

Does Oxygen Stable Isotope Composition in Primates Vary as a Function of Vertical Stratification or Folivorous Behaviour?

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Abstract

Stable isotopes of oxygen often vary within a community of primates. For example, folivorous monkeys that forage in the upper reaches of the forest canopy tend to evince high $\delta^{18}\text{O}$ values, whereas those that prefer the understory tend to have lower $\delta^{18}\text{O}$ values. Given that leaves also have high $\delta^{18}\text{O}$ values, particularly higher in the canopy, there is uncertainty as to which behavioural variable – vertical stratification or folivory – is the primary determinant of variation in $\delta^{18}\text{O}$ values. Here, we explore further $\delta^{18}\text{O}$ values from the Tai Forest monkeys ($n = 7$ species; $n = 33$ individuals) by examining the interaction between diet and vertical stratification, thereby allowing us to differentiate the effects of each covariate. We found that $\delta^{18}\text{O}$ values varied as a function of mean canopy height, but not folivory, resolving uncertainty about the primary cause of $\delta^{18}\text{O}$ variation. This outcome revolves largely, but not entirely, on the behaviours of *Procolobus verus*, a highly folivorous but understory forager. Relatively elevated values in *Cercopithecus diana*, a frugivorous but middle-to-high canopy forager, raises the possibility that plant reproductive tissues (e.g., fruits, flowers) may be increasingly sensitive to evaporative fractionation at higher forest canopy levels. Overall, our results further affirm the value of using $\delta^{18}\text{O}$ values to estimate the vertical behaviour of primate species in a fossil assemblage.

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Introduction

Stable oxygen isotope analysis has emerged as a useful tool for detecting ecological partitioning in mammalian communities. The reasons are twofold: first, variation in the isotopic composition of an assemblage stems from differences in forag-

ing behaviour [Clementz and Koch, 2001; Cerling et al., 2004; Crowley, 2014; Crowley et al., 2015] and water flux [Bryant and Froelich, 1995; Kohn et al., 1996; Levin et al., 2006; Podlesak et al., 2008; Blumenthal et al., 2017], and, second, this variation is preserved in the fossil record, allowing palaeoecological interpretations of diet and environmental conditions [Koch, 2007; Nelson, 2007, 2013; White et al., 2009; Patnaik et al., 2014]. A primate species will evince high $\delta^{18}\text{O}$ values when its body water is derived mainly from evaporated plant tissues [Crowley, 2012; Nelson, 2013; Carter and Bradbury, 2016] and/or because it is sensitive to evaporative fractionation from sweating or panting during thermoregulation [Kohn et al., 1996; Sponheimer and Lee-Thorp, 1999; Crowley et al., 2015]. Other species have low $\delta^{18}\text{O}$ values because they consume animal fats (e.g., carnivorans) and/or because they regularly recharge their body water by drinking directly from meteoric sources such as streams, lakes and pools (termed “obligate drinking”) [Fricke and O’Neil, 1996; Kohn et al., 1996; Levin et al., 2006; Moritz et al., 2012; Crowley et al., 2015; Blumenthal et al., 2017].

Within tropical forests, vertical variation in evapotranspiration and humidity leads to vertical variation in the $\delta^{18}\text{O}$ values of plant tissues [Sternberg et al., 1989; Ometto et al., 2005; Roberts et al., 2017]. For example, sun-exposed leaves in the upper canopy are particularly sensitive to evaporative fraction (higher $\delta^{18}\text{O}$ values due to the preferential evaporation of ^{16}O [Sternberg et al., 1989; Crowley et al., 2015]). Any diet consisting of canopy leaves is therefore expected to produce consumer tissues with relatively high $\delta^{18}\text{O}$ values, a prediction that was affirmed for the monkeys of Kibale Forest, Uganda [Carter, 2001; Nelson, 2013; Carter and Bradbury, 2016]. Indeed, there is a robust correlation between diet and the $\delta^{18}\text{O}$ values of Kibale primates – fully 84% of variation in oxygen isotope composition can be explained by the percentage of leaves in the diet ($R^2 = 0.84$; Fig. 1). In consequence, folivory is widely viewed as one of the main determinants of $\delta^{18}\text{O}$ variation within a given community of sympatric primates.

