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RESEARCH ARTICLE

Stable Isotopes Analysis of Black Lion Tamarins Reveals Increasing Arthropod Consumption When Fruit Productivity Decreases in Forest Fragments

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ABSTRACT

Given the cryptic and elusive nature of prey consumption, quantifying its contribution to the diet of free-ranging primates using behavioral methods is challenging. In this context, the use of carbon and nitrogen-stable isotopes represents a promising alternative approach. Here, we used stable isotope analysis to estimate the proportion of arthropods and fruits in the diet of black lion tamarins (*Leontopithecus chrysopygus*), an endangered primate endemic to the Brazilian Atlantic Forest. To do so, we ran stable isotope mixing models using isotopic data from hair samples of black lion tamarins living in six forest fragments showing different levels of habitat quality. Furthermore, we ran linear mixed models to assess the influence of habitat quality—fruit productivity (estimated by tree total basal area) and arthropod biomass – and individual characteristics (sex and body mass) on tamarins' $\delta^{15}N$ values (a proxy for trophic position). Our results revealed that arthropods contributed more to black lion tamarins' diet than reported in previous behavioral studies, suggesting that behavioral observations may considerably underestimate the importance of arthropodivory in the diet of arboreal primates. The degree of arthropodivory and frugivory was similar within groups, in line with the strong group cohesion and synchronization of feeding behaviors of this species and supporting the role of site-specific habitat characteristics on dietary choice. Arthropod consumption was higher in areas with lower fruit productivity and did not increase when arthropod biomass increased, suggesting that fruits represent a limiting but preferred resource for this species. These results demonstrate the dietary plasticity of black lion tamarins in areas of lower forest quality, where they manage to compensate low fruit productivity by shifting to a diet richer in arthropods. Considering that this species occurs within a highly fragmented landscape, preserving and protecting small forest patches remains crucial for the conservation of this species.

Amazone Raskin and Olivier Kaisin should be considered joint first authors.

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Summary

- Stable isotope analysis revealed that the black lion tamarin, which is considered mainly frugivorous, actually relies heavily on arthropods.
- Individuals living in the same forest fragment have similar $\delta^{15}N$ values, suggesting similar degrees of arthropodivory at the population level.
- $\delta^{15}N$ values increase as site-specific tree basal area decreases, indicating that arthropodivory is a strategy to cope with the decrease in fruit availability caused by habitat degradation.
- Our results, therefore, suggest that fruits represent a limiting resource for black lion tamarins.

1 | Introduction

The Brazilian Atlantic Forest has been subject to intense selective logging and habitat loss, resulting in a ~72% reduction of its forest cover since the beginning of the 16th century (Rezende et al. 2018). This severe habitat fragmentation and degradation can cause a reduction in the quality and availability of resources for species inhabiting forest remnants, possibly leading to lower carrying capacities (Arroyo-Rodríguez et al. 2013; Arroyo-Rodríguez and Mandujano 2006; Ingala et al. 2019; Johns and Skorupa 1987). Studies have shown that forest fragmentation can negatively affect species occurrence (Benchimol and Peres 2014), as well as individual foraging behaviors (Fahrig 2003). However, how particular species may be affected by fragmentation depends on intrinsic factors, such as the range of their diet and trophic plasticity, which may be difficult to estimate for free-ranging animals living in such complex habitats as tropical forests.

According to the optimal foraging theory, animals select their food resources according to a balance between the search and handling time and the energy content of resources (Stephens & Krebs, 1986). Several environmental factors, such as resource diversity and abundance, may influence the diet choice of animals and force them to consume nonoptimal fallback food, which may, in turn, affect their fitness (Emery Thompson 2017; Lambert and Rothman 2015; Radanovic et al. 2017). Optimal and nonoptimal food choices also depend on a species' nutritional needs (Lambert and Rothman 2015). Whenever available, omnivorous primates will often prefer sweet succulent fruits over less digestible items (e.g., leaves; Stanford and Nkurunungi 2003) and will target more nutritious resources (e.g., insects; Lambert 1998), even when they demand a greater energy-expenditure to acquire. For these species, fruit availability appears to be the most critical constraint on their diet habits (Clink et al. 2017; Johns and Skorupa 1987). As the abundance of nutritional fruits often decreases with habitat degradation (Irwin et al. 2010; Johns and Skorupa 1987), the capacity of a species to replace fruits with other alternatives resources may influence its ability to survive in fragmented forests (Kirika, Farwig, and Böhning-Gaese 2008). Accordingly, knowledge of a species' degree of behavioral plasticity is crucial to predict impacts of habitat change on its survival (Ménard et al. 2014).

Faunivory in primates comprises the consumption of both vertebrates and invertebrates. In general, the latter is more common, mostly includes insects and arachnids (Clutton-Brock and Harvey 1977), and is thus more accurately referred to as arthropodivory rather than insectivory. When observing wild primates in the field, it can be difficult to systematically assess arthropodivory because these predation events are generally opportunistic and hard to witness (Mallott, Malhi, and Garber 2015). Furthermore, animal material is usually better assimilated than plants as their elemental composition is closer to that of the consumers (Elser et al. 2000). Consequently, information provided by the ingestion rate of different foods, or the proportion of time spent feeding on a specific diet component, may not reflect actual assimilation rates, resulting in an inaccurate estimate of their respective contribution to the diet of omnivorous species (Navarro and Winter 1982). While frugivory and folivory are well characterized in omnivorous primates (Johns and Skorupa 1987; Kirika, Farwig, and Böhning-Gaese 2008), the importance of arthropodivory may be underestimated in terms of assimilated diet. In addition, the extent to which the degree of frugivory and arthropodivory is affected by changes in habitat quality has been poorly investigated.

Stable isotope analysis is a well-established technique in ecology, which has been widely applied to explore questions related to dietary habits across animals and ecosystems (Crowley 2012; Crowley et al. 2016; DeNiro 1987; Sandberg, Loudon, and Sponheimer 2012). Stable isotopes are useful because their ratios in consumers' tissues reflect those in their food items (Herrera et al. 2003; Warne, Pershall, and Wolf 2010). In particular, nitrogen isotope ratio ($^{15}N/^{14}N$) of consumers increases with increasing trophic position in any given food chain (Cotton and Sheldon 2013; Herrera, Rodríguez, and Hernández 2009). In the case of omnivores which feed on both plant and animal sources, the nitrogen isotope ratio should increase with higher contributions of animal sources, reflecting higher trophic positions (DeNiro and Epstein 1981). Thanks to these properties, stable isotopes can provide insights on resource partitioning (e.g., Crowley et al. 2013), resource use (e.g., Magioli et al. 2023), and trophic position of organisms (e.g., Schillaci et al. 2014).

