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Songs of Rusty Tinamou *Crypturellus brevirostris* and duetting in *Crypturellus* species

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SUMMARY.—Rusty Tinamou *Crypturellus brevirostris* is an elusive, ground-dwelling bird of *terra firme* forest. Although widespread across Amazonian Brazil, the Guiana Shield and extreme south-east Colombia, it is everywhere uncommon. Frequently, only its distinctive voice betrays its presence and therefore most contacts with this tinamou are auditory. Here, we analyse the vocalisations of Rusty Tinamou, a primary and secondary song, which may represent duetting between male and female of a mated pair. We also compare and discuss this vocal behaviour with duetting in other *Crypturellus* species.

Tinamous are sombre-coloured birds of the Neotropical forest floor, retiring and therefore difficult to observe for prolonged periods. More often heard than seen, their elusive behaviour and similar coloration among species make identification difficult when they are observed. Usually, only their distinctive songs betray their presence and permit identification (Davies 2002).

Rusty Tinamou *Crypturellus brevirostris*, which inhabits pristine Amazonian *terra firme* forest, is a poorly known species for which almost nothing is known concerning even basic aspects of its biology. The first record of its voice dates from December 1989, when T. A. Parker recorded a singing tinamou near Manaus, in the Brazilian state of Amazonas. Given that Bartlett's Tinamou *C. bartletti* had not been recorded north of the Amazon, that the type locality of *C. brevirostris* is Manaus, and that the voices of all other tinamou species in the area were already known, it was believed that the recorded song belonged to *C. brevirostris*, although in subsequent years there were no visual observations confirming this (Cohn-Haft *et al.* 1997). Once its voice was known, other birdwatchers and ornithologists obtained new records, but it remains a rarely recorded species even now. The observations and photographs published by Rufray *et al.* (2014) became the first irrefutable evidence that the above-mentioned songs were of *C. brevirostris*, which was not observed singing but heard close to the observers and then watched and photographed while foraging.

Here, we analyse and discriminate primary and secondary songs of this tinamou, and compare the secondary song with the similar-sounding, primary song of Cinereous Tinamou *C. cinereus*. We also discuss whether both songs are of a duetting male and female Rusty Tinamou, in view of duetting by Little *C. soui* and Variegated Tinamous *C. variegatus*. We also report observations of Rusty Tinamous responding to singing Variegated Tinamous.

Methods

For simplicity, we term all vocalisations that consist of more than a single note 'songs', even in the case of well-separated single whistles. This terminology does not assign any function to the vocalisation. For our analysis, we used eight available recordings of *C. brevirostris* song from different sources: four from French Guiana, one from Guyana and

three from Brazil. We rejected a doubtful record from Tefé, Brazil (Appendix 1; WA1258816), for being outside its known range and probably referable to Bartlett's Tinamou. We also checked eBird records of *C. brevirostris*, but because none provides details of voice or is accompanied by a sound-recording, they are not considered herein (eBird 2018).

For a comparison of the secondary song of *C. brevirostris* with the song of *C. cinereus*, we used seven www.xeno-canto.org (XC) recordings of the latter, all from the Guianan region: two from French Guiana, three from Suriname and two from Venezuela. For duetting behaviour of *C. soui*, we selected five recordings from the XC database: two each from Colombia and French Guiana, and one from Venezuela, while for *C. variegatus* we used XC221943 and XC284911, both from Brazil (Appendix 1), to supplement OC's observations.

Observations of *C. brevirostris*, *C. soui* and *C. variegatus* by OC were made in French Guiana during personal field work and studies for the Office National des Forêts and for the Groupe d'Étude et de Protection des Oiseaux en Guyane between 2005 and 2017. Observations of *C. brevirostris* by TVVC were made in *terra firme* forest north of Manaus, Brazil, in 2005–09. Observations of vocal interactions between *C. brevirostris* and *C. variegatus* were made in French Guiana by VP during field work for the Bureau d'Études Biotope in 2015–16, and by OC as above.

Results

Songs of *Crypturellus brevirostris*.—Rusty Tinamou has a characteristic song, typically commencing with a whistled note, followed by a series of more rapidly delivered whistles that rise slightly in pitch (Fig. 1). Occasionally, having reached its highest frequency, the series continues with additional notes that decrease in pitch and pace. Basic sound parameters of all eight recordings of this characteristic vocalisation, which we term primary song, were measured and these are summarised in Table 1. On average, the song comprises

TABLE 1

Measurements of basic voice parameters for three species of *Crypturellus* tinamous. Recordings used for the analysis (see Appendix 1): Rusty Tinamou *C. brevirostris*. Primary song ($n = 8$): ML80423 and 134458, WA47191, audio CD with two recordings (Naka *et al.* 2009), XC81200, 81202 and 253198, unpublished recording by VP. Secondary song ($n = 5$): ML80423 and 134458, WA47191, audio CD with one recording (Naka *et al.* 2009), unpubl. recording by VP. Cinereous Tinamou *C. cinereus* ($n = 7$): XC122487, 139218, 221821, 225380, 271934, 272430 and 272431.

