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ARTICLE

A reassessment of the taxonomy of *Crypturellus noctivagus* (Wied, 1820)

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ABSTRACT: *Crypturellus noctivagus noctivagus* (Wied, 1820) and *C. noctivagus zabele* (Spix, 1825) are endemic Brazilian tinamous restricted to Atlantic Forest and Caatinga, respectively. We used plumage, morphometric, vocal and oological characters to examine the validity of these taxa. Presence of sexual dimorphism in plumage only in birds occurring in Caatinga, and diagnostic differences in plumage pattern, tarsus color and egg color and shape allow us to recognize these two forms as distinct lineages, being considered here as *Crypturellus noctivagus* and *Crypturellus zabele*. We also provide updated diagnoses, descriptions, and geographic distributions for these two taxa.

KEY-WORDS: coloration, *Crypturellus zabele,* morphometrics, plumage, vocalizations.

INTRODUCTION

The genus *Crypturellus* Brabourne & Chubb comprises the majority of the South American tinamous (Sick 1997). Although several taxonomic revisions have been conducted (Hellmayr & Conover 1942, and references therein), much uncertainty persists in the taxonomy of this genus, in which considerable inter- and intraspecific variation is known to exist (Amaral & Silveira 2004). For example, at least 10 taxa have been considered subspecies of *Crypturellus noctivagus* (Wied, 1820), including *C. n. erythropus*, *C. n. atrocapillus*, *C. n. garleppi*, and *C. n. duidae* (Hellmayr & Conover 1942, Phelps & Phelps Jr. 1958, Blake 1977, Schwartz 1984). Many of these forms are currently considered species, such as *C. duidae*, *C. atrocapillus*, and *C. erythropus*, the latter two polytypic and likely requiring further taxonomic revision. Although most species in the genus *Crypturellus* are found in Amazonian and Andean forests, the two taxa presently allocated to *C. noctivagus* are endemic to eastern Brazil: *C. noctivagus noctivagus* (Wied, 1820), from the Atlantic Forest and *C. noctivagus zabele* (Spix, 1825), from the Caatinga.

Tinamus noctivagus Wied, 1820 (= *C. n. noctivagus*) and *Pezus zabelé* Spix, 1825 (= *C. n. zabele*) were described as separate species, but were later considered synonyms (Salvadori 1895, Hellmayr 1906, Ihering & Ihering 1907, Peters 1931, Pinto 1938). With more material available, Hellmayr & Conover (1942) recognized two subspecies, reviving the name *zabele* for the Caatinga birds and distinguishing them from nominal *C. noctivagus* by an overall paler color, a well-defined superciliary stripe, and broader bars in the wing-coverts and remiges. They also noticed possible sexual dimorphism in *C. n. zabele,* correcting the observations of Salvadori (1895), who described sexual dimorphism in *C. n. noctivagus* by using a female of *C. n. zabele* and a male of *C. n. noctivagus* in his analysis. Subsequent authors (Pinto 1964, Blake 1977, Pinto 1978, Mayr & Cottrell 1979, Cabot 1992, Sick 1997, Davies 2002, Grantsau 2010) followed the taxonomy proposed by Hellmayr & Conover (1942).

A proper investigation of the taxonomic status of these two forms requires the examination of a large and geographically diverse series of specimens, with a careful analysis of plumage variation and the inclusion of additional data of taxonomic interest, such as vocalizations, morphometrics, color of tarsus and eggs, and egg shape. Here we present a taxonomic revision of the *C. noctivagus* complex and provide updated diagnoses, descriptions, and geographic distributions.

METHODS

We analyzed 67 skins of adult *Crypturellus noctivagus* (38 males, 18 females and 11 unsexed), including the

holotypes of both taxa (*i.e.*, the nominal *noctivagus* and *zabele*), and 12 eggs (from four clutches), housed at the following institutions: American Museum of Natural History (AMNH), New York, USA; Field Museum of Natural History (FMNH), Chicago, USA; Zoologische Staatssammlung München (ZSM), Munich, Germany; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Brazil; Museu Nacional (MNRJ), Rio de Janeiro, Brazil; and Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. Juveniles, identified by distinct plumage and by smaller structural size (wing, bill and tarsus) which did not overlapped with the adults, were excluded from morphometric or plumage analyses and only considered for distribution analysis.

Characters analyzed included color and patterns of plumage, egg size, shape, and color, and tarsus color, as well as morphometric characters. All measurements and color data were taken by a single observer (B.M.T.). We analyzed the color of the supercilium, crown, nape, throat, breast, abdomen, and back, as well as the light barring in the tail and in the wing coverts, and the color of eggs and tarsus. We also analyzed the width of the light barring in the wings, supercilium length, and the presence of barring in the breast. Plumage colors were classified following Munsell (1994), comparing the specimens' colors to the reference colors provided by the charts, and then grouped in eight color categories (Table 1) to allow more straightforward comparisons. Tarsus color, although not preserved in the museum skins, could be analyzed through high-quality photos from birds in the wild (www.wikiaves.com.br) and also from information present on the specimens' labels. We also analyzed high quality photos of eggs when available (www.wikiaves.com.br). Morphometric analysis included wing and tarsus length, bill size (length, height and width) and egg size and shape (length, width and "roundness index", *i.e.*, length/width). All measurements were taken using calipers. To measure the wing bars, three bars from the middle coverts were selected, measured and the mean value was calculated. Student *t*-tests were conducted in PAST software v.2.15 (Hammer *et al*. 2001) and multivariate analysis (Principal Component Analysis) was carried out in SPSS 13.0. To avoid bias in the analyses, we did not consider *a priori* the provenance and previous identification of each specimen.

TABLE 1. Color categories and the original Munsell (1994) color codes from which they derived.

