Short Communication

No population genetic structure in a widespread aquatic songbird from the Neotropics

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ABSTRACT

Neotropical lowland organisms often show marked population genetic structure, suggesting restricted migration among populations. However, most phylogeographic studies have focused on species inhabiting humid forest interior. Little attention has been devoted to the study of species with ecologies conducive to dispersal, such as those of more open and variable environments associated with watercourses. Using mtDNA sequences, we examined patterns of genetic variation in a widely distributed Neotropical songbird of aquatic environments, the Yellow-hooded Blackbird (Icteridae, Chrysomus icterocephalus). In contrast to many forest species, Yellow-hooded Blackbirds showed no detectable genetic structure across their range, which includes lowland populations on both sides of the Andes, much of northeastern South America, Amazonia, as well as a phenotypically distinct highland population in Colombia. A coalescent-based analysis of the species indicated that its effective population size has increased considerably, suggesting a range expansion. Our results support the hypothesis that species occurring in open habitats and tracking temporally dynamic environments should show increased dispersal propensities (hence gene flow) relative to species from closed and more stable environments. The phenotypic and behavioral variation among populations of our study species appears to have arisen recently and perhaps in the face of gene flow.

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1. Introduction

Studies on the phylogeography of Neotropical lowland organisms have focused primarily on species inhabiting humid forest (reviewed by Aleixo and Rossetti, 2007; Moritz et al., 2000). Birds occurring in this habitat often show marked genetic structure, which likely reflects the interplay between their poor dispersal abilities (Moore et al., 2008) and the restrictions to gene flow imposed by features of the landscape such as major rivers (Aleixo, 2004; Capparella, 1988). In addition, the strong genetic structure often observed in rainforest bird species may reflect the effect of population isolation related to the purported historical contractions suffered by their favored environments as a consequence of climatic changes (Haffer, 1969). However, not all bird species from tropical lowland environments exhibit similar levels of genetic structure. For example, the levels of genetic divergence across geographic barriers are significantly stronger between populations of forest understory species than between populations of forest canopy species, a likely consequence of the higher dispersal propensity of the latter (Burney and Brumfield, 2009). Likewise, bird species of open-country environments such as the Brazilian *cerrado* appear to show considerably less population genetic differentiation than those of the understory of neighboring Amazonian forests, suggesting that *cerrado* birds have maintained relatively high levels of gene flow or that their populations have experienced rapid and recent geographic expansions (Bates et al., 2003).

The history of evolutionary diversification in the Neotropical lowlands has been profoundly influenced by the dynamics of extensive river and wetland systems, which once largely dominated the landscape in Amazonia (Hoorn et al., 2010). Species associated with riverine environments are an important component of the Neotropical lowland avifauna: 15% of the land bird species of the Amazon Basin are restricted to river-created habitats (Remsen and Parker, 1983). Because riverine environments (e.g. islands, successional vegetation on sandbars, flooded forests) are ephemeral at any given site and highly dynamic even over short temporal scales, avian species specializing on these environments are expected to show better dispersal abilities than closed-forest species, allowing them to track the changes in their less-stable habitats. This is expected to result in reduced levels of population genetic structure, but this prediction has not been evaluated in detail because, to

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our knowledge, few phylogeographic studies have focused on floodplain forest species (Aleixo, 2006) and no studies have examined patterns of genetic variation on widespread Neotropical bird species occurring in open environments associated with watercourses.

In this study, we use mitochondrial DNA sequence data to examine patterns of genetic variation across the range of a widely distributed Neotropical songbird from aquatic environments, the Yellow-hooded Blackbird (*Chrysomus icterocephalus*). This icterid species inhabits marshes and riverine habitats in the interAndean valleys and northern lowlands of Colombia, and east of the Andes in Colombia (north of the Río Guaviare), Venezuela and the Guianas, in Trinidad, and along the Amazon River from Peru to its mouth in northeastern Brazil (Jaramillo and Burke, 1999; Fig. 1). The species shows little geographic variation, except for an isolated high-elevation population (*Chrysomus icterocephalus bogotensis*) found in wetlands of the Altiplano Cundiboyacense, Cordillera Oriental of the Colombian Andes. The ecology and broad distribution of the Yellow-hooded Blackbird make it suitable for testing the prediction that Neotropical birds living in open habitats associated with marshy and riverine environments should show limited genetic structure relative to their rainforest interior counterparts.