	Mean	Standard deviation	Range
<i>Crypturellus brevirostris</i> : primary song ($n = 8$)			
No. of notes	16.3	5.0	12–27
Total length (seconds)	8.03	2.75	5.65–14.3
Fastest pace (notes/second)	2.43	0.17	2.22–2.70
Longest note (seconds)	0.40	0.13	0.28–0.54
Shortest note (seconds)	0.24	0.04	0.18–0.27
Longest pause (seconds)	0.60	0.19	0.38–0.85
Shortest pause (seconds)	0.185	0.025	0.15–0.22
Minimum frequency (Hz)	1,770	105	1,660–1,950
Max. frequency (Hz)	1,970	108	1,800–2,100
Frequency rise (Hz)	86	18	60–120
<i>Crypturellus brevirostris</i> : secondary song ($n = 5$)			
Note length (seconds)	0.50	0.10	0.38–0.62
Frequency (Hz)	2002	67	1,890–2,100
Minimum pause (seconds)	1.62	1.06	0.43–2.80
<i>Crypturellus cinereus</i> : primary song ($n = 7$) (monotypic, but all samples from Guianan Shield)			
Note length (seconds)	0.9	0.17	0.7–1.2
Frequency (Hz)	1,778	77	1,650–1,870
Minimum pause (seconds)	4.0	1.2	2.7–5.8

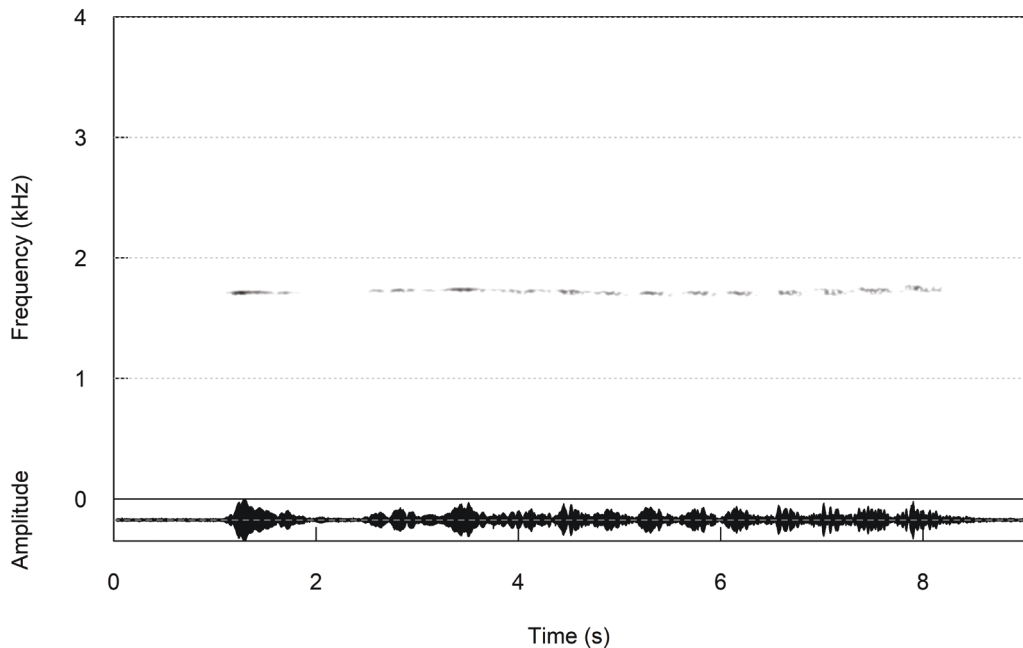


Figure 1. Typical primary song of Rusty Tinamou *Crypturellus brevirostris*, recorded by C. B. Andretti in *terra firme* forest north of Manaus, and published on the audio CD *Vozes da Amazônia brasileira / Voices of Brazilian Amazon* (Naka *et al.* 2009).

