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REVIEW ARTICLE

Perspectives and challenges on isotopic ecology of terrestrial birds in Brazil

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ABSTRACT. Although stable isotopes have been increasingly used in ornithology since 1980 in many places, Brazil has been slow in adopting this methodology, especially when it comes to terrestrial birds. The most common elements in bird ecology studies are carbon, nitrogen, hydrogen, and oxygen stable isotopes, which provide information on diet, trophic interactions, habitat use, migration, geographic patterns, and physiology. It is important that Brazilian ornithologists become aware of the potential of stable isotope analysis in ecological studies, and the shortcomings of this tool. The use of stable isotopes to study bird ecology has great potential in Brazil, since many ecological questions about Neotropical birds can be addressed by it (e.g., resource and habitat use, migratory routes, isotopic niches, anthropogenic impacts, individual specialization). Brazilian museums and other Natural History collections can provide samples to study long-term temporal dynamics in bird ecology. Additionally, the integration of avian tissue sample information into a database may increase the collaboration among researchers and promote sample reuse in a variety of studies. All biomes in Brazil have been under pressure from anthropogenic impacts (e.g., land-use change, habitat loss, fragmentation, intensive agriculture), affecting several taxa, including terrestrial birds. Considering the negative effects of human expansion over natural areas and that stable isotopes provide useful ecological information, ornithologists in Brazil should increase their use of this tool in the future.

KEY WORDS. $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$, $\delta^{18}O$, migratory birds, museum specimens, ornithology, trophic ecology.

The isotopic methodology generates ornithological information that used to be only possible with conventional approaches (e.g., regurgitates or stomach contents analyses, tracking with GPS and telemetry, bird ringing). Using a single sample that can be collected through a minimally invasive method, stable isotopes make it possible to gather long-term information about organisms (Newton 2016). Despite the advantages of this method, it has not been consistently employed in ornithological studies in Brazil. Brazilian studies are generally based on time-consuming and resource-demanding traditional methods that only offer a ‘snapshot’ of the diet of a bird.

Stable isotope analysis in ornithological studies is relatively recent worldwide, since the first studies were published in the 1980s (Hobson 2011). In Brazil, this methodology was first employed less than 20 years ago (Atkinson et al. 2005, Quillfeldt et al. 2008, Bugoni et al. 2008). In a literature review encompassing 2007–2009, Boecklen et al. (2011) reviewed the main studies in trophic ecology using stable isotopes. Birds were the fifth most studied group, particularly the ones inhabiting aquatic (ocean, estuaries, lake) and temperate environments (e.g., grassland, forest) (Boecklen et al. 2011). The representation of tropical birds in the literature was less than 10%, highlighting the urgency to apply stable isotopes in new studies to investigate bird ecology, particularly in terrestrial tropical environments.

Several studies have already been undertaken to compile the different facets of stable isotopes as a tool to understand bird ecology (e.g., Inger and Bearhop 2008, Hobson 2011, Wiley et al. 2017). None has focused on the Brazilian fauna, which is very distinct from the North American and European faunas. In this contribution, we discuss the potential of stable isotope studies in Brazil to better understand the ecology of terrestrial birds (Fig. 1).

