be considered otherwise distributed to the south, north and east of the Cerrado, does not appear clear-cut and requires further study of specimens and photographs from Brazil, or using phylogenetic techniques.

There are two named Amazonian populations: *albocinereus* of Western Amazonia (of Bolivia, Peru, Ecuador, Colombia, Venezuela and western Amazonas and Acre, Brazil) and *subcanescens* found north of the Amazon in British Guyana, French Guiana and Brazil from Manaus, Amazonas eastwards to Amapá and Pará states. Rivers seem not to form a barrier for *albocinereus*, whose range straddles the Amazon. Its distribution appears to be restricted by climatic or ecological factors, rather than to interfluves: there were no confirmed records uncovered in this study east of Leticia, Colombia or the border of Acre state. The form *subcanescens* is known only east of the rio Negro and north of the Amazon. Finally, *albogriseus* occurs in the Choco region from eastern Panama through western Colombia to north-western Ecuador.

The Chocó form *albogriseus* and Western Amazonian *albocinereus* were originally described as species and formerly treated specifically with respect to *sibilator* by some authors (e.g. Ridgway 1907). However, Hellmayr (1908) treated *albocinereus* and *atimastus* as "well-marked geographical forms" of *sibilator*. Subsequently, Hellmayr (1927) treated all congeners as conspecific. Most subsequent authors have followed this approach (Meyer de Schauensee 1966, Traylor 1979, Hilty & Brown 1986, Dunning 1987, Ridgely & Gwynne 1989, Ridgely & Tudor 1994, Salaman *et al.* 2001, 2010, Dickinson 2003, Restall *et al.* 2006, Schulenberg *et al.* 2007, McMullan *et al.* 2010, 2011, Remsen *et al.* 2013). However, Ridgely & Greenfield (2001), followed by Jahn *et al.* (2002), Hilty (2003), Gill & Wright (2006), Ridgely & Tudor (2009), McMullan & Navarrete (2013) and others, more recently treated *S. albogriseus* ("Western *Sirystes*") as a species separate from a broadly defined *S. sibilator* including all remaining taxa

("Eastern *Sirystes*"), based mainly on differences in vocalizations discussed in Ridgely & Tudor (1994). These differences have previously only been addressed through transcriptions in the field guide literature, in which available accounts have addressed only part of the genus' range.

Plumages have been discussed and illustrated in many publications (Ridgway 1907, Hellmayr 1908, 1927, Ridgely & Gwynne 1989, Sick 1993, Ridgely & Tudor 1994, 2009, Ridgely & Greenfield 2001, Souza 2002, Hilty 2003, Restall *et al.* 2006, Narosky & Yzurieta 2006, Schulenberg *et al.* 2007, Van Perlo 2009, McMullan *et al.* 2010, 2011, McMullan & Navarrete 2013). Most currently recognized taxa are illustrated in Figure 3. The salient plumage differences are summarized in Appendix 5. Western *Sirystes* *S. albogriseus* has two broad white wing bars and white wing covert edgings forming an extensively white proximal folded wing and a more extensively whitish tip to the tail than other taxa. It has an extensive white rump and grey underparts. In *albicinereus* of Western Amazonia and *subcanescens* of North Amazonia, the underparts are white with broad greyish or beige striations in the throat. Wings lack any extensive white markings except on the edge of flight feathers and in particular the tertials. There is also a broad area of white on the rump. In *atimastus*, the white on the rump is somewhat reduced and in *sibillator* almost absent. Subspecies *sibillator* and *atimastus* show dark streaking on the upperparts and narrow greyish edgings to the wing coverts, a feature which is barely visible in *subcanescens* and *albicinereus*. A supposed westward gradation in increasing whiteness of plumage led Hellmayr (1908, 1927) and Ridgely & Tudor (1994) to treat all *Sirystes* as one species. However, patterns of increasing or decreasing whiteness do not reflect a gradual west-east pattern for all plumage features: Amazonian *albicinereus* and *subcanescens* have almost no white on the wing coverts but the palest underparts of all *Sirystes*, whilst rump coloration is essentially equal for *albicinereus*, *albobrisesus* and *subcanescens*.

Previously known vocal variation in Sirystes

The first notes on vocalizations in *Sirystes* were published by Azara (1802-5), as cited by Vieillot (1818) in the original description of *sibillator*, of birds in Paraguay calling "*bi-bi-bi*". Modern studies of voice then began with Lanyon & Fitzpatrick (1983) who, based on fieldwork in the Western Amazonian region of Madre de Dios, Peru, described the "typical daytime vocalization given during active foraging" quite differently, as a "clear, ringing '*wher-pew*'". They stated that during more intense calling, intra-pair displaying, and dawn-singing, this frequently is lengthened into "*wher-pe-pe-pe-pew-pew*". The latter call was reportedly given more incessantly during nest visits.

Ridgely & Gwynne (1989) described the Panamanian population's calls as "*chup-chup-chup ...*" or "*prip-prip-prip ...*". Hilty & Brown (1986) included a note attributed to R. Ridgely about vocal differences between *Sirystes* populations each side of the Andes. Ridgely & Tudor (1994)

were then the first to detail these differences, using slightly modified versions of Lanyon & Fitzpatrick (1983)'s transcriptions to describe the calls of Amazonian birds ("*wher-pew*" or "*wher-pe-pe-pew-pew-pew*"). These authors noted the "rather different" and "huskier" calls west of the Andes, using Ridgely & Gwynne (1989)'s transcriptions. Ridgely & Greenfield (2001) used similar vocal transcriptions to Ridgely & Tudor (1994) but noted additional alternate calls "*wher-pewpu*" and "*wher-pew-pew-pew*" for Eastern *Sirystes* and "*chup-chip-chip*", "*prup-prip-prip-prip*" and "*che-che-che-che-che-chui*" for Western *Sirystes*. Hilty (2003) described the song of Eastern *Sirystes* in the south-eastern foothills of the Venezuelan Andes as "*wher whit-it*", "*wher whit*" and "*wher-pi'pi'pi'pi'pi'pi*", the latter considered an alarm call. Several of the above calls were cited in Restall *et al.* (2006). In Peru, Amazonian birds are described as calling "*p'weer-PEW-pu*", "longer series of '*pew*' notes, the number variable" and "quiet '*kew*' or '*pew*' notes given singly or in isolation" (Schulenberg *et al.* 2007).

Recordings of the kinds of vocalizations discussed in the above paragraphs for Eastern *Sirystes* have been made throughout Western Amazonia from Bolivia and Acre (Brazil) north through Peru and Ecuador to Venezuela, so are also presumably the vocalizations of birds in the Amazonian region of Colombia, from where there are no available recordings to date. This population corresponds to *albicinereus*.

Vocal differences between the Western Amazonian and other populations east of the Andes have not been highlighted to date in the literature, but are also evident from transcriptions of vocalizations in the field guide literature. Sick (1993) described the song of Brazilian populations as: "*ewe, ewe ewe, wee, wee, wee-WEEeh, tew, tew, ti, ti, ti, ti, ti, ti, ti, tew*". Van Perlo (2009) considered the song of Brazilian birds to be "*weew-weeuw-weeuw*" and its call a "short, rapid series of 4-7, slightly ascending fluted '*wuh-wiwi-wuh*' notes, the last note lowered". Honkala & Niiranen (2010) described south-east Brazilian birds as calling "*pee, pee, pee, pee ... with persistent tone*" (quite similar to Azara 1802-5) or "*peep-pep-pew-pew-pew*, descending at the end". Narosky & Yzurieta (2006) for Paraguay describe the song similarly to Van Perlo (2009) as "*fui-fui-fui-fui*". These songs correspond to the voice of birds occurring in Eastern South America including the Atlantic and Cerrado regions.

Vocalizations are considered innate (non-learned) in the Tyrannidae (Kroodsma 1984, 1989, Kroodsma & Konishi 1991). Although study of vocal differentiation in suboscines begun in this family, revisionary taxonomic studies using voice have focused recently on other groups such as the antbirds (e.g. Isler *et al.* 1999, 2006, 2007, 2009, Isler & Whitney 2011, Donegan 2012, Whitney *et al.* 2013a), tapaculos (e.g. Krabbe & Schulenberg 1997, Coopmans *et al.* 2001, Donegan & Avendaño 2008, Krabbe & Cadena 2010), antpittas (Donegan 2008, Carneiro *et al.* 2012) and

furnariids (Krabbe 2008). Although some recent taxonomic revisions of Neotropical Tyrannidae are based on voice (Donegan *et al.* 2009, Garrido *et al.* 2009), vocal characters have latterly been more often used to identify and diagnose cryptic new species (e.g. Coopmans & Krabbe 2000, Alvarez Alonso & Whitney 2001, Johnson & Jones 2001, Zimmer *et al.* 2001, Lane *et al.* 2007, Straneck 2007, Herzog *et al.* 2008, Whitney *et al.* 2013b,c, Zimmer *et al.* 2013). At the same time, various taxonomic revisions for the Tyrannidae based largely on molecular data have been published (e.g. Rheindt *et al.* 2008, 2009, Hosner & Moyle 2012). In this paper, I seek to document and discuss the implications of vocal variation in *Sirystes* and consider the taxonomic implications of vocal variation in the genus.