Although previous stable isotopes studies already examined the diet of various mammal species (e.g., armadillos, *Priodontes maximus* Magioli et al. 2023; peccaries, *Tayassu pecari* Bradham et al. 2018; or bears, *Ursus arctos marsicanus* Careddu et al. 2021), only a few studies have focused on extant primates. These studies analyzed, for example, resource partitioning and nutritional stress of lemurs (*Cheirogaleus* sp. and *Microcebus* sp.; Crowley et al. 2013), trophic niche adjustment in two howler monkey species (*Alouatta palliata* and *A. pigra*; Flores-Escobar et al. 2020), dietary shift in savanna chimpanzees (*Pan troglodytes verus*) along their distribution range (Wessling et al. 2019), or spatial isotopic variability of macaques (*Macaca fascicularis)* associated with canopy type (Schillaci et al. 2014). However, to our knowledge, no study to date has used this alternative method to evaluate how resource availability influenced the degree of frugivory and arthropodivory in a primate species across fragments with different habitat qualities.

In this study, we used carbon and nitrogen stable isotope analysis to explore the fruit and arthropod contributions to

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black lion tamarins' diet (BLTs, *Leontopithecus chrysopygus*), one of the 19 endemic primate species of the Brazilian Atlantic Forest (Culot et al. 2019; Graipel et al. 2017). Due to intense habitat loss and fragmentation, this species is considered endangered, with only about 1600 individuals remaining in the wild (Rezende et al. 2020). BLTs are considered primarily frugivorous and arthropodivorous (Coimbra-Filho and Mittermeier 1973). They have claw-like nails, a common feature in Callitrichids, that grants them vertical clinging, manipulative foraging, and bark-stripping capacity to locate concealed prey (Garber 1992). However, their feeding flexibility is still relatively unknown. Based on behavioral data using scan sampling, previous studies estimated that BLTs spent between $84.4 \pm 8.9\%$ and $93.5 \pm 4.7\%$ of their time eating fruits, $8.3 \pm 11.7\%$ and only $6.6 \pm 7.1\%$ to $6.7 \pm 4.7\%$ eating animal prey (Passos and Keuroghlian 1999; Keuroghlian and Passos 2001). Capturing such items may incur high energetics (Emery Thompson 2017; Kaisin et al. 2023). Another observational study based on ingestion events found a diet composed of $78 \pm 6.5\%$ of fruits, $8.3 \pm 11.7\%$ of exudates, and $12.5 \pm 2.5\%$ of animal prey (Valladares-Padua 1993). Animal sources mainly include insects and other arthropods, with BLTs occasionally feeding on small vertebrates and bird eggs (Garbino et al. 2022; Garbino et al. 2020; Valladares-Padua 1993). Given the rare and sporadic nature of vertebrate consumption, its contribution to the stable isotope signature of BLTs is considered trivial.

Furthermore, black lion tamarins adjust their foraging behaviors according to the daily, monthly, and seasonal cycles of prey availability (Garbino et al. 2022; Keuroghlian and Passos 2001). Additionally, behavioral plasticity and individual characteristics, such as age and sex, may also directly influence the specific diet of each individual (Chen et al. 2018; Nsi Akoue et al. 2017; Oelze et al. 2020). From this perspective, analyzing the nitrogen ($\delta^{15}N$) isotopic composition of BLTs could help estimate the influence of habitat quality (i.e., fruit productivity and arthropod biomass) on the proportion of fruits and arthropods in the diet of a given population and/or its component individuals.

Here, (1) we first analyze nitrogen stable isotope data of BLT hairs to determine whether $\delta^{15}N$ values (proxy for trophic position) vary according to (a) individual characteristics (interindividual variation) and (b) local arthropod biomass and fruit productivity (interpopulation variation). Given previous knowledge of primate and BLT feeding ecology, (1a) we expect that $\delta^{15}N$ values of BLTs should vary with individual age (Chen et al. 2018; Nsi Akoue et al. 2017; Oelze et al. 2020). On the one hand, the contribution of arthropods may be lower in the diet of adults compared to juveniles, as the latter should capture a higher proportion of animal prey, a relatively richer and more digestible protein source, to meet demands associated with growth (Cords 1986; Janson 1993; MacKinnon 2006). On the other hand, given their greater experience and dexterity, adults may be able to capture arthropods prey inaccessible to juveniles (Barnett et al. 2023), leading to a higher proportion of arthropods in the diet of the former. However, given the strong group cohesion and the lack of sexual dimorphism in lion tamarins, we expect no difference between sexes. (1b) Because many primate species are generalists, and can adapt their diet when their primary resources are not available (Keuroghlian and Passos 2001; Rothman et al. 2014), we expect $\delta^{15}N$ values of BLTs to vary according to local fruit productivity and arthropod prey biomass in the six forest fragments studied. Specifically, we predict a higher contribution of arthropods in the diet of BLTs inhabiting forest fragments with lower tree total basal area (TBA; an indicator of forest structure and maturity i.e., positively related to fruit availability). Second, (2) we calculate the assimilated diet of BLTs using two-tracer (C and N) stable isotope mixing models to estimate the contributions of fruits versus arthropods in the diet of BLTs and compare these contributions with in situ behavioral observations. We expect that the arthropod contribution to the BLT's diet would be greatly underestimated compared to previous behavioral observations.

2 | Methods

Ethics Statement

This study was conducted with the authorizations of the Chico Mendes Institute for Biodiversity Conservation (ICMBio; SISBIO; N°68253, 41345 and 41375), the Comissão Técnico-Científica do Instituto Florestal (COTEC; N°153/2021 D28/2021 PH and 167/2015), and the ethics committee of the São Paulo State University (UNESP; N°16/2019). BLTs being listed under Appendix I of the Convention on International Trade in Endangered Species (CITES), the necessary permits of exportation (N°21BR036613/DF) and importation (N°2021/BE00456/PI) of hair samples were obtained.

2.1 | Study Sites and Groups

BLTs are endemic to the Atlantic Forest of the State of São Paulo, inhabiting the inland seasonal semi-decidual forests of southeastern Brazil. This vegetation type is marked by strong climatic seasonality, holding typical regional plant species (Eisenlohr and de Oliveira-Filho 2015; Morrone 2017; Vieira et al. 2015), lower epiphyte diversity (Marcusso et al. 2022), and higher dominance of climbing plants (Vargas et al. 2018) compared to coastal rainforests. BLT populations are distributed across various federal and state protected areas and in multiple private and riparian forest fragments, all within the Paranapanema riverbasin (Albernaz 1997; Culot et al. 2015; Garbino, Rezende, and Valladares-Padua 2016; Moraes Rodrigues, Gagetti, and Piratelli 2016). Currently, the largest BLT population is in the Morro do Diabo State Park (MDSP).