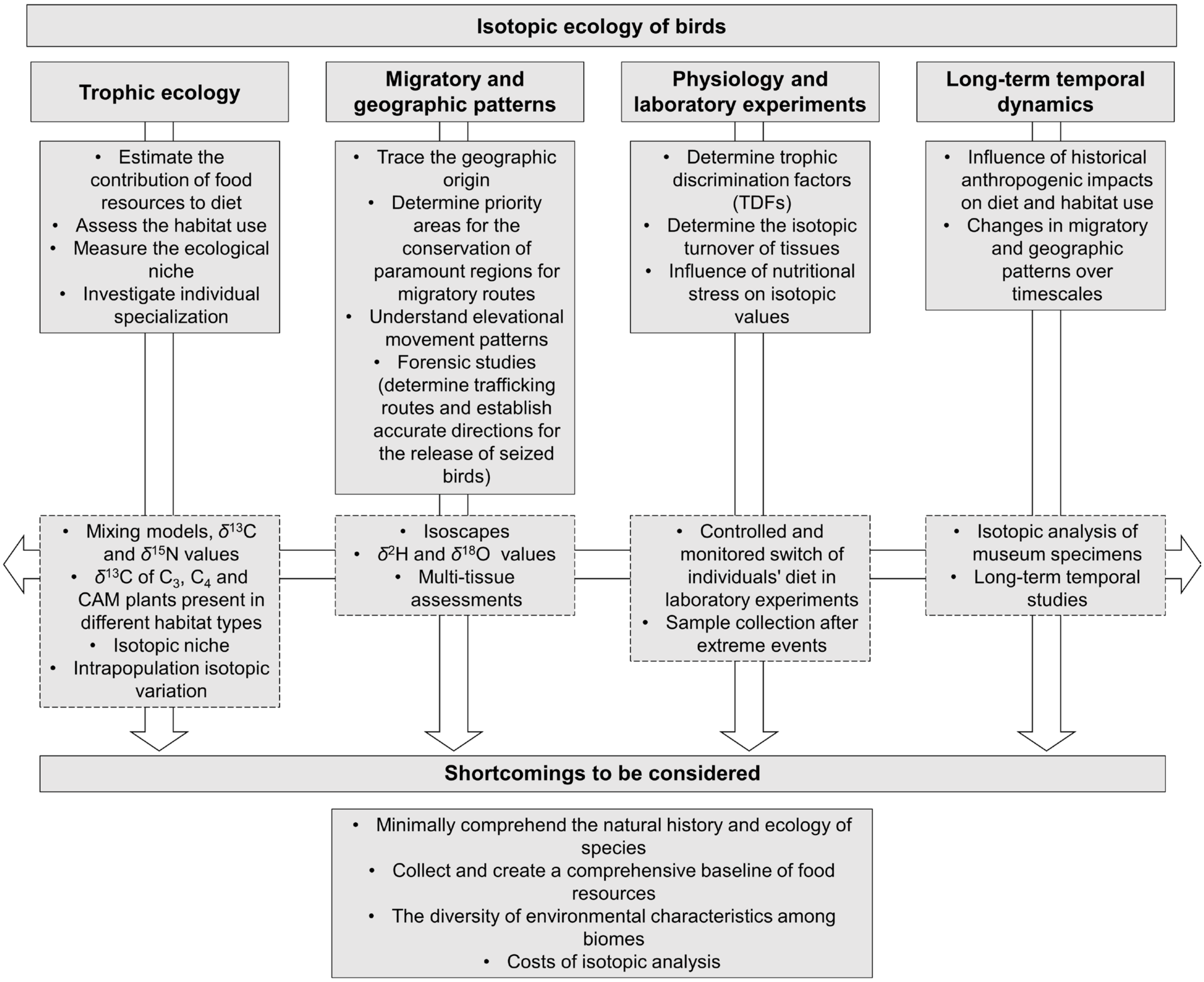

Figure 1. Flowchart of potential study themes (in bold) to be developed in isotopic ecology with terrestrial birds in Brazil. Each theme branches into several sub-themes that can be explored (first boxes below the themes) and the methods and approaches that can be employed to develop the studies (within the dashed boxes). Many methods and approaches are interchangeable among themes and subthemes (represented by the horizontal arrow). In addition, the shortcomings of stable isotope ecology that should be considered before or during the development of the studies.

What are stable isotopes and how to measure it (C, N, H, O)

Stable isotopes are the non-radioactive forms of the same element that contain different numbers of neutrons. The neutron-depleted isotope is usually called "light" and the neutron-enriched isotope is named "heavy". Although the amount of each stable isotope in each ecosystem varies naturally, the light isotopes are generally more common than the heavy isotopes (Fry 2008). The sentence "You are what you eat (plus a few per thousand)" represents the use of stable isotope analysis in ecology (DeNiro and Epstein 1976), meaning that organisms express the isotopic value of the resources they consume (but see Dodds et al. (2014) and Petta et al. (2020) for another viewpoint). Considering that the abundance of isotopes varies from one place to another, the proportion of each isotope in living organisms will also vary geographically. By analyzing different animal tissues with a mass spectrometer, it is possible to measure the proportion of each isotope in them, allowing the calculation of a ratio between heavy/light isotopes. The delta notation (δ) is used to describe the isotopic ratio of a sample as parts per thousand (per mille, ‰), following the equation '$\delta X = (R_{sample}/R_{standard} - 1)$', where X is the measured isotope of the element, R is the absolute isotopic ratio (R = heavy/light isotope) and $R_{standard}$ is the isotopic ratio of the international standard for each element (e.g., V-PDB for carbon; atmospheric air for nitrogen; V-SMOW for hydrogen and oxygen). The use of $R_{standard}$ is to standardize the values of δX to compare among the most different samples since δX will always be enriched or depleted regarding the heavier element (Bond and Hobson 2012).

Stable carbon isotopes (^{12}C and ^{13}C ratio; denominated as $δ^{13}C$) are commonly used to determine the habitat and resource use by an organism (Kelly 2000, Symes 2012, Wiley et al. 2017, Magioli et al. 2019). Terrestrial environments are highly associated with land use and cover (e.g., forest formation, anthropogenic areas), and plants vary in their isotopic values according to the photosynthetic cycle (C_3, C_4 e CAM). Tropical forests are mainly dominated by C_3 plants (usually trees), while C_4 plants are grasses associated with savannas and agricultural areas (e.g., pasture, sugarcane, maize). Neotropical C_3 plants have a wide range of isotopic values from -24‰ to -38‰, while C_4 plants range from -11‰ to -15‰ (Martinelli et al. 2009, 2020). Thus, through the values of $δ^{13}C$, it is possible to determine the environments used by birds, their food sources, and to compare the importance of forests versus anthropogenic areas in the ecology of a species (Ferger et al. 2013, Boesing et al. 2021, Navarro et al. 2021b). Nevertheless, in addition to the isotopic variation according to the photosynthetic cycle, other factors (i.e., water stress, light intensity, soil) can also influence the $δ^{13}C$ values of plants (Chesson et al. 2018, Sena-Souza et al. 2019). Therefore, it is crucial to consider the environmental conditions of the study site when collecting bird samples for isotopic analysis.

Nitrogen isotopes (^{14}N and ^{15}N ratio; denominated as $δ^{15}N$) are usually employed in studies of the dietary patterns and trophic processes. The ratio of nitrogen stable isotopes tends to be enriched by 3–4‰ as it moves towards the higher levels of the trophic chain. Consequently, top predators are expected to have higher $δ^{15}N$ values than primary consumers (Post 2002), making nitrogen isotope analysis an adequate tool to understand bird diet, the dietary differences among species or foraging groups, and trophic structuring (Herrera et al. 2003, McKinnon et al. 2017, English et al. 2018, Navarro et al. 2021b). Recently, new data has been published concerning the influence of nitrogen fertilizers on the $δ^{15}N$ values of birds inhabiting anthropogenic areas (Hebert and Wassenaar 2001, Møller et al. 2018). Synthetic and organic nitrogen fertilizers have distinct $δ^{15}N$ values due to the different nitrogen sources used for their production. The synthetic fertilizers have isotopic values closer to zero, since they are produced with nitrogen from atmospheric air, while those made from organic matter (e.g., animal waste) expresses greater $δ^{15}N$ (Hebert and Wassenaar 2001). In view of this data, nitrogen isotopes may be useful to clarify the effects of increased anthropogenic pollution, agriculture expansion and urbanization, on the diet of birds (Caron-Beaudoin et al. 2013).

The stable isotopes of hydrogen (^{1}H and ^{2}H ratio; denominated as $δ^{2}H$) and oxygen (^{16}O and ^{18}O ratio; denominated as $δ^{18}O$) can be used to uncover the geographic and migratory patterns of birds (Hobson 1999, 2011, Fox and Bearhop 2008, Hobson et al. 2019). The values of $δ^{2}H$ and $δ^{18}O$ vary according to latitude, precipitation patterns, temperature, elevation, and relative humidity, following the characteristics of the hydrological cycle in each geographic portion of the Earth (Rubenstein and Hobson 2004). The main sources of H and O isotopes in animal tissues are drinking water and water from the food they consume, but O isotopes also derive from the O_2 respiration process (Chesson et al. 2018). The values of $δ^{2}H$ and $δ^{18}O$ are usually represented as isoscapes, which are the isotopic values of landscapes. However, the analysis of $δ^{13}C$ and $δ^{15}N$ values has increased in studies involving birds and isoscapes (Hobson et al. 2012, Cheesman and Cernusak 2016, John Glew et al. 2018). Investigations on the association among different isoscapes are promising to promote a better understanding of the migratory patterns of terrestrial birds.