Color categories	Munsell (1994)
Black	5YR 2.5/1; 7.5YR 2.5/1; 10YR 2/1
Dark grayish brown	2.5YR 2.5/1; 2.5YR 3/1; 5YR 3/1; 7.5YR 3/2; 10YR 3/1; 10YR 3/2; 10YR 4/1
Grayish brown	5YR 4/2; 7.5YR 4/2; 10YR 4/2; 10YR 4/3; 10YR 5/2
Dark reddish brown	2.5YR 3/6; 5YR 2.5/2; 5YR 3/2; 5YR 3/3; 5YR 3/4; 7.5YR 2.5/2; 7.5YR 3/4; 10YR 2/2
Reddish brown	2.5YR 4/4; 2.5YR 4/6; 2.5YR 5/6; 2.5YR 5/8; 5YR 4/4; 5YR 4/6; 5YR 5/4; 5YR 5/6; 5YR 5/8; 5YR 6/8; 5YR 7/8; 7.5YR 4/6; 7.5YR 5/6; 7.5YR 5/8
Yellowish brown	7.5YR 6/6; 7.5YR 6/8; 10YR 5/4; 10YR 5/6; 10YR 5/8; 10YR 6/4; 10YR 6/6; 10YR 6/8
Yellow	7.5YR 7/6; 7.5YR 7/8; 7.5YR 8/6; 10YR 7/6; 10YR 7/8; 10YR 8/6
Pale	2.5YR 8/1; 7.5YR 7/4; 10YR 7/3; 10YR 7/4; 10YR 8/2; 10YR 8/3; 10YR 8/4

Vocal samples were obtained at the Arquivo Sonoro da Seção de Aves do MZUSP, on internet databases (www.wikiaves.com; www.xenocanto.com), and from colleagues. Sonograms were created and analyzed using the software Raven Pro 1.4 (Bioacoustics Research Program 2011). We only used recordings that produced clear and precise sonograms, with low or no background noise (sample size: n = 10 for *C. n. noctivagus*, n = 5 for *C. n. zabele*). The choice of vocal characters for the analysis was based on Isler *et al*. (1998) and Bertelli & Tubaro (2002), namely: the number of notes (a note being defined as an unbroken trace in the spectrogram), total duration of vocalization, maximum frequency, minimum frequency, bandwidth (max. freq. minus min. freq.), peak frequency (frequency at the point of highest amplitude), peak time (point in time of highest amplitude), and duration of each note and internote. Not all sonograms allowed precise note distinction; therefore, sample size varied for the analyses of note and internote duration. To minimize possible intra-individual differences, we followed Isler *et al*. (1998) and used a mean value when we had more than one vocalization for a single individual. The locality of each specimen was taken from their respective labels and from gazetteers (Paynter & Traylor 1991; Vanzolini 1992) and geographic data websites (*e.g.* http://www.fallingrain.com and http://www.bngb.ibge.gov.br/bngb.php), and mapped using the QuantumGis software.

RESULTS

Consistent differences in plumage color and pattern, morphometric characters, color of tarsus, egg color and egg shape were found. A very distinctive feature that stands out is the tarsus color. Tarsi are olivaceous in birds from the Atlantic Forest (currently *C. n. noctivagus*) and pure-

FIGURE 1. Ventral (above), lateral (center) and dorsal (below) views of *C. n. noctivagus* (from left to right MZUSP 43761, MZUSP 56384, MZUSP 48335 and MZUSP 49333) and *C. n. zabele* (male MZUSP 7603; female MZUSP 8496).

yellow in those from the Brazilian Caatinga (currently *C. n. zabele*). Another important difference between the two forms appears when we compare females. The upper breast of both males and females of *C. n. noctivagus* is solid gray, whereas the upper breast is solid gray only in males of *C. n. zabele*. The upper breast of females of *C. n. zabele* is barred rather than solid-gray (Figure 1). Therefore, breast color is a diagnostic difference between females of the two forms. As a consequence, *C. n. zabele* shows sexual dimorphism in plumage, which was not noticed in *C. n. noctivagus.* Although males of *C. n. noctivagus* tend to be more reddish than females, this is not a consistent difference (Table 2).

We found in almost every plumage character analyzed that *Crypturellus n. zabele* are paler than *C. n. noctivagus.* This is much more prominent in the wing bars and tail, and in the overall color of the throat, upper breast, and abdomen, which are darker and/or redder in *C. n. noctivagus* (Table 2). There is overlap in some of the characters analyzed; however, the color of the wing bars and tail coverts are distinct (Figure 1; Table 2). Even with a minor overlap in the color of the wing bars, the differences between the wings of the two forms become evident when we consider the larger bars in *C. n. zabele* wings (Table 3) combined with its overall paler colors. The color of the light bars in the tail coverts is particularly interesting: most *C. n. zabele* specimens showed a clear difference between the color of bars in rump (reddish brown) and tail coverts (pale), not observed in any *C. n. noctivagus*, which had darker tail covert bars. We also noted that the superciliary stripes tend to be not only paler in *C. n. zabele* (Table 2), but also broader and longer than in *C. n. noctivagus*, which usually had short, thin or even fragmented stripes (in *C. n. zabele* the stripes were evidently marked).

When sexual dimorphism for morphometric characters was analyzed, Student's *t*-test indicated that females of *C. n. noctivagus* are borderline significantly smaller than males for wing (t_{44} = 1.96, p = 0.05) and tarsus length (t_{44} = 2.06, p = 0.04). Males and females of *C. n. zabele* were indistinguishable when the same characters are compared (p > 0.05 in all cases). When comparing the same characters between males and females of each form, the tarsus length and wing bars of males of *C. n. noctivagus* significantly differed from males of *C. n. zabele* (t_{33} = 2.22, p = 0.03 and t_{27} = -3.96, p < 0.01, respectively), with males of the latter having smaller tarsi and broader wing bars than males of *C. n. noctivagus*. When females were compared, differences were only found in wing bars size, broader in *C. n. zabele* (t_{15} = -2.51, p = 0.03). It is important to notice that, except for the wing bars, these morphometric differences were very subtle (Table 3). When all birds were analyzed in the Principal Component Analysis (Figure 2), two factors explained 66.8% of the total variance between the two taxa. The taxa cluster with small overlap (Figure 2) suggesting the existence of morphometric differences between *C. n. noctivagus* and *C. n. zabele*, the latter with a tendency to have shorter tarsi and broader wing bars.

