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ARTICLE

Taxonomy and molecular systematics of the Yellow-green Grosbeak *Caryothraustes canadensis* (Passeriformes: Cardinalidae)

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ABSTRACT: The Yellow-green Grosbeak *Caryothraustes canadensis* is a South American passerine occurring in Amazon and Atlantic Forests. Currently, it comprises four subspecies: *Caryothraustes canadensis canadensis*, *Caryothraustes canadensis brasiliensis*, *Caryothraustes canadensis frontalis* and *Caryothraustes canadensis simulans*. No study has ever revisited its taxonomy, hindering a complete understanding of the available diversity in *Caryothraustes canadensis* complex. We examined color and morphometric variation in 259 scientific specimens and sequenced the mitochondrial gene ND2 of 29 tissue samples. We also quantitatively and qualitatively analyzed 52 spectrograms of vocal recordings. Molecular analyzes demonstrated the existence of two divergent lineages in *C. canadensis* complex, one from Amazonia and the other in the Atlantic Forest, which can also be distinguished by morphometric and plumage characters. Here we propose that the *C. canadensis* complex is composed of two full species: *C. canadensis* and *C. brasiliensis*. *Caryothraustes canadensis frontalis* shows no reciprocal monophyly in the phylogenetic analyzes, despite having weak plumage diagnostic characters; therefore, we suggest it should be considered a synonym of *C. brasilensis*.

KEY-WORDS: Amazon, Atlantic Forest, genetic analysis, Oscines, Pernambuco Endemism Center, phylogeny, vocal analysis.

INTRODUCTION

Caryothraustes canadensis was described by Linnaeus (1766) based on a plate of a yellow-bellied, black masked bird individual from Cayenne, French Guiana (not Canada as erroneously interpreted and used to name the species; Brewer 2016a). Long after, one related species with a distinctive gray belly and occurring in Central America – *Caryothraustes poliogaster* (Du Bus de Gisignies, 1847) – was described (Klicka *et al.* 2007, Brewer 2016b). Besides *C. canadensis* and *Caryothraustes poliogaster*, the genus had already included the Yellow-shouldered Grosbeak *Caryothraustes humeralis* (Lawrence, 1867). However, based on molecular analysis, *C. humeralis* is now in the monotypic genus *Parkerthraustes* (Remsen-Jr. 1997), family Thraupidae, while the genus *Caryothraustes* is allocated in the family Cardinalidae (Burns *et al.* 2014, Piacentini *et al.* 2015).

Currently, the Yellow-green Grosbeak comprises four subspecies of small-size (~17 cm) passerines, all of which inhabit the canopy of tropical lowland forests in Central and South America where they forage for fruits and seeds and emit a loud song (Brewer 2016a). *Caryothraustes canadensis canadensis* (Linnaeus, 1766) occurs in parts of the Brazilian Amazon Forest, Colombia, French Guiana, Guyana, Suriname and Venezuela. Other two sub-species are restricted to the Brazilian Atlantic Forest (Brewer 2016a): *Caryothraustes canadensis brasiliensis* Cabanis, 1851 occurs in eastern Brazil in the states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro, and *Caryothraustes canadensis frontalis* (Hellmayr, 1905) is endemic to the Pernambuco Endemism Center, *i.e.* the Atlantic Forest north of the São Francisco River (Silva *et al.* 2004, Brewer 2016a). Cabanis (1851) separated *C. c. brasiliensis* from *C. c. canadensis* based on its brighter yellow forehead and Hellmayr (1905) described *C. c. frontalis* based on the unique black-strip on the forehead. Ultimately, *Caryothraustes canadensis simulans* is exclusive to northern South America and Central America and was described based mostly on brighter colors, comprising more golden yellow on forehead, more yellowish olive green on back and larger and heavier bill (Nelson 1912, Brewer 2016a, b).

No other study has ever reanalyzed the taxonomy of this group, hindering a complete understanding of the diversity in *Caryothraustes canadensis* complex. Taxonomic

studies are of paramount importance in delimiting species and indicating the true diversity of a given region, aiding studies of phylogeny and biogeography (Silveira & Olmos 2007). Moreover, they are crucial to biodiversity conservation, as conservation programs frequently ignore threatened taxa at the subspecific or population levels (Zink 2004, Aleixo 2007). Accordingly, our aim was to integrate molecular data with traditional plumage coloration, morphometric and vocal data of the Yellow-green Grosbeak to revise the taxonomy of this species.

METHODS

Taxon sampling and laboratory procedures

Genetic analysis was conducted using tissue samples of 29 specimens of three subspecies of the Yellow-green Grosbeak, *C. c. brasiliensis* (*n* = 11), *C. c. frontalis* (*n* = 7), *C. c. canadenis* (*n* = 11). Vouchers are housed in the following institutions: *Museu de Zoologia da Universidade de São Paulo* (MZUSP, Brazil), Field Museum of Natural History (FMNH, EUA) and *Museu Paraense Emílio Goeldi* (MPEG, Brazil) (Table 1). We also added sequences available on Genbank for *C. c. simulans* (EF529916.1), *Caryotrhaustes poliogaster poliogaster* (EF529915.1), *Periporphyrus erythromelas* (EF529919.1), *Rhodothraupis celaeno* (EF529920.1) and *Cardinalis cardinalis* (JF795780.1). The last three were used as outgroups following Klicka *et al*. (2007) and *Cardinalis cardinalis* was used to root the trees.

Total genomic DNA was extracted using the Genomic DNA Mini Kit (Invitrogen). The mitochondrial molecular marker NADH Dehydrogenase Subunit 2 (ND2, 1041 bp) was amplified using primers L5215, H6313, L5758, H5766 (Hackett 1996, Sorenson *et al*. 1999) mitochondrial DNA (mtDNA. Polymerase chain reaction (PCR) amplifications were performed using an initial denaturation step at 94ºC for 2 min, followed by 35 cycles of 94ºC for 1 min, a 30 s annealing step at 50ºC, and a 72°C extension for 1 min, and the final extension was at 72°C for 7 min. In a 25 μL total volume, PCR amplifications contained approximately 20 ng of genomic DNA, buffer 10 ×, 200 mM of DNTPs, 1.5 mM of $MgCl_2$, 0.4 μM of each primer (forward and reverse), 0.2 × of BSA, and 0.1 U of Platinum™ *Taq* DNA Polymerase (Invitroven). PCR products were visually inspected in a 1% agarose gel, after electrophoresis, and positive results were purified using PEG precipitation protocol. Sequencing was carried out on an ABI 3130 automated capillary sequencer (Applied Biosystems) with the ABI Prism Big Dye terminator Kit. Both strands and one internal primer of each sample were sequenced. Sequences were edited and aligned using Geneious v. 9.1.2 (2016), it was checked if the sequences did not include stop codes or anomalous base, the alignment was performed using MAFFT v. 7 (Katoh *et al.* 2005) H-INS-i, F-INS-i and G-INS-i, in which pairwise alignment information are incorporated into objective function. These new options of MAFFT showed higher accuracy than currently available methods including TCoffee version 2 and CLUSTAL W in benchmark tests consisting of alignments of >50 sequences. Like the previously available options, the new options of MAFFT can handle hundreds of sequences on a standard desktop computer. We also examined the effect of the number of homologues included in an alignment. For a multiple alignment consisting of \u223c8 sequences with low similarity, the accuracy was improved (2\u201310 percentage points plug-in at Geneious.

Phylogenetic analyses

Phylogenetic relationships among individuals were inferred using the Maximum Likelihood (ML) in RAxML v. 7.2.7 (Stamatakis 2006), and Bayesian Inference (BI) in MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003), both on Cipres Science Gateway v. 3.1 (Miller *et al.* 2010). The best-fitting model of evolution for BI analysis was estimated using the Bayesian Information Criterion (BIC) in jModelTest v. 2.1.6 (Darriba *et al.* 2012) and HKY+G were selected as the best fitting model. BI analysis was performed using two independent runs with 10,000,000 generations each, 4 chains, the parametres and the trees were be sampled every 1000 generations and the burn-in was 20%, the posterior probabilities for each estimated node were obtained through a majority rule consensus of the remaining MCMC samples. ML analysis was done using a GTR-GAMMA model, with 100 independent searches, nodal support was estimated with 1000 bootstrap replicates. Additionally, mean pairwise *p*-distances among populations were calculated in MEGA v. 7.0 (Kumar *et al*. 2016).

