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ORIGINAL ARTICLE

Linking environmental indicators to blood, feather and claw $\delta^{18}O$ in the Saffron Finch (*Sicalis flaveola*) in the central Brazilian savannas

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Abstract

Understanding linkages between biotic and abiotic processes operating in highly seasonal environments such as the Savannas in the Neotropics is tremendously challenging but has been aided considerably through biogeochemical markers. Stable isotope ratios have been widely used as spatial and temporal integrative markers, signaling environmental information. Our objective in this study was to examine the relationship of tissue $\delta^{18}O$ and environmental factors and among multiple tissues in Saffron Finches, since this species is primary resident and abundant in the region. We conducted this study in a private farm in the central Brazilian savannas. We sampled 194 individuals in seven field samplings between January 2017 and March 2018. We collected whole blood, feathers and claws and analyzed them for $\delta^{18}O$ in both the yellow (YEL) and dull (DULL) plumage categories. We built different sets of environmental variables as predictors of blood $\delta^{18}O$. Median blood $\delta^{18}O$ varied widely throughout the year (13.4–18.8 ‰), differing in most pairwise comparison of months. Primary and tail feathers for both categories showed narrower isotopic median ranges compared to blood. Claw $\delta^{18}O$ showed smaller isotopic ratio variation than the other tissues. Our results showed that $\delta^{18}O$ values in avian blood are related to local climatic variables and reflect changes through time. The amount of precipitation, humidity and temperature were the most important environmental predictors. Therefore, the use of $\delta^{18}O$ in different avian tissues could be used as a proxy to infer different environmental and ecological aspects related to the Saffron Finch.

Keywords Oxygen-18 · Stable isotopes · Bird molting · Cerrado · Climate variables

Zusammenfassung

Umweltindikatoren und δ18O in Blut, Federn und Krallen der Safrangilbtangare (*Sicalis flaveola*) in den zentralbrasilianischen Savannen

Das Verständnis der Zusammenhänge zwischen biotischen und abiotischen Prozessen, die in stark saisonabhängigen Umgebungen wie den Savannen in der Neotropis ablaufen, ist eine enorme Herausforderung, die jedoch durch biogeochemische Marker erheblich erleichtert wurde. Stabile Isotopenverhältnisse werden häufig als räumliche und zeitliche integrative Marker verwendet, die Informationen über die Umwelt signalisieren. Unser Ziel in dieser Studie war es, die Beziehung zwischen Gewebe $\delta^{18}O$ und Umweltfaktoren sowie zwischen verschiedenen Geweben bei Safrangilbtangaren zu untersuchen, da diese Art in der Region primär ansässig und häufig ist. Wir führten diese Studie auf einer privaten Farm in den zentralbrasilianischen Savannen durch. Zwischen Januar 2017 und März 2018 haben wir 194 Individuen in sieben Felduntersuchungen beprobt. Wir sammelten Vollblut, Federn und Krallen und analysierten sie auf $\delta^{18}O$ sowohl in den

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gelben (YEL) als auch in den matten (DULL) Gefiederkategorien. Wir erstellten verschiedene Sätze von Umweltvariablen als Prädiktoren für $\delta^{18}O$ im Blut. Der mittlere Blut-$\delta^{18}O$-Wert schwankte im Jahresverlauf stark (13,4 bis 18,8 ‰) und unterschied sich in den meisten paarweisen Vergleichen der Monate. Primär- und Schwanzfedern wiesen für beide Kategorien im Vergleich zum Blut engere isotopische Medianbereiche auf. Das $\delta^{18}O$ der Krallen wies geringere Schwankungen im Isotopenverhältnis auf als die anderen Gewebe. Unsere Ergebnisse zeigen, dass die $\delta^{18}O$-Werte im Blut von Vögeln mit lokalen Klimavariablen zusammenhängen und Veränderungen im Laufe der Zeit widerspiegeln. Die Niederschlagsmenge, die Luftfeuchtigkeit und die Temperatur waren die wichtigsten Umweltprädiktoren. Daher könnte die Verwendung von $\delta^{18}O$ in verschiedenen Vogelgeweben als Proxy verwendet werden, um verschiedene Umwelt- und ökologische Aspekte in Bezug auf die Safrangilbtangare abzuleiten.

Introduction

Tropical savanna regions are known for their episodic and seasonal changes in rainfall. The central Brazilian savanna is a high biodiversity ecosystem and a hotspot for species conservation, occupying a vast territory in central Brazil, locally known as Cerrado. The Cerrado climate is seasonal, with a marked dry period. The Cerrado, with an area of about 205 million hectares, is considered one of the most threatened regions in the world (Hunke et al. 2015). The annual average rate of land cover changes in Brazil from 1990 to 2010 was 0.61% per year, and the remaining natural vegetation was reduced to 47% of the original (Beuchle et al. 2015). As a result, the region has high levels of endemic and threatened biodiversity (Mittermeier et al. 2011). The Cerrado is also a source and route of bird species exploited in the illegal wildlife trade (Destro et al. 2012).

Understanding environmental factors that influence bird populations is essential for assisting conservation actions. Environmental drivers in the Cerrado vary temporally and spatially, influencing the distribution of many bird species (Marini et al. 2009). Birds typically follow an annual cycle that includes periods of breeding, nesting, and molting tightly linked to wet–dry seasonality in this region (Marini et al. 2012). Other environmental features, such as relative humidity and temperature, are short-term signals for annual cycles, being related to a fine-tuning of the timing of the start of reproduction. Understanding linkages between biotic and abiotic processes operating in such highly seasonal environments is tremendously challenging but has been aided considerably through biogeochemical markers. Stable isotope ratios, in particular, have been widely used as spatial and temporal integrative markers, signaling environmental information (Dawson and Siegwolf 2007; Vander Zanden et al. 2016).