Methods

I assembled multiple digitized sound recordings (Appendix 1) initially with a view to considering the merits of the split of Western *Sirystes*. Subsequently, once the more complex variation in this group became evident, the study was expanded to better understand variation and assess species limits in the genus as a whole. Recordings were compiled largely from two major online compendia (www.xeno-canto.org and the Macaulay Library) and commercial CDs and DVDs (Appendix 1). These were supplemented with recordings from WikiAves Brazil from within the range of subspecies *subcanescens* and *albicinereus* only (due to large numbers of *sibilator/atimastus* recordings in other sources). Sonagrams were generated using the default settings of Raven Lite 1.0, sometimes adjusted for brightness and then expanded for time period and frequency to show the detail in Figures 1-2. Sound recordings were attributed to named taxa based on geographical distribution: (i) west of the Andes (*albogriseus*); (ii) Western Amazonia (*albicinereus*); (iii) North Amazonia (*subcanescens*); and (iv) Atlantic-Cerrado (*sibilator/atimastus*).

Sirystes populations were found to deliver various different sorts of vocalizations, with a vocal repertoire that is not particularly consistent in usage or nature between populations, presenting challenges to collating and analyzing data in a quantitative fashion. Four kinds of vocalizations were identified and studied here: short notes, whistles, chattering songs and downstroke songs. Each of these is discussed in turn below.

The first kind of call, apparently the only vocalization given by Western *Sirystes*, is a repeated single, short note ("short note": Figs. 1A-F). In Western Amazonia, short notes are delivered as part of more complex vocalizations usually commencing with a whistle (i.e. the "péw" of Lanyon & Fitzpatrick (1983) "*wher-péw*" or second or third syllable of Ridgely & Greenfield (2001)'s "*wheer-péwpu*" or Schulenberg *et al.* (2007)'s "*p'weer-PEW-pu*": Figs. 1G-L). The subsequent shorter notes only of the "*wheer-péw*" (and similar) vocalizations were measured as short notes, given some similarities in note shape to the short notes of Western *Sirystes*. In the Atlantic-cerrado population, single notes that might otherwise make up a part of a chattering song are

sometimes given as an isolated call (Figs. 2K-L) and are shorter than other calls of this group. Somewhat arbitrarily, these calls of eastern populations were treated as short notes for comparative purposes. It could alternatively be argued that Amazonian and Atlantic-Cerrado populations give no short notes at all, so this is a conservative approach.

The most common vocalization of Western Amazonian birds is a whistle. The whistle is followed immediately by a short note (Lanyon & Fitzpatrick (1983)'s "*wher-péw*": Figs. 1H, K, L), short notes (Ridgely & Greenfield (2001)'s "*wheer-péwpu*" or Schulenberg *et al.* (2007)'s "*p'weer-PEW-pu*": Figs. 1G, I, J), a downstroke song (Ridgely & Greenfield (2001)'s "*wheer-péw-péw-péw*" Figs. 1N-O) or a chattering song (Hilty (2003)'s "*wheer-pi'pi'pi'pi'pi'pi*": Fig. 1Q) in Western Amazonia. Because no other populations combine a whistle with other notes, the combination of notes in such sequences was not measured quantitatively. Instead, only the "*wheer*" part of these vocalizations ("whistle") was measured for Western Amazonian birds. This was compared to the single whistles of other eastern populations. In North Amazonian birds, whistles are given in sequences (Fig. 2A) or alone (Figs. 2B-D). In the Atlantic-cerrado population, whistles similar to those in the Western Amazonian and North Amazonian populations are not found in any recordings, but single long notes that might otherwise make up a part of downstroke songs are sometimes given as an isolated call (Figs. 2M-N). Somewhat arbitrarily, these calls of eastern populations were treated like whistles for comparative purposes. It could alternatively be argued that Atlantic-Cerrado populations give no whistles at all, so this is a conservative approach.

The small sample sizes of whistles and short notes for the Atlantic-Cerrado population (and other kinds of vocalizations which are not primary or secondary vocalizations in a particular population) should not be interpreted overly adversely as such samples generally reflect rare calls which are used for different communication purposes, rather than a lack of sampling. Statistical comparisons of primary vocalizations would render results showing much greater levels of differentiation than under this conservative approach.

For short notes and whistles: (i) individual note length (s), (ii) maximum acoustic frequency of the principal note (kHz), (iii) minimum acoustic frequency of the lower undertone (kHz), (iv) frequency bandwidth (difference between (ii) and (iii)), and (v) structure of vocalization in which the whistle is delivered, were measured or noted. Both short notes and whistles often have harmonic overtones, which in some instances allowed note length to be measured more accurately. However, the strongest and lowest principal note (usually the lowest tone visible on sonagrams) was always measured for frequency.

More complex vocalizations are also given by the Eastern populations of *Sirystes*. The first ("chattering song": Figs. 1P-R, 2G-I, 2O-W) corresponds to Azara (1802-5)'s "*bi-bi-*

bi", Van Perlo (2009)'s "*wuh-wiwi-wuh*", Honkala & Niiranen (2010)'s "*pee, pee, pee, pee ...*", Narosky & Yzurieta (2006)'s "*fui-fui-fui-fuio*" and the latter part of Hilty (2003)'s "*wheer-pi'pi'pi'pi'pi'pi*". The chattering song involves a series of few to many notes, often of variable length, in which individual notes are comprised of up-downstrokes with a region of thicker frequency bandwidth in the middle. Notes are often relatively symmetrical in shape and are delivered with short gaps between individual notes. Note length and song speed are highly variable in this sort of song. In Western Amazonian recordings, such vocalizations are rare and except in one recording (Fig. 1M) were delivered immediately following a whistle (Figs. 1P-R). In North Amazonia (Figs. 2G-I) and Atlantic-Cerrado (Figs. 2O-W) populations, these vocalizations did not follow whistles. Whistles of Western Amazonian birds were not included as part of the chattering song as a conservative approach in order to minimize differences between samples.

A second kind of song ("downstroke song": Figs. 1M-O, 2J, 2X-CH) corresponds to Schulenberg *et al.* (2007)'s "longer series of 'pew' notes", Van Perlo (2009)'s "*weew-weeuw-weeuw*", Honkala & Niiranen (2010)'s "*peep-pep-pew-pew-pew*" and the latter part of Ridgely & Greenfield (2001)'s "*wheer-péw-péw-péw*". This song involves a series of slower notes of essentially equal length in which the notes have a small initial upstroke and long descending part, with a less thick bandwidth at the peak, and a peak in acoustic frequency which occurs near to the start of the note. In the downstroke song, individual notes are more spaced out than in the chattering song.

For both chattering songs and downstroke songs, the following vocal variables were studied: (i) number of notes in song; (ii) total song duration; (iii) song speed (by dividing i by ii); (iv) max. acoustic frequency of highest note (kHz); and (v) peak in acoustic frequency—the relative position of the highest note (as a percentage, calculated as $(p-1)/(n-1)$ where p is the sequential position of the note with the highest frequency and n is the number of notes in the song, and in recordings with no discernible peak or with no ascending or descending pattern, this was instead determined as flat and the recording was ignored); and (vi), note shape (for downstroke songs only, owing to great intra-population note shape variation in chattering songs). Overtones were not often present in recordings of songs, but where present only the lower tones (principal notes) were measured. In some recordings, birds gave a chattering song and downstroke song rolled up one into the other without any break (e.g. Fig. 2X) or immediately following a whistle (e.g. Figs. 1N, O, Q). In such instances, each different sort of vocalization was treated separately.

Nominate or *atimastus* populations have been recorded giving a long, flat whistling alarm call (XC38102) and a fast trill (XC70770), but only a single example of each of these were available for a single population, so they were not studied further.

In *Sirystes*, vocalizations of one particular kind are given repeatedly (almost incessantly) by all taxa, particularly at dawn. Sometimes, other calls are interspersed with such vocalizations, but the predominant vocalization was abundantly apparent from each population sample. The methodology for sound recordings was not standardized, owing to the collaborative effort of many recordists whose recordings were studied used here. However, the large number of such recordists and broad range of localities for all taxa also means that a sampling or identification bias towards different sorts of vocalizations for different populations is unlikely. Primary vocalizations were identified quantitatively by counting the number of recordings inspected which included a vocalization of each kind and identifying which kind of vocalizations were found in at least 80% of the sample. In each case, the kind of recordings so identified were those which were also given in repeated long sequences in many recordings for the population. Secondary vocalizations were identified for most populations as those present in greater than 30% of recordings. Other recordings were classified as "rare". The kind of primary or secondary vocalization was identified and compared for each population.

Up to three different examples of each vocalization type were measured from each single recording analyzed. In total, 447 vocalizations were studied from 134 recordings, comprising 114 short notes, 108 whistles, 60 chattering songs and 165 downstroke songs (App. 2). Appendix 1 contains a list of recordings studied, with details of catalogue number, recordists and localities.

Recordings that were likely to be of the same individual, even if on different archived recordings, were treated as a single recording, with later recordings excluded from analyses. Additional recordings were therefore ignored where involving consecutive or near-consecutive serial numbers or made within two hours by the same recordist at the same locality and where recordings had similar mensural vocal variables. The number of assumed individuals for each vocalization type for each species is stated in Appendix 2. On most recordings, the first three vocalizations (where available) of each kind were studied, but in some recordings where the individual approached closer permitting greater definition on the sonagrams, later recordings were selected. In a handful of recordings with two individuals vocalizing, additional sets of data were taken per vocalization type per individual. Data from recordings that included only fragments of a song or call were ignored, save as stated above for whistles and short notes of *S. sibilator/atimastus*. As many recordings from as many localities as possible were included, where available, to determine the full range of variables. All recordings of individuals under natural conditions and after playback were included for the same reason. After compiling the data, the highest and lowest recorded values for each variable for each vocalization for each taxon were double-checked to verify upper and lower limits.