Taxonomic assessment

Supported clades in the phylogenetic analyses were used as a priori clades for the study of phenotypic diagnostic characters. We examined a total of 163 skins of the three *C. canadensis* subspecies (107 belonging to *C. c. canadensis*, 19 to *C. c frontalis* and 37 to *C. c. brasiliensis*) housed in the *Museu de Zoologia da Universidade de São Paulo* (MZUSP, Brazil) and the *Museu Paraense Emílio Goeldi* (MPEG, Brazil) (see Appendix I). We did not have personal access to *C. c. simulans*, what prevented us to include this taxa in this review. By the time this research was conducted, a spectrometer was not available, restricting colorimetric analysis to comparisons to color

Table 1. Voucher information of *Caryothraustes canadensis* tissue samples.

Museum	Taxon	Locality
MZUSP 91568	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Mata do Pacange, Reserva Michelin
MZUSP 91569	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Mata do Pacange, Reserva Michelin
MZUSP 98351	*Caryothraustes canadensis brasiliensis*	Brazil, Espirito Santo, Reserva Florestal CVRD
MZUSP 98352	*Caryothraustes canadensis brasiliensis*	Brazil, Espirito Santo, Reserva Florestal CVRD
MZUSP 98350	*Caryothraustes canadensis brasiliensis*	Brazil, Espirito Santo, Reserva Florestal CVRD
MZUSP 101537	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Camacan, Serra das Lontras
MZUSP 101536	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Camacan, Serra das Lontras
MPEG 70826	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Ilheus Ecoparque de UNA
MPEG 70827	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Ilheus Ecoparque de UNA
MPEG 70825	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Ilheus Ecoparque de UNA
MPEG 79859	*Caryothraustes canadensis brasiliensis*	Brazil, Bahia, Amargosa, Serra do Timbo
MZUSP 96547	*Caryothraustes canadensis canadensis*	Brazil, Amazonas, Sucunduri River (right margin), in front of Castanho Island
MZUSP 96548	*Caryothraustes canadensis canadensis*	Brazil, Amazonas, lower Canuma River (right margin)
MZUSP 96549	*Caryothraustes canadensis canadensis*	Brazil, Amazonas, lower Canuma River (right margin)
MPEG 65547	*Caryothraustes canadensis canadensis*	Brazil, Pará, Alenquer, ESEC Grao-Para
MPEG 65661	*Caryothraustes canadensis canadensis*	Brazil, Pará, Itaituba, FLONA Amaná, right margin Amana River
MPEG 65660	*Caryothraustes canadensis canadensis*	Brazil, Pará, Itaituba, FLONA Amaná, right margin Amana River
MPEG 66890	*Caryothraustes canadensis canadensis*	Brazil, Pará, Faro, Maracana Village, Xingu River
MPEG 74145	*Caryothraustes canadensis canadensis*	Brazil, Pará, Santarém, RESEX Tapajos/Arapiuns Capixaua
MPEG 74146	*Caryothraustes canadensis canadensis*	Brazil, Pará, Santarém, RESEX Tapajos/Arapiuns Capixaua
MPEG 74147	*Caryothraustes canadensis canadensis*	Brazil, Pará, Santarém, RESEX Tapajos/Arapiuns Capixaua
MPEG 76879	*Caryothraustes canadensis canadensis*	Brazil, Maranhão, Centro Novo, REBIO Gurupi
MZUSP 98475	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, São Miguel dos Campos, Usina Porto Rico
FMNH 427231	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra
FMNH 427232	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra
FMNH 427233	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra
FMNH 427234	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra
MPEG 70547	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra
MPEG 70548	*Caryothraustes canadensis frontalis*	Brazil, Alagoas, Ibateguara, Usina Serra Grande, Engenho Coimbra

catalogues. To standardize color analyses, only VRT compared forehead, crown, nape, back, rump, rectrices, throat, malar, ear coverts, breast, belly and primaries colors with a Villalobos & Villalobos (1947) color chart for all museums specimens analyzed and under the same light conditions.

We collected measurements of exposed culmen, distance between nostril and bill tip, lower jaw width, right tarsus, right wing chord (*i.e.* closed wing-lenght) and tail length with a caliper (precisions of 0.005 mm) and a ruler (for wing and tail measurements with a precision of 0.5 mm).

An additional 97 specimens housed in Muse*u de Biologia Professor Mello Leitão* (MBML, Brazil; 22 *C. c.*

brasiliensis), Mus*eu Nacional da Universidade Federal do Rio de Janeiro* (MNRJ, Brazil; 9 *C. c. brasiliensis*, 5 *C. c. canadensis* and 2 *C. c. frontalis*), *Colección Ornitológica Phelps* (COP, Venezuela; 39 *C. c. canadensis*), Museum of Natural Science of the Louisiana State University (LSUMZ, USA; 11 *C. c. canadensis* and 1 *C. c. simulans*), *Muséum National d'Histoire Naturelle* (MNHN, France; 4 *C. c. canadensis*) and *Museum für Naturkunde* (ZMB, Germany; 5 *C. c. canadensis*; Appendix I) were examined via high quality pictures taken by some of us and colleagues (see Acknowledgements). All specimens were photographed under white light. Although we did not compare the plumage of those individuals with color chart, we used their photographs as a *post hoc* analysis following valid species delimitation, aiming to confirm the usefulness of the putative diagnostic characters.

Vocal analysis

Following Catchpole & Slater (2008), we defined a note as a continuous line on spectrogram and a phrase as a sequence of similar notes followed each other by a short interval of time. Because the species emits two different types of phrase (defined here as Type-I and II; Fig. 1), we analyzed them separately. Type-I phrase is composed by "whistled" notes, and Type-II is composed by shorter notes followed each other by a very short time lapse, popularly known as "trill" (Fig. 1). We measured the maximum frequency (MaF), minimum frequency (MiF), bandwidth (BW), peak frequency (pF) and time duration for each single note in Type- I phrases and for all Type-II phrases and for all Type-II phrases as if they were a single note (Charif *et al.* 2010). We also counted the number of notes (NN) for all phrases.

Besides the quantitative measurements cited above, we analyzed the aspect of Type-I notes, shaped by frequency modulation. Frequency modulation occurs when the direction of frequency changes in y-axis of the spectrogram, thus causing inflections in the note (*i.e.* frequency modulation changes from ascending to descending or vice versa; Catchpole & Slater 2008). We used frequency and time resolution of 46.9 Hz and 1.06 ms respectively, and the qualitative analyses were performed using the same window size to avoid shape distortions in notes used in qualitative analysis (Charif *et al.* 2010). All notes were analyzed in black and white.

To perform vocalization analysis, we used RAVEN PRO v. 1.4 (Charif *et al.* 2010). From the 92 original recordings, only 52 (25 of *C. c. canadensis*, 17 of *C. c. brasiliensis* and 10 of *C. c. frontalis*) had a reasonable quality needed for analysis, *i.e.*, allowed accurate measures. Recordings were obtained from the following sound archives: Macaulay Library of Natural Sounds (CORNELL, Cornell University, USA); *Arquivo Sonoro Elias Coelho* (ASEC, UFRJ, Brazil); *Fonoteca Neotropical Jacques Vielliard* (FNJV, UNICAMP, Brazil); Xeno-Canto (XC, http://www.xeno-canto.org); and also from researchers who provided their personal recordings (see Appendix II). To measure MaF, MiF, BW, pF and duration we used only WAV sound files due their high quality and precision, and we used WAV as well as MP3 files to count NN and analyze note shapes.