We studied BLT groups from six distinct areas within the species' overall range (Figure 1): the Morro do Diabo State Park [MDSP; 33,845 ha; 22°37′21“S, 52°08′02“W], the Ponte Branca [PB; 1306 ha; 22°24′53“S, 52°30′48“W], San Maria [SMA; 515 ha; 22°14′20“S, 52°18′23“W] and Guareí [GUA; 105 ha; 23°25′07“S, 48°14′27”W] fragments, and the riparian forests of Angatuba [ASF; 79 ha;

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FIGURE 1 | General study area, showing the six forest fragments: (1) Morro do Diabo State Park (MDSP), (2) Ponte Branca (PB), (3) San Maria (SMA), (4) Guareí (GUA), (5) Angatuba (ASF), (6) Buri (BG).

22°27'26"S, 48°23'57"W] and Buri [BG; 78 ha; 23°47'19"S, 48°35'20"W]. During the study period, the mean annual temperatures and total annual precipitations were 21.9°C and 25.0°C, and 1067.9 mm and 1595.2 mm, respectively, for the Alto do Paranapanema region, in the eastern portion of the distribution range including GUA, ASF, and BG (altitudes ≅ 630 m) and the Pontal do Paranapanema region, in the western portion, including MDSP, PB, and SMA (altitudes ≅ 404 m) (*Agrometeorological Monitoring System*).

2.2 | Data Collection

2.2.1 | Sample Collection

2.2.1.1 | Hairs. Hair sample collection occurred between September 2017 and June 2021 (Supporting Information S1: Table 1). Hair samples were collected during BLT capture campaigns within the framework of multidisciplinary studies on health, movement ecology, behavior, and endocrinology, carried out by the Laboratory of Primatology (LaP, UNESP) and the Black Lion Tamarin Conservation Program (BLTCP, IPÊ). All captures were performed with a team of specialized field assistants, biologists, and veterinarians. BLTs were captured directly from the tree hollows in which they had spent the night, or with tomahawk traps (see Supporting Information S1: Text 1 in SI for capture details). Once captured, the tamarins were anesthetized intramuscularly with a combination of ketamine 12 mg/kg, (Dopalen; Ceva Saúde Animal Ltda., SP, Brazil) and midazolam 0.5 mg/kg (União Química Farmacêutica Nacional S.A, MG, Brazil), or using isoflurane, an inhalational anesthetic, to reduce stress during the whole procedure. Primary vital signs were monitored during the immobilization period. All animals were identified (ID), weighed (body mass) and sexed, and their age category was determined (adult vs. juvenile). Hairs were cut as close as possible to the root without damaging the skin from the interscapular and internal femoral regions, and stored in silica gel, away from light and at room temperature for isotopic analyses. As the $\delta^{15}N$ values of hairs from the interscapular and femoral regions were correlated (Wilcoxon test, $V = 9$, $p = 0.8438$), we included interscapular hair samples of BLTs from MDSP collected for a previous study, avoiding recapture of these individuals. Forty-four hair samples from 33 individuals (1–3 samples per individual) were collected in the field (Table 1), sometimes from different groups in the same fragment, including 11 replicates of 10 different individuals (Table 1). For the 10 individuals sampled two or three times, the time interval between samples varied from 0 to 18 months, and mean $\delta^{15}N$ values were calculated.

2.2.1.2 | Fruits. The resource data collection (i.e., fruits and arthropods) occurred from January 2021 to June 2021. The choice of species sampled was based on information on fruit consumption by BLTs compiled from data available in the literature (Keuroghlian and Passos 2001; Passos 1999), and from field observations of ongoing LaP/UNESP projects (Kaisin et al. 2023). Mature fruits were manually collected and whenever possible the same species were collected in all sites. We sampled a total of 139 trees, belonging to 11 orders, 13 families and 24 species (see Supporting Information S1: Table 2 for study areas details).

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TABLE 1 | Black lion tamarin hair samples of each age/sex category collected in the six forest fragments.

Site	Hair samples		Individuals	Groups	Adults		Juveniles	
	Dry	Rainy			♂	♀	♂	♀
ASF	12	0	6	1	3	1	2	0
BG	7	0	7	3	4	1	2	0
GUA	3	7	8	2	4	2	1	1
MDSP	5	1	5	1	3	2	0	0
PB	4	4	6	2	2	2	0	2
SMA	1	0	1	1	0	1	0	0
Total	**32**	**12**	**33**	**10**	**16**	**9**	**5**	**3**

Abbreviation: ASF = Angatuba, BG = Buri, GUA = Guarei, MDSP = Morro do Diabo State Park, PB = Ponte Branca, SMA = San Maria.

2.2.1.3 | Arthropods. BLTs are eclectic foragers that actively search for animal prey in epiphyte bromeliads, under tree bark, in tree hollows, and in palm sheaths. They prey on both mobile (e.g., grasshoppers, katydids, spiders) and non-mobile (e.g., cockroaches and coleoptera) arthropods (Valladares-Padua 1993). Based on previous feeding observations carried out over the past 6 years by the LaP/UNESP, arthropod samples were selectively, manually, and opportunistically sampled in the field. In addition, we collected arthropod samples from pitfall traps that were setup to assess arthropod prey biomass in each study site (see Section 3.3.b). In total, 625 arthropod items were collected, representing more than 50 morphospecies, belonging to seven orders known to be consumed by BLTs (i.e., Orthoptera, Blattodea, Hymenoptera, Coleoptera, Dermaptera, Hemiptera of the subphylum Hexapoda, and Araneae of the subphylum Chelicerata) (see Supporting Information S1: Table 2 for study areas details).

2.2.2 | Isotopic Sample Preparation and Analyses

After field collection, fruit and arthropod samples were dried in a laboratory oven at 50°C for a minimum of 2 weeks at the São Paulo State University (Brazil). For fruit samples, only the part known to be consumed by the lion tamarins was analyzed. Samples were then transferred to the Laboratory of Trophic and Isotope Ecology at the University of Liège (Belgium) where stable isotope analyses were conducted. Dried samples were ground with a mortar and a pestle to obtain a homogeneous powder (Gagnon and Hobson 2009). The powdered resource samples were then deposited inside carefully closed glass vials to prevent moisture contamination. Hair samples were placed in glass vials and cleaned three times with 2 mL of dichloromethane:methanol mixture (2:1) to remove exogenous contaminants (e.g., sweat and sebum). The hairs were ground to powder, then transferred to a 60°C incubator to dry for 24 h (Dammhahn, Soarimalala, and Goodman 2013).