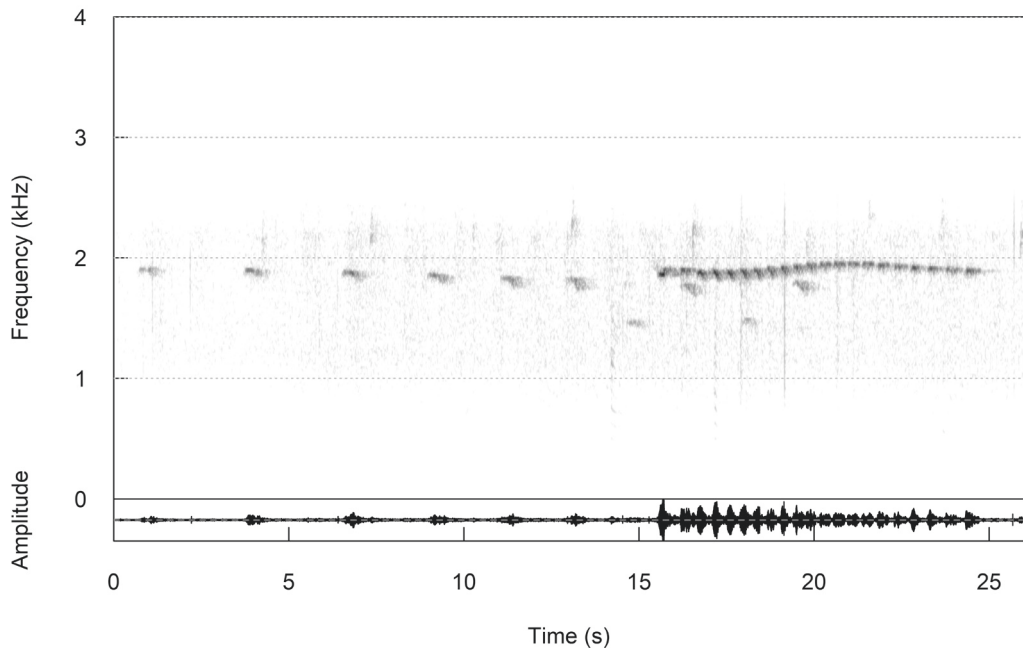


Figure 2. Secondary song followed by primary song of Rusty Tinamou *Crypturellus brevirostris*, recorded by Brian O'Shea in the Acary Mountains (Guyana), on 14 October 2006, and deposited in the Macaulay Library (ML134458).

c.16 notes with a total length of c.8 seconds, starting at a pitch of c.1,800 Hz, and rising to c.1,950 Hz. At its fastest pace, approximately 2.5 notes per second are delivered.

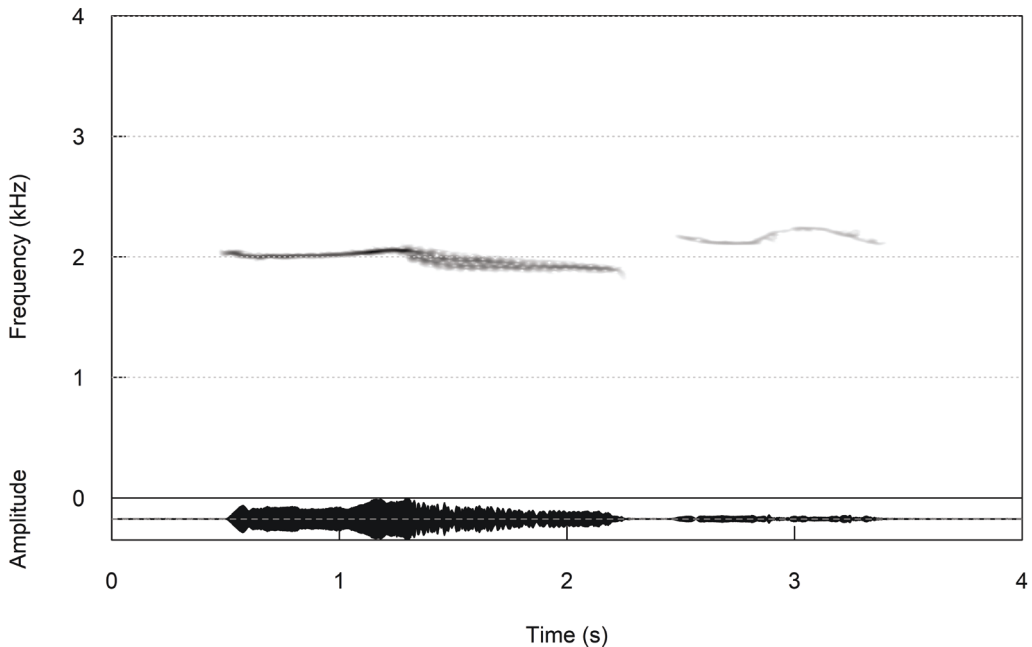


Figure 3. Typical duet of Little Tinamou *Crypturellus soui*, recorded by OC at the Piste de l'Anse, near Sinnamary, French Guiana, on 20 September 2015, and deposited on www.xeno-canto.org (XC282306).