Stable isotope ratios of oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) reflect the origins and routing of water in the hydrosphere (Clark and Fritz 1997). This approach is based on well-known biogeochemical processes that lead to differential discrimination between the heavier and lighter isotopes of these key elements. Values of $\delta^{18}O$ and $\delta^{2}H$ vary in environmental waters due to physical processes linked to the amount of rainfall, continentality, temperature, and altitude (Clark and Fritz 1997; Bowen 2010; Terzer et al. 2013; Baisden et al. 2016). These processes result in spatially explicit patterns or isoscapes (West et al. 2010). Isoscapes of $\delta^{18}O$ and $\delta^{2}H$ are widely used for studies of the hydrogeological cycle (Dansgaard 1964), paleo-records (Anchukaitis et al. 2008), forensic tracking of animal and plant provenance (Meier-Augenstein and Fraser 2008; Chesson et al. 2014), animal migration (Hobson and Wassenaar 2019), and food authentication (Carter and Chesson 2017).

Animal tissues incorporate isotopic values from local food and water, and for $\delta^{18}O$, also from the air (Bryant and Froelich 1995). Stable isotope values of keratin tissues (such as feathers, hair, and claws) become metabolically inactive once the tissue is formed, and thereby, its isotopic value does not change. In contrast, metabolically active tissues (such as blood and liver) reflect continuous changes in their isotopic values. Tissue integration of isotopic values from the diet, drinking, and other possible sources over a timescale are defined as tissue isotopic turnover rate, resulting from the balance between tissue synthesis and catabolism (reviewed by Vander Zanden et al. 2015). As feathers are synthesized during molt periods, they integrate the environmental conditions that preceded these events. If a species' molting phenology is known, it is possible to associate isotopic results from a sampled feather to the region where it was grown based on maps of spatial isotopic distributions (isoscapes). If the bird molts on wintering or breeding grounds, it carries local isotopic values in feathers before moving, which can be later examined to infer previous locations or habitat use. In this sense, $\delta^{2}H$ and $\delta^{18}O$ measurements have been widely used in animal migration studies (Hobson and Wassenaar 2019). Claws are continually growing from the base, but wear the tip, renovating in a period of about 2–5 months (Bearhop et al. 2003). Blood is being continually turned over, which is completed in about a month (Vander Zanden et al. 2015).

Measurements of $\delta^{2}H$ in feathers of migratory birds demonstrate a strong relationship with amount-weighted meteoric precipitation $\delta^{2}H$ at continental scales, especially in North America (Bowen et al. 2005; Hobson et al. 2014). In South America, the precipitation $\delta^{2}H$ isoscape is less

well developed but has been used to infer avian movements and molt origins at coarser scales (Garcia-Perez et al. 2013; García-Pérez and Hobson 2014). Migratory studies using δ^2H measurements clarify important aspects about movement and origin of birds (reviewed by Hobson and Wassenaar 2019), and other taxonomic groups, such as insects (Wassenaar and Hobson 1998; Flockhart et al. 2013), bats (Voigt et al. 2013; Cryan et al. 2014), and fish (Soto et al. 2013). Despite the close linkage between δ^2H and $\delta^{18}O$ in meteoric water, this association is not homogeneous throughout organisms (Bryant and Froelich 1995). For humans (Ehleringer et al. 2008), rodents, ungulates (Pietsch et al. 2011), and terrestrial carnivores (Koehler and Hobson 2019), this relationship is strong; however, feather of birds in North America correlates strongly with meteoric δ^2H, while $\delta^{18}O$ shows a weaker pattern (Hobson and Koehler 2015).

The Saffron Finch (*Sicalis flaveola*) is a small resident species that occurs throughout much of South America (Piacentini et al. 2015; Remsen et al. 2016). We focused on the subspecies *S. f. brasiliensis,* which is distributed in northeast and west-central Brazil. Natural habitats of this species include open areas with some shade or forest borders, usually associated with human farms (Palmerio and Massoni 2009). This species is the most frequently found in the illegal wildlife trade confiscations in the Brazilian territory (Alves et al. 2012; Costa et al. 2018).

Our purpose in this study was to examine the relationship of tissue $\delta^{18}O$ and environmental factors and among multiple tissues. As the climate is seasonal, we also expected a corresponding variation in finch isotopic values. Our objectives were to determine how tissue isotopic signals varied relative to those in environmental sources and determine if finch $\delta^{18}O$ values could be used as an environmental proxy. By answering these questions, we sought to understand tissue–environment isotopic linkages for oxygen and assist in better use of $\delta^{18}O$ measurements in animal ecology studies, including movement, physiology, and forensic applications.

Material and methods

Study site

We conducted this study at the Tabapuã dos Pireneus farm (15° 46′ 40″ S 48° 49′ 22″ W; elevation 1100 m a.s.l.), in the Municipality of Cocalzinho de Goiás, GO, Brazil. Predominant land uses are pastures and agriculture, while there are patches of natural forests along the streams and preserved areas (Cordeiro 2019). It also is adjacent to a 2822 ha natural area, the Pireneus State Park, with a predominance of savanna and grasslands (Pinto et al. 2009). The average annual rainfall is about 1500 mm, and the average annual temperature is 22 °C (Fig. 1). For the studied period (2016–2018), the average annual rainfall was 1,415 mm, and the average annual temperature was 21.9 °C (min 9.3 °C, max 35.6 °C). The average air humidity in the dry season was 53.3%, and during the rainy season, it was 71.2%. The climate is the Köppen Aw type (A: Equatorial, w: dry winter), characterized by two distinct seasons: a dry season between April and October, which corresponds to autumn/ winter, and a humid one, with relative heavy rains during the spring/summer period, which corresponds to November–March.