Factors affecting isotopic values in individuals and their environment

The use of stable isotopes in terrestrial ornithological studies is increasing, and results are promising. Certain methodological precautions, however, need to be taken before the analysis of samples and discussion of results (Rubenstein and Hobson 2004, Hobson 2011, Ben-David and Flaherty 2012). First, a minimal understanding of the natural history and ecology of the species (e.g., animal or plant-based diet, trophic guild, habitat preference) is fundamental to correctly interpret isotopic values. Animals showing similar isotopic values do not necessarily have the same diet, habitat use, or origin (Inger and Bearhop 2008). For example, it is possible to misinterpret data collected from nectarivore birds when the researcher does not consider a priori information on the influence of diet and physiology on $δ^{15}N$: although hummingbirds may express high $δ^{15}N$ values because they supplement their diet with arthropods (mainly spiders and flies) to meet their high metabolic requirements (Hardesty 2009), resulting in isotopic values that are similar to those found in strict insectivores, their primary food resource is in fact nectar.

Concerning the incorporation of food nutrients into animal tissues, it is important to remember that several biochemical reactions occur in organisms and in the ecosystems, leading to a process known as isotopic discrimination or more specifically, trophic discrimination factor (TDF). This biological process generates differences in isotopic values between the consumer and the resource consumed, which explains the "... (plus a few per mil)" in the sentence previously described (DeNiro and Epstein 1976). Each food source along with its stable isotopes are incorporated into the tissues of different organisms through different metabolic pathways. Consequently, the TDFs vary according to the tissue and the diet consumed (Healy et al. 2018). Additionally, the dynamics of isotopic incorporation vary among animal tissues, depending on physiological processes. Since the synthesis and replacement of each tissue of an animal will happen within a different period in time, it is possible to use multi-tissue analysis to uncover the consumption of resources at distinct phases of the life of an organism (Inger and Bearhop 2008). In the case of birds, while some tissues reflect the isotopic value of the resources consumed a few days ago (e.g., blood plasma, liver), others reflect the resources consumed months or years before (e.g., feathers, claws, bone collagen) (Hobson and Clark 1992, Bearhop et al. 2003). The discrimination and dynamics of isotopic incorporation may vary according to the species' phylogenetic relationships or similarity in dietary patterns (e.g., herbivores, carnivores, omnivores), highlighting the importance of carefully considering the use of correction factors (e.g., TDF) in bird isotopic ecology.

Another important consideration is to collect and create a comprehensive baseline of food resources (Post 2002). The baseline can be measured through the direct isotopic analysis of items consumed by the species or using phylogenetically related organisms as a proxy for resources (Casey and Post 2011). Creating a good baseline ensures that the isotopic comparisons among individuals are accurate, especially in dietary and food-web studies. In long-term studies, it may be difficult to sample historical resources to compose a baseline of the past. In this case, researchers should resort to museum collections in search of food items, or develop a robust proxy for the historical baseline (e.g., English et al. 2018, Mason et al. 2020). In Brazil, where biodiversity is high, a single bird species can consume many different food items (Durães and Marini 2005, Lopes et al. 2005, Siqueira et al. 2015). Thus, collecting and analyzing the complete baseline of a species may be unfeasible, highlighting the importance of developing good proxies from phylogenetically related organisms.

The diversity of environmental characteristics among biomes in Brazil (e.g., precipitation, vegetation type, soil, landscape composition) is also a reason for caution when investigating patterns in the isotopic ecology of birds. To be able to understand how abiotic factors influence species' isotopic values, it is important to examine refined isoscape maps for the Brazilian territory, which already incorporate several environmental variables in their models (Sena-Souza et al. 2019). Vegetation from distinct regions can also express isotopic variation or similarity (Vitória et al. 2018, Martinelli et al. 2020). For this reason, the isotopic values of the vegetation need to be considered, to correctly interpret the results of studies that incorporate a broad spatial area, especially because many birds have plant-based diets.

Stable isotopes in dietary, niche and food web studies

Stable isotopes can be broadly used in trophic ecology and foraging studies, for instance: estimating the proportion of items in the diet, assessing which environment is used more often to obtain food and as habitat, measuring different isotopic niche dimensions, and investigating foraging specializations among individuals, species, or groups (Table 1). Most dietary studies employ the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, which give more information on habitat and resource use, and the trophic levels of animal species (Kelly 2000, Inger and Bearhop 2008).

The ingestion of many food resources by an organism can be measured with stable isotope mixing models, which estimate how much each food source contributes to the diet of the individual's (Phillips and Gregg 2003, Phillips 2012). There are several mixing models that can be used to ascertain foraging patterns. Currently, the Bayesian models are favored, since they fully incorporate sources of uncertainty (but see Hopkins and Ferguson (2012) and Stock et al. (2018) for some different models and their particularities). González-Carcacía et al. (2020) used mixing models to unravel the greater contribution of C_3 plants (mainly forest-based) over CAM plants (cactus and agaves) in the diet of Neotropical birds in a semi-arid zone in Venezuela. Their results revealed the importance of forest patches for bird communities. Guaraldo et al. (2019) evaluated the diet of two congener species of *Elaenia* Sundevall, 1836 (one resident and one migratory) over their annual life cycles in the Brazilian Cerrado. Using mixing models, the authors showed that both species employ similar foraging strategies, contrary to the expectation that their diets would differ. Their study brings attention to the importance of new research to assess differences and similarities in the diet of birds that co-occur in species-rich tropical biomes. Mixing models encompass a wide range of research possibilities, but it is crucial to have a good experimental design for sample collection (both from birds and their food resources), and a prior knowledge of the analysis to be employed and its particularities (Phillips et al. 2014, Newton 2016). Especially in Brazil, where there is a great diversity of species and food resources, it is important to sample all possible food items to build an adequate isotopic baseline.