Carbon and nitrogen isotopic ratios were measured using continuous flow—elemental analysis—isotope ratio mass spectrometry (CF-EA-IRMS) at the University of Liège (Belgium), with a Vario MICRO cube C–N–S elemental analyzer (Elementar Analysensysteme GMBH, Hanau, Germany) coupled to an IsoPrime100 isotope ratio mass spectrometer (Isoprime, Cheadle, United Kingdom) (Das et al. 2017; Lepoint et al. 2016; Lepoint et al. 2016). Isotope ratios were expressed in ‰, using the δ notation (Coplen 2011). The weighing of the samples started by measuring two blanks (i.e., empty tin capsules). Measurements of elementary standards (glycine, $\delta^{15}N = 2.31 \pm 0.34‰$; $\delta^{13}C = -47.19 \pm 0.16‰$) and replicates of fruit, arthropod and hair samples from the study areas were repeated every 15 samples to calibrate isotopic samples and reduce experimental uncertainty (Lepoint et al. 2016; Lepoint et al. 2016). Standard deviations of multi-batch replicates were 0.34‰ ($\delta^{15}N$) and 0.31‰ ($\delta^{13}C$) for fruits, 0.39‰ ($\delta^{15}N$) and 0.05‰ ($\delta^{13}C$) for arthropods, and 0.39‰ ($\delta^{15}N$) and 0.04‰ ($\delta^{13}C$) for hairs. Then, IAEA (International Atomic Energy Agency) certified materials of ammonium sulfate (IAEA-N2, $\delta^{15}N = +20.27 \pm 0.31‰$) and sucrose (IAEA C-6, $\delta^{13}C = -11.05 \pm 0.17‰$) were analyzed at the start and end of each batch. Elemental data are expressed in %C and %N relative to dry weight. They were used to calculate C/N ratios (w:w) and constrain the isotopic mixing model (see Section 4.3).

2.2.3 | Habitat Quality Characterization

2.2.3.1 | Tree Total Basal Area. To estimate fruit productivity in the six study areas, we measured the total tree basal area (TBA). TBA is a well-established proxy for overall fruit productivity given that the latter is generally well-correlated with canopy diameter (Chapman, Chapman, and Wrangham 1992, 1995; Stevenson, Qulñones, and Ahumada 1998; Worman and Chapman 2006). This metric has been widely used to assess fruit availability in different environmental contexts (Rosenbaum et al. 1998; Develey and Peres 2000; Ordóñez-Gómez et al. 2016; Pessoa et al. 2017; Galán-Acedo, Arroyo-Rodríguez, and Chapman 2021). Although TBA does not take into account the relative abundance of lianas and vines, these plant forms only represent 5% of the diversity of plant species consumed by BLTs (unpublished data; Passos, 1992; Valladares-Padua 1993; Kaisin et al. 2023). Therefore, TBA remains a robust estimate of fruit availability for BLTs. To estimate TBA, we set up twenty 10 m x 10 m botanical plots, distant 200–400 m from each other, in each study area. The basal area of a tree is defined as the area (m^2) of the trunk at breast height (~1.3 m). We measured all trees with a circumference at breast height (CBH) ≥ 15 cm,

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corresponding to a diameter at breast height (DBH) ≥ 4.8 cm in each of the 20 botanical plots. This smaller DBH was chosen because, given their small size, BLTs also feed on smaller trees. To calculate the TBA of all trees inside the plots of each fragment, the areas of all trunks were summed.

2.2.3.2 | Arthropod Prey Biomass. To assess arthropod prey biomass, we set up 100 pitfall traps in each forest fragment. Pitfall trapping is a systematic method that has been widely used by ecologists to estimate relative arthropod prey abundance across different study sites (Hohbein and Conway 2018). Furthermore, in terms of habitat quality assessement, macroinvertebrate abundance has repeatedly been used to evaluate environmental changes (Haskell 2000; Hodkinson and Jackson 2005; Lamperty et al. 2020). We installed 10 pitfall traps in ten out of the twenty 10 × 10 m botanical plots (see Section 3.3.a). In each plot, the traps were set in two parallel lines of five traps, placed every one meter. Each pitfall trap consisted of a plastic pot (diameter = 25 cm, volume = 1 L) buried to ground level and filled with 150 mL of ethanol (70%) to preserve the arthropods (Lamperty et al. 2020). The lids of the pots, which were suspended 20 cm over the pitfalls using sticks, served as roofs to prevent detritus and rain from falling inside. The traps were left in the field for 5 consecutive days. Finally, the liquid from each trap was filtered to remove dirt and other detritus and captured arthropods classified to Order and then by morphospecies. Arthropod biomass was calculated based on the mean dry mass of each arthropod morphospecies in each forest fragment, weighed using an analytical balance. To accurately assess the relative abundance of arthropod prey, we only considered arthropods from the main orders consumed by BLTs (i.e., Orthoptera, Blattodea, Hymenoptera, Coleoptera, Dermaptera, Hemiptera, and Araneae). Furthermore, since BLTs do not seem to forage for microinvertebrates, we only collected arthropods > 5 mm. Whenever available, we weighed six individuals of each morphospecies to calculate its mean dry weight (Derraik et al. 2002, 2010). The mean dry weight of each morphospecies was subsequently multiplied by the number of individuals collected at each site (i.e., their abundance). We then calculated the total arthropod biomass in each site by summing the total weight of each morphospecies.

2.3 | Data Analysis

All analyses were performed in R (version 4.0.2) (R Core Team, 2017). To consider isotopic baseline variability across sites, we used corrected $\delta^{15}N$ values of BLTs as the dependent variable. Corrected values were obtained by subtracting the mean $\delta^{15}N$ values of *Syagrus romanzoffiana* samples of each site (a highly consumed fruit, therefore representing a main isotopic baseline) from raw $\delta^{15}N$ of BLTs from corresponding sites. The corrected $\delta^{15}N$ values followed a gamma distribution, tested using the Cramér von-Mises criterion. To determine intrinsic factors of variability in arthropod contribution to BLT diet, we tested the effect of individual characteristics (i.e., sex and age) on BLT corrected $\delta^{15}N$ values (see Section 4.1). To estimate the influence of resource availability on the trophic position of BLTs, we tested the effect of TBA and arthropod biomass on BLT corrected $\delta^{15}N$ values (see Section 4.2). The Akaike information criterion (AIC), combined with a likelihood-ratio test (Wilks 1938) was used to compare models, including the null model. Models with a delta AIC inferior to 2 were compared using the ANOVA function to choose the best model. Finally, we determined the fruit and arthropod contributions to the diet of BLT using an isotope mixing model (see Section 4.3).