2. Methods

We obtained 48 tissues samples of Yellow-hooded Blackbirds from the Magdalena Valley and Caribbean lowlands of Colombia, highlands of the Colombian Cordillera Oriental, and lowlands east of the Andes including open areas from Venezuela to Guyana and Central Amazonian Brazil (Fig 1; Appendix A). This sampling provided adequate coverage of much of the species' distribution because it included all major regions where it occurs. We lacked samples from the llanos of Colombia and Venezuela, from a seemingly disjunct population located in Guyana and Roraima (Brazil), and from the upper and lower reaches of the Amazon River (Fig. 1). However, these sampling limitations do not affect our conclusions about broad-scale patterns of genetic differentiation.

We extracted DNA from all samples and amplified and sequenced most of the mitochondrial ND2 gene (1034 base pairs) using standard procedures (Cadena et al., 2007). An additional sequence was obtained from GenBank, (accession number AF109934.1; Johnson and Lanyon, 1999), for a total of 49 individuals sampled.

Because genetic divergence in the ND2 gene was limited (see below), we examined relationships between individuals using a median-joining network constructed in the program Network v. 4.516 (Bandelt et al., 1999). To examine the geographic distribution of genetic variation within and among populations, we conducted an analysis of molecular variance (AMOVA) in the program Arlequin v. 3.0 (Excoffier et al., 2005). For this analysis, we defined seven populations, corresponding to different sampling localities (Fig. 1): subspecies *C. i. icterocephalus* from Falcón and Sucre states (Venezuela), Trinidad and Tobago, Guyana, Brazil, Atlántico and Cesar (Colombia), and subspecies *C. i. bogotensis* from Cundinamarca (Colombia). Similar results were obtained treating Atlántico and Cesar as separate populations. We also calculated values of nucleotide and haplotype diversity for each region and
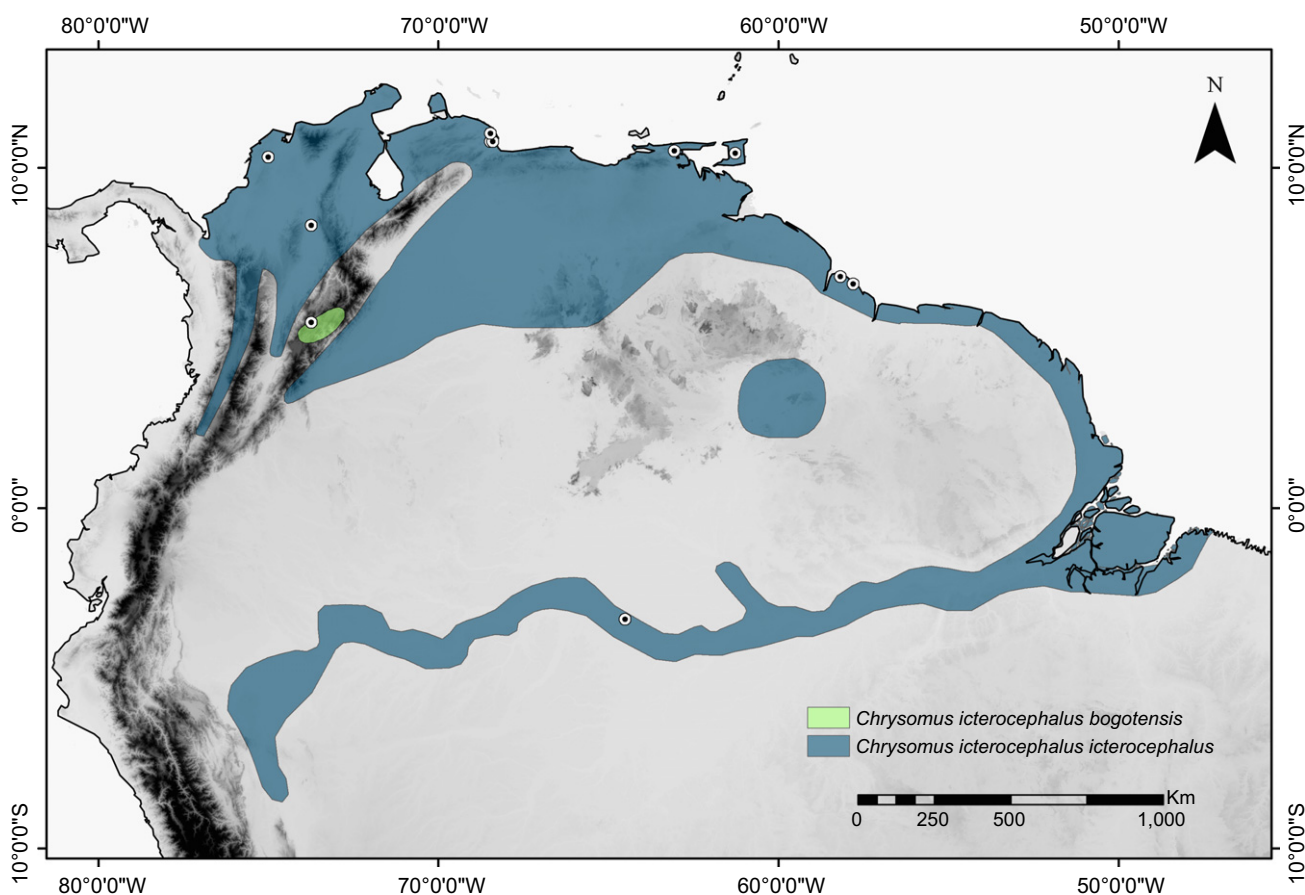