Statistical tests.—various tests of differentiation were applied for pairs of vocal and biometric variables of these populations in order to assess whether various postulated statistical tests considered relevant to species or subspecies rank had been passed, following Donegan (2008, 2012).

LEVEL 1: statistically significant differences at $p < 0.05$. A Bonferroni correction was applied for both vocal data and biometrics with the number of variables treated separately for each different call type (short notes and whistles: 4 variables each, $p < 0.0125$); chattering songs and downstroke songs: 5 variables, $p < 0.01$). An unequal variance (Welch's) t -test was used to test significance; for song speeds, a two-sample Kolmogorov-Smirnov test was applied as an additional test that must be satisfied for Level 1, to account for the possibility of a non-normal distribution. These calculations assess the statistical significance of differences between the means of populations, but do not address diagnosability, as they tolerate considerable overlap.

Further calculations, described below, were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, \bar{x}_1 and s_1 are the sample mean and sample standard deviation of Population 1; \bar{x}_2 and s_2 refer to the same parameters in Population 2; and the t value uses a one-sided confidence interval at the percentage specified for the relevant population and variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following one of Hubbs & Perlmutter's (1942) subspecies concepts, which is passed if sample means are two average standard deviations or more apart controlling for sample size, i.e. the sample mean of each population falls outside the range of 97.5% of the other population: $|(\bar{x}_1 - \bar{x}_2)| > (s_1(t_1 @ 97.5\%) + s_2(t_2 @ 97.5\%))/2$.

LEVEL 3: The traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size, which requires both the following tests to be passed: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_1 @ 99\%) + s_2(t_2 @ 75\%)$ and $|(\bar{x}_2 - \bar{x}_1)| > s_2(t_2 @ 99\%) + s_1(t_1 @ 75\%)$.

LEVEL 4: diagnosability based on recorded values (first part of Isler *et al.*'s 1998 diagnosability test) or, for plumage and subjective vocal characters (note shape and change of note shape), subjective diagnosability.

LEVEL 5: 'Full' diagnosability (where sample means are four average standard deviations apart at the 97.5% level, controlling for sample size): the second part of Isler *et al.*'s (1998) diagnosability test: $|(\bar{x}_1 - \bar{x}_2)| > s_1(t_1 @ 97.5\%) + s_2(t_2 @ 97.5\%)$.

A separate proposal for ranking species based on scores using a range of characters was recently developed by Tobias *et al.* (2010). Herein, a taxon pair that reaches Level 1 (but does not meet other tests) is treated as conforming to Tobias *et al.*'s (2010) 'minor magnitude' differences (less than two standard deviations between means). Level 2 is equivalent to their 'medium magnitude' (two standard deviations' difference between means), but the statistical test employed is more rigorous in that it also controls for sample size. Tobias *et al.* (2010) use five standard deviations'

difference without controlling for sample size for their 'major magnitude' differences; my Level 5 (four standard deviations apart, i.e. no overlap, but controlling for sample size) is treated as equivalent. Tobias *et al.* (2010) argued against some of the quantitative methods used above, where "calls of taxon A are comparable to songs of taxon B, or primary song of taxon A to secondary song of taxon B" as "Doing so will result in spurious estimates of phenotypic divergence." As a result, differences in primary vocalization type were also considered scorable as up to 3 each for kinds of primary vocalization which differ temporally or spectrally.

Museum specimens at BMNH and AMNH, including type specimens of *albogriseus* and *albocinereus*, and photographs on WikiAves Brazil were inspected to consider plumage differences, which were compared for all taxa.

Results

The results of vocal analyses are set out in Appendices 2-4. Four populations were found to meet the Tobias *et al.* (2010) test for species rank (App. 5).

"Western Sirystes" *S. albogriseus* has a dramatically different vocal repertoire from all populations East of the Andes. Western Sirystes has a different sort of primary vocalization from all other populations, and no recordings include whistles, chattering songs or downstroke songs. All available recordings involve repeated short notes, which can appear almost vertical on sonagrams. Recordings from across the species' range in Panama, Colombia and Ecuador are similar in this respect (Figs. 1A-E). Notes are quickly delivered downstrokes with a small initial upstroke (Fig. 1A-E). A comparison of the most similar call notes of the proximate (Western Amazonian) population – the second or third notes in the "wheer-péw" or "wheer-péw-péw" call – reveals statistical diagnosability in note length (Fig. 5B, App. 2-3). The small number of short note recordings in other populations occurring east of the Andes similarly show no overlap for note length. The vocal differences between Western and Eastern birds are substantial, with voices of the two being virtually unrecognizable from one another to the human ear or using sonagrams. These differences give strong support to Ridgely & Greenfield (2001)'s proposed split.

Whilst the vocal differences between populations either side of the Andes are well-known and supported by this study, significant variation in both vocal repertoire and quantitative vocal variables for whistles were found among the three populations occurring east of the Andes. All of them differ diagnosably (or in the case of a variable for one pair, near-diagnosably) in quantitative variables and in their usage of primary and secondary vocalizations:

- The most geographically distant pair: Atlantic-Cerrado versus Western Amazonian populations, differ: (i) in the kind of primary vocalization, which in the Atlantic-Cerrado are chattering songs and in Western Amazonia are whistles (App. 4); (ii) diagnosably in the song structure and.

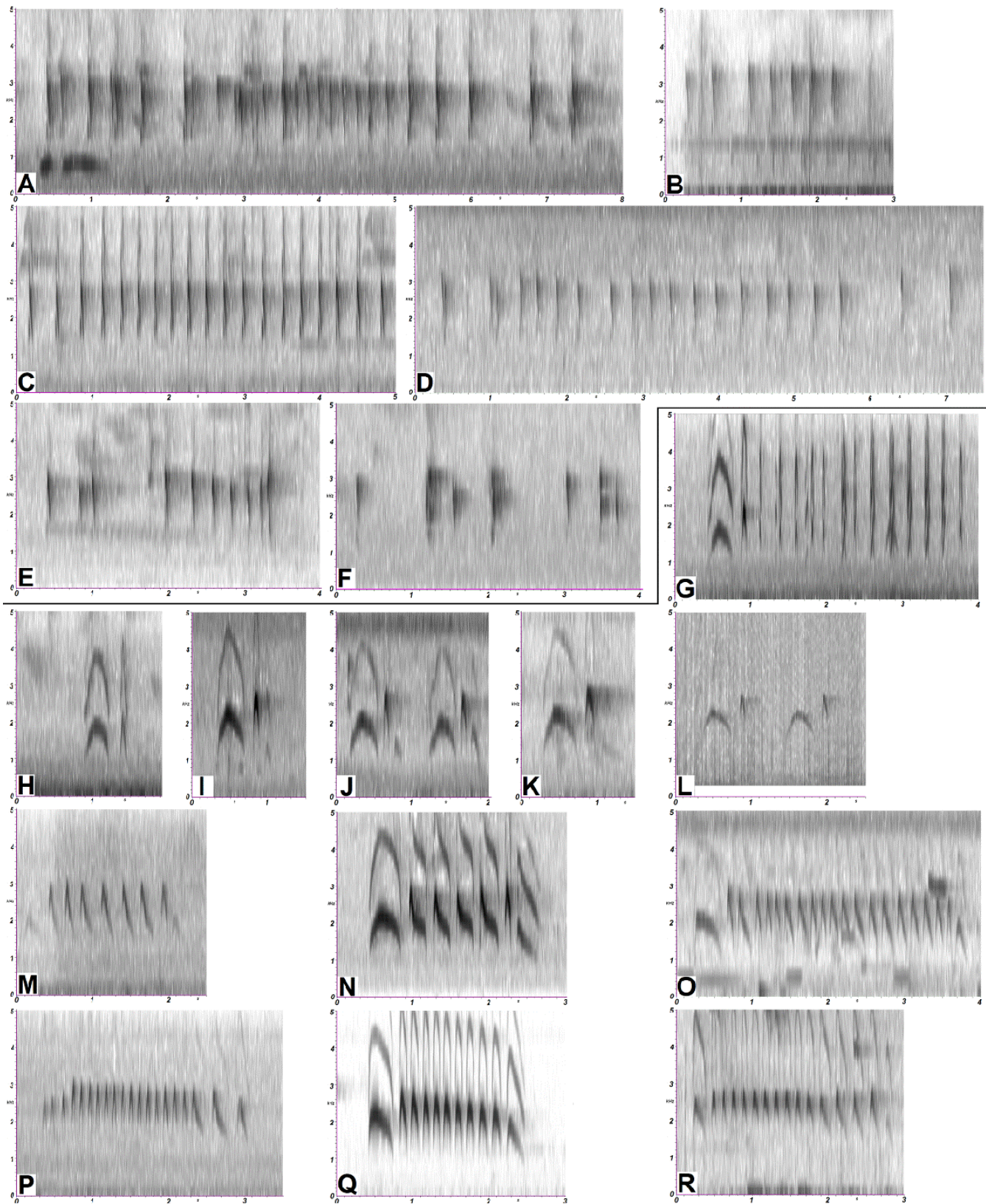


Figure 1: Sonograms of songs and calls of Western (Choco) *Sirystes S. albogriseus* of the Chocó (A-F) and White-rumped *Sirystes S. albocinereus* of Western Amazonia (G-R). Each sonogram here and in Fig. 2 shows 5 kHz of frequency bandwidth (y axis) and is on the same time scale (x axis) with number seconds noted; full details of recordings are in Appendix 1. Western (Choco) *Sirystes*, short notes – A-C: Darién, Panama (ML60335; Boesman 1999; ML31156) (near type locality of *albogriseus*); D: Chocó, Colombia (XC140775); E-F: Esmeraldas, Ecuador (Jahn *et al.* 2002; XC65721). White-rumped *Sirystes*, whistle and short notes – G. Barinas, Venezuela (ML66396); H: Apure, Venezuela (ML66397); I: Napo, Ecuador

(Krabbe & Nilsson 2003, track 156-1); J: Huánuco, Peru (ML17860); K: La Paz, Bolivia (ML52352); L: Acre, Brazil (WA1028668). White-rumped *Sirystes*, downstroke song – M: Barinas, Venezuela (ML66395); N: Napo, Ecuador (Boesman 2009), with initial whistle; O: Huánuco, Peru (ML17860), with initial whistle. White-rumped *Sirystes*, chattering song – P: Barinas, Venezuela (ML66395), with downstrokes at end; Q: Orellana, Ecuador (XC61441), with initial whistle; R: Madre de Dios, Peru (ML29607), with initial whistle and downstrokes at end.