Study species

Saffron Finches are predominantly granivorous, eat small arthropods, and forage on the ground (Rising and Jaramillo 2017). They drink from and take baths in puddles, troughs, and fountains (Marcondes-Machado 2002). They form pairs in the breeding season and are found in small-flocks in non-reproductive periods (Marques-Santos et al. 2018). Despite being a common species, few studies have focused on fundamental biological aspects, and the species' molt pattern has not yet been described. Saffron Finches have dull and yellow-colored plumage forms. Younger birds are dull and usually turn yellow after their second year, while females may delay this change for several years (Marques-Santos et al. 2018). We classified birds as dull (DULL) or yellow (YEL) according to their plumage as a proxy of the life stage of the bird (i.e., dull birds are young and yellow birds are older). Hollowed gourds are commonly provided and used as nest sites by the Saffron Finches. We checked for overall

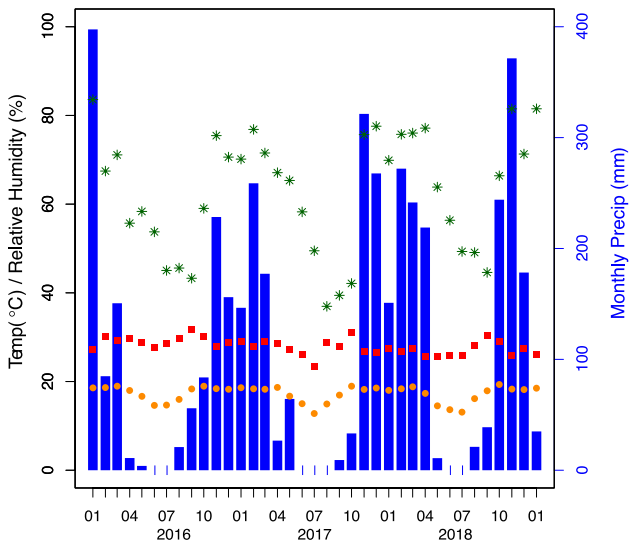

Fig. 1 Environmental variables for Brasilia weather forecast station, (National Meteorological Institute—15° 47′ 24.9″ S, 47° 55′ 22.9″ W). Numbers on horizontal axe are months between 2016 and 2018. Asterisk = relative humidity (%); square = maximum temperature (°C); circles = minimum temperature (°C); bar = precipitation (mm)

initiation and ending of reproductive activity (eggs and chick presence and chick feeding behavior) in these structures. We observed reproductive activity beginning in December and finishing around May. This period corresponds to the similar reproductive period of the Stripe-tailed Yellow-Finch (*Sicalis citrina*; (Gressler and Marini 2011) and other granivorous birds in the region, such as Blue-black Grassquits (*Volatinia jacarina*; Aguilar et al. 2008) and Double-collared Seedeaters (*Sporophila caerulescens*; Francisco 2006). Saffron Finch usually nests 1.8–2.5 nests per season and fledges 1.8–3.9 chicks in one reproductive season (Marques-Santos et al. 2018).

Bird capture and tissues sampling

We captured wild Saffron Finches with mist nets and marked individuals with numbered metallic bands. In total, we sampled 194 individuals in seven field samplings between January 2017 and March 2018, with a variable number of birds and recaptures (Table S1). We collected approximately 100 µL of whole blood by brachial venipuncture. All sampled blood was then air-dried on a glass slide. We collected whole feathers from the left wing (P1and P10), tail (R2), and body feathers. We cut a 1–2 mm tip fragment of the outer claw from the left foot in the first two sampling events. Feather and claw samples were stored in individual plastic bags and tagged. We visually examined each bird for the presence of newly grown or growing body coverts, wing primaries, and tail rectrix feathers as a signal of molt in these regions.

Laboratory analysis was done with all YEL or recaptured birds, while not all captured DULL birds were analyzed, as they were encountered more frequently. From DULL birds, we preferentially selected recaptured birds or selected them at random for analysis and balanced sample numbers (Table S1). Vander Zanden et al. (2015) estimated a 13.1-day half-life of blood for a 50 g bird. Saffron Finches weigh about 18 g, and so we expect a much shorter period of integration. Therefore, blood results were used as an independent variable since our samplings were at least two months apart. Correspondence in $\delta^{18}O$ values among different tissues should reveal the extent to which each period of integration matches environmental conditions. We performed an initial screening performing correlation tests with first-month sampled keratinized tissues, including claw, body, P1, and R2 feathers, correlating with P10 feathers. We continued isotopic analyses for a more extended period for P1, P10, and R2 feathers, as they would reveal more specific timely and spatial consistencies related to wing and tail molting. As flight feathers usually develop sequentially among Passeriformes, from inner to outer feathers (Silveira and Marini 2012), they should reflect incorporated isotope ratios relative to the period of each feather grown. We reasoned it would be possible to determine if there were discrepancies in $\delta^{18}O$ between feather types, representing individual movements or variations in environmental isotope ratios during the molt. Saffron Finches are resident, and so we expect that P1 × P10 feathers would be highly correlated. Similarly, we expected feathers from recaptured birds to have regrown sampled feathers in the study area. Therefore, deviations from P1 × P10 correlations and P10 expected values of recaptured birds should indicate the propensity of individual Saffron Finches to move throughout the year or during the time of feather growth. For some birds, one of the sampled feathers was developing (still with a blood irrigated bulb), which we used for calculating the conversion factor between blood and feather (Quillfeldt et al. 2008). We assume that claw tips would reflect diet from the previous 2–5 months (Bearhop et al. 2003), reflecting isotopic values from the last year. The procedures described here were approved by the Animal Use and Ethics Committee—University of Brasília (approval no. 55712/2016). Field collection permits were done under the Chico Mendes Institute for Biodiversity Conservation license (SISBIO no. 8745-1) and genetic use under the National System for the Management of Genetic Heritage and Associated Traditional Knowledge license (SISGEN no. A018ECD).