In five of the eight recordings, a second tinamou sings a different song in the background (Fig. 2). This latter consists of a rather irregular series of well-spaced short whistles. This song, which we term secondary song, has been recorded only in combination with primary song, and does not reach the lowest frequencies of the latter. Nevertheless, both primary and secondary songs cover a similar frequency range, but either one can start lower or higher, or end similarly, or display different mean frequencies.

Secondary song is produced before, simultaneously with, or following primary song, and therefore apparently constitutes an asynchronous duet in its simplest form, i.e. both members of a mated pair answering each other. It is also quite irregular in rhythm, sometimes being a series of very slightly accelerating whistles, while at other times it consists only of 1–2 well-spaced whistles. Tinamous of the Guianan and Amazonian lowlands generally vocalise mainly around dawn and dusk (Cabot 1992, Davies 2002). Rusty Tinamou does not sing frequently. Usually individuals sing just once, although they sometimes give a series of 2–4 songs, and once even a series of five songs over a period of two hours and 35 minutes was heard. The earliest song was heard before dawn at 05.45 h and the latest after sunset around 20.00 h; only rarely has the species been heard to sing in the middle of the night (OC, TVVC pers. obs.). Sometimes, individuals of *C. brevirostris* also respond to each other's primary song. However, they do not react readily to playback of song, on only one of many attempts did the bird in question react (OC pers. obs.).

Duetting in other *Crypturellus*.—On 20 September 2005, OC observed an individual of *C. soui* crossing a trail just a few metres ahead of him on the Piste de l'Anse at Sinnamary, French Guiana (05°21'N, 52°53'W). Following brief playback, the bird immediately began singing, and was answered by a second individual on the opposite side of the trail and c.10 m apart. The first to sing gave only the loudest song, a drawn-out pure whistle with a quavering terminus. The second bird answered with a pure whistle, slightly modulated and of weaker amplitude. Recordings XC282306 and XC282307 document this observation

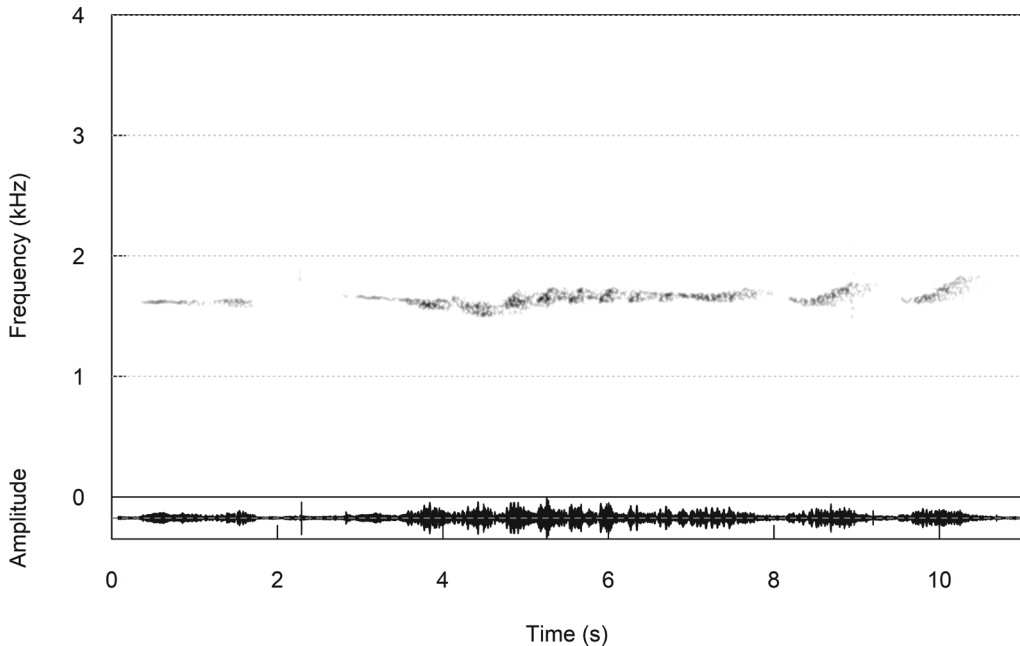


Figure 4. Typical duet of Variegated Tinamou *Crypturellus variegatus*, with the primary song by female followed by three notes by the male, recorded by PB at Rio Cristalino Jungle Lodge, Mato Grosso, Brazil, on 24 July 2005, and deposited on www.xeno-canto.org (XC221943).

(Fig. 3). This asynchronous duet, of which we have noted additional similar recordings, e.g. XC221883, XC273513 and XC275171, appears to be fairly common in *C. soui* (Appendix 1).