Yet, the most folivorous monkeys of Kibale also tend to forage in the emergent canopy [Gebo and Chapman, 1995], which produces a potentially confounding relationship between folivory and vertical height. Accordingly, Carter and Bradbury [2016] argued that folivory and canopy height were positive covariates of $\delta^{18}\text{O}$ values in Kibale primates, although they only directly tested the effect of folivory. In the Taï Forest, there is evidence that vertical stratification in dietary behaviour, rather than folivory per se, is the primary determinant of variation in $\delta^{18}\text{O}$ values [Krigbaum et al., 2013]. This distinction has produced uncertainty as to which behavioural variable – vertical stratification, folivory, or both in tandem – is the primary determinant of variation in primate $\delta^{18}\text{O}$ values. Reconciliation of these competing factors is important given one goal of linking $\delta^{18}\text{O}$ values to specific behaviours and ecologies in the primate fossil record [cf. Nelson, 2013].

Here, our aim is to augment published $\delta^{18}\text{O}$ values – based on bone carbonate from seven monkey species inhabiting the Taï Forest, Ivory Coast [Krigbaum et al., 2013] – with detailed data on folivory and habitat use. The seven species vary widely in their proclivity for consuming leaves, ranging from 1 to 91% of time spent feeding [Korstjens, 2001; Buzzard, 2006; McGraw et al., 2011; Kane and McGraw, 2017], and use of space in the vertical dimension [McGraw, 1996, 1998, 2000]. The West African-endemic olive colobus (*Procolobus verus*) holds particular interest to us because it is highly folivorous and yet averse to foraging in the upper canopy [Oates, 1988; Oates

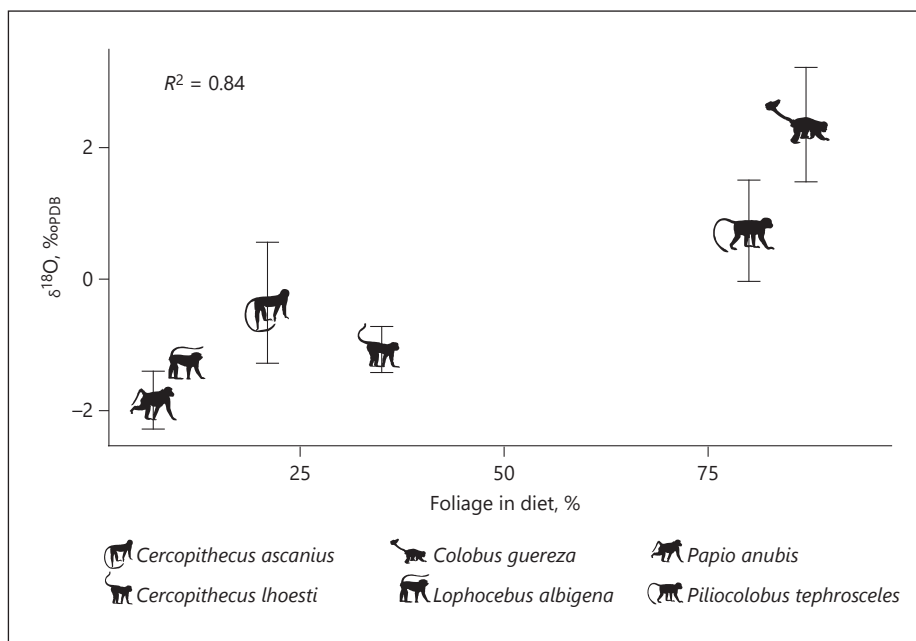


Fig. 1. Bivariate scatter plot based on published Kibale isotope data. To make the stable isotope values of Nelson [2013] (enamel) comparable to those of Carter and Bradbury [2016] (bone carbonate), we used an isotopic enrichment $\epsilon^*_{\text{bone-enamel}}$ of -0.815 (i.e., the mean $\epsilon^*_{\text{bone-enamel}}$ of two specimens of *Papio anubis*, KFB 16 and KFB 29, in common to both studies). PDB, Pee Dee Belemnite standard. Error bars represent one standard deviation. Sources of dietary data: *Cercopithecus ascanius* [Carter and Bradbury, 2016]; *C. lhoesti* [from Nyungwe Forest, Rwanda: Kaplin and Moermond, 2000]; *Colobus guereza* [Harris and Chapman, 2007]; *Lophocebus albigena* [Lambert et al., 2004]; *Papio anubis* [Carter and Bradbury, 2016]; *Piliocolobus tephrosceles* [Carter and Bradbury, 2016].

and Whitesides, 1990; McGraw, 1996]. It is therefore well suited for testing the hypothesis that folivory is a main determinant of high $\delta^{18}\text{O}$ values in a community of primates.