Stable isotope analyses

Feathers and claws were cleaned with distilled water and a mixture of methanol and chloroform (1:2). To eliminate residual humidity and improve water separation in laboratory analysis, we dried keratin tissues and blood in an oven at 60 °C for 24 h. We scraped blood from slides using a spatula, sliced small pieces of individual feather vane, and kept claws whole, weighed (1.2 mg) of each material, packed them in silver capsules, and sent them for oxygen stable isotope analysis at the Davis Isotope Facility, Davis, CA, USA (SIF). There, capsules were introduced into a zero blank carousel of a PyroCube (Elementar Analysensysteme GmbH, Hanau, Germany). Samples were combusted at 1400 °C in a glassy carbon reactor. CO was separated from any interfering N_2 on an adsorption trap and introduced into an interfaced Isoprime VisION (Isoprime Ltd., Stockport, UK, a unit of Elementar Analysensysteme GmbH, Hanau, Germany) mass spectrometer under helium flow.

During analysis at SIF, samples were interspersed with replicates of different laboratory reference materials. SIF uses international reference materials within each run as the scaling end-members. The within-run precision measurement errors for every laboratory reference material are shown in parenthesis. Nylon was used for every sample as laboratory reference material for order correction ($\delta^{18}O$ VSMOW = 7.8 ± 0.3‰). Alanine was used every four samples for size correction and elemental totals ($\delta^{18}O$ VSMOW = 20.5 ± 0.3‰). IAEA-600 and USGS-35 were

used every ten samples as international reference materials for normalization (δ ^{18}O VSMOW = − 3.5 ± 0.2 and 56.8 ± 0.4‰, respectively). Cellulose was used every ten samples for internal check (δ ^{18}O VSMOW = 31.2 ± 0.4‰). The long-term standard precision of the SIF for each of the reference materials is 0.4‰ for δ^{18}O.

Environmental variables

We obtained daily environmental data from the National Meteorological Institute website for 2016–2018 (Instituto Nacional de Meteorologia 2019). We used variables from the conventional measuring station located in Brasilia (Federal District), about 120 km apart from the study site. Daily data were downloaded from the following environmental variables: precipitation amount (mm), maximum temperature (°C), minimum temperature (°C), insolation (hours), average temperature compensated (°C), average relative humidity (%), and average wind speed (MPS). The temperature range (°C) was calculated as maximum temperature (°C)−minimum temperature (°C).

Statistical analyses

We used the robust Brown–Forsythe Levene-type test for testing the equality of group variances and Shapiro–Wilk to test for normality. Because monthly groups of isotopic data were not normally distributed, we used the non-parametric Kruskal–Wallis sum test for comparing between DULL and YEL groups and between monthly observations of blood, P10 wing and R2 tail feathers, and claw δ^{18}O. Post hoc Wilcoxon rank-sum tests were used for pairwise comparisons. We used the "fdr" *p* value adjustment method. We performed Spearman correlation tests between different tissue isotopic ratios. To test for differences in means between growing feathers and blood δ^{18}O, we performed a pairwise comparison of δ^{18}O values using a paired t-test. As suggested by Vander Zanden et al. (2014), to calculate tissue-to-tissue conversions, we used a linear regression equation for estimating the relationship between blood and feather tissues.

To understand climate effects on blood δ^{18}O, we fit the set of all possible models combining environmental variables as predictors of blood δ^{18}O. We used average estimates of environmental variables for a period between 10 and 30 days before blood sampling (i.e., we assumed a 20-day source–tissue integration period). The various combinations of the eight environmental variables resulted in 256 models. For assessing multicollinearity between two or more variables, we assessed the variance inflation factor (VIF) score computation for each model. Models having any variable with a score exceeding 4.0 were excluded (Zuur et al. 2009). After that procedure, we used Akaike's Information Criterion (AIC) to comparatively rank the 70 remaining models along a quantitative axis of model-data parsimony (Burnham and Anderson 2002).

Results

Molting observations

YEL birds showed a consistent pattern of primary wing molt in a short period. Wing molts were detected in May (1 mol in 5–20%) and July (5 molts in 7–71.4%—Fig. 2a, middle circle), after the breeding season. In contrast, DULL birds were observed molting in each of three different months. Molts were detected in January (1 molt in 8–12.5%), March (1 molt in 42–2.4%, considering 2017 and 2018), and May (3 molts in 39–7.7%,—Fig. 2a, inner circle). Less than 5% of DULL birds had wing molting in total (5 molts in 95, in all year), probably because first-year DULL birds may only molt after turning yellow adult birds (by molting body feathers first). Therefore, these molts accounted for the YEL category.

Feathers from tail and body showed a more protracted molt pattern through the year, having a less structured molting period. YEL tail molts were detected in March (1 molt in 12–8.3%), July (5 molts in 7, 71.4%), and December (1 molt in 8, 12.5%—Fig. 2b, middle circle). DULL tail molts were detected in March (5 molts in 42–11.9%, %, considering 2017 and 2018), May (8 molt in 39–20.5%), July (5 molts in 15–33.3%), and October (1 molt in 13–7.7%). YEL body molts were detected in January (2 molts in 10, 20%), March (1 molt in 12, 8.3%, %, considering 2017 and 2018), May (1 molt in 5, 20%) and July (3 molts in 7, 42.8%—Fig. 2c, middle circle). DULL body molts were detected in March (8 molt in 42–19%, %, considering 2017 and 2018), May (1 molt in 39–2.6%), July (6 molts in 15–40%), and October (3 molts in 13–23%—Fig. 2c, inner circle).