We also found differences between the two taxa in egg color and shape: eggs of *C. n. noctivagus* are greenish, while those of *C. n. zabele* are bluish; moreover, eggs of *C. n. zabele* are more elongated (greater length/width index; Table 3). However, owing to the small number of available clutches, these differences should be treated as tentative rather than definitive.

TABLE 2. Proportion (%) of specimens of *C. n. noctivagus* and *C. n. zabele* in relation to color characters analyzed. First line shows summed data of all specimens considered. The second line shows data of males and females separately.

Character	Taxa	Dark reddish brown	Reddish brown	Yellow/ Yellowish brown	Pale
Supercilium	*C. n. noctivagus*	4.35 (♂67.41 ♀0)	34.78 (♂37.04 ♀16.67)	41.3 (♂40.74 ♀50)	19.57 (♂14.81 ♀33.33)
	C. n. zabele		10 (♂25 ♀0)	30 (♂25 ♀0)	60 (♂50 ♀100)
Wing barring	*C. n. noctivagus*		2.13 (♂3.85 ♀0)	93.62 (♂92.31 ♀93.33)	4.26 (♂3.85 ♀6.67)
	C. n. zabele			10 (non sexed)	90 (♂100 ♀100)
Tail coverts bars	*C. n. noctivagus*	10.91 (♂9.68 ♀6.67)	89.09 (♂90.32 ♀93.33)		
	C. n. zabele		10 (non sexed)	50 (♂50 ♀66.67)	40 (♂50 ♀33.37)
Throat	*C. n. noctivagus*	9.26 (non sexed)	40.74 (♂16.13 ♀0)	29.63 (♂64.52 ♀66.67)	20.37 (♂19.35 ♀33.33)
	C. n. zabele			20 (♂25 ♀0)	80 (♂75 ♀100)
Abdomen	*C. n. noctivagus*		10.91 (♂12.90 ♀6.67)	69.09 (♂64.62 ♀73.33)	20 (♂22.58 ♀20)
	C. n. zabele			10 (♂0 ♀33.37)	90 (♂100 ♀66.67)

TABLE 3. Mean, maximum and minimum values of each morphometric character analyzed; all values are in centimeters. *p*-values of Student *t*-test were obtained from the comparison of males and females of each taxon separately. Asterisks indicate significant values at $p < 0.05$

Character	Gender	Sample size	*Crypturellus n. noctivagus*			Sample size	*Crypturellus n. zabele*			*p*-value
			Mean (SD)	Max	Min		Mean (SD)	Max	Min	
Wing length	♂	31	18.66 (0.63)	19.60	16.80	4	18.98 (0.59)	19.30	18.10	0.36
	♀	15	18.27 (0.67)	19.50	17.00	3	19.10 (0.36)	19.50	18.80	0.06
Tarsus length	♂	31	54.25 (2.26)	58.05	47.75	4	51.65 (1.50)	53.14	49.86	0.03*
	♀	15	52.72 (2.54)	56.25	46.30	3	51.24 (1.93)	53.31	49.50	0.36
Culmen	♂	31	30.20 (1.97)	34.50	25.15	4	30.29 (1.35)	31.65	28.43	0.93
	♀	15	30.10 (1.78)	33.20	26.65	3	30.26 (1.27)	31.71	29.37	0.89
Beak height	♂	28	6.34 (0.69)	8.80	5.40	3	6.48 (0.27)	6.73	6.20	0.74
	♀	15	6.03 (0.51)	7.10	5.00	2	6.70 (1.07)	7.45	5.94	0.14
Beak width	♂	31	6.71 (0.46)	7.65	5.60	4	6.49 (0.26)	6.81	6.20	0.35
	♀	15	6.52 (0.56)	7.70	5.90	3	6.77 (0.31)	7.10	6.49	0.47
Wing streaks	♂	26	1.70 (0.21)	2.17	1.35	4	2.19 (0.30)	2.60	1.91	<0.01*
	♀	14	1.79 (0.29)	2.42	1.40	3	2.27 (0.32)	2.63	2.05	0.02*
Egg length (L)		8	53.12 (1.74)	56.70	50.69	4	51.68 (1.68)	54.13	50.40	0.20
Egg width (W)		8	43.85 (0.59)	44.80	43.00	4	40.34 (0.78)	41.50	39.84	<0.01*
Egg (L/W ratio)		8	1.21 (0.04)	1.30	1.168	4	1.28 (0.02)	1.30	1.26	0.01*

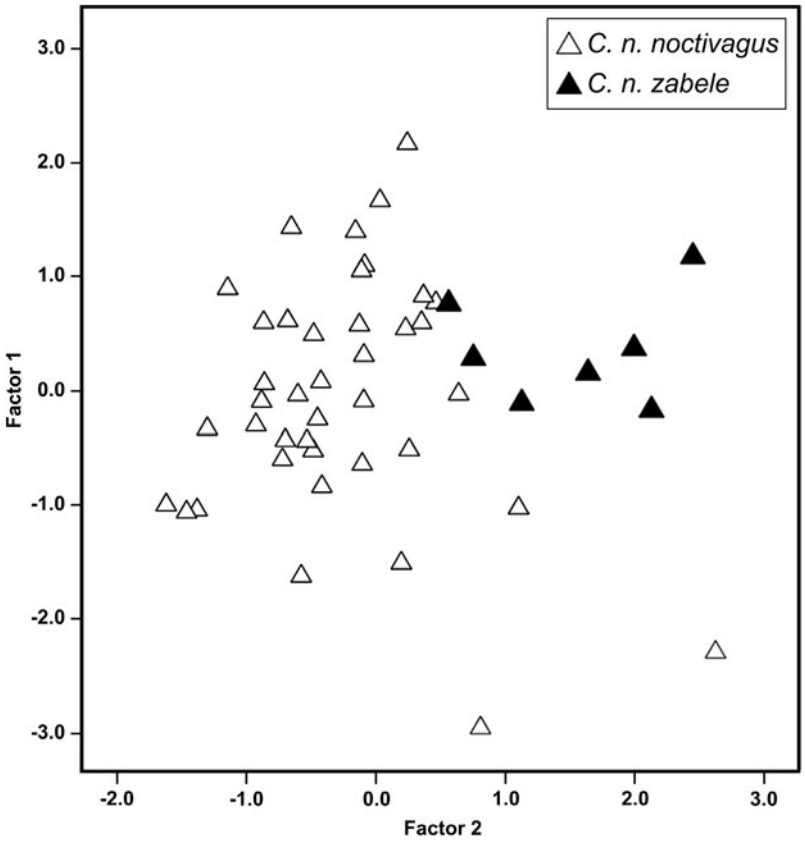

FIGURE 2. Results of the Principal Component Analysis (Eigenvalue: 66.8%), based on morphometrics (wing, tarsus, beak, wing streaks) of *Cryputrellus n. noctivagus* and *C. n. zabele* with each taxa represented by a different symbol.