Fig. 1. Geographic distribution of the Yellow-hooded Blackbird (*Chrysomus icterocephalus*) in northern South America, showing the ranges of the widespread nominate subspecies and of the highland-restricted *C. i. bogotensis*. Dots indicate localities sampled for this study.

for the whole range using the program DNAsp v.5 (Librado and Rozas, 2009).

To evaluate the demographic history of the species, we conducted Tajima's *D* test using DNAsp v.5 and a Bayesian skyride analysis (Minin et al., 2008) using BEAST v. 1.5.4 (Drummond and Rambaut, 2007). We ran the skyride analysis for 10 million generations, sampling every 1000 generations and discarding the first million as burn-in; this analysis employed the GTR + G nucleotide substiution model, which was selected as the best-fit to the data according to the AIC calculated in Mr. Modeltest (Nylander, 2004). We used a 2.1% substitution rate per million years (Weir and Schluter, 2008) to establish approximate dates for changes in population size.

3. Results

We found a total of 22 haplotypes in our sample of 49 Yellow-hooded Blackbirds; of the 1034 sites, only 29 were variable and nine were parsimony-informative. The variation we observed (see estimates of haplotype and nucleotide diversity in Table 1) was not clearly structured among the sampled populations; the more common haplotypes were shared among geographically distant populations and less frequent haplotypes were related to more common ones in a star-like fashion (Fig. 2a). Even the phenotypically differentiated and geographically isolated population from the Colombian highlands (*C. i. bogotensis*) shared one haplotype with populations of nominate *C. i. icterocephalus* from the Venezuelan, Brazilian and Colombian lowlands. The AMOVA indicated that most of the genetic variation (c. 84%) resided within populations (Table 2), confirming the lack of genetic structrure in the species.

Tajima's *D* was negative and significant ($D = -2.41$, $p < 0.01$), which is consistent with a recent population expansion or with positive selection. Further evidence for a recent population expansion was provided by the Bayesian Skyride analysis (Fig. 2b), which shows an increase in effective population size beginning at about

Table 1
Estimates of haplotype diversity and nucleotide diversity of Yellow-hooded Blackbirds for different regions and for the complete range-wide sample.