δ^{18}O differences among bird categories and months of collection

Median blood δ^{18}O in YEL and DULL finch categories were similar (Kruskal–Wallis Chi-squared = 0.49, $df = 1$, $p = 0.482$). However, median blood δ^{18}O varied widely throughout the year (13.4–18.8 ‰), differing in every pairwise comparison of months except for that between July/2017 and October/2017 (Kruskal–Wallis Chi-squared = 105.52, $df = 6$, $p = 2.2e{-}16$—Fig. 3a, b, Table 2S). Median P10 feathers δ^{18}O in YEL and DULL finch categories were also similar (Kruskal–Wallis Chi-squared = 3.31, $df = 1$, $p = 0.068$). However, pairwise monthly comparisons were in general similar, except from October/2017 and March/2018, which were similar between each other, while October/2017 differed from the other months and March/2018 differed only from March/2017 (Kruskal–Wallis

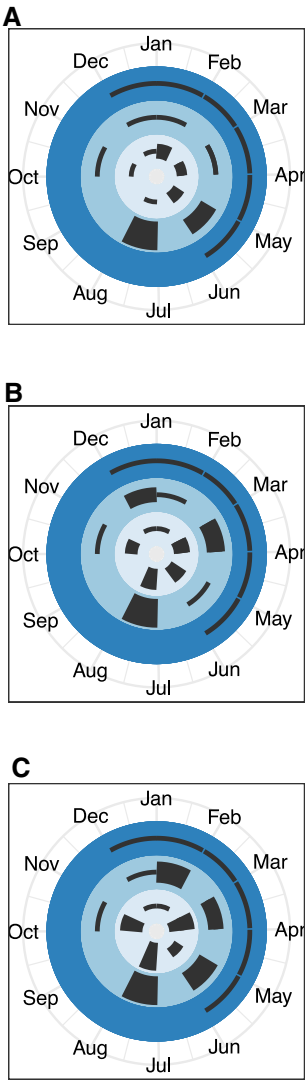

Fig. 2 Percentage of captured birds exhibiting molting in each category (inner circle—DULL molting, and intermediary circle—YEL molting, external circle—breeding season) and body region: **a** wing; **b** tail; **c** body. Thinner traces represent zero percentages or breeding season. Months representations are plotted in a clockwise direction. See text for sampling numbers and percentages values

Chi-squared = 19.03, $df = 6$, $p = 0.004$—Fig. 3c, d, Table S2). Median R2 feathers $\delta^{18}O$ in YEL and DULL finch categories differed (Kruskal–Wallis Chi-squared = 4.00, $df = 1$, $p = 0.045$). Hence, pairwise monthly comparisons were separated for each group. For DULLs, months were statistically similar (Kruskal–Wallis Chi-squared = 11.03, $df = 6$, $p = 0.08$—Fig. 3e, Table S2), while for YELs, some months were different and others similar (Kruskal–Wallis Chi-squared = 25.08, $df = 6$, $p = 0.0003$—Fig. 3f, Table S2). The P10 and R2 feathers for both categories showed narrower isotopic median ranges to blood (P10: 14.0–16.8 ‰; R2: 13.7–17.3 ‰ (Fig. 3c–f). However, for P10 feathers, YEL birds had a narrower range (15.4–17.5 ‰) than DULL (13.9–16.7 ‰, Fig. 3c, d). Median claw $\delta^{18}O$ sampled in Jan and March 2017 was 14.0 ‰, and was not significantly different between YEL and DULL categories (Kruskal–Wallis Chi-squared = 0.69, $df = 1$, $p = 0.41$) or among months (Kruskal–Wallis Chi-squared = 2.29, $df = 1$, $p = 0.13$, Fig. S1–supplementary material).

$\delta^{18}O$ correlations between tissues

On average, blood $\delta^{18}O$ values were 2.5 ‰ higher than new grown feathers ($t = -9.9$, $df = 7$, $p < 0{,}001$). Linear regression derived for blood–feather conversion was $y = 4.7 + 0.6x$ (Fig. 4a). P1 and R2 $\delta^{18}O$ were positively correlated with P10 $\delta^{18}O$ (P1 × P10, $r = 0.75$, $n = 43$, $p = 2.692e{-}09$, and R2 × P10, $r = 0.45$, $n = 86$, $p = 9.124e{-}06$, Fig. 4b, c), while body feathers $\delta^{18}O$ were not ($r = 0.47$, $n = 14$, $p = 0.067$, Fig. 4d). P10 $\delta^{18}O$ from birds recaptured two months later were not correlated with blood $\delta^{18}O$ from the previous capture ($r = -0.21$, $n = 10$, $p = 0.56$, Figs. S2 and S3–supplementary material). In these recaptured birds, blood isotopic values were also higher than feathers' (difference between means = 2.8‰, $t = -3.9$, $df = 9$, $p = 0{,}004$).

Correlations with environmental variables

Temporal variation in blood $\delta^{18}O$ was related to climatic variables. The first three most parsimonious models (delta AIC from 0.0 to 1.81) included the amount of precipitation, relative humidity, and individual or combined, temperature measures, such as maximum, minimum, or range. The top model included maximum temperature, precipitation amount, and relative humidity (adj. $r^2 = 0.83$, $df = 5$, logLik = − 164.4, AIC = 339.3, weight = 0.48, see Table 1, with the first ten ranked models and Table S3, with the total set of the ranked models). The amount of precipitation showed a clear linear relationship with blood $\delta^{18}O$ values, while humidity and temperature showed a nonlinear relationship with blood $\delta^{18}O$ values (Fig. S4–supplementary material).

Discussion

Our results show that $\delta^{18}O$ values in avian blood are related to local climatic variables and reflect changes through time. In the central Brazilian savannas, temperature, precipitation, and relative humidity were all related to $\delta^{18}O$ in the blood of Saffron Finches (Table 1). Avian blood $\delta^{18}O$ values can, therefore, be used as useful proxies for environmental conditions, and this may be a key advantage over the use of $\delta^{2}H$, which involves H exchange with body water and, analytically, with ambient lab vapor (Wassenaar 2019). There are advantages and disadvantages to using $\delta^{18}O$ measurements over the more common $\delta^{2}H$ even