Vocal and morphometric statistics

We assayed for morphometric and vocal differences between populations using parametric tests, when data showed normality and homoscedasticity, or their non-parametric equivalents when these two assumptions were not fulfilled (Gotelli & Ellison 2012). Analysis of variance (ANOVA; parametric) or Kruskal-Wallis (non-parametric) were used to compare morphometric and vocal differences between groups. The Tukey test, or its non-parametric equivalent Newman-Keuls, was used as *post hoc* tests to investigate for significant pairwise differences. Sexual dimorphism within putative groups was tested using the Student's *t* or Wilcox tests. We used 0.05 as critical value of *p* and we did not use any *p*-value corrections (*e.g.* Bonferroni) as this kind of correction is extremely conservative and its use has been discouraged

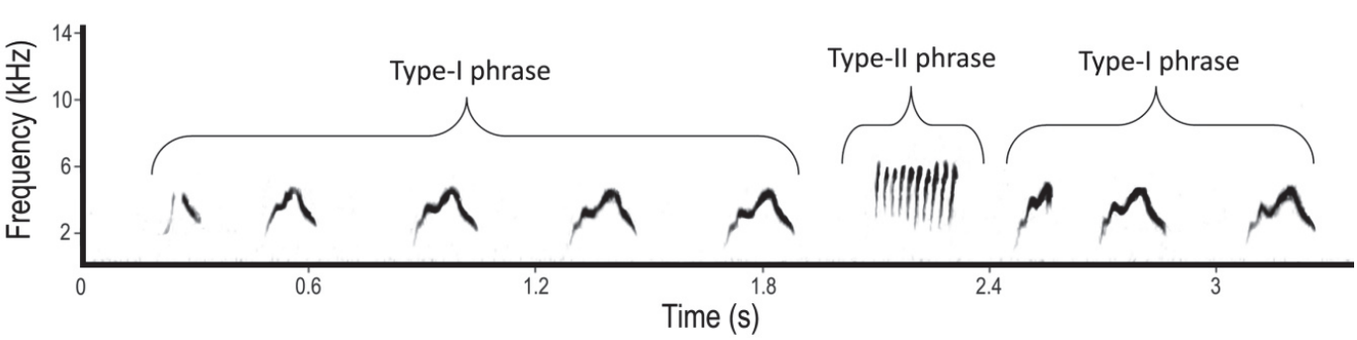

Figure 1. Spectrogram exemplifying a song (CORNELL 127847) with two Type-I and one Type-II phrases.

by some authors (Nakagawa 2004, Gotelli & Ellison 2012). To assess diagnosability between clades indicated by phylogenetic trees, we log-transformed measurements for all the individuals studied and conducted discriminant function analyses (DFA) in R software v. 3.2.2 (R Core Team 2017), clustering groups by 95% confidence intervals. Except for the Newman-Keuls test (performed in the "agricolae" package in the R software; Mendiburu 2015), we performed statistical analyses in the package "stats" (R Core Team 2017).

RESULTS

Molecular analysis

Maximum-likelihood and Bayesian analyses produced similar topologies with high support, indicating that both Atlantic Forest taxa belong to the same clade (Fig. 2). *Caryothraustes c. frontalis* and *C. c. brasiliensis* are closely related, with only 0.3% of mitochondrial divergence (mean *p*-distance, Table 2). On the other hand, individuals of *C. canadensis* from the Madeira-Tapajós interfluvium show 6.3% of mitochondrial divergence from *brasiliensis/frontalis*. Phylogenetic trees also indicate that *canadensis* is not a monophyletic group, since it comprises *C. c. simulans* and the *C. brasiliensis/frontalis* clade. In this sense, two distinct groups of *C. canadensis* form distinct Amazonian clades, one sister to the Atlantic form, restricted to the southern Amazon (from left bank of Madeira to both banks of Tapajós River, herein called population 1), and one containing individuals from northern and eastern Amazon Forest (population 2).

Morphometric analysis

Morphometry indicated higher similarity between birds from Atlantic Forest sites than those and Amazonian locations. Except for the exposed culmen length, measurements did not differ significantly between the two Atlantic Forest lineages ($P < 0.05$; Table 3). The discriminant analysis of morphometric variation (Fig. 3) showed that the clades *canadensis* population 2 and *brasiliensis/frontalis* are diagnosable mainly by differences in exposed culmen and wing length (factor 1). The clade *canadensis* population 1 overlaps in size with *brasiliensis/frontalis*, its sister group.

Plumage variation

Individuals from the Amazon Basin showed olive forehead coloration ranging mainly from Y-12°-6 (MZUSP 46064) to Y-12°-9 (MZUSP 46059; Fig. 4). There is weak plumage diagnosis between the two Amazonian clades pointed by phylogenetic trees, although the olive head distinguishes both from the Atlantic forms.

Although showing no genetic distinctiveness, the subspecies *C. c. frontalis* and *C. c. brasiliensis* show consistent differences in forehead color. Birds from the Atlantic Forest south of the São Francisco River, in Brazilian states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro can be distinguished by a bright-yellow forehead (YYO-12°-10; MZUSP 6274, or YYO-12°-11; MZUSP 24675). Forehead color did not vary in individuals from the Pernambuco Endemism Center; all birds from this region exhibited a discrete black forehead (Fig. 4). For specimens from the Amazon and Atlantic

Table 2. Genetic *p*-distance (%) between *Caryothraustes canadensis* subspecies estimated using NADH dehydrogenase 2 (ND2) sequences. *Caryothraustes canadensis canadensis* was divided into the two populations evidenced in the phylogenetic analyzes.

	C. c. brasiliensis	***C. c. frontalis***	***C. p. simulans***	***C. c. canadenis* (population 1)**
C. c. brasiliensis				
C. c. frontalis	0.3			
C. c. simulans	6.7	6.6		
C. c. canadensis (population 1)	6.2	6.1	6.5	
C. c. canadensis (population 2)	6.4	6.3	5.8	5.5

Table 3. Morphological measurements (in mm) as mean ± standard deviation and range in parenthesis for each sampled taxa.

Taxon	Culmen	Bill length	Bill width	Jaw height	Tarsus	Wing	Tail
C. c. canadensis	15.36 ± 0.96 (12.6 – 17.8)	11.51 ± 0.68 (9.6 – 13.4)	11.26 ± 0.51 (9.9 – 12.3)	6.6 ± 0.59 (5.65 – 11.5)	20.52 ± 0.97 (17.3 – 22.8)	88.9 ± 3.93 (72 – 99)	62.51 ± 6.08 (51 – 80)
C. c. brasiliensis	16.63 ± 0.8 (15 – 18.8)	12.33 ± 0.63 (11.2 – 13.55)	12.7 ± 0.69 (11.55 – 14.9)	7.41 ± 0.43 (6.9 – 9.02)	22.02 ± 1.24 (19.5 – 25.3)	96.16 ± 3.21 (90 – 103)	70.81 ± 4.39 (66 – 83)
C. c. frontalis	17.66 ± 0.83 (16.25 – 18.8)	12.8 ± 0.55 (11.9 – 13.85)	13.2 ± 0.57 (12.4 – 14.05)	7.6 ± 0.27 (6.95 – 7.85)	21.96 ± 1.29 (20.1 – 24.6)	95.18 ± 2.74 (90 – 100)	68.18 ± 3.41 (63 – 77)