| Region	*n*	Haplotype diversity ± SD	Nucleotide diversity ± SD
Venezuela	24	0.783 ± 0.081	0.00165 ± 0.00035
Falcón	13	0.718 ± 0.128	0.00124 ± 0.00040
Sucre	11	0.873 ± 0.071	0.00213 ± 0.00048
Trinidad and Tobago	4	1.000 ± 0.177	0.00274 ± 0.00066
Guyana	4	0.833 ± 0.222	0.00377 ± 0.00140
Brazil	6	0.867 ± 0.129	0.00158 ± 0.00044
Colombia	11	0.818 ± 0.119	0.00183 ± 0.00051
Lowlands	8	0.893 ± 0.111	0.00213 ± 0.00056
Cesar	2	1.000 ± 0.500	0.00308 ± 0.00154
Atlántico	6	0.800 ± 0.172	0.00158 ± 0.00044
Fúquene (HIghlands)	3	0.667 ± 0.314	0.00069 ± 0.00032
Whole range	49	0.810 ± 0.056	0.00172 ± 0.00028
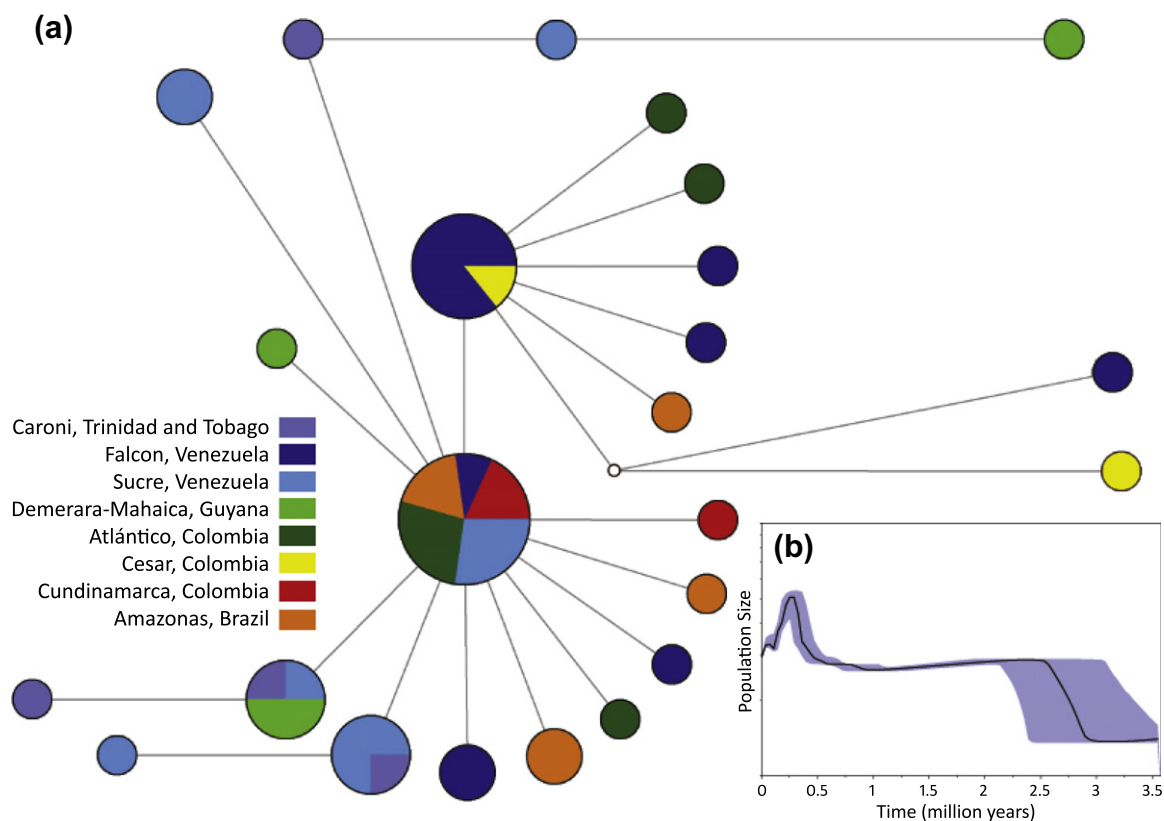
Fig. 2. (a) Median-joining haplotype network showing relationships among ND2 haplotypes of *Chrysomus icterocephalus* from populations across its geographic range. Size of each circle is proportional to the number of individuals carrying each haplotype (the smallest circles correspond to one individual); colors indicate sampling localities and the length of each line is proportional to the number of substitutions. Note the low divergence and haplotype sharing between areas, suggesting no genetic structure, and the star-like shape of the network consistent with a demographic expansion. (b) Bayesian skyride plot showing effective population size (the line indicates the median estimate and the shaded area the 95% credibility interval) as a function of time as inferred from ND2 variation in *Chrysomus icterocephalus*. Time zero is the present, with increasing numbers indicating time into the past in million years, back to the most recent common ancestor. Note the existence of two periods of demographic expansion (although credibility intervals are wide for the earlier one) and a more recent population decline.

Table 2
Results of analysis of molecular variance (AMOVA) showing that most of the genetic variation in Yellow-hooded Blackbirds resides within populations, confirming the lack of population genetic structure in this species.

Source of variation	d.f.	Sum of squares	Variance of components	Percentage of variation
Among groups	6	12.344	0.08428	7.43
Among populations, within groups	2	2.799	0.09758	8.60
Within populations	40	38.122	0.95305	83.98
Total	48	53.265	1.13492	

500,000 years before present and a later decline. An earlier demographic expansion is also suggested by the median estimate of population size at c. 3–2.5 million years before present (Fig. 2b), but credibility intervals around this estimate are too broad to reject a scenario of stable population size.