In addition to specifying the contribution of each food item to the diet of a species, stable isotopes in trophic ecology studies are also employed to assess which habitat is used by an animal to obtain resources (e.g., Guaraldo et al. 2016, Magioli et al. 2019, González-Carcacía et al. 2020). The habitat-level approach in foraging studies is important because it can serve as a guide for conservation, especially in landscapes that have been extremely modified by man. For instance, the isotopic results of Boesing et al. (2021) highlight the urgency to preserve forest patches and to design multifunctional landscapes for the maintenance of bird communities. Another consideration is that generalist species of the Brazilian Atlantic Forest, which appear to adapt well to environmental changes, in fact consume forest resources (mainly C_3 plants) more than they consume resources from agricultural areas (C_4 plants) (Boesing et al. 2021, Navarro et al. 2021b). Nevertheless, the dependence of birds on forest habitats is not exclusive to the Neotropics. Ferger et al. (2013), in a study using carbon isotopic values, discussed the importance of forests as a source of food for bird communities in Central Africa. Even though granivores are adapted to open environments (showing $\delta^{13}C$ values similar to C_4 plants), many other trophic guilds are highly dependent on forest resources, especially understory insectivores (Ferger et al. 2013). In a world facing rapid human-induced changes in landscape composition and struc-

Table 1. Examples of studies using stable isotope analysis to cover relevant themes and sub-themes of terrestrial bird ecology. The preference adopted for citation in the table was the existence of studies developed in Brazil or the Neotropics. We also cite studies from temperate regions that have not yet been developed in the Neotropics, showing the potential of development in Brazil.

Field	Study	Stable isotopes used	Organism	Aim	Method
Trophic ecology					
Diet	González-Carcacía et al. (2020)	$\delta^{13}C$, $\delta^{15}N$	Neotropical birds	Contribution of C_3 and CAM plants in the diet of species in a semi-arid zone in Venezuela, importance of forest remnants for species	Mixing models
	Guaraldo et al. (2019)	$\delta^{13}C$, $\delta^{15}N$	*Elaenia* sp.	Diet of two congener species over their annual life cycles in the Cerrado savannas of Brazil	Mixing models
Habitat use	Boesing et al. (2021)	$\delta^{13}C$, $\delta^{15}N$	Neotropical birds	Differences in habitat use by bird species in agricultural landscapes of the Atlantic Forest, Brazil	Comparison of $\delta^{13}C$ and $\delta^{15}N$ values and landscape composition
	Ferger et al. (2013)	$\delta^{13}C$, $\delta^{15}N$	Tropical birds	Influence of agricultural landscapes in the diet and habitat use of bird species in Central Africa	Comparison of $\delta^{13}C$ and $\delta^{15}N$ values and landscape composition
Niche	Bosenbecker and Bugoni (2020)	$\delta^{13}C$, $\delta^{15}N$	*Turdus* sp.	Isotopic niche width and overlap among three sympatric species of Turdus in southern Brazil	Isotopic niche
	Navarro et al. (2021b)	$\delta^{13}C$, $\delta^{15}N$	Neotropical birds	Comparison of the isotopic niche width of five trophic guilds between human-modified and natural landscapes	Isotopic niche
Individual specialization	Martínez del Rio et al. (2009a)	$\delta^{13}C$, $\delta^{15}N$	*Cinclodes* sp.	Dietary and isotopic variation among three species of Cinclodes in South America	Comparison of isotopic niches, $\delta^{13}C$ and $\delta^{15}N$ values among intrapopulation individuals
	Guaraldo et al. (2019)	$\delta^{13}C$, $\delta^{15}N$	*Elaenia cristata*	Differences in individual diet depending on the period of the year (breeding, molting, and non-breeding), and between adults and juveniles	Comparison of isotopic niches, $\delta^{13}C$ and $\delta^{15}N$ values among intrapopulation individuals
Migratory and geographic patterns					
Latitudinal migration	Cardenas-Ortiz et al. (2020)	$\delta^{2}H$	Neartic-Neotropical migrant birds	Inference of breeding origins of Neartic-Neotropical migrant birds captured in Colombia	Comparison of $\delta^{2}H$ values and isoscapes
Altitudinal migration	Hobson et al. (2003)	$\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$	Neotropical birds	Investigation of the potential of isotopic values to estimate altitudinal migration of hummingbirds in Ecuador	Comparison of $\delta^{2}H$, $\delta^{13}C$, $\delta^{15}N$ values and altitudinal gradients
Forensics	Andersson et al. (2021)	$\delta^{13}C$	*Cacatua sulphurea*	Isotopic analysis to monitor and regulate illegal trade of a critically endangered species	Compound-specific stable isotope analysis of $\delta^{13}C$ values among wild and captive individuals
Physiology and laboratory experiments					
Trophic discrimination factors (TDFs) and isotopic turnover rates	Martínez del Rio et al. (2009b), Vander Zanden et al. (2015)	$\delta^{13}C$, $\delta^{15}N$	Animals (including birds in general)	Summary about animal tissue isotopic turnover rate, TDFs and a call for more experimental studies	Review
Effects of stressful events	Ross et al. (2015)	$\delta^{13}C$, $\delta^{15}N$	*Ammodramus savannarum*	Influence of a severe storm to the increasing of pallid bands in juveniles' feathers	Comparison of $\delta^{13}C$ and $\delta^{15}N$ values and bird morphology
Long-term temporal dynamics					
Trophic ecology	Navarro et al. (2021a)	$\delta^{13}C$, $\delta^{15}N$	Neotropical birds	Influence of centenary anthropogenic impacts to the reduction of bird isotopic niches	Isotopic niche
	Mason et al. (2020)	$\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$	*Eremophila alpestris*	Influence of agricultural expansion to isotopic shifts and niche contraction	Isotopic niche
Physiology and morphology	Moller et al. (2018)	$\delta^{15}N$	*Somateria mollissima*	Impact of increased inorganic fertilizer use to feathers' quality between historical and contemporary individuals	Comparison of $\delta^{15}N$ values, bird morphology and fertilizer use
Geographic patterns	Hobson et al. (2010)	$\delta^{2}H$	*Euphagus carolinus*	Differences in geographical patterns between historical and contemporary individuals	Comparison of $\delta^{2}H$ values and breeding populations
	Jiguet et al. (2020)	$\delta^{2}H$	*Emberiza hortulana* and *Fringilla montifringilla*	Variation in latitudinal origin of historical and contemporary individuals of two declining species	Comparison of $\delta^{2}H$ values among different time-period individuals

ture, stable isotope analysis may help to better understand the various ecological aspects of birds in highly modified habitats.