The primary song of *C. variegatus* comprises a single introductory flat whistle followed by a pause of up to c.3–4 seconds, then a rapid series of c.5–12 shorter, quavering notes (Fig. 4). This song is frequently answered by another individual that gives 2–5 interrogative whistles, the secondary song. On 11–20 April 2016 in the nature reserve of La Trinité, French Guiana (04°35'N, 53°18'W) OC took detailed notes concerning songs of *C. variegatus*. Of 140 songs, 73 (52%) comprised primary song alone, 15 (11%) secondary song alone, 44 (31%) were duets with the primary song heard first, and eight (6%) were duets with the secondary song given initially. These proportions may vary with season, time of day, and paired (or unpaired) status of the individual birds. Only clear songs given from nearby were counted, to be certain whether there was an answer or not. Sometimes both birds were so vocal that it was difficult to assess which bird was answering which. Once, a primary song was answered by another primary song, and sometimes a third bird vocalised too. Duets appear more frequent in early morning and evening.

Vocal interactions between *Crypturellus brevirostris* and *C. variegatus*.—On several occasions in French Guiana, a Rusty Tinamou started singing a few seconds after a Variegated Tinamou sang in the same area. Song of *C. brevirostris* obviously triggered by a singing *C. variegatus* was heard on 8 February 2015 at Crique Léopard (04°57'N, 53°48'W) (VP pers. obs.), and again on 16 April, 9 July 2016 and 6 November 2017 near camp Aya in La Trinité reserve (04°35'N, 53°18'W) and along the forest track to Crique Naï near Mana (c.05°21'N, 53°47'W), respectively (OC pers. obs.). On 15 November 2016 along the Piste de Paul Isnard, near Saint-Laurent-du-Maroni (c.05°09'N, 53°57'W), a *C. variegatus* started to sing around 18.00 h. Immediately it was answered by a *C. brevirostris* on one side of

the track, and seconds later a second and third *C. brevirostris* answered with the species' primary song from the opposite side of the track (V. Rufay *et al.* pers. obs.) (Appendix 2).

Discussion

Rusty Tinamou appears to have a primary song, and a secondary song uttered by another individual (Fig. 2). The following points support this hypothesis. We can exclude with a high level of certainty that secondary song is given by another tinamou species. In the Guianan region, only the song of *C. cinereus* resembles this slow, secondary song. However, *C. cinereus* gives a repeated single whistle at a slower but more even pace (Fig. 5). Furthermore, the whistles fade, are longer in duration and slightly lower pitched (Table 1). Given that *C. cinereus* prefers somewhat different habitat, *várzea* forest and forest edges, rather than *terra firme* and forest interior, the possibility that it is present in precisely the same localities as *C. brevirostris* in five of nine recordings appears very small indeed. The secondary song is thus likely to be *C. brevirostris*. A territorial bird of the same species would probably respond with a similar territorial song. If the secondary song of *C. brevirostris* is triggered by primary song, the most likely option is that it represents response by a mate. The reason why secondary song of *C. brevirostris* has not been recorded individually might be because this song resembles that of *C. cinereus*. Another possibility is that being secondary song, it is heard much less frequently than territorial primary song, or it has simply been overlooked hitherto.

It would appear logical to assume that primary song represents male territorial song, while secondary song is given by a paired female. However, in *Crypturellus* tinamous roles are reversed between the sexes, i.e. courtship is initiated by females and incubation and care of chicks are male tasks (Cabot 1992). We therefore searched for data on the voice of males and females of other *Crypturellus*. Surprisingly, differences in voice between the sexes have