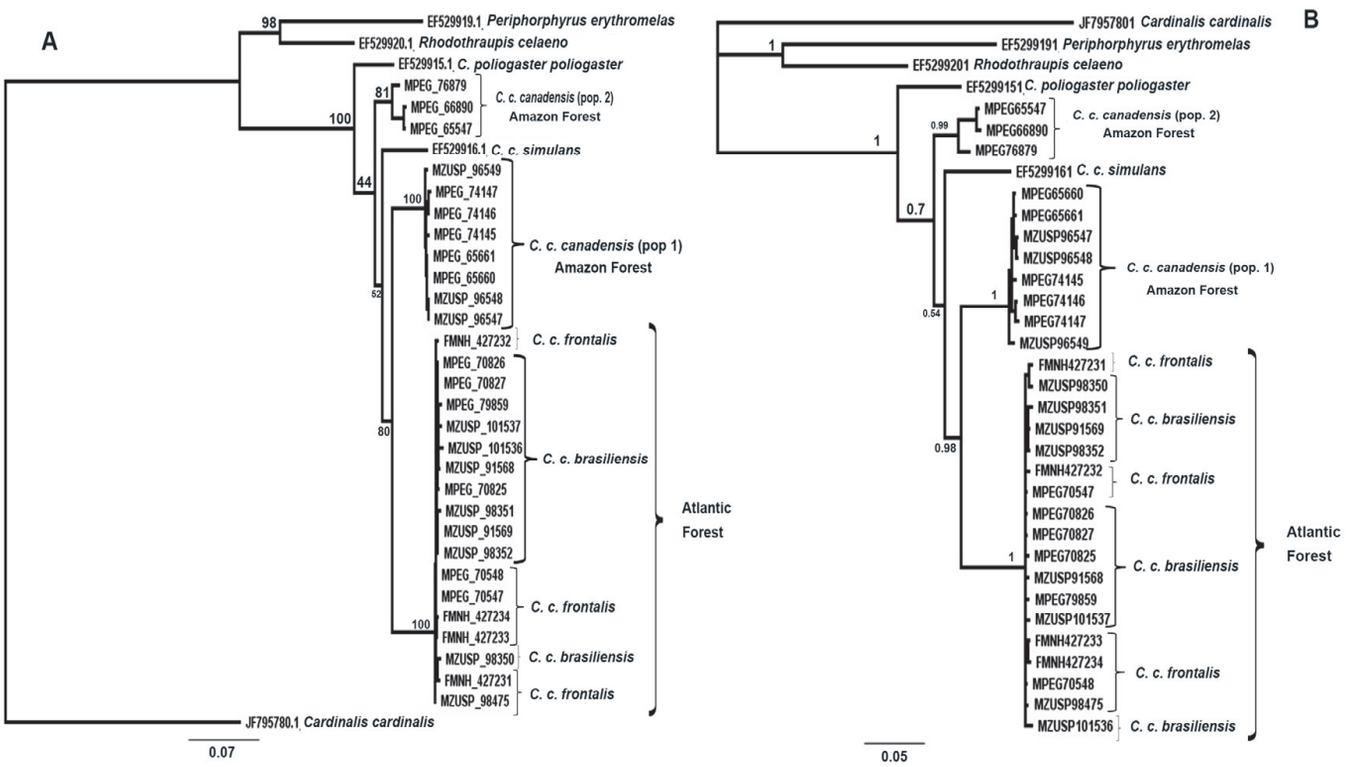

Figure 2. Phylogenetic relationships of *Caryothraustes canadensis*. (**A**) Maximum likelihood topology, nodes supports are bootstrap values. (**B**) topology obtained by Bayesian inference, node supports are posterior probabilities.

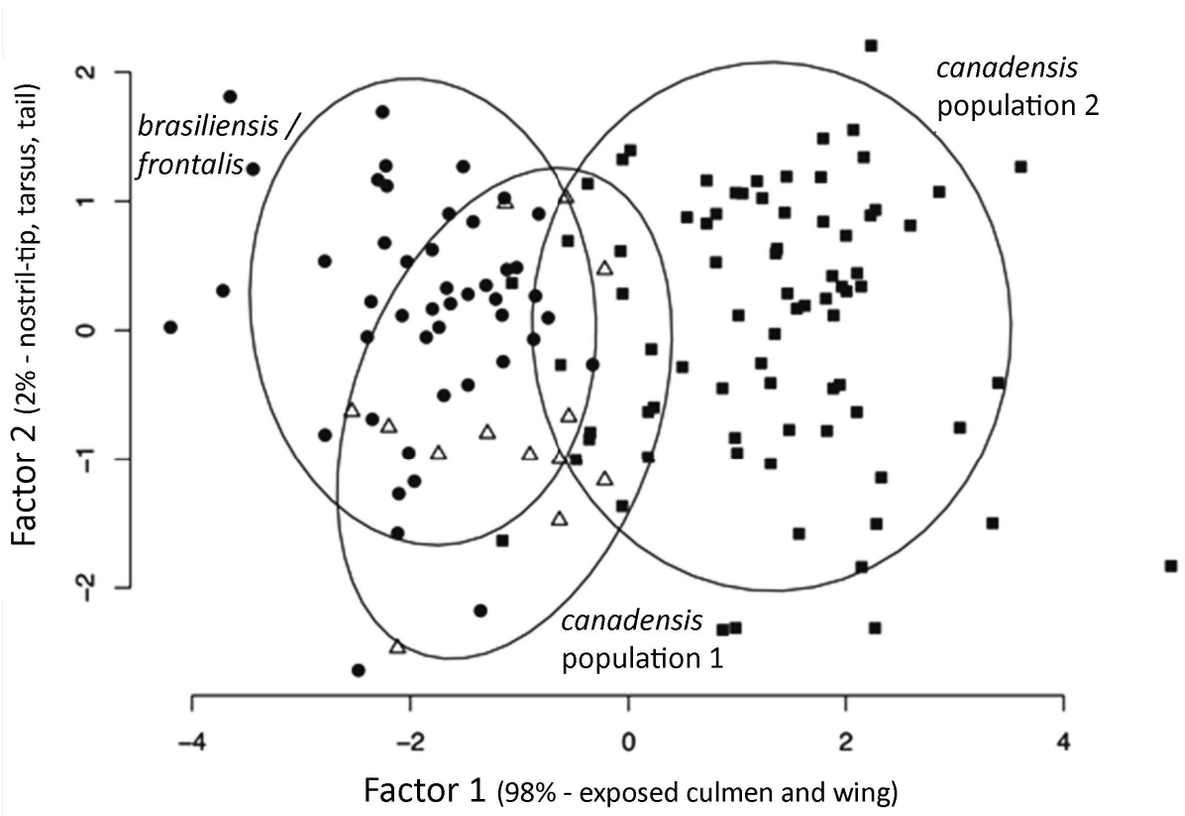

Figure 3. Discriminant function analysis. Ellipses indicate clusters of populations by 95% intervals.

Forest south of the São Francisco River crown and nape showed the same color as the forehead (olive and bright-yellow respectively), but of a slightly darker shade. The two Atlantic Forest subspecies showed the same pattern of crown and nape color (bright-yellow, Table 4), with small individual variation (ranging from YYO-12º-8; MZUSP 6274 to YYO-12º-10; MPEG 70547 for crown, and from YYO-12º-4; MZUSP 37733 to YYO-12º-6; MPEG 70827 for nape). Amazonian birds showed breast coloration ranging from olive-yellow (Y-12º-9; MZUSP 46072) to bright-yellow (YYO-12º-14; MZUSP 96546), whereas the Atlantic Forest birds consistently showed the same color (YYO-12º-11). The following parts of the body showed small, if any, variation between all individuals and cannot be used as diagnostics characters: back, rump, upper surface of tail, throat, malar parch, ear parch, belly and primaries (Fig. 5; Table 4). Through the analysis of the photographs, *C. c. simulans* show brighter underparts than the other specimens from Amazon basin. However, due to the low sample size (n = 1) we are not able to conclude if it can be considered a full species. We did not find sexually dimorphic features in any studied group.

Vocal variation

No significant differences (Newman-Keuls or Tukey tests $P > 0.05$) were observed in vocal characters between the songs of the three subspecies analyzed here (Tables 5 & 6). Of the 52 vocalizations analyzed, individuals emitted the Type-I phrase in 48 of them, and Type-II in 39. In most recordings (70%), both types of phrases were given, while in 23.5% and 5% only Type-I and II