2.3.1 | Intrinsic Factors of Variability in Arthropod Contribution to BLT Diet

To test for interindividual variations in corrected $\delta^{15}N$, we ran generalized linear mixed-effect models (GLMERs; "log" link) with the sex and body mass (i.e., a continuous variable highly correlated with age category; Pearson's $r = 0.88$, $p < 0.05$) of the 33 individuals set as fixed predictors. Sites were defined as random factors in the models since the study sites may have different uncontrolled characteristics. All continuous variables were standardized (i.e., $\delta^{15}N$, TBA, arthropod biomass, and individuals' body mass).

2.3.2 | Influence of Resource Availability

We ran generalized linear models (GLMs; "log" link) to explore the effect of resource availability on the relative contribution of arthropods to BLT diet. Interestingly, we found that fragment size did not predict fruit productivity (i.e., TBA) inside a forest fragment (Spearman correlation: rho = 0.543, $p = 0.297$). Due to the relatively small sample size ($N = 33$) and the fact that $\delta^{15}N$ values of BLTs were not significantly influenced by age and sex (see *Results*), we chose to simplify the habitat quality model using only three independent variables and avoided including random effects. We set TBA (m^2/ha), arthropod biomass (g) and region as fixed predictors, and corrected $\delta^{15}N$ values of BLTs as a response variable of the GLM.

2.3.3 | Arthropod and Fruit Contributions to the Diet of BLTs

To estimate the relative contribution of fruits and arthropods in the BLTs, we ran a two-isotope (C and N) Bayesian mixing model using the package MixSIAR (version 3.1.12) (Phillips et al. 2014; Stock and Semmens, 2016; Stock et al. 2018). Such models have been widely used in trophic ecology to determine the assimilated diet of various species in aquatic and terrestrial ecosystems in relation to environmental or individual trait variation (Crawford, Mcdonald, and Bearhop 2008; McKechnie 2004; Phillips 2012). We defined four groups of resources based on similarities in their C and N stable isotope composition: "Arth1" regrouping Araneae, Coleoptera and Hymenoptera, "Arth2" regrouping Orthoptera and Blattodea, "Fruits1" regrouping fruits from all available local plant species, dominated by C3 plants but also including a facultative CAM (*Pereskia aculeata*) which has isotopic composition close to C3 plants, and "Fruits2" including an obligatory epiphytic CAM plant (*Rhipsalis cereuscula*). The trophic discrimination factors

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(TDFs) used to account for the ^{13}C and ^{15}N enrichment between consumers and sources were those proposed by Kurle et al. (2014) for rats fed with vegetables and animal food: $\Delta^{13}C_{vegetables} = 3.4 \pm 0.5‰$, $\Delta^{15}N_{vegetables} = 2.4 \pm 0.2‰$, $\Delta^{13}C_{animal\ food} = 2.1 \pm 0.2‰$, and $\Delta^{15}N_{animal\ food} = 3.9 \pm 0.3‰$. We further used C and N concentration-dependencies function as prior since the C/N ratios of fruits and arthropods differed drastically, potentially contributing differently to carbon and nitrogen routing by lion tamarins. This function also allows us to model the difference in assimilation efficiency between fruit and animal food sources. We ran the models with 3×10^5 iterations, burn-in size was set as 2×10^5 with three parallel chains and a thinning interval of 100. The contribution of each resource group ($N = 4$) was calculated for each BLT individual ($N = 33$) within the six sites. Then, we aggregated sources into two groups *a posteriori*: arthropods and fruits. Based on posterior distributions derived from mixing model outputs, we calculated the proportions of arthropods and fruits as well as their median ± 95% credible interval in the diet of the tamarin groups living in the six study areas. Results of the SMA forest fragment were not presented due to the lack of replicates.

3 | Results

3.1 | Intrinsic Factors of Variability in Arthropod Contribution to BLT Diet

Raw isotope values of the 33 BLT hair samples are given in Supporting Information S1: Table 1. We examined 21 hair samples of males and 12 of females. All models had similar AIC support, but the inclusion of sex and body mass did not significantly improve the model. (ANOVA between Null and Sex & Weight models: $\chi^2 = 3.61$, $df = 2$, $p = 0.1648$). Therefore, there was no significant difference in corrected BLT hair sample δ15N values between males and females, and no influence of the body mass of adults and juveniles coming from the same study area (see Supporting Information S1: Table 3).

3.2 | Influence of Resource Availability

TBA and arthropod biomass from each study site are listed in Table 2. The best model exploring the effect of resource availability on corrected $\delta^{15}N$ values included both arthropod biomass and TBA. This model was significantly better than the null model (ANOVA between Null and TBA & Biomass models: $\chi^2 = 2.1748$, $df = 2$, $p < 0.05$; Table 3). Arthropod biomass and TBA both had significant negative effects on corrected BLT hair sample δ15N values (Tables 3 and 4; Figure 2). However, the effect size of arthropod biomass was very small (Table 4; see Supporting Information S1: Figure 1).

3.3 | Arthropods and Fruits Contributions to the Diet of BLTs

All BLT individuals were inside the mixing polygons (Figure 3), allowing proper use and building of the six mixing models. The

TABLE 3 | Results of the Generalized Linear Models for habitat quality variations (TBA and arthropod biomass) on baseline corrected $\delta^{15}N$ values of BLT hairs. The selected model (ΔAIC < 2) is highlighted in bold.

Model	K	*df*	AIC	ΔAIC	Wt
TBA+ Biomass	4	4	**102.05**	**0.00**	**0.99**
TBA	3	3	112.18	10.13	0.01
Biomass	3	3	148.16	46.11	0.00
Null	2	2	148.47	46.42	0.00

Abbreviations: AIC = The Akaike information criterion, ΔAIC = The difference in AIC score between the best model and the model being compared, df = Degrees of freedom, K = Number of parameters in the model, Wt = AIC weight, which is the relative likelihood of a model.

TABLE 4 | Parameters of selected generalized linear model testing the effect of habitat quality variations including total basal area of trees (TBA) and arthropod biomass on baseline corrected δ15N values of black lion tamarin hairs.

Effect	Estimate	Std. error	*t* value	*p*-value
TBA	−0.332	0.029	−11.22	< 0.001
Arthropod biomass	−0.004	0.000	−4.10	< 0.001

Note: Estimate of the coefficient with the corresponding standard error; *t* statistics and *p*-value of the calculated T distribution are presented.

