IBIS
international journal of avian science
Ibis (2025) doi: 10.1111/ibi.70001

Short Communication

Stable isotope data indicate origins of mislabelled historical bird specimens

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Natural history specimens provide valuable insights across diverse research fields, but those needing more accurate metadata have limited scientific value. We applied stable isotope analysis to investigate the origin of 19th century Atlantic Forest bird specimens attributed to the northeastern Brazilian state of Pernambuco, which are the only records for certain species in a highly threatened biodiversity hotspot. Carbon, nitrogen and sulphur isotope analyses indicate that these specimens were collected in Amazonia, not the Atlantic Forest. Stable isotope analysis is a promising tool for verifying specimen origins, enhancing their scientific value and resolving biogeographical questions.

Keywords: Amazonia, Atlantic Forest, Craven, natural history collections.

Natural history collections have long served as irreplaceable resources for addressing diverse biological and environmental questions, often extending far beyond their original purpose (Winker 2004, Holmes *et al.* 2016). Historically, such collections have been central to studies in systematics, evolution and biogeography (Mayr 1982), and more recently, their applications have expanded into fields such as ecology, conservation, agriculture and even human health (Remsen 1995, Shaffer *et al.* 1998, Graham *et al.* 2004, Suarez & Tsutsui 2004, Schmitt *et al.* 2018, Thompson *et al.* 2021, Blair 2024). A critical factor for many studies using natural history specimens is the availability of spatiotemporally accurate metadata. Unfortunately, many older specimens lack precise or reliable spatiotemporal information, significantly limiting their scientific value (Graham *et al.* 2004).

Stable isotope analysis has expanded the value of natural history collections as sources of tissue samples that can uncover various aspects of an organism's ecology (Navarro *et al.* 2022). For example, studies using stable isotopes have documented human-driven changes in avian migration ecology (Jiguet *et al.* 2020), habitat use (Navarro *et al.* 2021) and diet (Bond & Lavers 2014). A potential yet unexplored application of stable isotope analysis is in determining the geographical origin of natural history specimens lacking reliable spatial information. Stable isotopes can be an extremely useful tool to determine the origin of organisms at different spatial scales, especially if multi-isotopic approaches are employed to increase the precision of isoscape interpretation (Hobson 1999, Fowler *et al.* 2018). This technique could be particularly useful for specimens of species with broad geographical ranges inhabiting diverse ecosystems with distinct isotopic signatures, as these differences are displayed in isoscapes that can be used to help validate or infer specimen provenance.

In this study, we apply stable isotope analysis in a novel way to trace the origin of bird specimens attributed to the northeastern Brazilian state of Pernambuco, which have intrigued ornithologists for over a century. These specimens were reportedly collected by Charles Craven, a figure about whom little is known. In 1880, the English naturalist William Alexander Forbes mentioned Craven as an acquaintance in Recife, Pernambuco, noting Craven's interest in local natural history (Forbes 1881). The British Museum of Natural History (NHMUK) and the United States National Museum (USNM) hold numerous specimens labelled as Craven's collections from Pernambuco, including both verified local specimens collected alongside Forbes and others that Craven reportedly sent later. Many of these latter specimens are Amazonian species not otherwise recorded in Pernambuco, such as the Sand-coloured Nighthawk *Chordeiles rupestris* and the Paradise Jacamar *Galbula dea*, raising questions about their actual origin.

Craven's specimens are the only basis for the supposed historical occurrence of multiple Amazonian species in the Pernambuco Centre of Endemism, a highly threatened biodiversity hotspot within the Atlantic Forest of eastern South America with multiple documented cases of local and global avian extinctions (Pereira *et al.* 2014, Lees & Pimm 2015, Lima *et al.* 2022). For example, a specimen of the Variegated Antpitta *Grallaria varia* labelled 'Pernambuco' (NHMUK 1889.9.20.613), a species prone to local extinction in fragmented landscapes