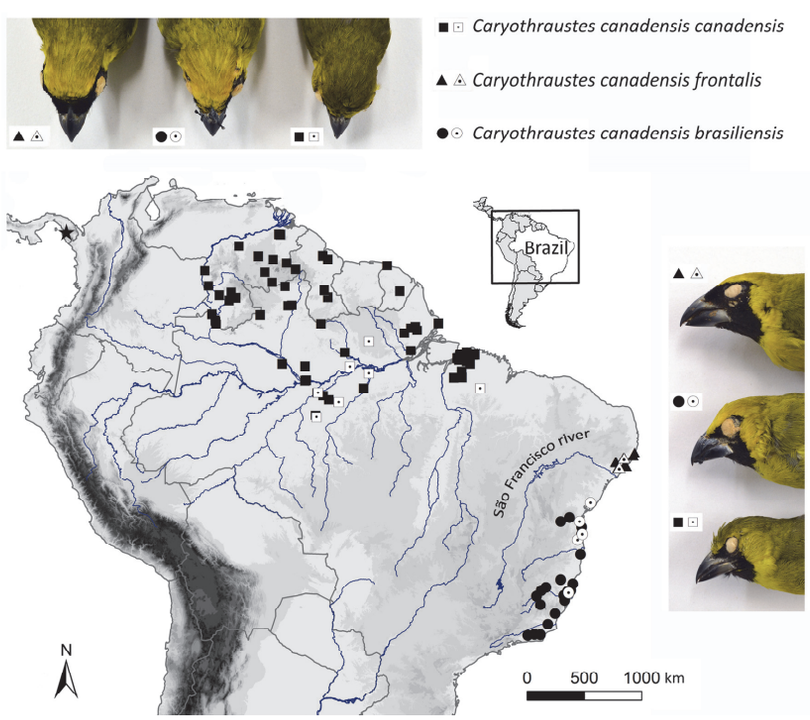

Figure 4. Lateral part of the head (upper left corner) and forehead (right side) of specimens: *Caryothraustes canadensis frontalis* (MZUSP 37731), *Caryothraustes canadensis brasiliensis* (MZUSP 34605) and *Caryothraustes canadensis canadensis* (MZUSP 46047). The distribution of all specimens analyzed is given in the map. Locations of genetic samples analyzed are represented by white symbols with black dots; specimens and recordings are represented by totally black symbols. Photograph location of *Caryothraustes canadensis simulans* is represented by a black star.

Table 4. Colors found in specimens examined. Numbers in parenthesis indicate the proportion of individuals showing the respective colors. O = olive; Y = yellow; B = black; BY = bright-yellow; OY = olive-yellow.

Taxon	Forehead	Crown	Nape	Back	Rump	Tail	Wing	Throat	Malar parch	Ear parch	Breast	Belly
C. c. canadensis (107 specimens)	O (97%)	O (100%)	O (100%)	O (100%)	O (100%)	O (100%)	OY (100%)	B (100%)	OY (100%)	O (100%)	Y (100%)	BY (100%)
C. c. brasiliensis (37)	BY (100%)	BY (100%)	BY (100%)	O (100%)	O (100%)	O (100%)	OY (100%)	B (100%)	OY (100%)	O (100%)	BY (100%)	BY (100%)
C. c. frontalis (19)	B (100%)	BY (100%)	BY (100%)	O (100%)	O (100%)	O (100%)	OY (100%)	B (100%)	OY (100%)	O (100%)	BY (100%)	BY (100%)

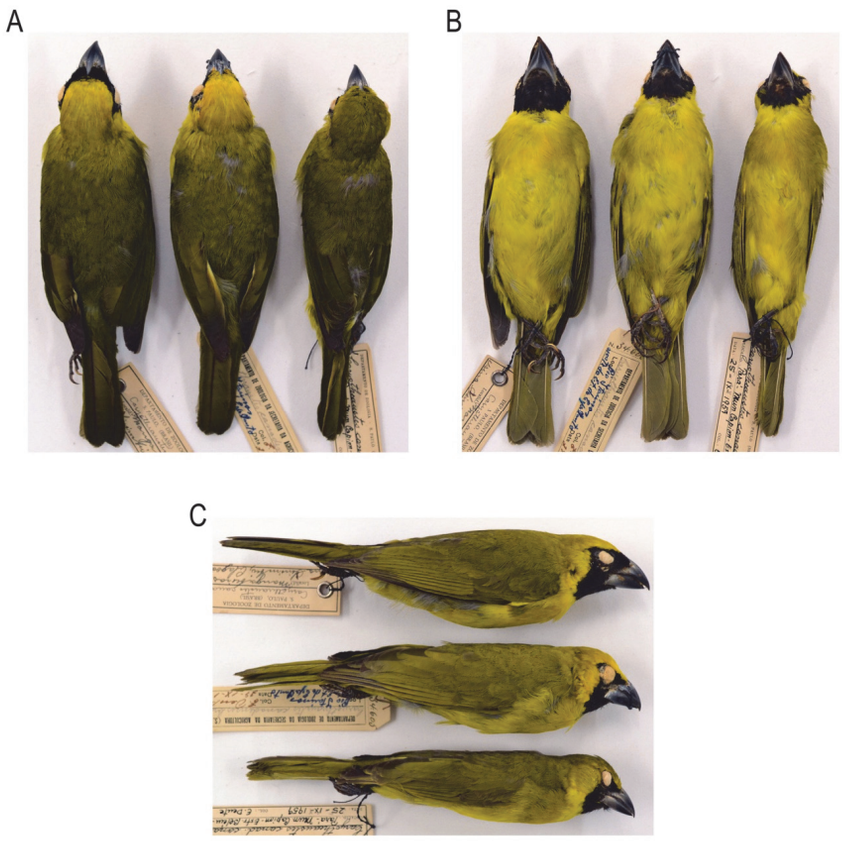

Figure 5. Dorsal (**A**), ventral (**B**) and lateral (**C**) parts of the body of specimens: *Caryothraustes canadensis frontalis* (MZUSP 37731; left A and B and upper C), *Caryothraustes canadensis brasiliensis* (MZUSP 34605; middle, south of São Francisco River) and *Caryothraustes canadensis canadensis* (MZUSP 46047; right A and B and bottom C).

Table 5. Measurements of vocal variables of Type-I phrases as mean ± standard deviation and range, in parenthesis, for each taxa. Each variable was measured for each single note. Number = number of notes within each phrase. As different recordings could have different number of phrases and notes, these values were extracted from the mean values of each recording.

Taxon	Maximum frequency (kHz)	Minimum frequency (kHz)	Bandwidth (kHz)	Peak frequency (kHz)	Time (s)	Number
Caryothraustes canadensis canadensis	5619 ± 938 (3773 – 8167)	1300 ± 230 (1003 – 1898)	4319 ± 944 (2439 – 7022)	3838 ± 444 (3155 – 5054)	0.148 ± 0.03 (0.087 – 0.247)	2.85 ± 1.17 (1 – 5.5)
Caryothraustes canadensis brasiliensis	5571 ± 1394 (3854 – 7534)	1160 ± 375 (846 – 2331)	4411 ± 1506 (2560 – 6687)	4147 ± 655 (3281 – 5343)	0.205 ± 0.02 (0.134 – 0.239)	2.01 ± 0.72 (1 – 3)
Caryothraustes canadensis frontalis	6732 ± 1478 (4360 – 8464)	1215 ± 248 (816 – 1584)	5571 ± 1538 (3333 – 7562)	4197 ± 534 (3416 – 5203)	0.184 ± 0.02 (0.147 – 0.22)	2.57 ± 0.81 (1 – 4)

Table 6. Measurements of vocal variables of Type-II phrases as mean ± standard deviation and range, in parenthesis, for each taxa. Each variable was measured for each entire phrase. Number = number of notes within each phrase. As different recordings could have different number of phrases and notes, these values were extracted from the mean values of each recording.