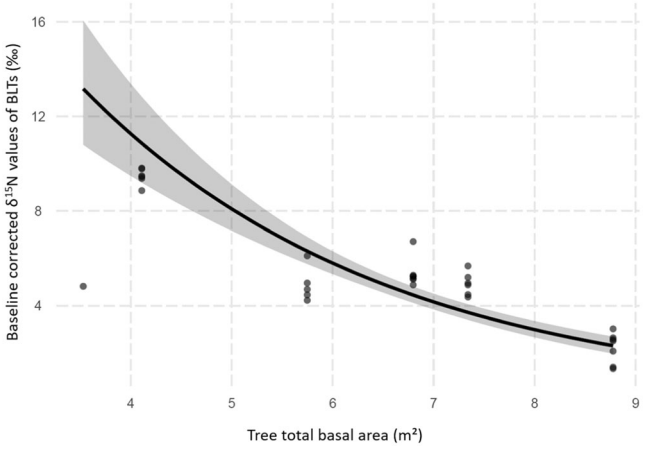

FIGURE 2 | Relationship between baseline corrected $\delta^{15}N$ values of black lion tamarin hairs (‰) and the total basal area of trees (m²).

TABLE 2 | Total basal area of trees (TBA in m²) and arthropod biomass (g) estimated for the six study areas.

Habitat quality variables	ASF	BG	GUA	MDSP	PB	SMA
TBA (m²)	7.36	6.80	8.52	5.50	4.25	2.91
Arthropod biomass (g)	6.84	8.20	8.91	141.51	65.42	147.85

Abbreviations: ASF = Angatuba, BG = Buri, GUA = Guarei, MDSP = Morro do Diabo State Park, PB = Ponte Branca, SMA = San Maria.

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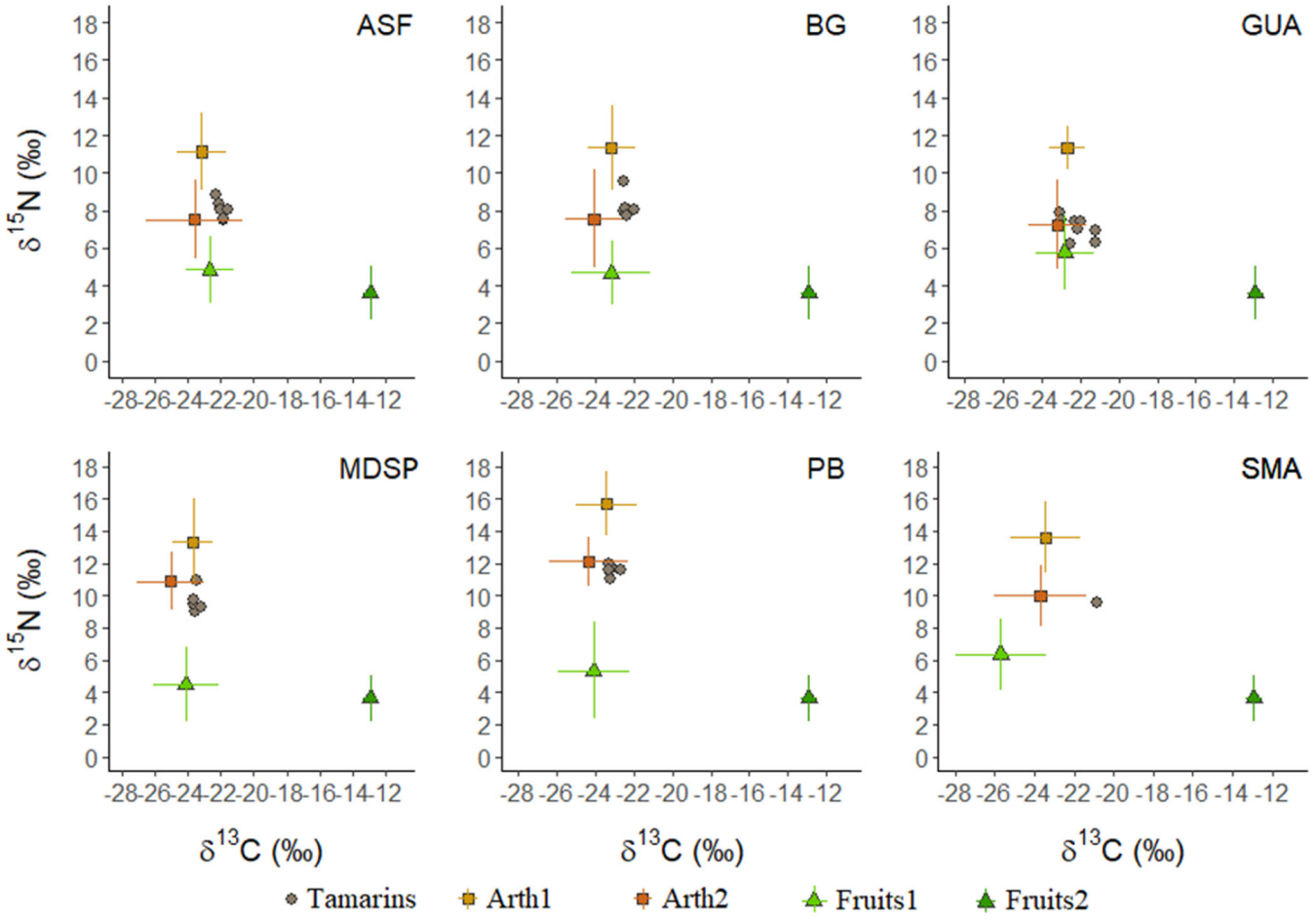

FIGURE 3 | Isotope space of carbon and nitrogen for the black lion tamarins and their food resources within the six study areas. Food sources were corrected by their respective trophic discrimination factors. ASF=Angatuba, BG=Buri, GUA=Guareí, MDSP=Morro do Diabo State Park, PB=Ponte Branca, SMA=San Maria.

medians of resource contributions showed a higher proportion of fruits (from 51.7% to 63.7%) than arthropods in the diet of BLTs, except in the Buri fragment where fruit proportion was 39.4% (Figure 4; see Supporting Information S1: Table 4 for resource contribution details of each BLT population). In addition, isotopic mixing models showed similar arthropod and fruit contributions in the diet of individual living in the same study area (see Supporting Information S1: Table 5).

4 | Discussion

Resource availability is key for the survival of animals, including Neotropical primate species (Kirika, Farwig, and Böhning-Gaese 2008; Radanovic et al. 2017). Dietary choice and feeding behavioral plasticity can thus be determinant for the sensitivity and resilience of species living in degraded environments (Johns and Skorupa 1987). Our study showed that the isotopic composition of black lion tamarins (BLT) did not vary with sex or body mass of individuals (i.e., age) and that they relied more on arthropods in areas with lower fruit productivity. Indeed, we found that $\delta^{15}N$ values of BLTs increased with decreasing TBA but not with increasing arthropod biomass. We also found that arthropods contributed more to BLTs' diet than reported in previous behavioral studies.