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(Stratford & Stouffer 1999), has been widely cited as evidence of the species' occurrence in this region (Sclater 1890, Cory & Hellmayr 1924, Pinto 1978, Krabbe & Schulenberg 2003). While some researchers have questioned the provenance of Craven's specimens (Salvadori 1891, Naumburg 1939), others have argued they should be given the benefit of doubt (Papavero & Teixeira 2001). The latter point of view seems reasonable, as several ostensibly 'Amazonian' species have disjunct populations in the Pernambuco Centre of Endemism (e.g. Brazilian Tinamou *Crypturellus strigulosus*, Lettered Aracari *Pteroglossus inscriptus*, White-shouldered Antshrike *Thamnophilus aethiops*; Lima *et al.* 2022). However, many species that Craven collected are not particularly prone to local extinction, as they are generally common and abundant throughout their ranges, and are unlikely to have escaped detection by subsequent ornithologists surveying the region (Lima *et al.* 2022), casting further doubt on their origins.

The Amazon and Atlantic rainforests exhibit distinct isotopic signatures in elements such as carbon, nitrogen and sulphur (Sena-Souza *et al.* 2019, Martinelli *et al.* 2021). These differences are useful in producing isoscapes for provenance studies (Newton 2021, Tarrant & Richards 2024), making it possible to test whether Craven's specimens originated from the Amazon or the Atlantic Forest. Carbon ($\delta^{13}C$) values are generally lower in the Amazon than in the northeastern Atlantic Forest (Sena-Souza *et al.* 2019), especially because the Atlantic Forest has more altered landscapes with increased abundance of C_4 plants, which is reflected in higher $\delta^{13}C$ values in animal tissues (Diniz-Reis *et al.* 2024). Nitrogen ($\delta^{15}N$) values typically show the reverse pattern, with lower values in Atlantic Forest plants, although this difference is subtle and should be taken with caution because uncertainty over spatial patterns of $\delta^{15}N$ are common in South America ecosystems (Sena-Souza *et al.* 2020, Martinelli *et al.* 2021). Although sulphur ($\delta^{34}S$) isoscapes have not yet been developed for these regions, geophysical and biological processes typically affect $\delta^{34}S$ values, creating a gradient from coastal to inland areas (Tarrant & Richards 2024). This could result in higher $\delta^{34}S$ values in the northeastern Atlantic Forest, given its proximity to the coast. Because feathers incorporate the isotopic composition of the environment through the bird's diet during the moulting period, and remain metabolically inert after synthesis, these isotopic differences are preserved over time in specimen tissues (Wiley *et al.* 2017), potentially allowing us to determine if specimens originated in the Amazon or the Atlantic Forest. Although some isotopic overlap exists between these regions (Martinelli *et al.* 2021), analysing multiple elements is expected to improve the ability to differentiate them. Here, we compare the isotopic signatures of Craven's specimens with those of known-origin specimens from the same period to resolve this long-standing biogeographical mystery.

METHODS

The availability of comparative material dictated that this analysis be restricted to two sets of specimens: one comprising six Ringed Woodpeckers *Celeus torquatus* and the other including seven specimens of the family Bucconidae (puffbirds and allies, Table 1). The first set included two *Celeus torquatus tinnunculus* from the Atlantic Forest, three *C. t. torquatus* from Amazonia and one *C. t. torquatus* allegedly collected in the Atlantic Forest of Pernambuco by Craven. The second set included two Spot-backed Puffbirds *Nystalus maculatus* and one Crescent-chested Puffbird *Malacoptila striata* from the Atlantic Forest, two Rufous-necked Puffbirds *M. rufa* from Amazonia, and two *M. rufa* allegedly collected in the Atlantic Forest of Pernambuco by Craven. These two specimen sets were chosen to allow for an isotopic comparison between Craven's specimens and specimens known to have been collected in the Amazon and in the Atlantic Forest in the same period (i.e. late 1800s). Although the second set of specimens includes multiple species, these taxa generally inhabit similar environments and have similar diets (Rassmussen & Collar 2002). This enables a meaningful comparison, as isotope values in feathers reflect the diet of the individuals rather than species identity (DeNiro & Epstein 1978, 1981).