Taxon	Maximum frequency (kHz)	Minimum frequency (kHz)	Bandwidth (kHz)	Peak frequency (kHz)	Time (s)	Number
Caryothraustes canadensis canadensis	8704 ± 938 (6674 – 9897)	2060 ± 297 (1633 – 2851)	6644 ± 945 (4941 – 8208)	6130 ± 955 (4392 – 7838)	0.124 ± 0.03 (0.08 – 0.23)	6.17 ± 1.44 (4 – 10)
Caryothraustes canadensis brasiliensis	8063 ± 1162 (5963 – 10001)	1961 ± 347 (1565 – 2827)	6101 ± 1229 (4036 – 7872)	5571 ± 586 (4664 – 6773)	0.176 ± 0.02 (0.131 – 0.231)	7.343 ± 1.26 (5 – 9)
Caryothraustes canadensis frontalis	8478 ± 613 (7284 – 9159)	1827 ± 348 (1323 – 2565)	6650 ± 613 (5502 – 7526)	5996 ± 190 (5713 – 6304)	0.169 ± 0.04 (0.11 – 0.235)	7.6 ± 1.79 (5 – 10)

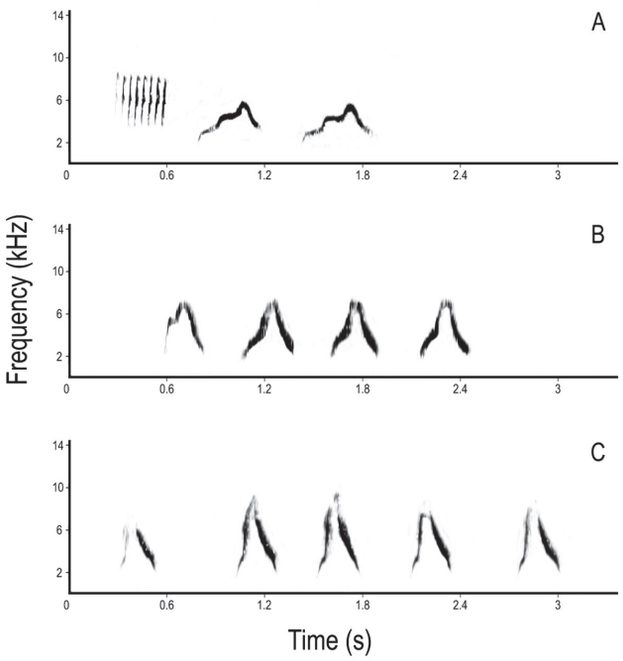

Figure 6. Spectrograms exemplifying individual variation found in qualitative voice analysis. Above are two recordings of *Caryothraustes canadensis brasiliensis* from Espírito Santo state, Brazil (FNJ 9140 [**A**]; ASEC JMB07514 [**B**]) and below is one recording of *Caryothraustes canadensis canadensis* from the Amazonas state, Brazil (CORNELL 127705 [**C**]). Contrary to expectations, we observed more similarity between the recordings B and C (different species) than between A and B (same species).

were observed, respectively. A total of 859 Type-I notes (in 349 Type-I phrases) and 210 Type-II phrases were individually measured. We measured all Type-I notes and all Type-II phrases available in all analyzed recordings. As the recordings did not have the same number of notes and phrases, we performed the tests using a simple mean for each recording to avoid pseudoreplication. Qualitative analysis of Type-I phrases, measured by visual analysis of the shape of the notes, showed a great variation even within the same locality and, therefore, could not be used to diagnose taxa (*e.g.* Fig. 6).

DISCUSSION

Plumage variation and diagnosis

Our phylogenetic trees support the existence of two Amazonian clades, that although weakly diagnosable between them in terms of size, voice and plumage, are both different in forehead color when compared to the Atlantic forms. Here we propose that the Amazonian clades should be treated as *Carytohraustes canadensis* until genomic data or more detailed morphological data reveal if they should be treated as separate species (Bocalini *et al.* in prep.).

In the Atlantic Forest, we suggest that both forms should be treated as *Caryothraustes brasiliensis*, since it has priority over *C. c. frontalis*. Beside the black forehead, Hellmayr (1905) cited the bright-yellow breast as a diagnostic character for *C. c. frontalis* compared to specimens from other parts of the Atlantic Forest. Although for some specimens (*e.g.* MPEG 70547) we found slightly brighter breast when compared to some individuals of *C. brasiliensis* (*e.g.* MZUSP 91569), this was due to intraspecific variation and cannot be used to distinguish the two Atlantic Forest populations. In this sense, both groups share almost all plumage colors except on the forehead. Our phylogenetic trees indicate that *C. c. brasiliensis* and *C. c. frontalis* form a unique clade with very shallow divergence. As our results do not indicate reciprocal monophyly between the two taxa, here we synonymize *C. c. frontalis* in *C. brasiliensis*. Further analysis using genomic markers, such as ultraconserved elements (Bocalini *et al.* in prep.) could clarify if the variation on forehead color corresponds with phylogenetic divergence of the two populations putatively isolated by the São Francisco River barrier.

Besides that, the clade formed by *C. c. simulans* is supported by our phylogenetic trees, and photography analyses reveal slight plumage differences when compared to *C. canadensis* and the Atlantic forms. However, as we used only one sequence from the GenBank and few specimens were studied by us, we prefer to keep its current status until we collect enough morphometric, voice and genomic data (Bocalini *et al.* in prep.).

Vocal analysis

Within the order Passeriformes there is a dichotomy between the usage of song in taxonomy of species included in the Oscines and Suboscines suborders (Raposo & Höfling 2003). Laboratory experiments and field studies have suggested that some suboscine species songs are innate (*i.e.* genetically defined, without changes associated to learning) and the species are unable to learn their songs (Stein 1963, Payne & Budde 1979, Kroodsma 1984). Conversely, variations observed in oscine songs have been thought as consequence of a learning ability, and theoretically with no taxonomic value (Marler & Tamura 1962). These assumptions made decades ago and for a limited species have been used to support the separation of a variety of suboscine taxa (*e.g.* Willis 1992, Whitney *et al.* 1995, Isler *et al.* 1998, Zimmer 2008, Carneiro *et al.* 2012), while few attempts have been made to use song in the taxonomy of oscine species (Raposo & Höfling 2003, but see Cadena & Cuervo 2010). However, based on recent empirical evidence, this dichotomy has been

revised (Payne 1986, Trainer *et al.* 2002, Price & Lanyon 2002, Cadena & Cuervo 2010, Kroodsma *et al.* 2013).

Although the use of oscine vocalization in taxonomy is encouraged by some authors (Raposo & Höfling 2003) and could be used to diagnose species in *Arremon torquatus* complex (Cadena & Cuervo 2010) in addition to corroborating phylogenetic relationships for *Dendroica* Warblers (Payne 1986) and Oropendolas (genera *Psarocolius*, *Gymnostinops*, and *Ocyalus*) (Price & Lanyon 2002), our analysis found that none of the vocalization characters used were useful in delimiting the proposed species. This was similar to other study with Wrens *Troglodytes* (Rice *et al.* 1999); these birds also have a complex and highly-variable song. Despite the relatively small sample size (52 recordings analyzed), high levels of individual variation in qualitative analysis prevented us from identifying diagnosable groups. For example, it is possible to find greater differences in the shape of notes between single recordings of birds from the state of Espírito Santo (Fig. 6A & B), than between recordings from Espírito Santo and Amazonas (Fig. 6C). This was contrary to the expectation that recordings from individuals that belong to the same species (*e.g. C. brasiliensis*, Figs. 6A & B) would be more similar than recordings of different species (*e.g. C. brasiliensis*, Figs. 6B and *C. canadensis*, Fig. 6C). This likely reflects song-learning ability within *Caryothraustes* species. In relation to quantitative analysis, as well as shape of notes, it is possible that high levels of variation prevented us from diagnosing the groups of individuals by their song. However, because oscine song proved useful in taxonomic and systematic previous studies (see above), we suggest it should be tested with other passerines and at different taxonomic levels (*e.g.* populations) in an attempt to delimit differentiated taxa (Raposo & Höfling 2003).

Distribution remarks

Recent records on the right bank of the Parnaíba River, in the Brazilian state of Piauí (Simas 2016) may represent the southeastern range limit of *C. canadensis*. Northwest Piauí occurs in a very extensive ecological transition zone between the Amazon, Cerrado and Caatinga domains and has semideciduous forests as its predominant vegetation type (IBGE 2012). Bird inventories in the western part of that state have recorded Amazonian taxa (*e.g.* the Pied Puffbird *Notharchus tectus* and the Rufous-capped Antthrush *Formicarius colma amazonicus*; Santos *et al.* 2010).

Additionally, there is an apparent gap in the distribution of *C. canadensis* in the Tapajós-Tocantins interfluvium, in southern Amazonia, as well as in the Inambari Center of Endemism. These absences might not arise from sampling problems, once these regions have historically been as much sampled as the others – see, for example, that some of the best sampled Amazonian localities (Serra dos Carajás and Fartura Farm) are within Tapajós-Tocantins interfluvium and has no record of the Yellow-green Grosbeak (Pacheco *et al.* 2007, Somenzari *et al.* 2011, Aleixo *et al.* 2012) and other well-sampled regions west from Madeira River have also not accounted for the species (Gyldenstolpe 1945, 1951, Guilherme 2012). A few other Amazonian species show similar distributions patterns (*i.e.* present in some interfluvium and absent in others), albeit not exactly as *C. canadensis*, such as Chestnut-crowned Foliage-gleaner *Automolus rufipileatus*, Dusky-capped Greenlet *Hylophilus hypoxanthus*, and Black Bushbird *Neoctantes niger*, which present disjunct populations with an absence area in the intermediate region (Ridgely & Tudor 2009).