Spectographic (sonogram) analysis did not show significant differences in the vocal characters analyzed (Table 4). Songs of both *C. n. noctivagus* and *C. n. zabele* consist of three to four notes with equally variable note and internote duration, as well as varied frequency and amplitude time (peak time) (Figure 3). The point of highest amplitude (peak time) can happen on the first or second note, and both patterns appeared in vocalizations of a single individual. Therefore, we analyzed peak time considering the mean of each individual, as was done for

TABLE 4. Mean, maximum and minimum values of each vocal character analyzed with p-values of Student *t*-test comparing the two taxa. Bandwidth is the maximum frequency minus minimum frequency, peak frequency is the frequency at the point of higher amplitude, and peak time is the point in time of highest amplitude (represented as a percentage of the total vocalization). Peak time was calculated for the mean of each specimen vocalizations and for grouped vocalizations in which the highest amplitude was in the first or second note. Not all sonograms allowed precise note distinction; therefore sample size varied for the analysis of note and internote duration.

Vocal character	Sample size	*Crypturellus n. noctivagus*			Sample size	*Crypturellus n. zabele*			*p*-value
		Mean (SD)	Max	Min		Mean (SD)	Max	Min	
Max Freq (Hz)	10	1112.79 (102.22)	1311.45	966	5	1003.38 (135.6)	1106.53	819.10	0.11
Min Freq (Hz)	10	429.78 (101.64)	592.5	291.45	5	413.04 (92.7)	550.98	298.40	0.70
Bandwidth (Hz)	10	683.01 (194.97)	1020	400.7	5	590.34 (211.32)	792.60	346.08	0.41
Peak Freq (Hz)	10	752.24 (72.6)	861.3	689.1	5	684.04 (52.47)	750	602.9	0.08
Total length (s)	10	1.46 (0.12)	1.65	1.34	5	1.44 (0.12)	1.56	1.28	0.67
1st note duration (s)	7	0.56 (0.06)	0.66	0.48	5	0.54 (0.14)	0.75	0.4	0.75
1st space duration (s)	7	0.13 (0.09)	0.26	0.02	5	0.21 (0.03)	0.25	0.18	0.06
2nd note duration (s)	7	0.24 (0.04)	0.29	0.19	5	0.25 (0.04)	0.30	0.19	0.56
2nd space duration (s)	7	0.07 (0.07)	0.21	0.02	5	0.03 (0.03)	0.07	0.00	0.23
3rd note duration (s)	7	0.29 (0.08)	0.4	0.16	5	0.21 (0.06)	0.28	0.15	0.09
3rd space duration (s)	5	0.04 (0.02)	0.07	0.01	4	0.06 (0.05)	0.11	0.01	0.43
4th note duration (s)	5	0.2 (0.08)	0.29	0.09	4	0.19 (0.04)	0.23	0.14	0.83
Peak time - mean (%)	10	27.63 (12.44)	51.33	11.91	5	38.46 (21.87)	61.59	12.82	0.23
Peak time - 1st note (%)	16	20.63 (7.2)	34.1	11.63	7	15.9 (6.78)	31.05	11.25	0.15
Peak time - 2nd note (%)	3	53.62 (12.1)	66.7	42.83	3	61.42 (0.38)	61.67	60.99	0.32

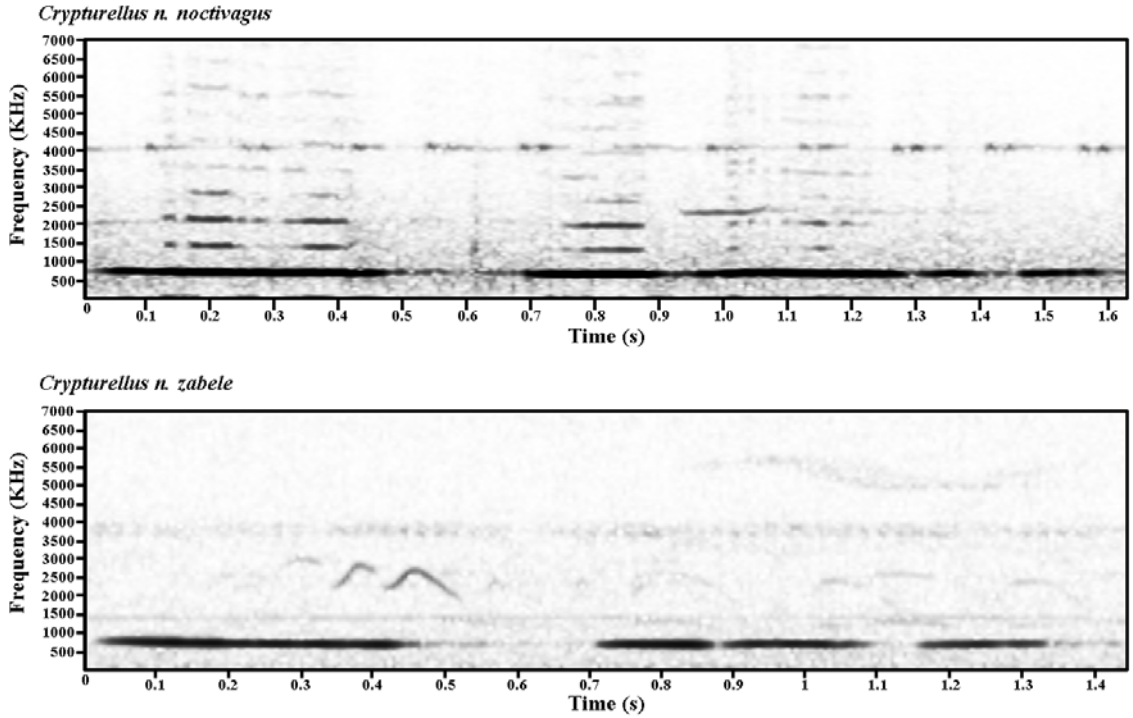

FIGURE 3. Representative sonograms for *C. n. noctivagus* (São Paulo, Itanhaém) and *C. n. zabele* (Bahia, Lagoa Real). The voice of both taxa consists in 3 to 4 notes and appears as black horizontal bars in the sonogram.