4. Discussion

Our analyses of mtDNA variation in the marsh-dwelling Yellow-hooded Blackbird revealed little to no phylogeographic structure over its broad distribution in the Neotropical region. Such lack of structure contrasts markedly with the strong patterns of population genetic variation seen in many rainforest species (Antonelli et al., 2010), but is consistent with patterns seen in species associated with riverine environments such as floodplain forests (Aleixo, 2006) and with relatively open vegetation such as the *cerrado* (Bates et al., 2003). The lack of phylogeographic structure in the Yellow-hooded Blackbird is not unexpected because dispersal in this species and in other aquatic taxa is not constrained by open areas and rivers, which represent barriers to gene flow for forest birds. Moreover, stretches of ocean have not been an insurmountable barrier for Yellow-hooded Blackbirds, which occur in the island of Trinidad and have been recorded as vagrants in the Netherlands Antilles (Voous, 1985). The Trinidad birds are not appreciably differentiated genetically from mainland populations (Figs. 1 and 2). Wetland environments are strongly seasonal and ephemeral owing to rainfall patterns, natural succession and changes in the courses of rivers, so species that occur in these environments are expected to be highly dispersive in order to track the dynamics of their favored habitats. Indeed, populations of Yellow-hooded Blackbirds are known to move between seasonal marshes and permanent lakes tracking habitat changes associated with rainfall (Wiley and Wiley, 1980). Therefore, the natural history of the species suggests that gene flow among populations should be substantial, which is consistent with our results.

An alternative, non-exclusive explanation for the observed lack of population genetic structure in the Yellow-hooded Blackbird is that populations have recently expanded, and our analyses of historical demography indicates that this hypothesis is plausible. Population expansions from presumably smaller distributions have also been suggested for avian species inhabiting the *cerrado* (Bates et al., 2003) and occurring along Amazonian rivers (Aleixo, 2006). More studies are necessary to determine whether this pattern is general for species occupying these environments and to correlate patterns of range expansion to climatic and geomorphological events. We note, however, that our inferred demographic expansion of the Yellow-hooded Blackbird in the Pleistocene is likely not a consequence of a recent origin of the habitats it favors because such habitats have existed for many million years in the Neotropical lowlands (Hoorn et al., 2010).

Our data indicate low divergence and even haplotype sharing between the high-elevation subspecies *C. i. icterocephalus* from the Colombian Andes and representatives of the lowland nominate subspecies from much of its range. The highland form occurs at c. 2550–3100 m elevation and differs from lowland populations, which rarely range above 600 m, in its substantially larger size and the much darker female plumage (Chapman, 1914). Our results imply that this phenotypic differentiation, which might be adaptive and is presumably heritable, has proceeded in the absence of neutral genetic differentiation, and perhaps even in the face of gene flow. Similar results have been noted for a variety of other bird species for which phenotypic and mtDNA variation have been examined (Ballentine and Greenberg, 2010; Pérez-Emán et al., 2010; Pruett and Winker, 2010; Zink, 2004). The lack of genetic structure in the Yellow-hooded Blackbird also contrasts with geographic variation in breeding biology and social systems documented for this species (Naranjo, 1995), which likely reflects plasticity in response to environmental conditions.

The wetland system to which *C. i. bogotensis* is restricted is considered one of the major centers of diversification of water birds in the Andes (Fjeldså, 1985). The region (i.e. the Altiplano Cundiboyacense) is unusual in that it harbors disjunct populations of other predominantly low-elevation marsh-associated species (e.g. *Gallinula melanops*, Rallidae) and of species occurring in distant geographic regions such as the Holarctic (*Eremophila alpestris*, Alaudidae) and the central and southern Andes and Patagonia (*Muscisaxicola maculirostris*, Tyrannidae). The wetland system of the Altiplano Cundiboyacense likely originated close to the time when this section of the Cordillera Oriental attained its current elevations, some 3.2 million years before present (Torres et al., 2005). However, our results are consistent with a recent origin of the high-elevation population of Yellow-hooded Blackbird in the area, as proposed by Fjeldså (1985). Comparative phylogeographic studies (e.g. Carstens et al., 2005) considering additional species with disjunct populations as well as species endemic to the region (e.g. *Rallus semiplumbeus*, Rallidae; *Synallaxis subpudica*, Furnariidae; *Cistothorus apolinari*, Troglodytidae) should shed further light on the origin of this distinctive avifauna.