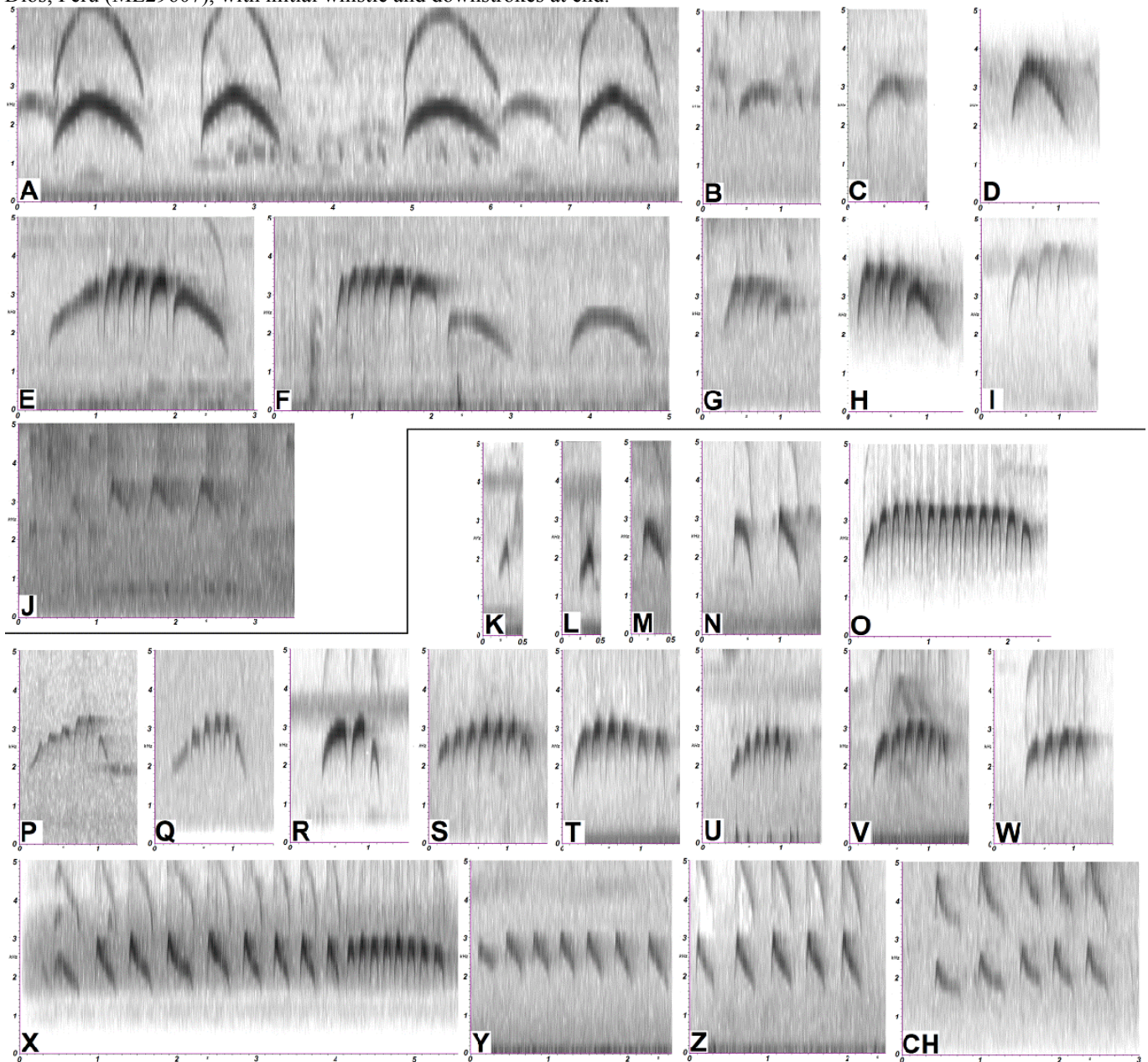


Figure 2: Sonagrams of songs and calls of Todd's *Sirystes S. subcanescens* of North Amazonia (A-J) and Sibilant *Sirystes S. sibilator* of the Atlantic and cerrado regions (K-Z & CH). Todd's *Sirystes*, whistle – A: Amazonas, Brazil (ML127365); B: Guyana (ML98716); C: French Guiana (XC74402); D: north Brazil (XC49721). Todd's *Sirystes*, chattering song – E-F: Amazonas, Brazil (ML42831; ML42831), latter with two whistles following; G: Guyana (ML98716); H: north Brazil (XC49721); I: Pará, Brazil (XC126301). Todd's *Sirystes*, downstroke song – J: French Guiana (XC59331). Sibilant *Sirystes S. sibilator* short note (fragment of chattering song) – K: São Paulo, Brazil (ML66398); L: Rio Grande do Sul, Brazil (ML19527). Sibilant *Sirystes S. sibilator* whistle (fragment of downstroke song) – M: Concepción, Paraguay (ML54296); N: Rio Grande do Sul, Brazil (ML68463). Sibilant *Sirystes S. sibilator* chattering song – O: Paraná, Brazil (XC60864); P: Pará, Brazil (XC13732); Q: Maranhão, Brazil (XC1426); R: Bahia, Brazil (XC82406); S: São Paulo, Brazil (XC7042); T: Rio Grande do Sul, Brazil (ML19369); U: Mato Grosso, Brazil (XC86650); V: Misiones, Argentina (XC8196); W: Caazapá, Paraguay (ML54254). Sibilant *Sirystes S. sibilator* downstroke song (to 4s), then chattering song – X: Caazapá, Paraguay (XC55850). Sibilant *Sirystes S. sibilator* downstroke song – Y: Rio de Janeiro, Brazil (XC58340); Z: Chapada (near type locality of *atimastus*), Mato Grosso, Brazil (XC23724); CH: Misiones, Argentina (XC51980).

note shape of whistles, which in Western Amazonia are always followed by one or more short notes, a chattering song or downstroke song but in the Atlantic-Cerrado population, to the extent fragments of downstroke songs can be considered the equivalent of a whistle, are delivered alone or in sequences of such notes and have a less symmetrical and more sharply peaked note shape (Figs. 1-2); (iii) to the extent fragments of downstroke songs can be considered the equivalent of a whistle, diagnosably and significantly in the maximum acoustic frequency of whistles (App. 3; Fig. 4A); and (iv) significantly but not diagnosably in other vocal variables set out in Appendix 3.

- North Amazonian and Atlantic-Cerrado populations differ: (i) in the kind of primary vocalization, which in North Amazonia are whistles and in the Atlantic-Cerrado are chattering songs (App. 4); and (ii) in the kind of secondary vocalization, which in North Amazonia are chattering songs and in the Atlantic-Cerrado are downstroke songs (App. 4); (iii) diagnosably and significantly in the length of whistles (App. 3; Fig. 4A); (iv) provisionally (based on a single recording from North Amazonia), in the note shape of downstroke songs, with the North Amazonia recording having an initial upstroke which is slower in reaching the peak; and (v) significantly but not diagnosably in other variables set out in Appendix 3.
- Western Amazonian and North Amazonian populations differ: (i) diagnosably in the song structure of whistles, which are the primary vocalization for both populations, which in Western Amazonia are always followed by one or more short notes, a chattering song or downstroke song but in North Amazonia are delivered alone or in sequences of whistles; (ii) significantly in maximum acoustic frequency of whistles (App. 3; Fig. 4A), which narrowly missed the statistical test of diagnosability perhaps due to sample sizes from North Amazonia, but showed no overlap; (iii) in secondary vocalization type (which is the chattering song in North Amazonia versus downstroke song in West Amazonia) (App. 4); (iv) provisionally (based on a single recording from North Amazonia), in the note shape of downstroke songs, with the North Amazonia recording having an initial upstroke which is slower in reaching the peak; and (v) significantly but not diagnosably in other variables set out in Appendix 3.

Each of these four populations scores at least Tobias et al. (2010)'s "seven points" required for species rank with respect to each of the others (Appendix 5).