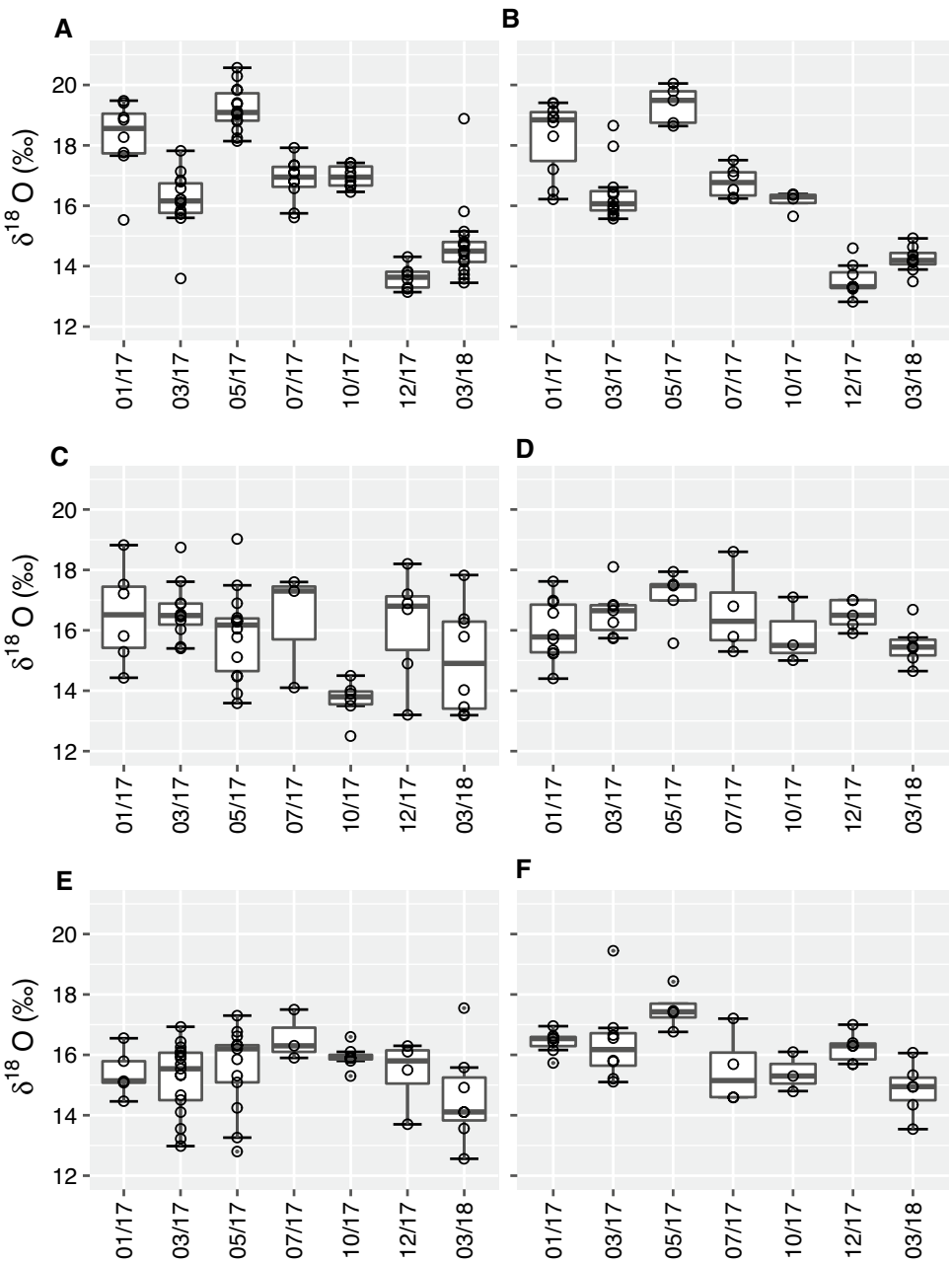

Fig. 3 Boxplots of $\delta^{18}O$ in bird categories and tissues by month collected. **a** Blood of dull birds; **b** blood of yellow birds; **c** P10 primary of dull birds; **d** P10 primary of yellow birds; **e** R2 rectrix of dull birds and **f** R2 rectrix of yellow birds. Points are individual observations

though both are closely connected through the meteoric relationship. One advantage for $\delta^{18}O$ measurements is that they do not involve analytical complications related to ambient exchange with water vapor which may be tissue-dependent and require calibration standards that appropriately account for tissue type (Soto et al. 2013). However, one potential disadvantage is that the range in $\delta^{18}O$ values in the environment is compressed (~ 15 ‰) as compared to $\delta^{2}H$ (~ 150 ‰), although some of that difference is also associated with lower analytical errors (between 0.3 and 0.4 ‰, Bontempo et al. 2014, and this study) for $\delta^{18}O$ measurements as compared to $\delta^{2}H$ measurements (~ 2‰, Bontempo et al. 2014). Oxygen stable isotopes seem to have a less predictable relationship between animal tissues' average precipitation isotopic values because oxygen can be derived from water, diet, and air, whereas hydrogen is only derived from water and diet. Understanding factors that influence $\delta^{18}O$ incorporation to animal tissues is crucial for more refined ecological applications, especially those related to forensics and tracking of animal provenance.

Processes controlling broad-scale patterns in environmental oxygen isotopes are relatively well understood and relate to large-scale water cycle dynamics and surface–atmosphere vapor fluxes. The amount of precipitation and temperature are major environmental drivers of stable isotope ratios of