other characters, but we also measured it considering each vocalization, grouping vocalizations with the peak time in the first and second note, but significant differences were not found. However, *C. n. zabele* peak time seemed to occur slightly later than the peak time of *C. n. noctivagus*. The voice of *C. n. zabele* also seemed to have a slightly lower frequency than that found in *C. n. noctivagus*, but there was a great overlap between the two taxa.

Regarding distributions, the two taxa do not overlap. *Crypturellus n. zabele* is endemic to the Caatinga, also marginally inhabiting the Cerrado (Figure 4), and occurs in northeastern Brazil from Piauí to northwest Minas Gerais states, whereas *C. n. noctivagus* is endemic to the Atlantic Forest, occurring from Bahia to Rio Grande do Sul states (Figure 4). However, in the present, due to the severe deforestation of the Atlantic Forest, which resulted in its replacement by open, drier vegetation similar to the Caatinga, *C. n. zabele* distribution can be extended closer to the western limits of the nominate form in Espírito Santo and southern Bahia states.

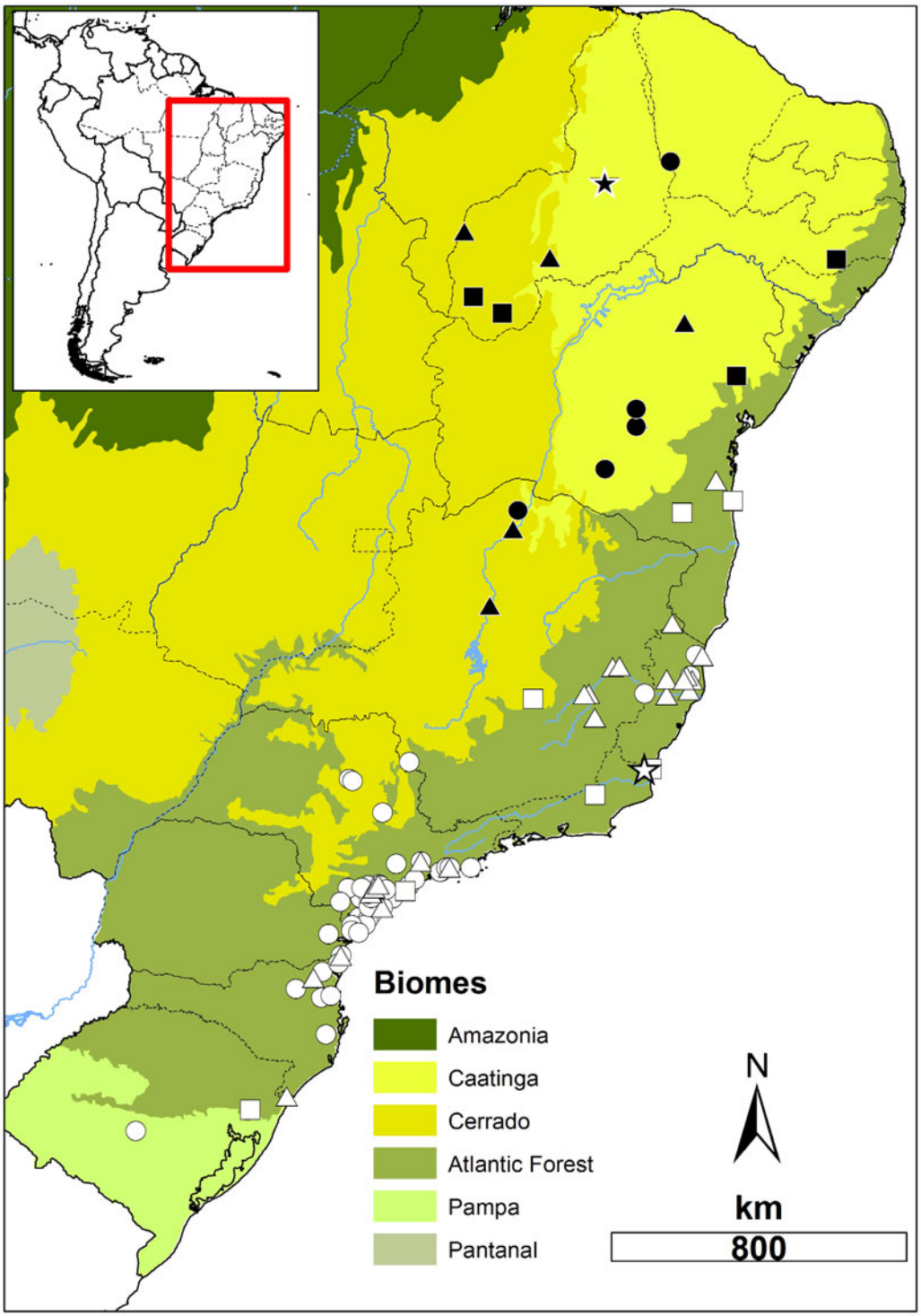

FIGURE 4. Distribution of *C. n. noctivagus* (open symbols), and *C. n. zabele* (closed symbols). **Triangles:** museum specimens (skins); **stars:** Type-localities; **circles:** recent records (literature, photos or vocal records); **squares:** historical records. Biomes according to IBGE & MMA (2004).