Studies in trophic ecology may estimate the isotopic niche metrics of bird species. Understanding a species' niche, which includes diet, habitat use, and geographic patterns, is very important to understand the natural history of a species (McGill et al. 2006). The isotopic niche is correlated with the ecological niche, since the δ-space is comparable to the n-dimensional space of the niche concept (Newsome et al. 2007). Bosenbecker and Bugoni (2020) investigated isotopic niche width and overlap in three sympatric species of *Turdus* Linnaeus, 1758 in southern Brazil. Even though the contribution of each food item is slightly different among thrushes, niche overlap shows that the three species share similar resources, mainly C_3 plants and invertebrates (Bosenbecker and Bugoni 2020). Navarro et al. (2021b) documented a decrease in the width of the isotopic niche of many trophic guilds in human-modified landscapes when compared to birds in natural areas of the Atlantic Forest biome. Although the niche of granivore birds tends to expand in human-modified landscapes, the niche of frugivore, insectivore, nectarivore, and omnivore birds becomes narrower in response to the anthropogenic impacts in southeastern Brazil (Navarro et al. 2021b). Several Brazilian biomes have struggled with human expansion and, consequently, with their negative environmental effects, such as habitat loss, fragmentation, and savannization (e.g., Ribeiro et al. 2009, Carvalho et al. 2009, Silvério et al. 2013, Sales et al. 2020, Magioli et al. 2021). Contrasting with this situation, little has been done in the field of isotopic niche studies to produce information that could guide the conservation of bird species and their habitats in the Neotropical region.

The isotopic niche approach provides practical solutions to several questions regarding the ecology of birds. Nevertheless, it is worth mentioning that this method, which is backed up by helpful analytical software packages (e.g., SIBER – Jackson et al. 2011, rKIN – Eckrich et al. 2020), is still recent and has some shortfalls. To avoid them, it is important to make a detailed assessment of the isotopic variation of baseline resources (Inger and Bearhop 2008). Moreover, we do not know the diet of many Neotropical bird species, highlighting the need for a careful interpretation of the results, and expanding our knowledge about the natural history of those species.

Stable isotope analysis has proven a valuable tool to identify foraging specializations in individuals or species (Araújo et al. 2007, Layman et al. 2012). Species may exhibit varying degrees of intra-population specialization in food resource exploration and habitat use, which can be identified through multi-tissue isotopic analysis (Araújo et al. 2011, Bond et al. 2016). Martínez del Rio et al. (2009a) compared intrapopulation isotopic variation among three species of *Cinclodes* G.R. Gray, 1840 in South America. Each of the species has a seasonal foraging singularity. Representatives of one species are generalists and consume terrestrial/freshwater and marine resources. Individuals of a second species have both generalist and specialist individuals, and a third species has specialist individuals strictly dependent on marine invertebrates (Martínez del Rio et al. 2009a). Guaraldo et al. (2019) showed that the diet of *Elaenia cristata* Pelzeln, 1868, a terrestrial migratory bird in Brazil, varies depending on the time of the year (breeding, molting, and non-breeding), and between adults and juveniles. Some birds may have distinct individual dietary preferences, so it is possible to observe isotopic variations among individuals of different ages and sexes (Fox and Bearhop 2008). Nevertheless, although Brazil has a vast territory inhabited by several species with different degrees of specialization, stable isotope analysis has not been employed to its full potential to allows us to understand these patterns.

The concept of isoscapes and the use of stable isotopes to track migratory species

Detecting large-scale movement patterns in migratory species may be time consuming and financially costly, especially when conventional methodologies are employed (e.g., telemetry, mark-recapture, leg banding) (Hobson and Norris 2008). It is increasingly evident that isotopic analysis is a great cost-effective tool to obtain information on the geographic patterns of birds through the use of isoscapes and individual values of δ^2H and δ^{18}O (Hobson 2011, Hobson et al. 2019, Table 1). There has been a growing appeal among researchers to explore Neotropical regions, in association with North America studies, to construct an isotopic atlas for migratory birds (Hobson et al. 2014). This effort aims to facilitate the understanding of migratory dynamics, and to develop more effective approaches to the conservation of species. Even though Brazil has a great diversity of migratory birds and is also in the migratory route of several species (Somenzari et al. 2018), few studies conducted in the country have used stable isotopes to address this theme.

Brazil stretches over a wide latitudinal and longitudinal extent, which provides markedly distinct isoscapes (Sena-Souza et al. 2019). Isoscapes are the geographic patterns of isotopic values of landscapes, represented by maps of δ^2H, δ^{18}O, and others. The different Brazilian biomes have particular water regimes and, therefore, each may show different values of δ^2H and δ^{18}O (Bowen et al. 2005). Although seasonal variations in atmospheric circulation slightly influence in isoscapes annually, isotopic spatial patterns are stable on a large temporal scale, providing robust data to trace the geographic origin of individuals analyzed (Nardoto et al. 2017).

Migrant birds have different breeding and wintering sites. Usually, they molt during one of these periods, before the migration event. Thus, the values of δ^2H and δ^{18}O of the feathers, an inert tissue, reflect the isotopic value of the region in which the molting was performed (Hobson 1999). Certain tropical regions are obligatory routes for several migratory species. If stochastic events and anthropogenic impacts reach these areas, the conservation of the birds passing through these routes may be impacted. Cardenas-Ortiz et al. (2020) observed that populations of some migratory birds from distinct North American sites mixed spatial-temporally in an area of Colombia. Populations that do not have distinct migratory routes may compete for resources in the same region at the same time, representing a possible bottleneck for the survival of these species (Cardenas-Ortiz et al. 2020). South America receives many migratory birds escaping from the winter of the Northern Hemisphere. Forest areas in northern Brazil have been impacted by changes in land-use for agricultural purposes, which may pose a threat not only to resident species but also to migrant birds. Using isotopic analysis to track the origin of individuals may be helpful for the determination of priority areas for conservation of paramount sites on migratory routes.