In an initial study, Atlantic (*sibilator*) and cerrado (*atimastus*) populations were treated separately, but only small differences were evident, the most substantial of which was in song speed of chattering songs (mean 5.29 ± 1.07 s.d. (Minimum 3.21- maximum 8.22) ($n=126$) for Atlantic; 6.60 ± 0.98 (5.28-8.62) ($n=17$) for cerrado), but this did not attain 50% diagnosability.

Discussion

The proposed split of Western from Eastern *Sirystes*, which are trans- and cis-Andean populations of isolated lowland populations, is well documented (Ridgely & Tudor 1994) and here corroborated. However, other distributions of this group do not present simple cases of geographic replacements across known divides (Fig. 5). The Amazon River may be a geographical barrier in the lowermost part of the basin for the *subcanescens* and members of the *sibilator/atimastus* group, with proximate identifiable recordings from both north (Fig. 2I) and south (Fig. 2P) of the Amazon in Pará, Brazil. However, the species is very rare in Pará (A. Lees *in litt.* 2013) and records may therefore relate to austral wanderers whose distribution should not be limited to interfluvial regions. Further upstream, neither the Amazon River nor its major tributaries form a barrier between populations of *albocinereus*, which is distributed from Peru, Bolivia and Brazil north through Colombia to Venezuela. The limits between Western Amazonian *albocinereus* and North Amazonian *subcanescens* are not presently known. In Venezuela and northern Colombia, the former is known only in Andean foothills, with no records in the Venezuelan Amazon, although it extends at least east to Iquitos in Peru (BMNH specimen: Fig. 3) and is reported east to Leticia in Colombia (Hilty & Brown 1986).

The form *albocinereus* is known from specimens in Meta, eastern Colombia (App. 6), various localities near the East Andes base in the llanos region and a sight record in Leticia (Hilty & Brown 1986), which is close to a specimen record from Iquitos, Peru (Fig. 3(iv)). However, there were no confirmed records of *Sirystes* uncovered during this study from east of Colombia to Manaus or in Brazilian Amazonia south of the river outside Acre, despite various authorities mapping presence in the region (e.g. Ridgely & Tudor 1994, 2009, Souza 2002, Van Perlo 2009). Historical specimens (e.g. Rio Purus: Carnegie Museum P88176, P93535) and modern collections (Museu Paraense Emilio Goeldi 26485-6, 58026) from south of the Amazon in Brazil are all from Acre state and westernmost Amazonas, not elsewhere, despite quite extensive collections having been made in southern Amazonia. Cohn-Haft *et al.* (2007) do not list this species for either side of the Rio Madeira. There are records from Reserva Natural Palmari on its website (in westernmost Amazonas, so presumably *albocinereus*). Other reported localities in southern Brazilian Amazonia such as Pousada Rio Roosevelt (Whittaker 2009) and rio Urucu (Peres & Whittaker 1991) lack archived sound recordings in the databases studied here and no confirmatory materials or details of the observations are available (A. Whittaker *in litt.* 2013).

The northernmost records of the *sibilator* group come from northern Mato Grosso and south-eastern Pará states. The species is rare in the well-inventoried Alta Floresta region (Lees *et al.* 2013) and may be an austral migrant or vagrant to this area (A. C. Lees *in litt.*). Sick (1993) also considered the *sibilator* group to be a partial migrant in southern part of its range. However, Greenberg & Marra (2005) found no

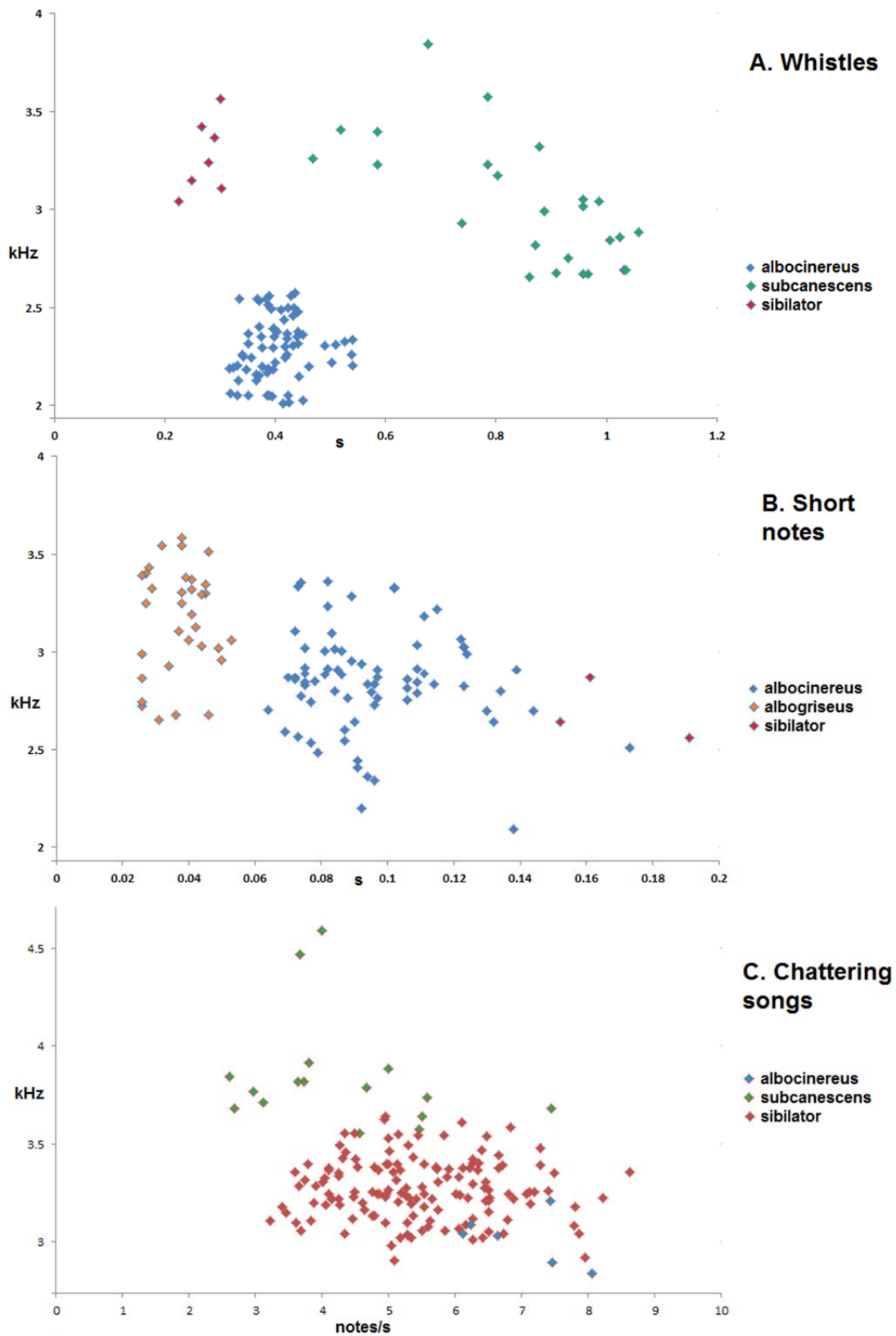


Figure 4: Scatter graphs showing vocal differentiation for selected variables between *Sirystes* taxa. A. song length (s) (x-axis) versus maximum acoustic frequency (kHz) (y-axis) for whistles. B. song length (s) (x-axis) versus maximum acoustic frequency (kHz) (y-axis) for short notes. C. song speed (notes/s) (x-axis) versus maximum acoustic frequency (kHz) (y-axis) for chattering songs.



Figure 3: Examples of the series at BMNH of (left to right): (i)-(ii) Western (Choco) *Sirystes S. albogriseus* Veragua, Panama (both, close to topotypical); (iii) White-rumped *Sirystes S. albocinereus* cotype, "Bogotá"; (iv) *S. albocinereus* Iquitos, Peru (paralectotype); (v) *S. sibilator atimastus* Chapada, Brazil (topotypical); (vi) *S. s. sibilator* Paraguay (topotypical); (vii) *S. s. sibilator* Rio de Janeiro, Brazil. *S. subcanescens* is not illustrated. © Natural History Museum.

evidence for seasonal distributional change and there are sound recordings in the sample from Paraguay, Argentina and southernmost Brazil for all months except December-February and May-July, so it is better considered a wanderer or partial migrant at most. Migration or seasonal movements are not reported in the other taxa

The plumage differences between the various vocally differentiated groups identified in this study are substantial in the context of Tyrannidae. In one of *Sirystes*' hypothesized closest relatives, *Myiarchus*, sympatric species are characterized by strong vocal but minor plumage differentiation.

The split of Western from Eastern *Sirystes* is strongly supported by differentiation in vocal (Figs. 1-2, 4, App. 2-4) and morphological (Fig. 3) characters. The vocal differences between three of the Eastern populations are less dramatic but still significant within the Tyrannidae. All these populations meet proposed benchmarks or points of reference for species rank in other suboscine groups (Isler *et al.* 1998) and species scoring tests (Tobias *et al.* 2010) vis-a-vis one another. A further pair (*atimastus* and *sibilator*) do not meet the same level of vocal differentiation nor the requirements of species scoring tests and are better treated as subspecies of a single species. The vocal and plumage differences, combined with distribution data, suggest a long-standing lack of gene flow between four populations. Four populations would be afforded species rank under a biological species concept, following modern treatments (Helbig *et al.* 2002, Remsen 2005, Tobias *et al.* 2010).