DISCUSSION

The overall plumage of *C. n. zabele* is paler than in *C. n. noctivagus* and they also differ in morphometric characters and egg shape and color. However the most striking differences appear when we compare the tarsus coloration and the females' breast plumage. These diagnostic characters are critical to the recognition of these taxa as two distinct, independent lineages, which must be considered as separated species under the Phylogenetic Species Concept.

The first description of a specimen from the *Crypturellus noctivagus* complex was provided by Wied (1820), who described *Tinamus noctivagus* (= *Crypturellus n. noctivagus*) based on a type specimen from Muribeca Farm, Itabapuana River, Espírito Santo state. It was characterized as possessing dark gray-reddish brown upper parts, reddish rust-brown lower back and rump, ashy gray lower neck and rusty-yellow bright brownish breast. The author did not mention tarsus color, and no plate accompanies his description. Five years later, Spix described *Pezus zabelé* (= *Crypturellus n. zabele*) based on a specimen from Oeiras, Piauí state. A plate accompanied the description, where the yellowish wing and tail bars, as well as the yellow legs, can be clearly seen (although the superciliary stripe is absent).

Several authors attempted to analyze these taxa such as Salvadori (1895) and Miranda-Ribeiro (1938), but Hellmayr & Conover (1942) provided the most accurate description to date, with the recognition of two forms: *C. n. noctivagus* and *C. n. zabele*. They noticed that while females of *C. n. zabele* had barred breasts, males of the same subspecies did not, so they recognized the existence of a sexually dimorphic character in this form. Hellmayr & Conover (1942) were unsure about their female analysis, having a single adult female, but our analysis with more specimens allow us to recognize the bars in female breasts as a diagnostic character of *C. n. zabele*. Hellmayr & Conover (1942) also pointed that *C. n. zabele* would be distinguishable from *C. n. noctivagus* due to several paler characters, wings more broadly barred with pinkish buff and distinctive superciliary stripes. We could recognize all these characters in our analysis, but most of them had a small degree of overlap with *C. n. noctivagus*.

Salvadori (1895) treated these two taxa as synonyms under the name *Crypturus noctivagus* and proposed that the species is sexually dimorphic: females were suggested to show more distinct wing barring than males, yellow buff and more barred rump and tail coverts, with the black bars wider and better defined than the chestnut ones, paler yellowish buff or rufescent upper tail covert bars, and more heavily barred flanks, with the brown-black bars extending from the flanks to the sides of the breast. However, Salvadori's description of the male corresponds to *C. n. noctivagus* while the female corresponds to *C. n. zabele* (Hellmayr & Conover 1942). Our data support the conclusions of Hellmayr & Conover (1942).

Miranda-Ribeiro (1938:739, 754) did not consider *C. n. zabele* as valid, but instead reported sexual dimorphism in *C. noctivagus*. He had at hand a very small series (five specimens), and his description of *Orthocrypturus noctivagus* includes characters found in both taxa. Miranda-Ribeiro (1938) indicated that females have a more ochre and distinct superciliary stripe, as well as a more ferruginous neck and upper breast than males. In *C. n. zabele*, the more ferruginous and barred upper breast does occur in females, instead of having the solid gray upper breast observed in females of *C. n. noctivagus*.

Further studies after Hellmayr & Conover (1942) did not expand or deepen the discussion over the taxonomic status of these tinamous. Pinto (1964), however, suggested possible sexual dimorphism in *C. n. noctivagus* based on the presence of black bars on the entire back, rump and tail coverts in females (in males, present mainly in the tail coverts). Nevertheless, according to our analysis, barred back and rump are found in both males and females. Pinto (1964) also mentioned a specimen (MZUSP 14031) as an intermediate form, here classified as a typical *C. n. noctivagus*.

A different explanation for the plumage differences of the two forms would be the Gloger's Rule. It indicates that darker plumage is associated with more humid habitats, and one can also argue that differences in habitat lighting condition can cause different plumage coloration in birds, such as red or orange in closed habitats (McNaught & Owens 2002). Indeed, the humid forest inhabitant *C. n. noctivagus* is darker in plumage than *C. n. zabele*, which inhabits the open, sunny Caatinga.

However, we noticed consistent diagnostic characters such as the tarsus color and the breast plumage of females, along with a distinct, non-overlapping distribution, and habitat preferences. Therefore, these taxa can be recognized as distinct species under the Phylogenetic Species Concept, and hereafter would be treated as such. The recognition of the two forms under the Biological Species Concept (BSC) is less evident. However, the presence of sexual dimorphism only in *C. zabele,* differences in eggs' color and shape, and absence of hybrids even in areas where the distribution of two taxa approaches suggests that these two closely related forms could be reproductively isolated and that could be also recognized as a full species under the BSC.

This revised taxonomic status may be important for future conservation efforts, including captive breeding and reintroductions. *Crypturellus noctivagus* is considered threatened in Brazil and also São Paulo, Paraná and Rio Grande do Sul states (Straube *et al.* 2004, Tomotani

2010, Corrêa *et al*. 2010, MMA 2014) and is probably extinct in Rio de Janeiro (Pacheco *et al*. 1996), with hunting and deforestation being the main causes for the population decrease. *Crypturellus zabele,* although still quite common in some national parks such as Serra das Confusões (Silveira & Santos 2012), is also threatened at national level (MMA 2014). We also speculate that the destruction of the Atlantic Forest in eastern Brazil, where it is being replaced by more open, secondary vegetation, could contribute for a south/eastward expansion of *C. zabele* in areas originally dominated by Atlantic Forest (and thus previously inhabited by *C. noctivagus*).

TAXONOMY

This section summarizes our taxonomic recommendation and provides revised diagnoses for the taxa involved.

Crypturellus noctivagus (Wied, 1820)

Tinamus noctivagus Wied 1820: 158 (footnote).

Crypturus noctivagus: Tschudi 1844: 307 (n. 277); Burmeister 1856: 320; Reinhardt 1870: 47; Salvadori 1895: 539.

Nothocercus noctivagus: Bonaparte 1856: 881.