Altitudinal migration is another geographic pattern performed by several Neotropical birds and which can be measured using the isotopic analysis of hydrogen. Variations in precipitation rates and atmospheric dynamics along altitudinal gradients promote different values of δ^2H through the environment and, consequently, in migrant individuals (Hobson et al. 2003). By analyzing different tissues, it is possible to track the altitudinal migratory route, since each has a distinct turnover rate. This means that each tissue will provide the δ^2H value of the environment in which it was formed (e.g., low or high elevation) (Newsome et al. 2015). Nevertheless, it is fundamental to consider the seasonal variations in the precipitation patterns of a region to correctly interpret the isotopic values of birds (Villegas et al. 2016). Studies that evaluate altitudinal migration in the Brazilian territory using stable isotopes are recent and are few and far in-between. Adopting this methodology might facilitate the understanding of the elevational movement patterns of birds, especially considering the influence of climate change in modifying the migratory dynamics of species.

Understanding physiological and stressful events that might affect birds through laboratory experiments

The accuracy of isotopic analysis depends on incorporating corrections to individual values that consider the physiological dynamics of the species (Table 1), such as isotopic discrimination. Correctly measuring the discrimination values between consumers and food resources is essential for applying mixing models and estimating the trophic position of individuals (Martínez del Rio et al. 2009b). Nonetheless, estimating the discrimination factors is not trivial. Studies have proposed tools to help researchers estimate trophic discrimination factors (TDFs) to correct isotopic values for species, without the need for experimental work (e.g., Caut et al. 2009, Healy et al. 2018). Still, exploring this theme in further studies is essential to fine-tune the isotopic analysis methodology (Hobson 2011), especially concerning Brazil's native birds, since their TDFs have not, for the most part, been calculated. Through controlled and monitored changes in the diet of individual birds in the laboratory, it is possible to measure the TDF of a species (Bearhop et al. 2002). In this type of experiment, researchers must give the animals a diet with different isotopic values at preset intervals (e.g., starting with C_3 resources and switching to C_4) and, concomitantly, monitor the isotopic values of the tissues until the change in the diet can be identified. In these types of experiments, it is important to determine the growth rate of the target tissue for analysis. Ornithologists interested in this topic may rely on zoos and legal breeding programs to develop laboratory experiments, while keeping in mind that the physiological patterns of captive and wild individuals may differ (Hobson 2011).

The isotopic turnover of each tissue may vary greatly in time (from days to years) depending on the physiology of the species (Vander Zanden et al. 2015). Several studies have already focused on determining the turnover rates of various tissues of birds and other taxa (Boecklen et al. 2011). Nevertheless, the dynamics of isotopic incorporation among tissues is also a relatively new topic for Brazilian ornithologists. The same approach (switching diets in the laboratory) can be used to monitor the turnover rate of each tissue that one intends to use in the isotopic analysis (Newton 2016). Considering that species from diverse Brazilian biomes may present particular physiologies, it is desirable to understand whether they show distinct turnover rates for the same tissue.

There is still no consensus among researchers about the influence of nutritional stress on the isotopic values expressed by bird tissues. Some studies have shown that δ^{13}C and δ^{15}N values can vary slightly or greatly due to stressful events, depending on the physiology of the species (e.g., Hobson et al. 1993, Graves et al. 2012). Extreme events such as starvation and natural disasters may have serious physiological consequences for birds, including defects in the feather, for instance fault bars (Ross et al. 2015, Jovani and Rohwer 2017). Ross et al. (2015) analyzed juvenile individuals of *Ammodramus savannarum* (J.F. Gmelin, 1789) after a severe storm, comparing individuals with and without pallid bands (a type of fault bar). Juveniles containing pallid bands showed lower values of δ^{15}N than individuals with normal feathers, due to the environmental stressors they experienced. Other studies point to the lack of a relationship between the isotopic values found in bird tissues and stressful events, such as food restriction and disease infection (e.g., Kempster et al. 2007, Yohannes et al. 2011). None of these studies have been developed with birds from Brazilian biomes. Thus, ornithologists must make efforts to understand the relationship among physiology, stressful events, and isotopic values of species occurring in Brazil.

Using isotopic analysis to unravel long-term temporal dynamics in bird ecology

Understanding the historical patterns in the ecology of a bird is essential for the development of conservation practices. To that end, it is possible to obtain broad temporal information through the analysis of stable isotopes. All sub-themes already covered in this review may be subject to studies aimed to understand the history of a bird's ecology, such as diet, habitat use, and geographic and physiological patterns (Table 1). To that end, natural history museums play a fundamental role in preserving metabolically inert tissues (e.g., feathers, bones, claws) that serve as a source for isotopic analysis (Wiley et al. 2017). Generally, museum specimens are useful and is the only way to access historical samples (Winker 2005).

Although ornithological collections are a rich source of historical samples for the analysis of stable isotopes, museum specimens have not been broadly used in studies, particularly in the Neotropics. Considering the lack of extensive specific literature with isotopes and terrestrial birds on a temporal scale in Brazil, studies from temperate environments will be discussed to illuminate some prospects to be employed in tropical regions. Anthropogenic impacts such as land-use changes, habitat loss, and agriculture expansion can be directly associated with historical alterations in the ecology of birds, which can be observed through $\delta^{13}C$ and $\delta^{15}N$ values (Mason et al. 2020, Navarro et al. 2021a). Navarro et al. (2021a) showed that over 100 years of human expansion in a region of southeastern Brazil, the isotopic niche width of several trophic guilds (frugivores, granivores, insectivores, nectarivores, and omnivores) have been drastically reduced. Mason et al. (2020) also observed the narrowing of the niche of *Eremophila alpestris* (Linnaeus, 1758) since 1916, that is a widespread species in the northern hemisphere. Both studies suggest that the agricultural expansion in the study areas has decreased the amount and availability of food for these birds, consequently affecting their niche width. Given the severe land-use changes that can be observed in the Brazilian territory since the European colonization and markedly during the last hundred years, the use of isotopic analysis with museum specimens is important to understand the modifications in the ecology of tropical birds.