- A. **Western *Sirystes*** *Sirystes albogriseus* of eastern Panama, western Colombia and north-western Ecuador. Where Eastern *Sirystes* is split further, this could be renamed as "**Choco *Sirystes***".
- B. **Eastern *Sirystes*** *S. sibilator*, which in turn can be treated as a superspecies comprising the following three biological species:
 1. **White-rumped *Sirystes*** *S. albocinereus* of the upper Amazon region in Venezuela, Colombia, Ecuador, Peru, Brazil and Bolivia.
 2. **Todd's *Sirystes*** *S. subcanescens* of the Guyana shield and lower Amazon region north of the Amazon river, in Brazil, Guyana and French Guiana.
 3. **Sibilant *Sirystes*** *S. sibilator* (including subspecies *atimastus*) of the Atlantic region and eastern South America in much of Brazil south to eastern Paraguay and north-easternmost Argentina.

The vernacular names set out above are those of Hellmayr (1927) except that for Western *Sirystes*, which is Ridgely & Greenfield (2001)'s preference over Ridgway (1907) and Hellmayr (1927)'s "Panama *Sirystes*".

Further molecular analyses for this group could shed light on how the vocal differences between *Sirystes* populations arose, in particular: (i) whether the most vocally divergent and vocally simple population, *albogriseus*, is basal to more vocally variable populations found East of the Andes or recently derived; and (ii) if differences in the kinds of primary and secondary vocalizations between Todd's and Sibilant *Sirystes* are linked with greater or lower levels of molecular variation than between White-rumped and Todd's *Sirystes*, which are similar in plumage and differentiate vocally on more quantitative grounds.

A re-assessment of the conservation status of the newly split taxa is called for: whilst the split species are still relatively widely distributed, their populations are doubtless undergoing reductions due to accelerated habitat loss in many parts of their ranges. *S. albogriseus* in particular may be threatened or near-threatened.

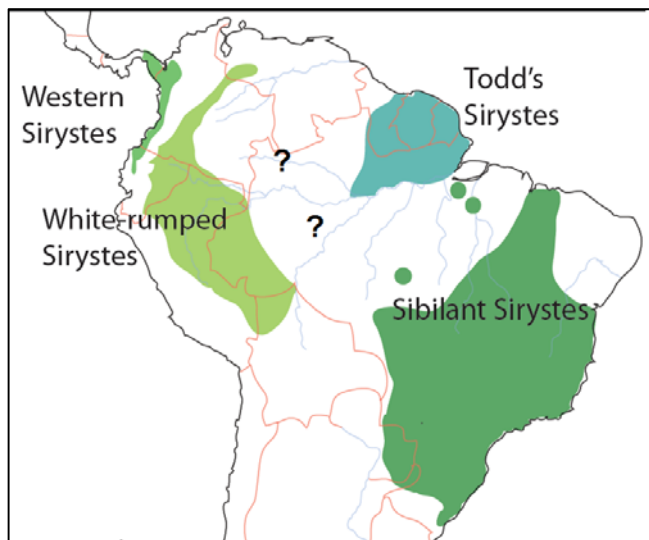


Figure 5: Map of *Sirystes* distributions by M. McMullan.

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Appendix 1

Sound recordings inspected.

All sound-recordings used in analyses are cited below. Coordinates are taken from the relevant database or publication and converted where necessary into degrees and minutes. Dashes refer to a series of different cat. nos. starting and ending with the number in question. Taxonomy in all appendices follows the new arrangement presented in the main text. The split of recordings between *sibilator* and *atimastus* is provisional and complicated due to their close similarity and the lack of a detailed morphological study on birds of this region here. Further research is needed to determine the limits between these two forms. Catalogue numbers refer to: ML=Macaulay library; XC=www.xeno-canto.org, WA = WikiAves Brazil.

Choco *Sirystes S. albogriseus*

Panama Darién: Cana (70°51'N, 77°38'W; 500 m) (XC60676: K. Allaire; Boesman 1999). Cerro Jefe (ML31223: T. Davis). Darién (ML31156: T. Davis). Cerro Pirre (ML60293, 60315, 60332, 60335 [latter two treated as same recording]: P. Coopmans).

Colombia Chocó: Utría National Park Trail (06°04'N, 77°23'W) (XC140775: N. Athanas).

Ecuador Esmeraldas: Playa de Oro, Santiago (00°51'N, 78°46'W; 60-300 m) (XC65721-2 [treated as same recording]: A. Spencer; Jahn *et al.* 2002, track 27-3: P. Mena Valenzuela). **Pichincha:** 17km NW Pedro Vicente Maldonado (00°15'N, 79°12'W; 300 m) (XC71119, 71140 [treated as same recording]: D. Lane).

White-rumped *Sirystes S. albocinereus*

Venezuela Apure: El Nula (07°29'N, 71°53'W) (ML66397: P. Schwartz). **Barinas:** Rio Masparro (08°47'N, 70°7'W) (ML66395-6 [treated as same recording]: P. Schwartz).

Ecuador Napo: Sacha Lodge, río Napo (00°32'S, 76°23'W; 250 m) (XC94987, 94990-1 [latter two treated as same recording]: D. Lane; Boesman (2009): J. Moore; Krabbe & Nilsson (2003) track 156.1). La Selva Lodge, (00°24'S, 76°20'W; 300 m) (XC4888: D. Jones; Krabbe & Nilsson (2003) tracks 156.2-3). **Orellana:** Yasuni Research Station, Parque Nacional Yasuni (00°40'S, 76°24'W; 250 m) (XC61440-1, 61434 [all treated as same recording]: A. Spencer).

Peru Huánuco: 35 km NE of Tingo Maria, Santa Elena (09°00'S, 75°00'W) (ML17860, 17863, 2 individuals [latter treated as same recording]: V. Emanuel; ML18330: J. Cartwright). **Ucayali:** Puntijao, 15.4 km. SSE mouth of Rio Cohengua, (10°25'S, 73°57'W) (ML166290: G. Seeholzer).

Madre de Dios: Cocha Cashu, Manu National Park (11°52'S; 71°22'W) (ML29582, 29607, 29999: T. A. Parker III; XC64190-1; J. Tobias & N. Seddon). ARCC (12°03'S; 69°41'W; 150 m) (XC39828-9: D. Geale). 35.0 km W of Puerto Maldonado, Tambopata (12°30'S, 69°00'W) (ML35176: L. Kibler; ML12835: T. A. Parker III). Explorer's Inn, río Tambopata, Puerto Maldonado, (12°50'S; 69°18'W) (ML28846: A. van den Berg; XC516: J. van der Woude). Sachavacayoc Lodge, Tambopata (12°51'S; 69°22'W; 270 m) (XC55, 737, 25801; B. Planqué).

Bolivia La Paz: Alto Rio Madidi Camp (ML52352, 52357: T. A. Parker III).

Brazil Acre: Senador Guiomard (WA730793: E. Guilherme). Assis (WA1028668: F.I. de Godoy)

Todd's *Sirystes S. subcanescens*

Guyana. Upper Takutu-Upper Essequibo: Right bank of Rewa River at Corona Falls, (03°11'N, 58°41'W) (ML98716: D. Finch).

French Guiana. Sinnamary, route de St Elie (05°20'N, 53°06'W; 15 m) (XC74402: A. Renaudier). Roura, Montagne Maripa (04°27'N, 52°22'W; 20 m) (XC59331: R. Alexandre).

Brazil: "Amapá" (Amazonas?): Torre ZF-2 (XC49721: R. Fraga). **Pará:** Almeirim (01°06'S, 52°39'W) (XC126301: C.B. Andretti). **Amazonas:** ZF-2, INPA research tower (02°35'S, 60°07'W) (ML127365: C. Marantz). Manaus (02°35'S, 59°56'W) (XC119125: G. Leite). ZF-2, ca. 30 km. W BR-174, trail to second (LBA) tower (02°36'S, 60°13'W) (ML127479: C. Marantz). 80 km N of Manaus (02°26'S, 60°00'W) (ML42816, 42831: R. Bierregaard). Presidente Figueiredo (WA290276: G. Leite).

Sibilant *Sirystes S. sibilator*

Brazil: Pará: Tucuruí dam, right margin of the lake (04°14'S, 49°25'W; 70 m) (XC13732; S. de Melo Dantas).

Bahia: Road to Remanso, Lençóis, Chapada Diamantina (12°35'S, 41°22'W; 400 m) (XC80120, 81643; J. Minns). Lencois (12°36'S, 41°24'W; 400 m) (XC82406: J. Minns). Boa Nova, Wet Forest (14°23'S, 40°06'W; 825 m) (XC80220, 80268, 81667, 82248, 82317: J. Minns).

Espirito Santo: Reserva Biológica de Sooretama (19°01'S, 40°01'W; 60 m) (XC65307, 85155, 85159; J. Minns). Reserva Florestal de Linhares (19°05'S, 39°54'W) (ML115333: C. Marantz). Reserva Natural da Vale - Linhares (19°09'S, 40°04'W; 40 m) (XC80096-7: J. Minns).

Reserva Biológica A. Ruschi (19°53'S, 40°35'W; 750 m) (XC81687: J. Minns). Duas Bocas, Cariacica, (20°17'S, 40°28'W; 150 m) (XC21070: F. T. & J. Silvério Lemos). Fazenda Caetes, Vargem Alta (20°27'S, 40°60'W) (XC28364, 70768, 70770-1: D. Lane; XC29501: F. Lambert).