Crypturellus noctivagus noctivagus: Peters 1931: 22; Pinto 1938: 8; Hellmayr & Conover 1942: 59; Pinto 1964: 09; Grantsau 2010: 15 (pl. 2).

Orthocrypturus noctivagus: Miranda-Ribeiro 1938: 754.

Holotype: AMNH 6740 (♂, Muribeca, Espírito Santo state; examined).

Common name

Portuguese (Brazil): *jaó-do-sul*. English: Yellow-legged Tinamou. *C. noctivagus* and *C. zabele* share the popular "Yellow-legged Tinamou" name, but only the latter show such coloration; *C. noctivagus* has olivaceous legs and the English name should be adjusted for this species.

Diagnosis

Distinguished from *C. zabele* by solid gray upper breast in females and olivaceous tarsus. Also generally darker and/or more reddish overall coloration than *C. zabele*, especially in the wing and tail covert bars, but also commonly seen in the abdomen and throat. Usually thinner wing covert light bars. Superciliary stripe usually smaller, thinner and less marked. Eggs more rounded and greenish than in *C. zabele*.

Re-description

Crown and nape until back black, dark reddish brown or dark grayish brown. Superciliary stripe variable in width and length, usually small; reddish brown, yellowish brown or pale colored. Throat color from pale to reddish brown. Upper portion of breast dark grayish brown, grayish brown or dark reddish brown. Lower portion of breast reddish brown or yellowish brown. Abdomen from reddish brown to yellowish brown or pale. Wing pattern: alternating black or dark reddish brown bars and reddish brown, yellowish brown or pale bars (pattern may uncommonly consist of non-distinguishable black or dark reddish brown and yellowish brown irregular markings and spots instead of defined bars). Tail coverts pattern: alternated black or dark reddish brown bars and reddish brown bars (same color as lower portion of rump). Males usually redder. Tarsus olivaceous. Eggs greenish.

Distribution

Atlantic Forest, from southern Bahia (coastal lowlands), Espírito Santo and eastern Minas Gerais to Rio Grande do Sul states. No specimen from Rio de Janeiro state was found in collections, but Pacheco *et al*. (1996) list the species for this state. The species is considered threatened in São Paulo and Paraná (Straube *et al.* 2004, Tomotani 2010), probably extinct in Rio de Janeiro (Pacheco *et al*. 1996) and was considered extinct in Rio Grande do Sul (Bencke *et al*. 2003), until the recent record in a gallery forest (Corrêa *et al*. 2010).

Examined material (n = 67)

Bahia: Gongogi River (MZUSP 14031 ♂). **Minas Gerais:** Mairinque (MZUSP 7792 ♀); Doce River, Governador Valadares (MNRJ 22340 ♂); Doce River, Baixo Suaçuí (MZUSP 24470 juvenile ♂, 24471 ♂, 24796 ♂, 24797 ♂, 24798 nd, 24799 nd, 24804 ♂); Doce River (right margin), Baixo Piracicaba (MZUSP 24466 ♀, 24467 ♂, 24468 ♂, 24469 ♀); Doce River (right margin) (MZUSP 24462 ♀, 24463 ♀, 24464 nd, 24465 ♂, 24800 ♂, 24801 ♀, 24802 ♂, 24803 ♂); Raul Soares (MNRJ 25489 ♂, 25490 ♂). **Espírito Santo:** Muribeca (AMNH 6740 ♂, holotype); Fazenda Boa Lembrança, Itaúnas River, Conceição da Barra (MNRJ 39739 ♂); Cupido, Linhares (MNRJ 26798 ♀, 26799 ♀); Córrego Cupido, Barra Seca River, Sooretama (MNRJ 39586 ♂); São José River (MZUSP 28054 ♂, 28055 ♀); São Domingos (MNRJ 19404 ♂); Linhares (MNRJ 26264 ♂); Rancho Fundo, Colatina (MNRJ 19402 ♀, 19405 juvenile ♀), not specified (AMNH 317184 ♂; MNRJ 19401 nd, 19403 ♂, 19406 nd). **São Paulo:** Varjão do Guaratuba (right

margin) (MZUSP 43761 ♂); Ipiranga (MZUSP 49335 ♂); Iguape (AMNH 469092 ♂, 469093 nd; MZUSP 245 - 2 eggs); Barra das Corujas River (MZUSP 56384 ♀); Rocha, Ribeirão Fundo (MZUSP 49332 ♂, 49333 ♀, 49334 ♀, 2257 - 5 eggs); Ipiranga River, Tamanduá, Juquiá (MZUSP 47486 nd, 47487 nd); Primeiro Morro (MZUSP 49331 ♀); Fazenda Poço Grande, Juquiá River (MZUSP 24374 ♂, 24375 juvenile nd, 24376 juvenile nd, 24377 ♂, 24378 ♂). **Paraná:** Limeira, Serra da Prata, Guaratuba (MHNCI 4387 ♀). **Santa Catarina:** Colônia Hansa (MZUSP 1906 nd). **Rio Grande do Sul:** Lagoa do Morro do Forno, Dom Pedro de Alcântara (AMNH 313713 ♂, 313714 ♂); not specified (MZUSP 1955 – 1 egg).

Crypturellus zabele (Spix, 1825)

Tinamus noctivagus: Wied 1821: 111 (*non* Wied, 1820).

Pezus Zabelé Spix, 1825: 62 (pl. 77).

Crypturus noctivagus: Wagler 1827: 19, sp. 6; Tschudi 1844: 307 (n. 277); Burmeister 1856: 320; Forbes 1881: 360; Salvadori 1895: 539; Hellmayr 1906: 701.

Nothocercus noctivagus: Bonaparte 1856: 881.

Crypturornis noctivagus noctivagus: Hellmayr 1929: 477.

Crypturellus noctivagus noctivagus: Peters 1931: 22; Pinto 1935: 54; Pinto 1938: 8.

Orthocrypturus noctivagus: Miranda-Ribeiro 1938: 754.

Crypturellus noctivagus zabele: Hellmayr & Conover 1942: 60; Pinto 1964: 09; Grantsau 2010: 15 (pl. 2).