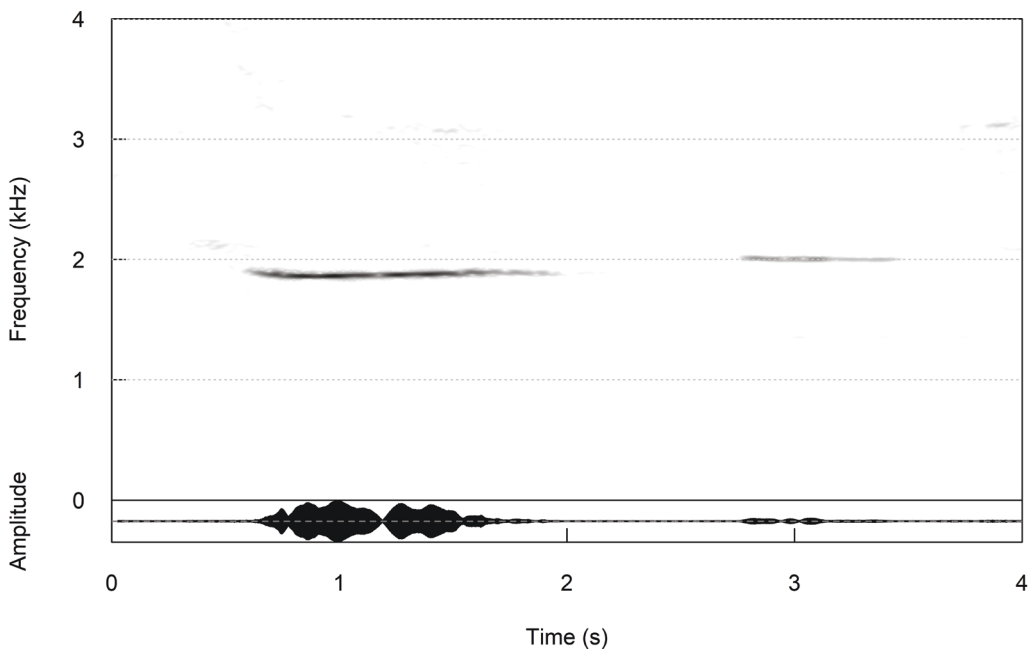


Figure 5. Duet of Cinereous Tinamou *Crypturellus cinereus*, recorded by PB at Peperpot, Commewijne, Suriname, on 14 March 2007, and deposited on www.xeno-canto.org (XC272432).

been documented for only a few *Crypturellus* (Cabot 1992, Sick 1993, Magalhães 1999, Cabot *et al.* 2014) and firm evidence that *Crypturellus* perform male–female duets is mentioned in the literature only for Tataupa Tinamou *C. tataupa* (Davies 2002).

The life history of *C. variegatus* was studied in detail by Beebe (1925). This species appears to be polyandrous, with courtship initiated by the female and primary song is always given by the female. In this species, the most vocal sex is the female, with the male only occasionally answering with secondary song.

Thicket Tinamou *C. cinnamomeus* was thoroughly studied by Leopold (1959). Very different from *C. variegatus*, this species appears to be monogamous, and although males incubate the eggs and provision the chicks, they are also the primary singers. Twelve singing birds that were collected were all males.

Lancaster (1964a,b) reported on Slaty-breasted Tinamou *C. boucardi*. In this species, the male is again the primary singer, the female having a different, more nasal, whining and subdued vocalisation, typically uttered in response to the male. This species is polygamous, with males incubating several broods belonging to different females.

Magalhães (1999) reported vocal differences related to sex in Brown *C. obsoletus* and Small-billed Tinamous *C. parvirostris*, but without much detail.

For the widespread and common *C. soui*, surprisingly, the literature is less clear. Schäfer (1954) indicated that both sexes utter the drawn-out tremulous whistle. In a study of *C. soui* by Skutch (1963), he observed that ‘when a male started whistling in the evening a female would respond and this would go on for longer than about 20 minutes, it came across as if it were a call to the female initially then when the response was received a sing-song melody proceeded as if they were ‘talking to each other’. How Skutch identified male and female in the field in the twilight is less clear. In two pairs studied in captivity, females initiated courtship behaviour (Brooks 2015). Duet calls were more frequently initiated by females than higher-pitched males, and were elicited on separation of paired birds. Both