Minas Gerais: Viçosa (20°47'S, 42°53'W) (XC115568: N. Eiterer). **Rio de Janeiro:** Conceição do Castelo, Fazenda Pindobas IV (20°18'S, 41°17'W; 1,200 m) (XC85390: J. Minns). Parque Nacional Itatiaia (22°23'S, 44°38'W and environs; 700-1,150 m) (ML32052, 47984: P. Isler; XC46724, 58323-4, 58339-40: B. López-Lanús; XC64841, 64847: R. Gagliardi; XC5971, 17609: N. Athanas; XC62636, 64907: H. van Oosten).

São Paulo: São Jose dos Campos (23°02'S, 46°02'W; 800 m) (XC7042: C. Candia-Gallardo; XC120008: G. Leite). Intervalles State Park, Carmo road (24°17'S, 48°26'W; 800 m) (XC82407: J. Minns; XC91619: J. Honkala). Fazenda Barreiro Rico; Anhemi (ML66398: P. Schwartz). Alto Ribeira State Park (PETAR) (24°32'S, 48°43'S) (XC112627: R. Silva e Silva).

Santa Catarina: Rio Tigre, Guatambu (27°08'S, 52°47'W; 290 m) (XC23827, 23830: A. Eisen Rupp). Reserva Volta Velha, Itapoá (26°05'S, 48°38'W; 10 m) (XC81682: J. Minns). Ribeirão Quati, Parque Nacional da Serra do Itajaí, Indaial (27°03'S, 49°13'W; 600 m) (XC41912: A. Eisen Rupp).

Parque Nacional da Serra do Itajaí, Presidente Nereu (27°10'S, 49°13'W; 500 m) (XC41894: A. Eisen Rupp). Barra do Monte Alegre, Chapecó (27°14'S, 52°35'W; 385 m) (XC23826: A. Eisen Rupp). Campo Belo do Sul (27°54'S, 50°45'W; 1,017 m) (XC85853: C. Espinola).

Paraná: PN do Iguazu-Pozo Preto (XC60864: M. Castelino). **Rio Grande do Sul:** 40 km NW of Tenente Portela, Turvo Forest Reserve (27°12'S, 54°01'W) (ML19369, 19376: W.

Belton; ML68463: D. Finch). 6 km NW of Garruchos; São Borja (28°10'S, 55°34'W) (ML19391, 19527: W. Belton).

Paraguay Concepción: San Luis National Park (22°40'S, 57°21'W) (ML54296, 54307: M. Robbins). **San Pedro:** Laguna Blanca (XC55849; M. Velázquez). **Caazapá:** 7.5–8 km E of San Carlos, Cordillera de Caaquazu (26°07'S, 55°44'W) (ML54254, 54476: M. Robbins). Reserva Tapyta (XC55850: M. Velázquez).

Argentina Misiones: 20 km S of Foz de Iguazú; Iguazu National Park (25°40'S, 54°26'W; 190 m) (ML22142, 23720: T.A. Parker III; XC69473: F. Lambert). Yacutinga Lodge, Andresito (25°43'S, 54°25'W) (XC51980: B. López-Lanús). Paraje María Soledad, Dpto Gral Belgrano (25°51'S, 53°59'W; 330 m) (XC8196: G. S. Cabanne). PN Iguazu-Macuco (XC49720: R. Fraga). Parque Provincial El Pinalito (26°25'S, 53°50'W) (ML132971: P. Hosner). Parque Provincial Cruce Caballero (26°31'S, 53°59'W) (ML132942: P. Hosner). Reserva Natural Cultural Papel Misionero

(27°00'S, 54°06'W) (ML164298: M. Lammertink). PP Mocona (XC53040: C. Ferrari).

Cerrado recordings subset:

Brazil Maranhão: Mancha Verde, São Joao dos Patos (06°36'S, 43°37'W) (XC1426: G. R. R. Brito). **Minas Gerais:** Cavernas do Peruaçu National Park (15°02'S, 44°15'W; 750 m) (XC84486; J. Minns). Itacarambi (15°05'S, 44°07'W; 550 m) (XC82405: J. Minns). **Goiás:** Goiânia, (16°41'S, 49°16'W; 640–690 m) (XC38102 (alarm call): N. D'Acosta). **Mato Grosso:** Cristalino Jungle Lodge, Trilha da Serra Mato Grosso (09°35'S, 55°55'W) (ML126768: C. Marantz). 20 km W of Alta Floresta (09°50'S, 56°19'W) (XC86650: A. Lees). Casa de Pedra area, Chapada dos Guimaraes (XC23724: P. Donahue). **Mato Grosso do Sul:** Estancia Mimosa, Bonito (310 m) (XC8595: D. De Granville). Bonito, Serra da Bodoquena (21°05'S, 56°52'W; 315 m) (XC82176: J. Minns).

Appendix 2

Vocal data

In each table in this appendix, for each taxon / song, data are presented as follows: mean ± standard deviation (lowest value–highest value) (n = no. of vocalizations analyzed). $n_{ai}=x$ in respect of each vocalization for each population, refers to the assumed no. of individuals sampled.

A. Short notes

Taxon	Call length (s)	Max. frequency (kHz)	Min. frequency (kHz)	Freq. bandwidth (kHz)
Choco Sirystes <i>S. albogriseus</i> Chocó ($n_{ai}=11$)	0.037 ± 0.008 (0.026–0.053) ($n=33$)	3.16 ± 0.27 (2.65–3.58) ($n=33$)	1.43 ± 0.22 (1.17–1.91) ($n=33$)	1.71 ± 0.27 (1.08–2.21) ($n=33$)
White-rumped Sirystes <i>S. albocinereus</i> West Amazonia (second and third notes of "wher-péw" call) ($n_{ai}=26$)	0.096 ± 0.021 (0.064–0.173) ($n=74$)	2.84 ± 0.27 (2.09–3.36) ($n=76$)	1.10 ± 0.17 (0.72–1.44) ($n=56$)	1.75 ± 0.29 (1.21–2.37) ($n=56$)
Sibilant Sirystes <i>S. sibilator</i> Atlantic-Cerrado (chattering song fragments) ($n_{ai}=2$)	0.168 ± 0.020 (0.152–0.191) ($n=3$)	2.69 ± 0.16 (2.56–2.87) ($n=3$)	1.31 ± 0.35 (1.06–1.71) ($n=3$)	1.38 ± 0.19 (1.15–1.50) ($n=3$)

B. Whistles

Taxon	Call length (s)	Max. frequency (kHz)	Min. frequency (kHz)	Freq. bandwidth (kHz)
White-rumped Sirystes <i>S. albocinereus</i> West Amazonia (first note of "wher-péw" and other calls commencing with a similar whistle) ($n_{ai}=26$)	0.41 ± 0.05 (0.32–0.54) ($n=70$)	2.29 ± 0.16 (2.01–2.57) ($n=75$)	1.06 ± 0.13 (0.81–1.38) ($n=61$)	1.21 ± 0.24 (0.72–1.76) ($n=61$)
Todd's Sirystes <i>S. subcanescens</i> N Amazonia ($n_{ai}=9$)	0.85 ± 0.17 (0.47–1.06) ($n=25$)	3.03 ± 0.32 (2.65–3.46) ($n=25$)	1.59 ± 0.31 (1.05–2.10) ($n=25$)	1.43 ± 0.29 (0.70–1.96) ($n=25$)
Sibilant Sirystes <i>S. sibilator</i> Atlantic-Cerrado (downstroke song fragments) ($n_{ai}=5$)	0.27 ± 0.03 (0.23–0.30) ($n=7$)	3.27 ± 0.19 (3.04–3.57) ($n=7$)	1.36 ± 0.15 (1.09–1.60) ($n=7$)	1.92 ± 0.25 (1.70–2.28) ($n=7$)

C. Downstroke songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency (kHz)	Position of peak (%)
White-rumped Sirystes <i>S. albocinereus</i> West Amazonia ($n_{ai}=13$)	7.06 ± 3.65 (4–20) ($n=18$)	1.46 ± 0.64 (0.77–3.19) ($n=18$)	4.89 ± 0.92 (3.33–6.39) ($n=18$)	3.07 ± 0.18 (2.75–3.36) ($n=18$)	0.25 ± 0.32 (0.00–1.00) ($n=18$)
Todd's Sirystes <i>S. subcanescens</i> N Amazonia ($n_{ai}=1$)	4 ($n=1$)	1.92 ($n=1$)	2.08 ($n=1$)	3.74 ($n=1$)	1.00 ($n=1$)
Sibilant Sirystes <i>S. sibilator</i> Atlantic-Cerrado ($n_{ai}=26$)	7.24 ± 3.06 (3–17) ($n=41$)	2.41 ± 1.14 (0.91–6.50) ($n=41$)	3.08 ± 0.57 (2.06–4.40) ($n=41$)	3.25 ± 0.12 (2.90–3.53) ($n=41$)	0.36 ± 0.22 (0.00–1.00) ($n=38$)