Appendix A

Voucher number, geographic origin, and GenBank ND2 sequence accession numbers of the 49 samples of *C. icterocephalus* used in this study. Museum acronyms: FMNH: Field Museum of Natural History; LSUMZ: Louisiana State University Museum of Natural Science; NMNH: National Museum of Natural History, Smithsonian Institution; INPA: Instituto Nacional de Pesquisas da Amazônia; ANDES-BT: Museo de Historia Natural, Universidad de los Andes.

Taxon	Voucher no.	Accession no.	Locality
C. i.icterocephalus	FMNH 339750	HQ289836	Venezuela: Falcón, Tucacas
C. i. icterocephalus	FMNH 339751	HQ289837	Venezuela: Falcón, Tucacas
C. i. icterocephalus	FMNH 339766	HQ289820	Venezuela: Falcón, Tucacas
C. i. icterocephalus	FMNH 339767	HQ289821	Venezuela: Falcón, Tucacas
C. i. icterocephalus	FMNH 339768	HQ289822	Venezuela: Falcón, Tucacas
C. i. icterocephalus	FMNH 339752	HQ289838	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339753	HQ289839	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339754	HQ289840	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339755	HQ289841	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339757	HQ289816	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339758	HQ289817	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339759	HQ289818	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339769	HQ289823	Venezuela: Falcón, Boca del Tocuyo
C. i. icterocephalus	FMNH 339760	HQ289849	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339761	HQ289850	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339762	HQ289851	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339763	HQ289852	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339764	HQ289853	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339765	HQ289819	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339770	HQ289824	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339771	HQ289825	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339772	AF109934.1	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339773	HQ289826	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	FMNH 339774	HQ289827	Venezuela: Sucre, Guaraunos
C. i. icterocephalus	LSUMZ B35929	HQ289854	Trinidad and Tobago: Caroni
C. i. icterocephalus	LSUMZ B35943	HQ289855	Trinidad and Tobago: Caroni
C. i. icterocephalus	LSUMZ B35945	HQ289856	Trinidad and Tobago: Caroni
C. i. icterocephalus	LSUMZ B35947	HQ289857	Trinidad and Tobago: Caroni
C. i. icterocephalus	NMNH 623064	HQ289846	Guyana: Demerara-Mahaica, Demerara
C. i. icterocephalus	NMNH 623065	HQ289848	Guyana: Demerara-Mahaica, Demerara
C. i. icterocephalus	NMNH 625916	HQ289847	Guyana: Demerara-Mahaica, Demerara
C. i. icterocephalus	NMNH 627460	HQ289845	Guyana: Demerara-Mahaica, Mahaica
C. i. icterocephalus	INPA 128	HQ289810	Brazil: Amazonas, Tefé
C. i. icterocephalus	INPA 1326	HQ289811	Brazil: Amazonas, Tefé
C. i. icterocephalus	INPA 1330	HQ289812	Brazil: Amazonas, Tefé
C. i. icterocephalus	INPA 1331	HQ289813	Brazil: Amazonas, Tefé
C. i. icterocephalus	INPA 1332	HQ289814	Brazil: Amazonas, Tefé
C. i. icterocephalus	INPA 1523	HQ289815	Brazil: Amazonas, Tefé
C. i. icterocephalus	ANDES-BT 452	HQ289834	Colombia: Cesar, Gamarra
C. i. icterocephalus	ANDES-BT 453	HQ289835	Colombia: Cesar, Gamarra
C. i. icterocephalus	ANDES-BT 454	HQ289828	Colombia: Atlántico, Santa Lucía
C. i. icterocephalus	ANDES-BT 455	HQ289829	Colombia: Atlántico, Santa Lucía
C. i. icterocephalus	ANDES-BT 456	HQ289833	Colombia: Atlántico, Santa Lucía
C. i. icterocephalus	ANDES-BT 457	HQ289831	Colombia: Atlántico, Santa Lucía
C. i. icterocephalus	ANDES-BT 458	HQ289832	Colombia: Atlántico, Santa Lucía
C. i. icterocephalus	ANDES-BT 459	HQ289830	Colombia: Atlántico, Santa Lucía
C. i. bogotensis	ANDES-BT 27	HQ289842	Colombia: Cundinamarca, Fúquene
C. i. bogotensis	ANDES-BT 28	HQ289843	Colombia: Cundinamarca, Fúquene
C. i. bogotensis	ANDES-BT 29	HQ289844	Colombia: Cundinamarca, Fúquene

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