The human impact on the isotopic values of birds has also been addressed in ecological studies. For instance, changes in the $\delta^{15}N$ values of birds may reflect an increased use of fertilizers in agriculture, or even an increase in garbage disposal (Blight et al. 2015, Møller et al. 2018, Navarro et al. 2021a). Navarro et al. (2021a) discussed the reduction in $\delta^{15}N$ values between historical and modern birds of different trophic guilds and its possible relationship with the increased use of synthetic nitrogen fertilizers in Brazil. Møller et al. (2018) also showed the association among changes in $\delta^{15}N$ values in contemporary birds, increased use of fertilizers in agriculture, and their negative consequences in the health of the feathers of *Somateria mollissima* (Linnaeus, 1758) in Denmark. Brazilian lands are known worldwide for their agricultural productivity and consequent negative influence on biodiversity (Moraes et al. 2017). Notwithstanding, we still lack information on the influence of nitrogen fertilizers applied in landscapes on the morphological characteristics of native bird species.

Stable isotopes also allow us to ascertain changes in the migratory and geographic patterns of birds over time (e.g., Hobson et al. 2010, Jiguet et al. 2020). Hobson et al. (2010) evaluated whether historical and contemporary individuals of *Euphagus carolinus* (Statius Muller, 1776), a North American migratory species, have altered their geographic patterns since the nineteenth century. The results of $\delta^{2}H$ indicate that the small changes in the eastern populations may result from changes in the quality and availability of habitat and food resources, which generated a valuable direction in conservation strategies for this bird (Hobson et al. 2010). Jiguet et al. (2020) also found no geographical changes over the last 160 years for two declining migrant species in Europe, but argued that similar $\delta^{2}H$ patterns between historical and modern individuals may result from a homogeneous latitudinal decrease in the populations of these birds. In Brazil, there is a diversity of migratory species that may be struggling against the negative effects of climate change on their movement patterns. The application of isotopic analysis can be a useful tool to understand these spatiotemporal changes.

Although long-term temporal studies are an expanding theme in bird ecology, some practical precautions in the use of isotopic analysis must be employed for the correct interpretation of the results. A representative sampling of the environmental isotopic baseline is essential in dietary studies, since it can represent a bias if it is not well addressed with adequate values that reflect the resources used in the time scale analyzed (Casey and Post 2011). In this situation, natural history museum collections and herbariums are a significant source of food resource samples from the past, contributing to build an isotopic baseline. Another relevant precaution is the need to correct for isotopic values following temporal variations in the isotopic constitution of ecosystems and the atmosphere. The Suess effect represents a change in $\delta^{13}C$ values in the atmosphere over the years, as a result of an increase in CO_2 from anthropogenic activities (Revelle and Suess 1957), and it should be considered in studies that aim to analyze historical biological data (Dombrosky 2020).

Protocol for feather collection in field samplings

The use of mist-nets in ecological studies to capture birds is common across Brazil. The Brazilian government agency responsible for standardizing the bird ringing process (CEMAVE/ICMBio) has already counted approximately one million individuals banded since 1977 (Sousa and Pereira 2020). Despite the numerous projects involving bird capture, few efforts have been made to consolidate a feather collection protocol for isotopic analysis (Smith et al. 2003). The rewards of building a solid isotopic database are enormous, as discussed elsewhere in this text.

Feathers are the most recommended tissue among ornithologists to build a comprehensive collection, since they are easy to collect and to store, and it is also an inert tissue for isotopic analysis (Smith et al. 2003, Rutkowska et al. 2018). More than one type of feather should be collected (primaries, rectrices, and breast contour), since the isotopic values between them may vary according to their molting period (Grecian et al. 2015). Multi-feather collection is also important in the case of migratory species, since the molting period may be correlated with the environmental aspects and geographic origin of the individuals (Costa et al. 2021). Collecting other tissues (e.g., blood, claw) is also relevant, since it can complement information on a temporal scale within the same individual. In this case, researchers must be trained specialists and comply with the ethics committees and animal welfare laws.

Besides tissue samples, some additional information is needed to build a strong database for the interpretation of isotopic data (Smith et al. 2003). Researchers should identify each bird to the lowest possible taxonomic level, annotate the exact collecting location (geographic coordinates are preferable), and the date of collection (day, month, and year). Whenever possible, ornithologists should accurately report the sex and age of the individuals sampled. The food resources (e.g., invertebrates, fruits, seeds, flowers) available in the environment are valuable to compose the isotopic baseline, so it is important to emphasize the relevance of collecting some items by opportunistic search or through gut contents expelled by birds during the capture (e.g., regurgitates or feces). Food resources should preferably be stored dry or frozen, without chemical preservation methods (e.g., ethanol, formaldehyde), since preserving invertebrates in ethanol may alter their isotopic values (Jesus et al. 2015). The recommendation for a widespread feather collection should not inhibit the traditional collection of museum specimens, but serve the purpose of increasing the availability of samples for isotopic and molecular analyses (Smith et al. 2003, Rocque and Winker 2005). The AviSample Network metadata repository is a global initiative that provides an opportunity for ornithologists to share all the information related to stored tissue samples, contributing for new collaborations among researchers and the reuse of avian samples (Brlík et al. 2022).

The role of Brazilian museums in providing data and tissue samples

Natural History Museums are rich repositories of data that have been traditionally employed in studies of taxonomy and systematics. More recently, collections have been also used in ecological studies, including studies in isotopic ecology (Rocque and Winker 2005, Wiley et al. 2017). Up to twenty years ago, the worldwide use of isotopic analysis in museum bird specimens was not common. In Brazil, ecological studies using this approach are even more recent and under-explored (Navarro et al. 2021a). Brazilian museums, particularly the following three examples holding vast Neotropical bird collections, have enormous potential for stable isotope research: Museu de Zoologia da Universidade de São Paulo, Museu Paraense Emílio Goeldi, and Museu Nacional – UFRJ. Additionally, other museums and private collections throughout Brazil may prove valuable.