Methods

We used published $\delta^{18}\text{O}$ values from 33 samples of bone carbonate. Each sample stems from a naturally deceased monkey collected between 1994 and 2009 (for a detailed description of sample preparation, see Krigbaum et al. [2013]). Briefly, bioapatite carbonate samples were collected from rib bones and prepared using a modified Kruger method. Organics were initially removed from the samples with 2.5% NaOHCl. Each sample was then rinsed to a neutral pH with DI H_2O before secondary carbonates were removed with 0.2 M CH_3COOH . The pretreated samples were run on a Finnigan MAT 252 IRMS with a Kiel Device. $\delta^{18}\text{O}$ values were reported relative to the Vienna Pee Dee Belemnite standard.

In addition, we used published data on mean strata height [McGraw, 1996, 1998, 2000] and dietary behaviour [Korstjens, 2001; McGraw et al., 2011; Kane and McGraw, 2017] (online suppl. material Table S1; for all online suppl. material, see www.karger.com/doi/10.1159/000502417).

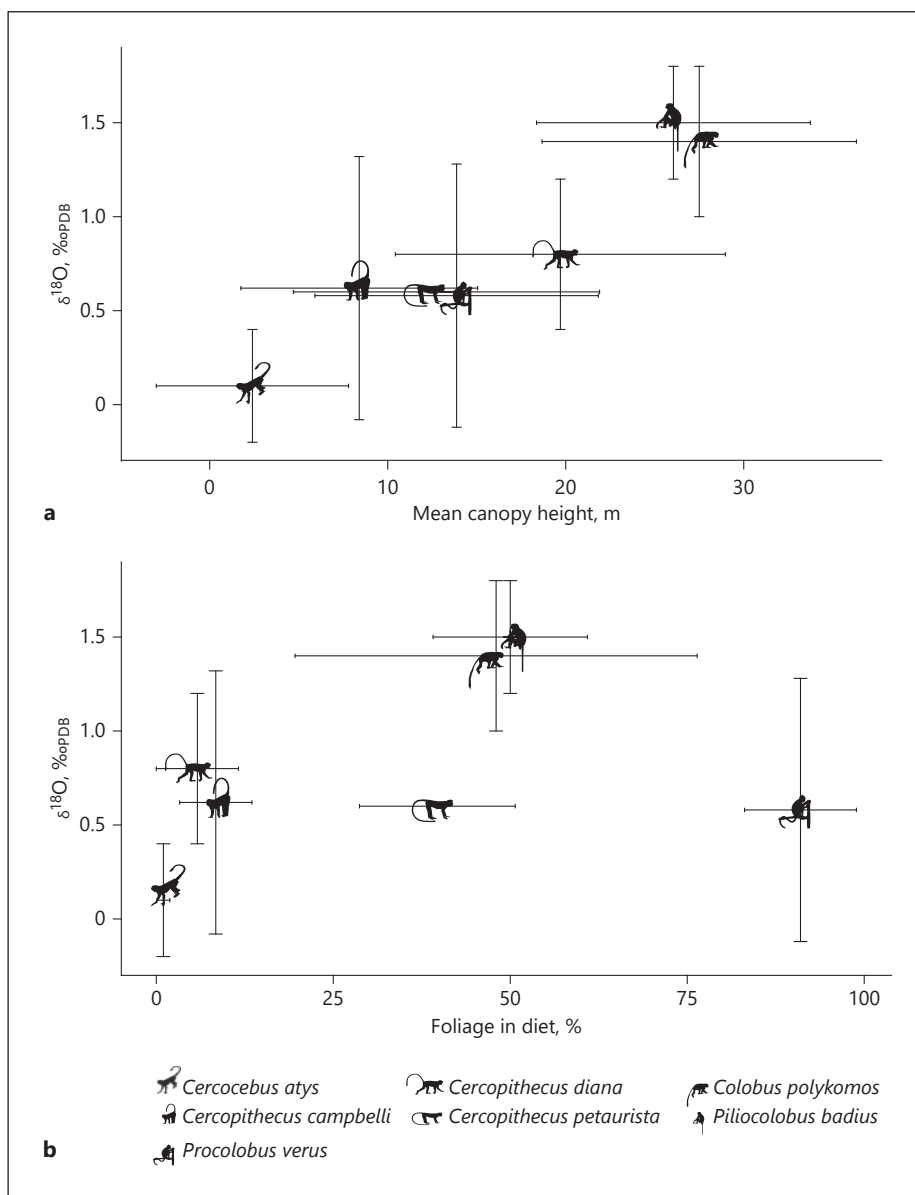


Fig. 2. Bivariate scatter plots of mean $\delta^{18}\text{O}$ values for each of the seven Tai monkey species in the study against mean canopy height (m; **a**) and foliage consumed (% of diet; **b**). PDB, Pee Dee Bel-
emnite standard. Error bars represent one standard deviation.

We used $\delta^{18}\text{O}$ values for all specimens ($n = 33$) in a multiple regression model that included average mean canopy height (m), percent foliage consumed and an interaction effect (mean canopy height percent foliage) as predictor variables. We determined overall model significance via an analysis of variance (ANOVA) and used an R^2 to evaluate the overall fit of the model. We evalu-

ated the strength of each predictor variable with standard beta coefficients (β). In a post hoc analysis, we also evaluated the underlying relationship between canopy height and percent folivory for each species with an independent linear regression. Model fit and significance for this test were also determined with an ANOVA. Significance was tested in all models, with $\alpha = 0.05$. All statistics were run in JMP 13 for Mac.

Results and Discussion