Taxonomy of the Yellow-green Grosbeak

***Caryothraustes canadensis* (Linnaeus, 1766)**
English name: Yellow-green Grosbeak
Portuguese name: Furriel
Loxia canadensis Linnaeus 1766: 304
Pitylus viridis Sclater 1886: 306
Pitylus canadensis Snethlage 1914: 461
Caryothraustes canadensis canadensis Peters 1970: 224
Type-locality: Cayenne, French Guiana
Diagnosis: individuals can be distinguished from other *Caryothraustes* species by the presence of olive color on forehead, crown and nape. Although Amazonian birds have significantly smaller body size in comparison to the other two species (Fig. 3; Table 3), due to overlap in measurements it cannot be used as a diagnostic character. Average dimensions (mm): bill length 11.5; tail 62.5; tarsus 20.5; wing 89.
Distribution: mostly Amazon Basin in southern Colombia, eastern and southern Venezuela, in most parts of Guyana, French Guiana and Suriname and on both banks of Negro, Trombetas and Jari Rivers in Brazil. In the southern Amazon it occurs in the Madeira-Tapajós interfluve and on the right bank of Tocantins River. It seems that the southeastern range limit to its distribution occurs on the east bank of Parnaíba River, out of Amazon Basin and in the municipality of Altos, Piauí, Brazil (Simas 2016.

***Caryothraustes canadensis simulans* Nelson 1912**
English name: Cana Green Grosbeak
Type locality: Cana, eastern Panama
Diagnosis: underparts yellowish olive green and smaller than other members of *C. canadensis* (Nelson 1912, Hellmayr 1938). Average dimensions (mm): bill length 18; tail 66; wing 86 (Hellmayr 1938).
Distribution: eastern Panama and northern Colombia (Hellmayr 1938).

***Caryothraustes brasiliensis* Cabanis, 1851**
English name: Yellow-faced Grosbeak
Portuguese name: Furriel-do-sul
Caryothraustes brasiliensis Cabanis 1851: 144
Pitylus brasiliensis Sclater 1886: 306
Pitylus canadensis frontalis Hellmayr 1905: 277
Caryothraustes canadensis brasiliensis Peters 1970: 226
Caryothraustes canadensis frontalis Peters 1970: 225
Type-locality: Bahia, Brazil
Diagnosis: specimens north to the São Francisco River show distinctive black stripe on the forehead in contrast to southern forms, which possess a bright-yellow forehead, both different from the olive forehead of Amazonian species (Fig. 4). Average dimensions (mm): bill length 12.8; tail 70.8; tarsus 22; wing 96.7.
Distribution: Atlantic Forest from Pernambuco, eastern Bahia and Minas Gerais, to the lowland forests in Espírito Santo and Rio de Janeiro.

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APPENDIX I

Specimens examined. For collection acronyms see Methods.

Caryothraustes canadensis frontalis – 21: **BRAZIL:** São Miguel dos Campos (1♂ 1♀ MZUSP 98475, MNRJ 34361); São Miguel (1♂ 2♀ MZUSP 37728, MZUSP 37729, MZUSP 37730); Mangabeiras, Usina Sinimbu (7♂ 4♀ MZUSP 37731, MZUSP 37732, MZUSP 37733, MZUSP 37734, MZUSP 39304, MZUSP 39305, MZUSP 39306, MZUSP 39307, MZUSP 39309, MZUSP 39308, MZUSP 39310); Quebrangulo, Engenho Riachão (1♀ MZUSP 39311); Ibateguara, Usina Serra Grande, Engenho Coimbra (2♀ MPEG 70547, MPEG 70548); Murici (1♂ 35819); Igarassú, Recife, Usina São José (1? MNRJ 24749).

Caryothraustes canadensis brasiliensis – 66: Porto Seguro, Estação Veracruz (2♂ MZUSP 76257, MZUSP 76258); Bahia (1♂ MZUSP 2538); Jequié, Serra do Talhão (1♂ MZUSP 14323); Ilhéus (1♂ 1♀ MZUSP 33874, MZUSP 33875); Pacangê, Michellin Reserve (1♀ 1? MZUSP 91568 MZUSP 91569); Ilhéus, Ecoparque de Una (2♂ 1? MPEG 70825, MPEG 70826, MPEG 70827); Ilhéus, Fortuna River (2? MNRJ 25199, MNRJ 25200); Ilhéus (1♂ MNRJ 28011); Camumu (MNRJ 38130). Doce River, lower Suassuí (3♂ 5♀ MZUSP 25280, MZUSP 25285, MZUSP 25289, MZUSP 25290, MZUSP 25287, MZUSP 25286, MZUSP 25288); Doce River, lower Piracicaba, right margin (1♂ 1♀ MZUSP 25281, MZUSP 25282); Doce River, right margin (1♂ 1♀ MZUSP 25283, MZUSP 25284). Reserva Florestal CRVD (2♂ 1♀ MZUSP 98351, MZUSP 98350, MZUSP 98352); P. Cachoeiro (2♀ MZUSP 6155, MZUSP 6156); Espírito Santo (1♀ 1♂ MZUSP 6274, MBML 6155); Pau Gigante (2♂ MZUSP 24675, MNRJ 7877); São José River (1? MZUSP 28124); Itaúna River, north of state (2♂ 1♀ MZUSP 34603, MZUSP 34604, MZUSP 34605); Terra Alta (1♂ MBML 6235); Santa Tereza (7♂ 2♀ MBML 6136, MBML 6138, MBML 6139, MBML 6140, MBML 6146, MBML 6147, MBML 6148, MBML 6152, MBML 6143); Santa Tereza Biological Station (1♂ MNRJ 44411); Santa Lúcia Biological Station (1♂ MNRJ 44410); Colatina (1♀ MNRJ 10500); Linhares (1♂ 2♀ MNRJ 39558, MBML 6149, MBML 6144); Aracruz, Santa Cruz (4♂ 3♀ MBML 6137, MBML 6141, MBML 6142, MBML 6145, MBML 6150, MBML 6154, MBML 6156); São Mateus (2♂ MBML 6151, MBML 6153). Muriaé River, Cardoso Moreira (1♂ MZUSP 27323); Petrópolis (1♂ MPEG 23645).