Breast contour feathers were cleaned in 2:1 chloroform:methanol (Paritte & Kelly 2009), then c. 0.8 mg of cut feathers were weighed out in preparation for carbon, nitrogen and sulphur stable isotope measurement. The samples were encapsulated in tin and loaded into a Thermo Fisher Scientific (TFS; Waltham, MA, USA) IsoLink Elemental Analyser coupled to a TFS Delta V Plus isotope ratio mass spectrometer. We used isotopically disparate laboratory reference materials (CNS1, CNS2 and CNS3) to correct for linearity and instrument drift, checked against international standards USGS42 and USGS43 (human hair; Coplen & Qi 2012) and USGS88 (marine fish collagen; Schimmelmann *et al.* 2020). Reproducibility was 0.12‰ for $\delta^{13}C$, 0.16‰ for $\delta^{15}N$ and 0.12‰ for $\delta^{34}S$.

After standardizing our dataset using the *scale* function from the base R package (R Core Team 2023), we conducted *k*-means clustering based on a dissimilarity matrix for the *Celeus* and Bucconidae specimens separately. We employed the Canberra method to compute distances between sample pairs using the R packages 'cluster' (Maechler *et al.* 2022) and 'factoextra' (Kassambara & Mundt 2020).

RESULTS

Two separate clusters were evident in isotopic variation plots: one comprising samples from Amazonia and the other from the Atlantic Forest (Fig. 1). In *Celeus*, there was some overlap between Amazonian and Atlantic specimens when analysing $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$

Table 1. Samples measured for stable isotope composition ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values).

Catalogue number	Taxon	Region	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
1888.8.5.565	*Celeus torquatus tinnunculus*	Atlantic Forest	−21.1	9.6	16.8
1889.2.26.319	*Celeus torquatus tinnunculus*	Atlantic Forest	−21.5	9.2	17.4
1889.2.26.316	*Celeus torquatus torquatus*	Amazonia	−22	7.6	18.1
1892.1.16.23	*Celeus torquatus torquatus*	Amazonia	−21.8	10.4	13.5
1895.11.27.67	*Celeus torquatus torquatus*	Amazonia	−21.5	9.6	13.1
1889.2.26.318*	*Celeus torquatus torquatus*	Uncertain	−22.1	8.7	15.4
1888.8.22.93	*Malacoptila striata striata*	Atlantic Forest	−24.5	9.1	18.7
1890.8.28.47	*Nystalus maculatus maculatus*	Atlantic Forest	−16.5	11.5	17
1888.8.22.82	*Nystalus maculatus maculatus*	Atlantic Forest	−18.4	10.2	18.9
1890.8.28.66	*Malacoptila rufa rufa*	Amazonia	−23.7	8.5	6.2
1890.8.28.65	*Malacoptila rufa brunnescens*	Amazonia	−23.3	7.4	14.3
1890.8.28.67*	*Malacoptila rufa rufa*	Uncertain	−23.4	7.8	12.3
1890.8.28.68*	*Malacoptila rufa rufa*	Uncertain	−24	7.7	11.5

All samples are from the NHMUK. Craven specimens are marked with an asterisk.

individually. However, when considering these isotopes together, specimens from the two regions formed separate clusters (Fig. 1a). Variation in $\delta^{13}C$ was particularly informative in separating *Celeus* specimens from the Amazon and Atlantic rainforests, with Craven's specimen showing a $\delta^{13}C$ value (−22.1‰) closer to Amazonian specimens (−22 to −21.5‰) than Atlantic specimens (−21.5 to −21‰), a result also supported by the dissimilarity matrix. For Bucconidae, $\delta^{15}N$ and $\delta^{34}S$ were more useful than $\delta^{13}C$ in differentiating regions. Variation in the latter isotope alone did not clearly separate specimens from the Amazon and Atlantic rainforests, although there was a tendency for Amazonian specimens to have lower $\delta^{13}C$ values. There was no overlap in $\delta^{15}N$ and $\delta^{34}S$ values between Amazonian and Atlantic specimens, and again, Craven's specimens were closer to Amazonian than Atlantic specimens (Fig. 1b). Dissimilarity matrices that combined $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values further supported that the Craven specimens are closer to Amazonian (*Celeus* 1.7–2.8, Bucconidae 0.4–1.3) than Atlantic specimens (*Celeus* 3.0, Bucconidae 2.1–3.0), because differences in distance measures are smaller between the Craven and Amazonian specimens (Fig. 2).