4.1 | Intrinsic Factors of Variability in Arthropod Contribution to BLT Diet

In some primate species, adults and juveniles have different dietary intakes and juveniles tend to have higher $\delta^{15}N$ values than adults (Crowley 2012). Contrary to these previous findings, our stable isotope analysis showed that BLTs of a specific fragment had similar $\delta^{15}N$ values, regardless of age class. Additionally, our results confirmed our hypothesis that males and females have similar arthropod proportions in their diets due to the lack of sexual dimorphism in their behaviors. Isotopic mixing models provided congruent results, indicating similar trophic positions and proportions of animal matter in the diet of individuals living in the same forest fragment. These results are coherent with the fact that, like most callitrichid species, BLTs live in small monogamous or polyandrous groups characterized by a high intragroup cohesion, which involves the synchronization of feeding activities and homogenization of diets (Kaisin et al. 2023; Garber 1988; Valladares-Padua 1993). We also found that, even in study areas where more than one group were sampled, individuals from the same study consumed a similar proportion of fruits and arthropods regardless of their group. This suggests that, in addition to intra-group cohesion, the diet of BLTs seems to be governed by the resources available in their habitat. Therefore, studying

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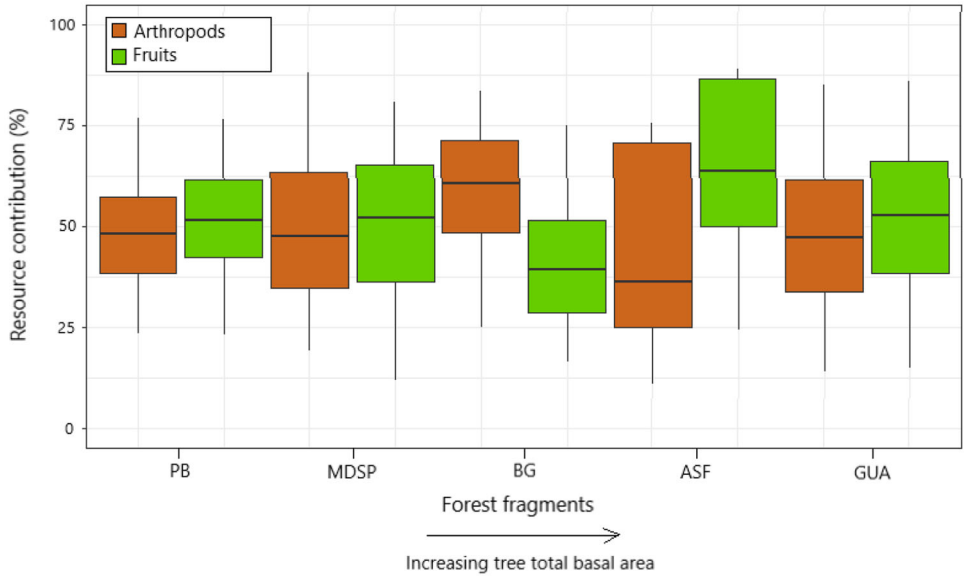

FIGURE 4 | Arthropod (orange) and fruit (green) contributions in the diet of black lion tamarin populations within five study areas. ASF=Angatuba, BG=Buri, GUA=Guareí, MDSP=Morro do Diabo State Park, PB=Ponte Branca.

habitat quality through resource availability remains essential to understand the determinants of diet variations among BLT populations.

While these preliminary isotopic analyses provide novel insights on the contribution of arthropods in the diet of BLTs, revealing that individuals from the same group tend to have similar trophic levels (i.e., proportions of animal matter in their diets), they still may present interindividual differences in the types of prey consumed. Depending on the individual's age or sex, it may forage for different animal prey that requires more or less effort and expertise to capture. For example, a recent study revealed that adult white-fronted capuchins (*Cebus albifrons*) predate wasp larvae, a high-yield resource that juveniles do not yet have the expertise to extract (Barnett et al. 2023). While our results do not allow to respond to this question, DNA metabarcoding represents, in this context, a powerful complementary tool to accurately identify items in the diet of primates (Ruppert, Kline, and Rahman 2019). This DNA-based method has the potential to reveal the frequency at which small vertebrates (e.g., frogs) or other invertebrate (e.g., snails or annelids) are present in the feces of BLTs, uncovering the relative importance of these other animal matter sources in their diet (Quéméré et al. 2013; Rowe et al. 2021; Brun et al. 2022). Combining stable isotope analyses with DNA metabarcoding offers extensive possibilities for future research in primate feeding ecology.

4.2 | Influence of Resource Availability

As expected, $\delta^{15}N$ values of BLTs were mainly influenced by fruit productivity. As TBA (i.e., fruit productivity) increased the $\delta^{15}N$ values of BLT hairs decreased. Since $\delta^{15}N$ values are positively correlated to higher consumption of animal matter (DeNiro and Epstein 1978), our results show that BLTs consume more arthropods when fruit productivity is lower. However, $\delta^{15}N$ values of BLT did not increase with increased arthropod biomass, suggesting that fruits might be the only limiting resource for this primate species. As it has been documented in the golden lion tamarin (Villela et al. 2008), BLTs are able to adjust their feeding habits in areas with lower fruit productivity by increasing arthropod consumption. Our results, therefore, support that fruits are the preferred resource of BLTs and that the consumption of arthropods is determined by the abundance of the former, implying a more important time investment, in line with optimal foraging theory (Emlen 1966; MacArthur and Pianka 1966). However, we cannot exclude that the small effect size of arthropod biomass might be due to an imperfect sampling. Indeed, since our pitfall traps estimated the ground-dwelling arthropod biomass—the most efficient method according to our tests in the field—instead of the canopy arthropod biomass, which might generate some errors if both community biomasses are not correlated.

Interestingly, we found that there was no correlation between TBA and forest fragment size, suggesting that area is not necessarily a good indicator of fruit productivity or habitat quality. As a consequence, this finding suggests that small healthy Atlantic Forest fragments might constitute appropriate habitats for this generalist neotropical primate with a flexible diet and small home range. In this sense, in the current contact of habitat fragmentation, preserving even small forest fragments, while assuring their connectivity, may prove to be crucial for the conservation of this species.