Caryothraustes canadensis canadensis – 157: **BRAZIL:** Paca, right margin of Abacaxis River (1♀ MZUSP 77097); Camarão, right margin of Abacaxis River (1♀ MZUSP 77099); Camarão, left margin of Abacaxis River (1♂ MZUSP 77098); right margin of Canunmã River, lower part (1♂ MZUSP 96549); right margin of Canunmã River (1♂ 1♀ MZUSP 96548, LSUMZ Field number B-81337); right margin of Sucunduri River, Across Ilha do Castanho (4♂ 1? MZUSP 96546, MZUSP 96547, LSUMZ Field number B-85545, LSUMZ Field number B-85543, LSUMZ Field number B-96547); right margin of Sucunduri River, Igarapé da Cabaça (1♂ LSUMZ Field number B-80869); Manaus, Ducke Reserve (2♂ 1♀ MPEG 30055, MPEG 30056, MPEG 30057); Tootobi River, tributary of Demini River (1? MPEG 37549); Jau River, left margin, Novo Airão (1♀ MPEG 50688); Itacoatiara (2♂ MNRJ 32808, MNRJ 32809). Serra do Navio (1♂ MZUSP 65511, 1♀ MNRJ 29265); Araguari River, right margin (1♂ 2♀ MPEG 21649, MPEG 21649, MPEG 21652); Amapari River, Macapá (1♂ 1♀ MPEG 23643, MPEG 23644); Amapari River, Serra do Navio (1♂ MPEG 24103); Igarapé Novo, left margin Igarapé Amazonas, left margin Iratapuru River (1♀ MPEG 29386). Igarapé Açu (2♂ MZUSP 6759, ZMB 281736); Capanema (3♂ 1♀ MZUSP 32791, MPEG 23613, MPEG 23614, MPEG 23615); Belém, Utinga (2♂ 5♀ MZUSP 36061, MZUSP 36060, MZUSP 46074, MZUSP 46075, MZUSP 46076, MZUSP 46077, MNRJ 10904); Belém (3♂ 1♀ MZUSP 42814, MPEG 1541, MPEG 23616, ZMB 19026, 1♂ ZMB 31179); Município de Capim, Estrada Belém Brasília km 93 (19♂ 11♀ 2? MZUSP 46044, MZUSP 46045, MZUSP 46042, MZUSP 46043, MZUSP 46070, MZUSP 46046, MZUSP 46047, MZUSP 46048, MZUSP 46049, MZUSP 46051, MZUSP 46068, MZUSP 46069, MZUSP 46053, MZUSP 46057, MZUSP 46055, MZUSP 46054, MZUSP 46060, MZUSP 46058, MZUSP 46056, MZUSP 46059, MZUSP 46061, MZUSP 46062, MZUSP 46063, MZUSP 46050, MZUSP 46071, MZUSP 46072, MZUSP 46073, MZUSP 46067, MZUSP 46064, MZUSP 46065, MZUSP 46066, MZUSP 46052); Tailândia, Agropalma Reserve (1♂ 1♀ MZUSP 77583, MZUSP 77584); Jubatituba (1♀ MPEG 898); Peixe Boi Experimental Station (1♂ MPEG 5664); Quatipuru River, Flor do Prado (2♂ MPEG 12629, MPEG 12630); Belém Brasília Road km 96 (4♂ MPEG 14343, MPEG 14344, LSUMZ 67926, LSUMZ 67927); Belém Brasília Road km 86 (1♂ 1♀ MPEG 17977, MPEG 17978); Benevides, Baía do Sol, Retiro do Sol (2♂ 1♀ MPEG 22148, MPEG 22156, MPEG 22183); Santa Barbara do Pará (1♂ MPEG 22194); Castanhal/Manaparim Road, km 86 (1♂ MPEG 23631); Acará-Mirim River, left margin, Tomé-Açu, Massaranduba (2♂ 1♀ 1? MPEG 26336, MPEG 26337, MPEG 26338, MPEG 26339); Bragança, Benjamin Constant, Sítio Manoel Horácio (1♀ MPEG 32331);

Castanhal, Curuça Road (1♀ MPEG 35217); Santa Bárbara, Morelândia Farm, Genipaúba Road km 6 (1♀ MPEG 55920); Aveiro, Tapajós River, left margin, Escrivão (1♂ MPEG 64329); Alenquer, ESEC Grão-Pará (1♂ MPEG 65547); Itaituba, FLONA Amaná, right margin of Amaná River (1♂ 1♀ MPEG 65660, MPEG 65661); Faro, Maracanã Village, Xingu River (1♂ MPEG 66890); Tomé Açu (1? MPEG 70274); Benevides (2♂ MPEG 8436, ZMB 8435); Baião (1♀ ZMB 31177); Bragança (1♀ 1♂ MNRJ 10907, LSUMZ 67925). Mucajaí, Apiaú Colony (2♂ 1♀ MPEG 46269, MPEG 46270, MPEG 46271); Couto de Magalhães River, Garimpo União (1♂ MPEG 49385). **FRENCH GUIANA:** French Guiana (2? MNHN 790, MNHN 1064). **GUYANA:** British Guiana (1♂ MZUSP 6760); Guiana (2♀ MNHN 2493, MNHN 2494); Kopinang River, 7 km SW Kopinang (2♂ LSUMZ 175537, LSUMZ 175537). **VENEZUELA:** Salto Maiza, Paragua River (1♀ 1? COP 30837, COP 30841); Paragua River, Raudal (1♀ COP 26702); Paragua River, Raudal (1♀ 1♂ 1? COP 22805, COP 26701, COP 26698); La Faisca, mina Cerro Paraui-Tepui (1♀ 2♂ 2? COP 33166, COP 33162, COP 33163, COP 33164, COP 33165); Campamento Cruz, Yarra (1♀ 2♂ COP 34782, COP 34783, COP 34784); San Fernando de Atabapó (1♀ 2♂ COP COP 22185, COP 22186, COP 22187); Puerto Yapacana (4♀ 5♂ COP 39779, COP 39778, COP 39781, COP 39782, COP 39784, COP 39785, COP 39786, COP 39787, COP 39780); Carabobo, Cuyum River (1♂ COP 46700); El Nenamo (1♂ COP 68100); Salto Guaiguinima, Paragua River (1♂ COP 30838); Paragua River, Cerro Tabarerupá (2? COP 26699, COP 26700); Puerto Yapacana (2? 1♂ COP 39783, COP 39778, 39777); Icabarú River (1♀ COP 42268); Culebra, Cunucunuma River (1♀ COP 74970); M. Parima (1♀ COP 70866); São Carlos of Negro River (2♂ COP 41883, COP 41884); Camp Jaime Benitez, slopes of Mt. Marahuaca (1♀ LSUMZ 25269).

Caryothraustes canadensis simulans – 2: **PANAMÁ:** Prov. Darien, *c.* 9 km NW Cana on slopes of Cerro Pirre (2♂ LSUMZ 104752, LSUMZ 104753).

APPENDIX II

Recordings examined. For collection acronyms see methods.

Caryothraustes canadenses frontalis – 10: **BRAZIL:** Usina Serra Grande, Engenho Coimbra (2 CORNELL 127847, CORNELL 127855); Santa Justina Farm (2 ASEC LPGD02715, ASEC LPGD02616 a-c); Ibateguara, Usina Grande (1 ASEC LPGD03056); Campo Alegre, Mata Matão (1 Laherte Lobo de Araújo). Usina Trapiche, Mata do Tanguá (3 ASEC LPGD03223, ASEC LPGD03227, ASEC LPGD03308); Barreiros (1 Sidinei Dantas).

Caryothraustes canadenses brasiliensis – 17: **BRAZL:** Jaguaquara (2 Vagner Cavarzere); Itacaré (1 Leonardo Patrial); Boa Nova (1 XC 84457). Pirapetinga (1 ASEC LPG08108). Linhares reserve (3 CORNELL 115347, CORNELL 115390, CORNELL 115401); Conceição da Barra, São Joaquim Farm (2 FNJV 8940, FNJV 9604); Santa Tereza, Nova Lombardia Reserve (2 FNJV 9140, FNJV 9142); Cafundó Farm (1 JMB07514); FLONA of Preto River (1 ASEC RR04122). Casemiro de Abreu (1 ASEC LPGDA1247-48); Guapiaçu Ecological Reserve (1 Ricardo Gagliardi); Casemiro de Abreu, União Biological Reserve (1 ASEC LPGD06903).

Caryothraustes canadensis canadensis – 25: **BRAZIL:** Manaus (4 Marcelo Villegas, FNJV 7122); Presidente Figueiredo (1 XC 76377); Projeto de Assentamento Puxurizal (1 CORNELL 127705); Cachoeira Porteira, Cachorro River (2 FNJV 9978, FNJV 7123); Santa Bárbara, Mosqueiro (1 FNJV 7121). **FRENCH GUIANA:** Mana, piste ONF Dardanelles (1 XC 44065). **GUYANA:** E bank Waruma River (1 CORNELL 134927); Upper Demerara-Berbice 10.0 km N of Linden (1 CORNELL 85816). **VENEZUELA:** Capuchinbird Road, Bolívar (1 XC 12161); San Carlos of Negro River (1 Cornell 63330); Cuyuni River (1 CORNELL 63329); Grande River (4 CORNELL 63325, CORNELL 63326, CORNELL 63327, CORNELL 63328); Grande River, El Palmar (3 CORNELL 63321, CORNELL 63322, CORNELL 63323); La Tigra, El Palmar (1 CORNELL 63320); E of El Palmar, along road in Grande River Forest (1 CORNELL 60563); 19.0 km S of Las Claritas (1 CORNELL 112218).