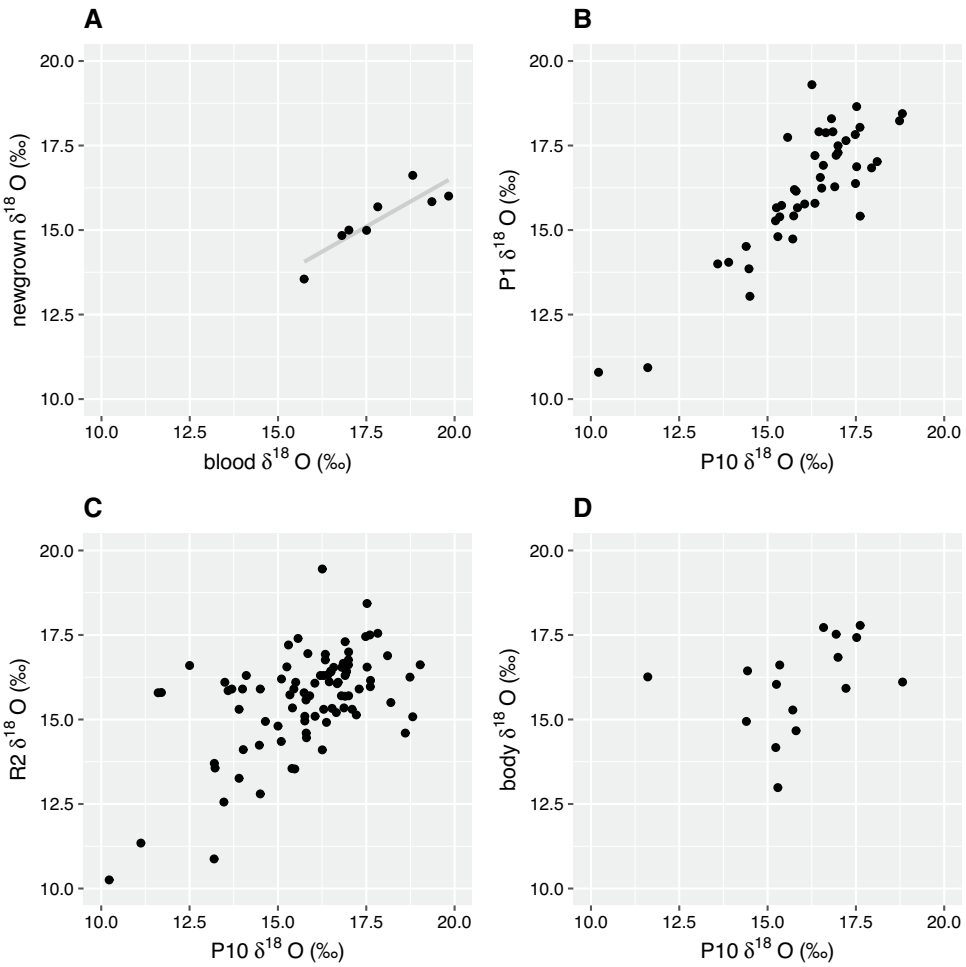

Fig. 4 Scatterplots between blood and new grown feathers $\delta^{18}O$ (**a**), and between feathers $\delta^{18}O$ from different parts of the body of the Saffron Finch: **b** P10 and P1 primaries (Spearman correlation, $r=0.75$, $n=43$, $p=2.692e{-}09$), **c** P10 and R2 feathers $\delta^{18}O$ (Spearman correlation, $r=0.45$, $n=86$, $p=9.124e{-}06$) and **d** P10 and body feathers (Spearman correlation, $r=0.47$, $n=14$, $p=0.067$)

Table 1 AIC results for regressions of blood $\delta^{18}O$ on environmental covariates from 133 Saffron Finches

Rank	Int	Ins	Prec	max-t	av-t	min-t	ran-t	hum	Wind	Adj. r^2	*df*	logLik	AIC	ΔAIC	Weight
1	1.18	–	−0.04	0.43	–	–	–	0.09	–	0.83	5	−164.4	339.3	0.00	0.48
2	1.52	–	−0.04	0.46	–	–	−0.08	0.09	–	0.83	6	−164.2	341.0	1.73	0.20
3	1.37	–	−0.04	–	–	0.47	0.38	0.09	–	0.83	6	−164.2	341.1	1.81	0.19
4	0.89	–	−0.04	–	0.43	–	0.23	0.10	–	0.82	6	−165.6	343.8	4.52	0.05
5	15.57	–	−0.03	–	–	0.30	–	–	−1.05	0.82	5	−167.3	345.1	5.89	0.03
6	16.81	–	−0.03	0.29	–	–	−0.37	–	−1.07	0.82	6	−166.8	346.3	7.03	0.01
7	16.67	–	−0.03	–	–	0.29	−0.09	–	−1.07	0.82	6	−166.8	346.3	7.09	0.01
8	16.62	–	−0.03	−0.08	–	0.38	–	–	−1.07	0.82	6	−166.9	346.4	7.10	0.01
9	3.07	–	−0.04	–	0.47	–	–	0.09	–	0.82	5	−168.1	346.8	7.50	0.01
10	17.97	–	−0.03	–	0.24	–	−0.20	–	−1.17	0.81	6	−168.5	349.6	10.31	0.00

Models were evaluated using AIC ranking between models (ΔAIC) and AIC weight. The coefficients of the variables included in the first 30 ranked models are exhibited. Birds were captured and sampled at the Tabapuã dos Pireneus farm (15° 46′ 40″ S 48° 49′ 22″ W), in the Municipality of Cocalzinho do Goiás, GO, Brazil. Sampling was made in Jan, Mar, May, Jul, Oct, and Dec/2017 and Mar/2018

int intercept, *ins* insolation (h), *prec* amount of precipitation (mm), *max-t* maximum temperature (°C), *av-t* averaged temperature (°C), *min-t* minimum temperature (°C), *ran-t* temperature range (°C), *hum* relative humidity (%), *wind* wind speed (MPS)

precipitation water (reviewed by Bowen 2010). Although less explored, other drivers, such as humidity, may also contribute to evaporative processes, leading to more pronounced fractionation of stable isotopes in more xeric conditions (Gat et al. 2011; Giustini et al. 2016). In this study, climatic factors were likely drivers of Saffron Finch $\delta^{18}O$ variation

through time. The amount of precipitation, temperature and relative humidity were strong predictors present in the most weighted models.