DISCUSSION

Our analysis indicates that three specimens of dubious origin collected by Charles Craven are likely to have originated in Amazonia, not in the northeastern Brazilian state of Pernambuco as stated on their original labels. The lower $\delta^{13}C$ value observed in the *Celeus* specimen of uncertain origin aligns with the slight differences in carbon isotopic values between regions, which are generally lower in Amazonia compared to the Atlantic Forest (Sena-Souza *et al.* 2019). Nevertheless, the differences in $\delta^{13}C$ isotope values between these two regions can be subtle and may be covered by the varying proportions of different resources in the organisms' diets (Diniz-Reis *et al.* 2024). This variability could explain the lack of distinction among $\delta^{13}C$ values in the Bucconidae specimens. For the Bucconidae, the $\delta^{15}N$ and $\delta^{34}S$ values were significant indicators of the specimens' geographical origin. Typically, $\delta^{15}N$ values are lower in the northeastern Atlantic Forest than the Amazon; however, we found higher $\delta^{15}N$ values in Bucconidae specimens from the Atlantic Forest. The reason for this unexpected pattern remains unclear, highlighting the need for further research to understand regional $\delta^{15}N$ variation in birds, especially given the current scarcity of comparative isotopic studies involving avian taxa across the Amazon and Atlantic Forest. Although this result deviates from the patterns of Brazilian $\delta^{15}N$ isoscapes based on soil and foliar samples (Sena-Souza *et al.* 2020, Martinelli *et al.* 2021), our combined isotopic analysis ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) justifies the attribution of the Amazon as the geographical origin of Craven's specimens. Additionally, the $\delta^{34}S$ values of the Bucconidae specimens were consistent with expected isotopic differences between regions in terms of their proximity to the coast. The specimen collected by Craven exhibited a low $\delta^{34}S$ value, mirroring the pattern observed in Amazonian specimens far from the coast.

Our findings justify doubts on the geographical origin of many other Craven specimens allegedly collected in Pernambuco raised by other ornithologists (Salvadori 1891, Naumburg 1939). These biogeographically unlikely specimens are mostly species otherwise only known from Amazonia, but also including some species otherwise only known from northern (e.g. Baudo Guan *Penelope ortoni*, USNM 107214) or southern (e.g. White-throated Hummingbird *Leucochloris albicollis*, USNM 107185) South America. These specimens may have been collected in other regions and mislabelled as originating from

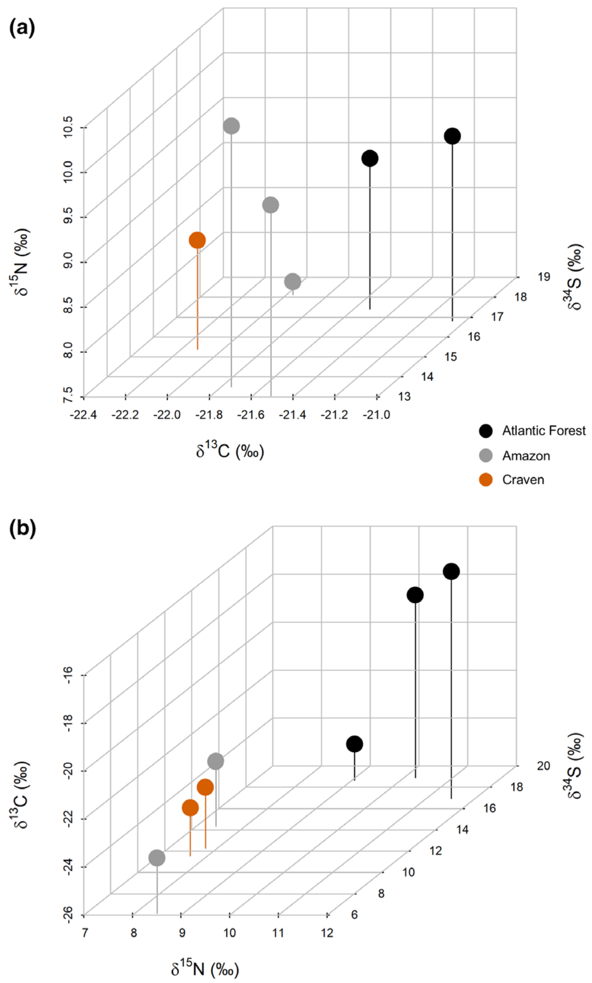

Figure 1. Values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ of each specimen of (a) Ringed Woodpecker *Celeus torquatus* and (b) Bucconidae from the Atlantic Forest (black dots), Amazon (grey dots) and Craven's specimens (orange dots). The *x*- and *y*-axes are flipped between (a) and (b) to emphasize the significant elements of each taxon on the *x*- and *z*-axes for better cluster visualization.