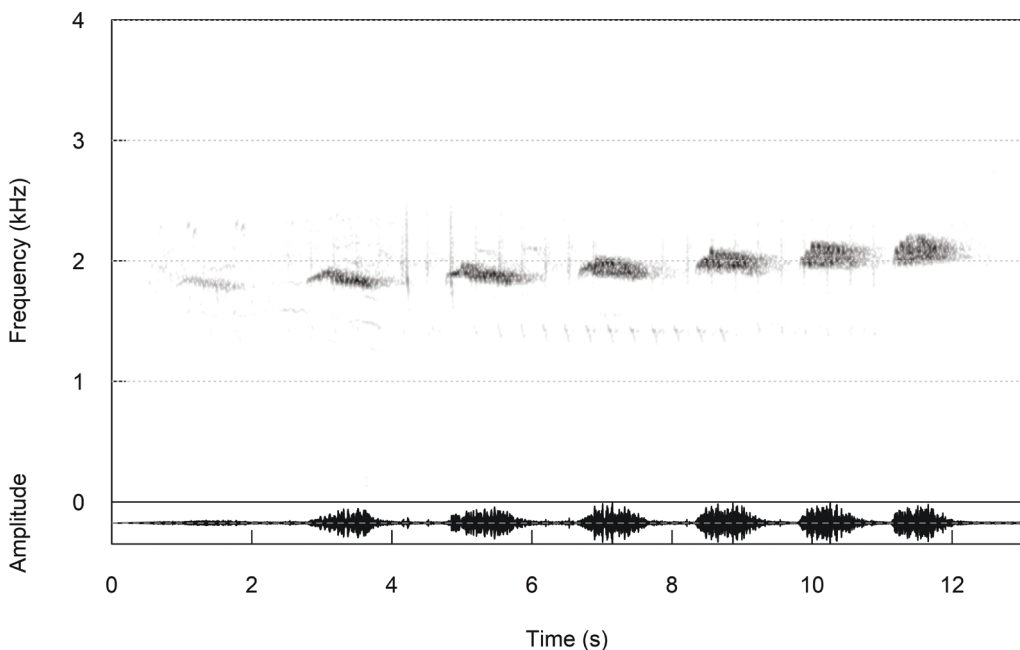


Figure 6. Typical primary song of Little Tinamou *Crypturellus soui*, recorded by PB at Zanderij, Suriname, on 14 March 2014, and deposited on www.xeno-canto.org (XC272579).

sexes uttered the drawn-out whistle with a tremulous ending (D. M. Brooks *in litt.* 2017). Consequently, the vocal repertoire of *C. soui* appears quite diverse, including a rising series of whistles typically given at dawn and dusk, and often considered to represent the primary song of unknown sex (Ridgely & Greenfield 2001, Schulenberg *et al.* 2007; Fig. 6), a drawn-out whistle with tremulous ending sometimes termed daytime song and either given by one bird, a pair or possibly two territorial birds, and a pure whistle mainly given in a duet by birds of unknown sex.

Of the 21 *Crypturellus*, most species have been studied in even less detail, but for several species at least there are also indications of duetting and vocal differences between the sexes. For example, *C. cinereus* regularly can be heard counter-singing on slightly different pitches, either by two territorial birds or a duetting pair, e.g. XC221826 (Appendix 1). Both *C. obsoletus* and *C. parvirostris* possess two distinct and frequently heard vocalisations.

In the four species discussed above (Sick 1993), we have examples of principally female singers, principally male singers, species in which the sexes appear almost equally vocal, and breeding systems ranging from polygamy to polyandry.

Among tinamou species for which vocal behaviour are available, *C. brevirostris* is closely related to *C. variegatus*, but this does not necessarily mean that their vocal behaviour is identical, as *C. variegatus* may or may not represent an exceptional case. At present, we can conclude only that there is no evidence that either the male or female of *C. brevirostris* is the primary singer.

Another question raised by our observations concerns *C. brevirostris* responding to the song of *C. variegatus*. Both species possess a similar introductory whistle, albeit on a slightly different pitch. Whether this similarity is sufficient to trigger a Rusty Tinamou to sing, or whether this behaviour indicates true interspecific territoriality, is unclear and also merits further investigation.

Tinamous in the forested lowlands are more frequently heard than seen and, when seen, observations are often limited to a brief glimpse barely sufficient to identify the species, let alone to determine the sex involved. It is thus unsurprising that duetting and identification of the sex of each singer has very rarely been appropriately documented with evidence. In the case of *C. brevirostris*, it would require intensive and dedicated field work to confirm that secondary song is uttered by this species and to determine the sex. Because the sexes are similar in coloration, study of marked birds, the sexes of which could be inferred by in-hand anatomical examination or using chromosomes, would be necessary. Alternatively, birds in captivity could be studied, as performed with Elegant Crested Tinamou *Eudromia elegans* (Schuster *et al.* 2012) and Little Tinamou *C. soui* (Brooks 2015) for other purposes. To what extent vocal behaviour in captivity is representative of natural conditions requires clarification. Apparently, in many *Crypturellus*, e.g. *C. obsoletus*, *C. parvirostris*, *C. tataupa* and *C. soui*, vocalisations in captivity appear virtually identical to those given by wild individuals (L. F. Silveira pers. comm.).

Careful sexing of specimens collected after their voice has been recorded is also desirable to clarify possible sexual differences in the vocalisations of *C. brevirostris*, as well as among other tinamous that duet. It is clear that there is still much to be learned concerning the vocal behaviour of *Crypturellus* tinamous.

Acknowledgements

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field work in the nature reserve of La Trinité, and TVVC thanks Mario Cohn-Haft, the Tropical Ecology, Assessment and Monitoring (TEAM) Network, and the Instituto Nacional de Pesquisas de Amazônia (INPA) for supporting his field work north of Manaus. We thank the Comité d'Homologation de Guyane for access to its database. We received additional information from Daniel Brooks and Mark Robbins, and we greatly appreciate comments by Des Jackson and Luís Fábio Silveira on a draft of this paper. Guy M. Kirwan, Brian O'Shea and Christopher J. Sharpe made useful comments on the submitted manuscript.