Some studies have demonstrated that $\delta^{18}O$ in animal tissue is a reasonable proxy for seasonal variability in climate (Auerswald et al. 2011; Zazzo et al. 2015). The Cerrado experiences annual dry and rainy seasons, marked by a difference in the amount of precipitation between the two seasons (Fig. 1), yet the same clearly seasonal pattern was not as apparent in intra-annual patterns of oxygen isotopic variation in avian blood (Figs. 3a, b, 4b).Here, we considered the integration period of oxygen from environment to blood to occur over 20 days, a period much shorter than the typical multi-month climatic season. Partitioning environmental data on this more refined temporal scale provided better approximating models for the weekly to monthly patterns in blood oxygen isotope variation. In fact, even in wet seasons, there are oscillations of extremely rainy and drought periods, and these smaller-scale variations could have been involved in our system. In this sense, blood $\delta^{18}O$ may be used as an environmental marker to track ecosystem activity on a more refined temporal scale. Specific animal ecophysiological responses to the environment might be, thus, evaluated, such as mate pairing, nesting, and hatching behaviors within a single breeding season.

While yellow birds showed a short molting period for primaries, dull birds showed a more protracted pattern. Isotope values in feathers reflected this difference where $\delta^{18}O$ was more variable in dull than in yellow birds (Fig. 3c–f). According to the dull/yellow classification adopted here, first-year individuals were placed in the same category as second-year individuals that had not yet molted. Therefore, all dull birds acquired their remiges during the breeding season in which they hatched, which may or may not have been the same year they are captured or sampled. This may help to explain the larger ranges of $\delta^{18}O$ observed in feathers from dull birds.

Correlations between body, rectrices, and wing feather isotopic values varied from no correlation to strong correlation (Fig. 4). Strong correlations imply similar environmental conditions and metabolic pathways during the growth of these tissues that must be associated with the integration of isotopic values. Considering the molting of the wing, from proximal to distal positions, P1 and P10, $\delta^{18}O$ correlation showed that these feathers were likely grown close in time and environmental space. Other tissue isotopic signals were not so strongly correlated with P1. This result has practical applications for forensic or provenance studies: feather sampling should favor wing primaries instead of feathers from other parts of the body. We found a − 2.5‰ blood to feather conversion factor (Fig. S3), which falls within the range of − 3.5 to − 1.4 ‰, as reported for House Sparrow (*Passer domesticus*) between plasma and red blood cells, respectively, and feathers (Wolf et al. 2011). Claw $\delta^{18}O$ values cannot be directly compared with other tissues, as they reflect 2–5 months before sampling, which did not overlap with other tissues sampled in this study. However, despite the small sample size, they may be useful as a finer time integration tissue, as their isotopic variation was generally smaller than that of other tissues (Fig. S1).

Animals incorporate ^{18}O from different sources, mainly from drinking water, metabolic O_2 from food, and atmospheric O_2. Differences in the importance of these inputs are related to species ecology and physiology (Magozzi et al. 2019). Studies suggest that larger animals are prone to ingest more water than small animals (Bryant and Froelich 1995), but climate may also affect water ingestion, mainly temperature and humidity (Abeni et al. 2015). Animals adapted to dry habitats ingest less water than animals in humid habitats (Bryant and Froelich 1995). The less water, or water associated with food ingested, the less influence of meteoric isotopic values in tissues. If a higher proportion of body oxygen originates from food sources, there are many other uncertainties related to vegetal or animal food items. For example, plant $\delta^{18}O$ assimilation is related to hydraulic properties of the plant, where relative humidity is closely related to the isotopic enrichment in leaf water (reviewed by Cernusak et al. 2016). Different prey may assimilate ^{18}O differently (Pietsch et al. 2011), complicating efforts to estimate the relative quantities of food items ingested, digested, and absorbed by animals unless the diet is well known. During metabolism, oxygen reacts with macromolecules, generating water and carbon dioxide. Liquid water generated is eliminated mainly as urine, fecal water, and sweat, which are in equilibrium with total body water, not affecting its $\delta^{18}O$ values (Bryant and Froelich 1995). Therefore, environmental factors may play a role in many different phases of isotopic tissue assimilation.

The incorporation of ^{18}O in Saffron Finch blood is obviously influenced by the concentration of oxygen isotopes in local meteoric waters (Table 1). Saffron Finches are primarily granivorous, but they also consume small arthropods. Saffron Finches also drinks local water directly. Therefore, the amount of precipitation and temperature should seasonally influence $\delta^{18}O$ in Saffron Finch tissues. Relative humidity may operate either on climatic events affecting evaporative processes of precipitation water or directly on respiration demands of animals, in turn affecting the relative enhancement of water ingestion or water evaporation and fractionation in food sources. Magozzi et al. (2019), proposed that relative humidity is an essential link between isotopes in precipitated water and bird keratin, especially in regions where humidity is highly variable, such as on the European continent. In this sense, Saffron Finch may be a good species for studying

geographical and local variation in precipitation isotopic values.

Although results presented here are specific to the Cerrado region and the Saffron Finch, they open an avenue for incorporating another tool to the isotopic toolbox for ecological and forensic wildlife studies (Vander Zanden et al. 2016). Our data clearly showed that the use of a single isotope in different avian tissues can be used to infer different environmental and ecological aspects related to the Saffron Finch. While blood reflected the seasonal environmental variability of the Brazilian central savannas, feathers might be useful as indicators of important ecological aspects of molting and reproductive periods. The molting period for the Saffron Finch could be investigated by retrospectively tracking environmental variables and blood $\delta^{18}O$ values that corresponded to the period of the feather formation. The knowledge of the temporal variability in isotope values can be used for refining spatial models, making inferences of geographical origins of confiscated birds more accurate (Vander Zanden et al. 2018). These inferences may guide reintroduction of individuals to nature and enforcement actions in criminal hotspots. Therefore, knowing key aspects of bird ecology will ultimately be essential to a better understanding of how life cycle influences isotopic interpretations relevant to species and human illegal exploitations and guide environmental policies or enforcement actions against local threats.

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Author contributions FJVC and GBN contributed to the study conception and design. Material preparation and data collection were performed by FJVC. KAH and MBW contributed to the data interpretation, statistical analysis and manuscript outline and writing. The first draft of the manuscript was written by FJVC and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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