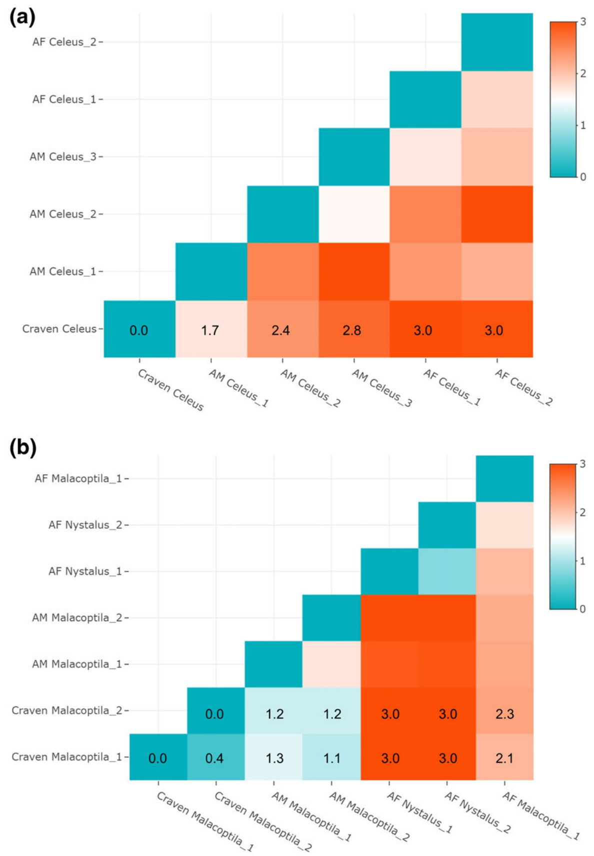

Figure 2. Dissimilarity matrix for (a) Ringed Woodpecker *Celeus torquatus* and (b) Bucconidae specimens showing distance measures between specimen pairs based on the three isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) combined. Smaller values indicate greater similarity in isotopic signature. AF, Atlantic Forest; AM, Amazonia.

Pernambuco, perhaps after being shipped from Recife to foreign collections. Additionally, Craven may have been the dealer rather than the collector of these specimens, which may have been obtained by third parties in multiple different locations across South America and subsequently sent to Craven in Pernambuco. Our results suggest that all these specimens should be assigned uncertain provenance, and the species must be removed from lists of historically occurring species in northeastern Brazil. Stable isotope analysis offers a promising tool for verifying the origins of specimens with uncertain locality data, enhancing their scientific value, and resolving biogeographical and evolutionary questions.

We thank the NHMUK for maintaining and providing the samples used in this analysis, and Mark Adams for help with sampling and export of samples. We thank the reviewers, the Associate Editor Stuart Marsden and Editor Rauri Bowie for helpful comments on the manuscript. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

AUTHOR CONTRIBUTIONS

Rafael Dantas Lima: Conceptualization; data curation; writing – original draft; writing – review and editing. **Ana Beatriz Navarro:** Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Jason Newton:** Resources; methodology; writing – review and editing. **Alexander Charles Lees:** Conceptualization; writing

– review and editing. **Luís Fábio Silveira:** Funding acquisition; writing – review and editing.

ETHICAL NOTE

This study used historical museum specimens. No permits or ethics approval were required.

FUNDING

This work was primarily funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grant no. 17/23548-2 to L.F.S.). The authors also thank FAPESP (grant nos. 2020/07619-0 and 2021/10339-1 to A.B.N. and R.D.L.) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant no. 381507/2024-6 to R.D.L.) for financial support.

CONFLICT OF INTEREST

None of the authors have any conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available in Table 1.

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Received 26 November 2024;
Revision 1 June 2025;
revision accepted 29 September 2025.
Associate Editor: Stuart Marsden