D. Chattering songs

Taxon	No. of notes	Song duration (s)	Song speed (notes/s)	Max. frequency (kHz)	Position of peak (%)
Choco Sirystes <i>S. albogriseus</i> Chocó ($n_{ai}=0$)	N/A	N/A	N/A	N/A	N/A
White-rumped Sirystes <i>S. albocinereus</i> West Amazonia ($n_{ai}=5$)	11.50 ± 3.23 (9–20) ($n=6$)	1.65 ± 0.56 (1.11–2.70) ($n=6$)	6.98 ± 0.78 (6.05–8.05) ($n=6$)	3.03 ± 0.15 (2.84–3.26) ($n=6$)	0.08 ± 0.13 (0.00–0.33) ($n=6$)
Todd's Sirystes <i>S. subcanescens</i> N Amazonia ($n_{ai}=6$)	5.75 ± 4.27 (3–21) ($n=16$)	1.52 ± 1.54 (0.67–7.08) ($n=16$)	4.27 ± 1.29 (2.61–7.44) ($n=16$)	3.84 ± 0.29 (3.56–4.59) ($n=16$)	0.32 ± 0.32 (0.00–0.33) ($n=16$)
Sibilant Sirystes <i>S. sibilator</i> Atlantic-Cerrado ($n_{ai}=65$)	6.06 ± 3.24 (3–29) ($n=145$)	1.14 ± 0.58 (0.41–4.46) ($n=143$)	5.45 ± 1.14 (3.21–8.62) ($n=143$)	3.26 ± 0.16 (2.90–3.64) ($n=146$)	0.56 ± 0.18 (0.00–1.00) ($n=144$)

Appendix 3:

Vocal differences between *Sirystes* taxa

The following codes are used in the table below. For vocal variables, the first symbol refers to the type of call: σ : short note; λ : whistle; ϕ : chattering song; δ : downstroke song. The immediately following letters refer to vocal variables: NN: number of notes; SL: song length; SS: song speed; MF: maximum acoustic frequency; mF: minimum acoustic frequency; PP: position of peak in acoustic frequency; FV: acoustic frequency bandwidth; PP: position of peak; NS: song structure or note shape; PV: primary vocalization type; SV: secondary vocalization type. Numbers 1,2,3,4 and 5 in brackets refer to the diagnosability levels met by the variable, based on the tests set out under Methods. For PV and SV, vocalization codes refer to the kind of primary or secondary vocalization respectively for each taxon. The code "(pres/abs)" refers to one of the taxa in question not giving the kind of vocalization at all in the sample studied. Degrees of freedom can be calculated by taking the lower value of the two taxa for the relevant variable under '($n=x$)' in Appendix 2, and subtracting 1. The taxon with the higher or lower of the relevant variable can be seen in Appendix 2. Note that some populations may appear 'less diagnosable' for certain variables than they may actually be due to sample size.

Taxon	White-rumped Sirystes <i>S. albocinereus</i> West Amazonia	Todd's Sirystes <i>S. subcanescens</i> N Amazonia	Sibilant Sirystes <i>S. sibilator</i> (inc. <i>atimastus</i>) Atlantic-Cerrado
Choco Sirystes <i>S. albogriseus</i> Chocó	σ NS(4) σ SL(1,2,3,4,5)* σ MF(1) σ mF(1) PV(σ/λ) λ (pres/abs) δ (pres/abs) ϕ (pres/abs)	PV(σ/λ) σ (pres/abs) λ (pres/abs) δ (pres/abs) ϕ (pres/abs)	σ SL(1,2,3,4,5) σ MF(1) PV(σ/ϕ) λ (pres/abs) δ (pres/abs) ϕ (pres/abs)
White-rumped Sirystes <i>S. albocinereus</i> West Amazonia	X	λ SL(1,2) λ MF(1,2,4) λ mF(1) λ NS(4) λ FV(1) δ SS(4) δ MF(4) δ NS(4) ϕ SS(1,2) ϕ MF(1,2) SV(ϕ/δ)	σ SL(1,2) λ SL(1,2,4) λ MF(1,2,3,4,5) λ mF(1) λ NS(4) λ FV(1) δ SS(1) δ SL(1) δ MF(4) δ NS(4) ϕ SS(1) ϕ PP(1,2) PV(λ/ϕ)
Todd's Sirystes <i>S. subcanescens</i> N Amazonia	X	X	λ SL(1,2,3,4,5) λ FV(1) ϕ SS(1) ϕ MF(1,2) ϕ PP(1) PV(λ/ϕ) SV(ϕ/δ)

* The level 5 test was missed for this vocalization variable and taxon pair based on the full sample, by a tiny margin of distance between means less than the number of significant figures for which raw data were taken. The test was passed in some instances of random removal of data from the set for each taxon, so was here treated as if passed.

Appendix 4

Use of different vocalization types by *Sirystes* taxa

In the table below, the number of recordings out of the sample for each population containing the kind of vocalization mentioned are noted, then expressed as a percentage of the sample and identified as a primary (>80%), secondary (>30%) or rare (<20%) vocalization. Note that percentages do not add up to 100% by taxon, because many recordings contain examples of more than one vocalization type.

Taxon	Choco <i>Sirystes</i> <i>S. albogriseus</i> Chocó	White-rumped <i>Sirystes</i> <i>S. albocinereus</i> West Amazonia	Todd's <i>Sirystes</i> <i>S. subcanescens</i> N Amazonia	Sibilant <i>Sirystes</i> <i>S. sibilator</i> Atlantic-Cerrado
σ (short note)	Primary voc. 100%: 12/12	See under whistle	/	Rare voc. 3.7%: 3/81
λ (whistle)	/	Primary voc. 83.3%: 25/30 (part of wheer-chip")	Primary voc. 81.8%: 9/11	Rare voc. 4.9%: 4/81
δ (downstroke song)	/	Secondary voc. 43.3%: 13/30	Rare voc. 9.1%: 1/11	Secondary voc. 32.1%: 26/81
φ (chattering song)	/	Rare voc. 16.7%: 5/30	Secondary voc. 54.5%: 6/11	Primary voc. 80.2%: 65/81
Other	/	/	/	Alarm: 1.2%: 1/81 Faster song: 1.2%: 1/81

Appendix 5

Species scoring tests

In the table below, scores based on Tobias et al. (2010) are allocated to each taxon studied here. Seven points is the benchmark for species rank. Only up to three plumage characters, one temporal vocal character and one spectral vocal character are available for consideration for each pair, so this is not an exhaustive list of morphological differences. Neither biometrics nor habitat differences were used here: these could yield increased scoring.

Taxon	White-rumped <i>Sirystes</i> <i>S. albocinereus</i> West Amazonia	Todd's <i>Sirystes</i> <i>S. subcanescens</i> N Amazonia	Sibilant <i>Sirystes</i> <i>S. s. atimastus</i> Cerrado	Sibilant <i>Sirystes</i> <i>S. s. sibilator</i> Atlantic
Choco <i>Sirystes</i> <i>S. albogriseus</i> Chocó	Voice (6) Ext. white on wing coverts (3) More ext. white tail tip (1) Pale underparts (3) Total: 13	Voice (6) White tail tip (3) Ext. white wing coverts (3) White tail tip (2) Total: 14	Voice (6) Striations on back (3) Ext. white on wing coverts (3) Ext. white on rump (3) Total: 18	Voice (6) Striations on back (3) Ext. white wing coverts (3) Ext. white on rump (3) Total: 18
White-rumped <i>Sirystes</i> <i>S. albocinereus</i> West Amazonia	X	Voice (5) Marginal versus no white tail tip (1) Throat / breast shade (2) Total: 8	Voice (6) Ext. striations on back (1) Ext. white rump (3) Ext. white lower wing cov. (2) Total: 12	Voice (6) Ext. striations back (1) Ext. white rump (3) Ext. white lower wing cov. (2) Total: 13
Todd's <i>Sirystes</i> <i>S. subcanescens</i> N Amazonia	X	X	Voice (6) Ext. of white on lower wing coverts (2) Throat and breast shade (2) Ext. of white on rump (1) Total: 11	Voice (6) Ext. white lower wing coverts (2) Ext. white rump (2) Throat and breast shade (2) Total: 12
Sibilant <i>Sirystes</i> <i>S. s. atimastus</i> Cerrado	X	X	X	Voice (1) Paler belly (2) Ext. of white rump (1) Total: 4

Appendix 6

List of Colombian specimens

Few specimens of *Sirystes* exist from Colombia and several of these have been overlooked by previous authors (e.g. Meyer de Schauensee 1945, who considered ANSP 148061 the only Colombian specimen of *albogriseus*). All specimens found by Biomap Alliance Partners (2012) for Colombia are cited below. Dashes refer to a series of different specimen cat. nos. starting and ending with the number in question. Specimens are listed in order of institution and cat. no. Acronyms: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, Tring (BMNH); Museo de Historia Natural, Universidad de la Salle, Bogotá (MLS); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (FNS); Smithsonian Institution, National Museum of Natural History, Washington (USNM); Museo de Historia Natural, Universidad del Valle, Cali (MHNUV). Only AMNH and BMNH specimens were inspected during this study.

Choco *Sirystes S. albogriseus*. ANSP 148061 (Juradó, Chocó). MHNUV 5823 (Bajo Calima, Valle del Cauca). USNM 411925-6 (Montelíbano, Córdoba), 411927 (Nazaret, Valencia, Córdoba), 443382-3 (Nuquí, Chocó).

White-rumped *Sirystes S. albocinereus*. AMNH 130673 (Puerto Barrigón, Puerto López, Meta). BMNH 1888.1.13.765 ("Bogotá") (type of *albocinereus*). FNS 43843 ("Bogotá"). MLS 4420 (río Ariarí, Meta), 4421 (Hacienda La Realidad, Puerto López, south of Villavicencio, Meta), 4422 (Vista Hermosa, río Guapaya, Macarena, Meta).