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Appendix 1: voice recordings of *Crypturellus* species

Given are: source and reference number (ML: Macaulay Library; WA: Wikiaves; XC: xeno-canto), locality of recording, date of recording, recordist, type of song.

Rusty Tinamou *Crypturellus brevirostris*

- ML80423, Manaus (Amazonas, Brazil), January 1990 (?), T. A. Parker. Primary and secondary song.
- WA1258816, Tefé, on right bank of Solimões River (Amazonas, Brazil), 2 July 1993, J. F. Pacheco. Secondary song?
- ML134458, Acary Mountains (Guyana), 14 October 2006, B. O'Shea. Primary and secondary song.
- WA47191, km 34 along road ZF-2 in Cuieiras Reserve, north of Manaus (Amazonas, Brazil), 11 March 2007, T. V. V. Costa (this recording is the same as that on *Voices da Amazônia brasileira*, see below). Primary and secondary song.

Audio CD, *Voices da Amazônia brasileira / Voices of the Brazilian Amazon*, vol. 1, INPA, Manaus (Naka *et al.* 2009).
 Two recordings: one by T. V. V. da Costa, km 34 along road ZF-2 in Cuieiras Reserve north of Manaus (Amazonas, Brazil), 11 March 2007 (same as WA47191), primary and secondary song, and one by C. B. Andretti, in *terra firme* forest north of Manaus, primary song.
 XC81200 and XC81202, inselberg Savane-roche Virginie near Régina, French Guiana, 29 May 2011, A. Renaudier. Primary song.
 XC253198, Aya, Réserve Naturelle de la Trinité, French Guiana, 18 April 2015, O. Claessens. Primary song.
 XC386694, Crique Moussinga, Bassin du Maroni, Apatou, French Guiana, 12 August 2013, V. Pelletier. Primary and secondary song.

Cinereous Tinamou *Crypturellus cinereus*

XC221821, Junglaven area, Amazonas, Venezuela, 11 January 1993, P. Boesman.
 XC221826, Serra dos Carajás, Salobo area, Pará, Brazil, 17 January 2005, P. Boesman.
 XC272430 and 272431, Peperpot, Commewijne, Suriname, 14 March 2007, P. Boesman.
 XC225380, Río Caura south of Maripa, Bolívar, Venezuela, 4 March 2010, J. Klaiber.
 XC122487, track to the Crique Dardanelles, Mana, French Guiana, 25 December 2012, J. King.
 XC139218, village of Cacao, Roura, French Guiana, 19 June 2013, T. Thai.
 XC271934, Cola Creek, Para, Suriname, 22 March 2014, P. Boesman.

Little Tinamou *Crypturellus soui*

XC221883, El Pauji road, Bolívar, Venezuela, 31 July 2002, P. Boesman.
 XC272579, Zanderij, Suriname, 14 March 2014, P. Boesman.
 XC273513, Reserva Natural de las Aves El Paujil, Santander, Colombia, 2 February 2011, P. Boesman.
 XC275171, Playa de Oro, Esmeraldas, Ecuador, 10 May 1996, P. N. Valenzuela.
 XC282306 and XC282307, Piste de l'Anse, Sinnamary, French Guiana, 20 September 2015, O. Claessens.

Variiegated Tinamou *Crypturellus variegatus*

XC221943, Rio Cristalino Jungle Lodge, Mato Grosso, Brazil, 24 July 2005, P. Boesman. Duet, the female first, answered by the male who sings three times.
 XC284911, Caruari, Amazonas, Brazil, 28 July 2015, G. A. Leite. Duet.

Appendix 2: vocal interactions between *Crypturellus brevirostris* and *C. variegatus* in French Guiana.

Given are: reference in database Faune-Guyane, locality of observation, date of observation, observer(s) and no. of CHG record.

http://www.faune-guyane.fr/index.php?m_id=54&id=448161, Crique Léopard, Saint-Laurent-du-Maroni (04°57'N, 53°48'W), 8 February 2015, V. Pelletier, CRYBRE 2015-4.

http://www.faune-guyane.fr/index.php?m_id=54&id=348630, nature reserve of La Trinité (04°35'N, 53°18'W), 16 April 2016, O. Claessens, CRYBRE 2016-3.

http://www.faune-guyane.fr/index.php?m_id=54&id=362262, forest track to Crique Nâi, Mana (c.05°21'N, 53°47'W), 9 July 2016, O. Claessens, CRYBRE 2016-4.

http://www.faune-guyane.fr/index.php?m_id=54&id=383582, Piste de Paul Isnard, Saint-Laurent-du-Maroni (c.05°09'N, 53°57'W), 15 November 2016, T. Deville, C. Gosset, G. Léotard, C. Lermite, V. Ruffray, CRYBRE 2016-7.