The three predictor variables in our model explained approximately 63% of variation for all $\delta^{18}\text{O}$ values collected from the seven species (online suppl. material Table S2). Mean strata height explained a significant level of variation ($\beta = 0.82$, $p < 0.0001$; Fig. 2a), whereas percent foliage in the diet ($\beta = 0.48$, $p = 0.4899$; Fig. 2b) and the interaction between mean strata height and percent foliage ($\beta = 0.10$, $p = 0.2021$) did not. Furthermore, the relationship between mean canopy height and folivory did not reach statistical significance either ($R^2 = 0.167$, $F_{1,5} = 1.00$, $p = 0.3625$; online suppl. material Fig. S1), indicating that in the Taï Forest (and unlike the general pattern in the Kibale Forest [Fig. 1]), the high-canopy monkeys were not also the most folivorous.

This expanded data set from Taï upholds the conclusions of Krigbaum et al. [2013], i.e., that vertical stratification is the best predictor of $\delta^{18}\text{O}$ values in a community of monkeys (online suppl. material Table S2). Much of this statistical outcome hinges on *P. verus* (average Cook's distance = 0.22, online suppl. material Table S1), the most folivorous monkey species at Taï (Fig. 2b). Tellingly, it has relatively low $\delta^{18}\text{O}$ values that resemble those of much less folivorous species – e.g., *Cercocebus atys*, *Cercopithecus campbelli* and *Cercopithecus petaurista* (Fig. 2b) – each of which forages in the understory or on the forest floor rather than in the high canopy, the preferred stratum of *Colobus* and *Piliocolobus* at Taï (Fig. 2a) and Kibale (Fig. 1). In effect, the olive colobus is a West African anomaly of convenience, allowing us to clearly differentiate between the effects of folivory (as a categorical concept) and vertical stratification. Compellingly, statistical significance was achieved even when *P. verus* was removed from the model: the strongest predictor of $\delta^{18}\text{O}$ values still remained canopy height ($\beta = 0.63$, $p = 0.0381$), not folivory ($\beta = 0.25$, $p = 0.35$).

In contrast, the other two major folivores – *P. badius* and *C. polykomos* – exerted minimal leverage on the linear model (average Cook's distance of 0.0069 and 0.016, respectively) compared to the more frugivorous taxa (online suppl. material Table S1). Thus, the observed effect of vertical stratification on $\delta^{18}\text{O}$ values cannot be attributed to the collective influence of colobine monkeys. The Diana monkey (*C. diana*) is a testament to the overall effect of vertical stratification – it is a highly frugivorous middle-canopy forager with $\delta^{18}\text{O}$ values that resemble those of *P. badius* and *C. polykomos*. Further, the three main understory-level foragers (*C. petaurista*, *C. campbelli*, *P. verus*) have widely varying diets but indistinguishable $\delta^{18}\text{O}$ values (online suppl. material Table S1).