Holotype: ZSM unnumbered (♂, Oeiras, Piauí; examined). The original (Spix, 1825) reads "in limite sylvarum campestrium (Catingha)". Hellmayr & Conover (1942) suggested the type locality Oeiras.

Common name

Portuguese (Brazil): *zabelê*. English: Yellow-legged Tinamou.

Diagnosis

Distinguished from *C. noctivagus* by grayish barring on upper breast of females and by pure yellow tarsus. Also generally paler coloration than *C. noctivagus*, never so red; light bars on wing coverts broad; and more marked difference between color of tail covert bars (pale) and rump covert bars (reddish brown). Superciliary stripe usually broader, longer and more marked. Eggs bluish, apparently more elongated than in *C. noctivagus*.

Re-description

Crown and nape until back black, dark reddish brown or dark grayish brown. Superciliary stripe large and broad, yellowish brown or pale. Throat pale or yellowish brown. Upper portion of breast dark grayish brown or grayish brown in males; grayish bars in a reddish brown or yellowish brown background in females. Lower portion of breast reddish brown or yellowish brown. Abdomen yellowish brown or pale. Wing pattern: alternating black or dark reddish brown bars and large pale bars. Tail coverts pattern: alternating black or dark reddish brown and pale or yellowish brown bars (gradually darken and/or become redder until rump). Tarsus yellow. Eggs bluish.

Distribution

Mainly in Caatinga, from Piauí to northern Minas Gerais states, does not occur on coastal lowlands. Records from the literature indicate that the species was also found in Pernambuco state (Forbes 1881), however no specimen from this region was found in museum's collections.

Examined material (n = 17)

Piauí: Oeiras (ZSM no number ♂ holotype); Correntes (AMNH 240962 ♂, 240963 ♂, 240964 ♀); P.N. Serra das Confusões (MZUSP 77621 nd). **Bahia:** Vila Nova (MZUSP 7603 ♂, 7604 ♂, 7606 juvenile ♂, 183 - 4 eggs); Macaco Seco, Andaraí (FMNH 47486 ♂); not specified (AMNH 469094 ♀, 469095 nd). **Minas Gerais:** Gruta do Tatu - São Francisco (MNRJ 4510 nd); Rio São Francisco, Pirapora (MZUSP 8496 ♀).

Additional examined material

Without locality (n = 4): AMNH 185893; MNRJ 4509, 4511, 4512.

Captivity (n = 3): MHNCI 2024 nd; MNRJ 33187 juvenile nd, 39740 nd.

Vocalization (voc), photography (pho) and historical record (hr) examined for vocal analysis (^{v}) and/or map confection (^{m}) with respective number of recording, author, year and source.

Crypturellus noctivagus **(n = 24): Minas Gerais:** Rio Doce State Park (XC1223 voc^{vm}, Jones D. 1997, Xenocanto; XC85039 voc^{vm}, Minns J. 1997, Xenocanto); Lagoa dos Patos (hr^{m}, Salvadori 1895). **Rio de Janeiro:** Cantagallo (hr^{m}, Euler 1867 *apud* Hellmayr & Conover

1942). **São Paulo:** Bertioga (vocalization[vm] from 2008 provided by Cavarzere V.); Cananéia (WA329285 voc[m], Souza M.J. 2010, Wikiaves); Carlos Botelho State Park (XC4902 voc[m], Planqué C. 2005, Xenocanto); Curucutu, Itanhaém (vocalization[vm] from 2007 provided by Schunck F.); Eldorado (WA251118 voc[m], Kaseker E.P. 2010, Wikiaves) Ibiúna (WA504913 voc[m], Mervinskas M. 2011, Wikiaves); Guaratuba (WA105021 voc[vm], Kaseker E.P. 2010, Wikiaves); Pariquera-Açu (WA585083 pho[m], Souza M.J. 2012, Wikiaves) Peruíbe (WA551282 voc[m], Faitarone A. 2012, Wikiaves); Registro (WA482781 voc[vm], Sanches D. 2011, Wikiaves); São Sebastião (WA519772 voc[vm], Lopes B.J. 2011, Wikiaves); Sítio do Cervo, Miracatu (XC18996 voc[vm], Hirsch T. 2008, Xenocanto). **Paraná:** Guaraqueçaba (WA480308 voc[vm], Deconto L.R. 2011, Wikiaves); Guaratuba (WA576531 voc[m], Gussoni C. 2012, Wikiaves); Mãe Catira (XC92171 voc[m], Luijendijk T. 2011, Xenocanto) **Santa Catarina:** Blumenau (WA221952 voc[m], Legal E. 2009, Wikiaves); Ilhota (WA484960 voc[m], Encarnação J. 2011, Wikiaves); Reserva Volta Velha, Itapoá (XC28292 voc[vm], Patrial E. 2008, Xenocanto). **Rio Grande do Sul:** Arroio Grande, near Taquara (hr[m], Berlepsch & Ihrering, 1885 *apud* Hellmayr & Conover, 1942); São Sepé (WA533224 pho[m], Corrêa L.L.C. 2011, Wikiaves); Taquara do Mundo Novo (hr[m], Berlepsch & Ihrering, 1885 *apud* Hellmayr & Conover, 1942).

Crypturellus zabele **(n = 11):** Piauí: Gibués (hr[m], Hellmayr & Conover 1942) Parnaguá (hr[m], Hellmayr & Conover 1942). Ceará: RPPN Olho D'água do Urucu, Parambu (XC13536 voc[vm], Albano C. 2007, Xenocanto). Pernambuco: Garanhuns (hr[m], Forbes 1881). Bahia: Boqueirão, Rio Pardo (hr[m], Wied 1821); Lagoa Real (XC40027 voc[vm], Albano C. 2009, Xenocanto); Lamarão (hr[m], Hellmayr & Conover 1942) Lençóis (XC15592 voc[m], Athanas N. 2007, Xenocanto); Mucugê (XC82085 voc[vm], Santos S.S. 2003, Xenocanto). Minas Gerais: Cavernas do Peruaçu National Park (XC11923 voc[vm], Beadle D. 2002, Xenocanto; XC85041 voc[vm], Minns J. 2002, Xenocanto).

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