Despite the recent efforts to employ the isotopic tool and the accessibility of ornithological collections to molecular analyzes, there is still a need for greater interaction between Brazilian museum curators and isotopic ornithological research. One concern that may worry curators is the destruction of tissues from specimens (mainly feathers). Nevertheless, most studies require a small amount of feather sample (e.g., 1 mg or 0.5 cm^2) to accurately analyze stable isotopes, and this does not visually alter the specimen (Wiley et al. 2017). A small piece of sample is sufficient to bring relevant results to understand the ecology of endangered species and assist in planning the conservation of target birds (Tawa and Sagawa 2021). Another point to be considered, is the creation of an integrated open access database of bird isotopic values, which will help to avoid the re-sampling of feathers and other tissues from species in museums and collections that have already been sampled. Besides that, this initiative would also stimulate scientific partnership among researchers to explore other aspects of a species' ecology or to provide complementary information to other analytical methods.

Improving tools to assist forensics and illegal bird trade

Isotopic analysis can also be employed in forensic studies to help determine the geographic origin of seized birds (Nardoto et al. 2017, Andersson et al. 2021). In Brazil, besides the impacts of fragmentation and habitat loss, the illegal trade of species is one of the major threats to bird diversity (Marini and Garcia 2005). Approximately 23% of Brazilian bird species are traded illegally, many of which are classified into threatened categories of IUCN (Alves et al. 2013). Associating isoscapes and isotopic values of seized individuals may be useful to determine trafficking routes in Brazil, and target more effective strategies to fight against illegal bird trade (Sena-Souza et al. 2019). Additionally, the release of seized and recovered birds in unsuitable locations (outside their geographic range) may pose a potential risk to wild populations (Marini and Garcia 2005, Efe et al. 2006). Thus, isotopic analysis can be a relevant tool to identify the origin of individuals and establish appropriate places for their release.

The continuous generation of isoscapes for the Brazilian territory will increase the robustness of isotopic analysis in forensics. Efforts are already being implemented to understand the isotopic differences among distinct vegetation types and precipitation patterns in the Brazilian biomes (e.g., Gastmans et al. 2017, Martinelli et al. 2020). Expanding these efforts may help to fight against the illegal trade of wildlife, such as increasing coverage from the Global Network of Isotopes in Precipitation (GNIP), which provides data on temporal and spatial variations of environmental isotopes in precipitation. Another important process that should be better understood to improve the stable isotope tool in forensics is the molting periods of distinct bird taxa, promoting the correct interpretation of individual isotopic values and geographic origin. More recently, the use of compound-specific isotope analysis (CSIA) has gained interest. It consists of obtaining the isotopic value of amino acids rather than of bulk tissues (Ishikawa 2018). Since essential amino acids do not undergo biochemical reactions, their isotopic values directly reflect the food ingested and isotopic data from diet sources are not necessary (Whiteman et al. 2019). This recent advance promises more accurate and informative isotopic values, helping to improve the forensic tool used to fight illegal bird trade (Andersson et al. 2021).

Financial and sample size shortcomings

Despite the advantages of using stable isotopes as a tool to understand the ecology of species, there is still a financial constraint that prevents researchers from considering this method. The analysis can cost $10–20 US dollars per sample, depending on the number of isotopes of interest and whether the researcher already sends the samples prepared for the analysis, or not. If the samples are sent for analysis outside of Brazil, there are additional shipping costs and the samples must be registered with the SISGEN system (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado). The cost of an isotopic study depends on the total number of samples analyzed, which may vary according to objectives of the research. Ecological studies usually use the rule of thumb to determine a reliable sample size (n = 30), but this should not be unconditional, since the experimental design must follow the assumptions of the analyzes employed (Martínez-Abraín 2014). Some isotopic niche analyzes suggest a minimum of 10–15 samples per group, to obtain consistent and robust results (Jackson et al. 2011, Eckrich et al. 2020) although studies with other approaches may require more samples. It is relevant to point out that using conventional methodologies is not necessarily cheaper, as it requires greater field effort and the acquisition of other tools to achieve the same results obtained with stable isotopes. Even so, although isotopic analysis is not expensive, it is not yet widely available nor is it under consideration by Brazilian researchers when designing new project funding proposals. Additionally, it is desirable to establish collaboration between researchers in ornithology and isotopic ecology, increasing the analytical power of the study.

Final remarks

The Brazilian scenario for exploring the isotopic analysis of terrestrial birds is promising. There are many ecological topics that can be approached with this tool. Even the most common stable isotopes in ecology studies (carbon, nitrogen, hydrogen, and oxygen) are still not frequently used in studies originating in Brazil. Trophic ecology is one topic that may benefit from the use of isotopic analysis, since it provides robust information about the diet, use of habitat, and species' niche (e.g., Kelly 2000, Newsome et al. 2007, Boecklen et al. 2011). Detecting the migratory and geographic patterns of birds is another interesting topic to be addressed with stable isotopes (e.g., Inger and Bearhop 2008, Hobson 2011), especially in a territory where there is great diversity of migratory species. Studies on physiology and laboratory experiments are crucial to improve the isotopic method, adapting it to the reality of native species (e.g., Martínez del Rio et al. 2009b, Hobson 2011). Additionally, valuing museums and ornithological collections may promote desirable opportunities to increase our knowledge about the ecological history of birds and to compare it with the contemporary ecology, to help devise conservation strategies (e.g., Wiley et al. 2017).

Despite so many opportunities for studies in the Brazilian territory using stable isotopes and birds, there are still some challenges to be considered before the enthusiasm for the tool grows. Researchers interested in employing isotopic analysis must know the methodological shortcomings to correctly interpret the results (Inger and Bearhop 2008, Caut et al. 2009, Casey and Post 2011). If precautions are taken, however, the benefits of using isotopes to broaden our knowledge of bird ecology will become increasingly evident. In a country with such a vast territory, composed of six biomes, all under intense pressure from anthropogenic impacts (land-use changes, habitat loss, fragmentation), the use of isotopic analysis in new ornithological studies is promising.

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