Overall, our findings raise the possibility that all plant tissues, including reproductive tissues such as fruits and flowers, are increasingly sensitive to evaporative fractionation at higher canopy levels. Such an interpretation is premature in the absence of systematic data from plant tissues, but it does invite reassessment of basic assumptions. For example, it is often suggested that fruits have relatively lower $\delta^{18}\text{O}$

values compared to leaves due to reduced rates of evapotranspiration [Nelson, 2013; Crowley et al., 2015; Carlson and Crowley, 2016; Carter and Bradbury, 2016]. Nevertheless, in Sri Lanka tropical forests, Roberts et al. [2017] found that the $\delta^{18}\text{O}$ values for primate foods did not consistently differ between fruits and mature leaves within the same forest stratum. Although Roberts et al., [2017] did not give a specific mechanistic reason for the lack of consistent $\delta^{18}\text{O}$ differences between these plant tissues, it could be that some high-canopy fruits with greater cuticle permeability may have elevated evapotranspiration rates [Schreiber and Riederer, 1996], resulting in similar $\delta^{18}\text{O}$ values to adjacent canopy leaves [Roberts et al., 2017]. This premise is corroborated by studies that report a positive association between air temperature variation and the $\delta^{18}\text{O}$ values of some fruit tissues [Jahren et al., 2001; Pustovoytov et al., 2010]. In this vein, the reproductive biology of figs holds particular interest, especially those with potential for photosynthesis and respiration; by this reasoning green figs are predicted to have higher $\delta^{18}\text{O}$ values than other fruits (see Dominy et al. [2016]).

In addition, our findings suggest that it is essential to combine stable isotope data with morphological inferences when interpreting the relationship between vertical behaviour and diet in the primate fossil record. For example, colobines (both extant and extinct) are usually, but not always, high-canopy foragers, as reflected by their relatively high $\delta^{18}\text{O}$ values [White et al., 2009; Nelson, 2013; Carter and Bradbury, 2016]. If a fossil colobine is undifferentiated from an obvious frugivore, the equivocal result could be evidence of high-canopy foraging by the frugivore or understory foraging by the colobine (provided uniformitarian principles are at work). Likewise, if morphological interpretations of diet are limited due to fragmentary remains or lack of diagnostic dental features, it cannot always be expected that a high $\delta^{18}\text{O}$ value will coincide with greater levels of folivory. Rather, high $\delta^{18}\text{O}$ values could be an outcome of high-canopy foraging behaviour (folivorous, frugivorous or otherwise) [Krigbaum et al., 2013; Nelson, 2013] or foraging in open environments [Crowley, 2012; Nelson, 2013]. In this latter case, tandem use of carbon and oxygen stable isotopes can clarify habitat conditions because closed-forest, high-canopy foragers tend to have lower $\delta^{13}\text{C}$ values than those which rely on plants in open habitats [Nelson, 2013].

Taken together, the significance of our results is threefold. First, we demonstrate that vertical stratification, not folivory per se, is the primary determinant of variation in $\delta^{18}\text{O}$ values in the community of cercopithecids at Taï, providing further support for the results of Krigbaum et al. [2013]. Second, our findings raise the possibility that plant reproductive tissues (flowers, fruits) are also sensitive to evaporative fractionation to some extent [cf. Roberts et al., 2017]. Third, we show that oxygen stable isotope data, when combined with distinct functional morphological traits, have the potential to inform the fossil record, particularly interpretations of diet [Carter and Bradbury, 2016] and vertical stratification [Krigbaum et al., 2013; Nelson, 2013]. At the same time, our results do call further attention to a large empirical void in the discipline: namely, the oxygen stable isotope composition of primate foods, both generally and in the vertical dimension. Further filling this void, while continuing to explore patterns of oxygen isotope values in a greater diversity of living primate communities, is certain to be instructive.

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Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

The authors have no conflicts of interest to declare.

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Author Contributions

L.D.F. and W.S.M. conceived the research idea, W.S.M. collected specimens for isotope study and contributed new data, L.D.F. and W.S.M. analysed data, L.D.F. and W.S.M. wrote the paper.

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