4.3 | Dietary Contribution of Arthropods and Discrepancies Between Stable Isotopes Analyses and Behavioral Observations

Mixing models revealed that BLTs are, on average, as arthropodivorous as frugivorous. We found that the contribution of arthropods in their diet calculated using isotopes was considerably higher than expected based on behavioral data where

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the time spent consuming arthropods was very low (Kaisin et al. 2023; Passos, 1999, 2001; Valladares-Padua 1993). Indeed, feeding behavioral observations based on Kaisin et al. (2023) indicate 0.86% to 2.97% of arthropod consumption events compared to stable isotopes revealing 36.3% to 60.6% of arthropod proportion in the diet of BLTs (see Supporting Information S1: Table 6). We posit that the proportion of arthropods in the diet of BLTs may be underestimated in scan sampling data when compared to the results obtained by isotope analyses. This is also congruent with the fact that, while stable isotope results contrast significantly with previous feeding behavioral studies showing a relatively low arthropod contribution (Kaisin et al. 2023; Passos, 1999, 2001; Valladares-Padua 1993), they provide new information on the proportions of fruits and arthropods in the assimilated diet of BLTs. Multiple factors may play a role and interact to produce the observed discrepancy between stable isotope analysis and behavioral observations. The fact that this species is arboreal and elusive makes observations of its behavior extremely difficult. Consequently, feeding behavior observations, especially techniques using scan sampling, may underestimate arthropod prey consumption and be inappropriate to quantify arthropodivory for this small-bodied primate in a forest environment with low-visibility conditions (Amato, Van Belle, and Wilkinson 2013). Although the consumption of fruits is a conspicuous behavior as tamarins from the same group usually eat synchronously (Kaisin et al. 2023; Dixson, 2012; Garber 1988; Kleiman & Rylands, 2002; Valladares-Padua 1993), the consumption of arthropods is a swift, opportunistic, and thus elusive behavior. The probability that the scan sampling occurs at the exact time of invertebrate consumption is relatively low. In addition, direct observations fail to properly quantify indirect consumption of arthropods (e.g., arthropods potentially present inside or on ingested fruits). Interestingly, two recent studies have shown that spider monkeys (*Ateles* spp.) and red-nosed cuxiús (*Chiropotes albinasus*) prefer insect-infested fruits (Barnett et al. 2023; dos Santos-Barnett et al. 2022). Therefore, black lion tamarins may also be intentionally, or unintentionally, consuming fruits containing insects, which could increase the proportion of arthropods in their diets.

Although measuring food intake or ingestion rate (i.e., the quantity of food items ingested per time unit; Rothman, Chapman, and Van Soest 2012; Schülke, Chalise, and Koenig 2006) remains the most accurate direct method to estimate ingested diet, stable isotope analyses represent a powerful indirect tool. They provide information on what is truly assimilated by a consumer to constitute its own tissues. In omnivorous consumers, the "assimilated" diet may be significantly different from the "ingested" diet. Indeed, omnivorous species typically feed on a mix of high- and low-quality food items in terms of ecological stoichiometry that will not be assimilated with the same efficiency. This implies that food items closer to the consumer tissues, in terms of elemental ratios (e.g., animal tissues), are generally better assimilated by omnivores and can therefore contribute more to their tissue composition than lower-quality food items (e.g., plant tissues) (Elser et al. 2000).

Stable isotope analyses have the potential to reveal the importance of specific food items that may be largely overlooked when relying solely on assessment techniques relating to what is ingested as opposed to assimilated. Thus, this method gives new insights on the feeding ecology of BLTs and open perspectives to study arboreal primate species that have an omnivorous diet and can be difficult to follow and observe in the field (Crowley et al. 2013; DeNiro and Epstein 1981; Magioli et al. 2023). Nevertheless, behavioral observations remain essential to complement stable isotope analyses since they may be crucial in allowing ecological interpretations that may not be formulated using stable isotopes alone (Lejeune et al. 2018). For example, behavioral data allows the quantifications of the time, and by extension, the energy that the individuals need to spend to fulfill their nutritional requirements. This is demonstrated by the substantial foraging efforts observed in two populations of BLTs (MDSP = 20.2%, GUA = 23.0%) although direct arthropod consumption was very low (Kaisin et al. 2023). This suggests that behavioral observations may have important implications to evaluate the fitness and survival ability of different tamarins' populations and further support the idea that both stable isotope analyses and behavioral observations are complementary and should be used in parallel to study feeding ecology of consumers (Crowley, Rasoazanabary, and Godfrey 2014; Schoeninger, Iwaniec, and Glander 1997). Note that the lack of information on hair growth patterns for this species prevents us from establishing the exact time frame that a 5–6 cm BLTs' hair represents. An interesting perspective for a more detailed analysis of BLTs' diet over time would be to establish hair growth patterns to be able to precisely link stable isotope variation in hairs to the period of growth.

5 | Conclusion

Overall, our findings demonstrate that *L. chrysopygus* living in the same forest fragment have the same diet pattern in which fruits represent the main resource. As a result, the proportion of fruits in their diet increases according to tree productivity inside the fragments. Our results also revealed that BLTs increase their consumption of arthropods when fruits are scarce, highlighting the plasticity of their diet and their adaptability to different habitats. Trophic plasticity may therefore play a key role in the survival and resilience of BLTs living in degraded forests, where fruits might represent a limited resource. Since smaller fragments do not always present lower fruit productivity, it is crucial to preserve all forest fragments, independently of their size. This research confirms that stable isotope analyses represent a valuable tool to estimate the trophic level and relative proportions of fruits and arthropods in primates' diet and support its wider use to explore the feeding ecology of any terrestrial mammal. In parallel with stable isotope analyses, future studies should focus on the fitness of primates to assess the extent to which primates can shift their diets without affecting their fitness and identify limiting resource in a context of habitat degradation (Ingala et al. 2019; Johns and Skorupa 1987).

Author Contributions

Amazone Raskin: conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); writing–original draft (lead); writing–review & editing (lead). **Olivier**

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Kaisin: conceptualization (equal); data curation (lead); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (lead); project administration (supporting); supervision (equal); writing–original draft (equal); writing–review & editing (lead). **Loïc N Michel:** formal analysis (supporting); writing–review & editing (supporting). **Benjamin Lejeune:** formal analysis (supporting); writing–review & editing (supporting). **Gilles Lepoint:** formal analysis (supporting); investigation (supporting); methodology (supporting); supervision (supporting); writing–review & editing (supporting). **Rodrigo Gonçalves Amaral:** data curation (equal); writing–review & editing (supporting). **Gabriel Pavan Sabino:** data curation (supporting); writing–review & editing (supporting). **Márcio Silva Araújo:** formal analysis (supporting); methodology (supporting); resources (supporting); writing–review & editing (supporting). **Gabriela Cabral Rezende:** data curation (supporting); writing–review & editing (supporting). **Fany Brotcorne:** methodology (supporting); project administration (supporting); supervision (equal); writing–original draft (supporting); writing–review & editing (equal). **Laurence Culot:** conceptualization (lead); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (equal); Project administration (lead); resources (lead); supervision (lead); writing–original draft (equal); writing–review & editing (equal).

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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