Journal of Human Evolution 101 (2016) 1–16

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Comparative isotope ecology of African great apes

Vicky M. Oelze [a, b, *], Geraldine Fahy [c, d], Gottfried Hohmann [a], Martha M. Robbins [a], Vera Leinert [a], Kevin Lee [a], Henk Eshuis [a], Nicole Seiler [a], Erin G. Wessling [a], Josephine Head [c], Christophe Boesch [a], Hjalmar S. Kühl [a, b]

[a] Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany
[b] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[c] Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution, Deutscher Platz 6, 04103 Leipzig, Germany
[d] University of Kent, School of Anthropology and Conservation, Marlowe Building, CT2 7NR Canterbury, UK

ARTICLE INFO

Article history:
Received 27 May 2015
Accepted 27 August 2016

Keywords:
Carbon
Nitrogen
Habitat
Feeding ecology
Seasonality
Isotopic baseline

ABSTRACT

The isotope ecology of great apes is a useful reference for palaeodietary reconstructions in fossil hominins. As extant apes live in C_3-dominated habitats, variation in isotope signatures is assumed to be low compared to hominoids exploiting C_4-plant resources. However, isotopic differences between sites and between and within individuals are poorly understood due to the lack of vegetation baseline data. In this comparative study, we included all species of free-ranging African great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla sp.*). First, we explore differences in isotope baselines across different habitats and whether isotopic signatures in apes can be related to feeding niches (faunivory and folivory). Secondly, we illustrate how stable isotopic variations within African ape populations compare to other extant and extinct primates and discuss possible implications for dietary flexibility. Using 701 carbon and nitrogen isotope data points resulting from 148 sectioned hair samples and an additional collection of 189 fruit samples, we compare six different great ape sites. We investigate the relationship between vegetation baselines and climatic variables, and subsequently correct great ape isotope data to a standardized plant baseline from the respective sites. We obtained temporal isotopic profiles of individual animals by sectioning hair along its growth trajectory. Isotopic signatures of great apes differed between sites, mainly as vegetation isotope baselines were correlated with site-specific climatic conditions. We show that controlling for plant isotopic characteristics at a given site is essential for faunal data interpretation. While accounting for plant baseline effects, we found distinct isotopic profiles for each great ape population. Based on evidence from habituated groups and sympatric great ape species, these differences could possibly be related to faunivory and folivory. Dietary flexibility in apes varied, but temporal variation was overall lower than in fossil hominins and extant baboons, shifting from C_3 to C_4-resources, providing new perspectives on comparisons between extinct and extant primates.

1. Introduction

The feeding ecology of different primate species is a valuable reference for reconstructing the ecological niche of extinct hominoids. In particular, great apes reveal a diversity of behavioral traits and ecological adaptations that provide a unique framework for ecological reconstructions in our earliest ancestors in Pleistocene Africa (e.g., Stanford, 2006). For fossil hominins, various lines of evidence (e.g., skeletal and dental morphology, dental wear and plant residuals in calculus) can provide information on feeding behavior (e.g., summarized by Ungar and Sponheimer, 2011). Recently, stable isotope analysis in both extant and extinct primates is increasingly utilized to link past and present feeding ecology (Ungar and Sponheimer, 2011; Antón et al., 2014).

However, our current knowledge on the feeding ecology diversity of wild apes may be biased by the small number of communities that are subject to long-term research. Increasing evidence from previously unstudied wild great ape populations suggests general classifications may be over-simplified. Each unstudied population can be expected to preserve its own unique behavioral or even cultural traits (Whiten et al., 1999). At the same

* Corresponding author.
E-mail address: viktoria_oelze@eva.mpg.de (V.M. Oelze).

http://dx.doi.org/10.1016/j.jhevol.2016.08.007
0047-2484/

time, ape populations are declining at high rates and have already gone extinct in many regions (Junker et al., 2012; Tranquilli et al., 2012). Hence, there is a need to develop new techniques and strategies to compare the ecology of extant great apes across populations, habitats, and species in a standardized, yet timely manner.

Isotope analysis is a well-established tool in the study of wildlife ecology (Wolf et al., 2009) and in paleoanthropology (Ungar and Sponheimer, 2011; Sponheimer et al., 2013). The stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are increasingly utilized biochemical markers to reconstruct the feeding ecology of primates, particularly in populations that cannot be directly observed (Schoeninger et al., 1998; Schoeninger, 2009). The differentiation into separate or overlapping ecological niches can be assessed in sympatric primate species (Schoeninger et al., 1998; Macho and Lee-Thorp, 2014; Oelze et al., 2014). Stable isotope analysis in hair keratin is a particularly useful approach when investigating temporal and inter- and intra-individual dietary variation in great apes (Oelze et al., 2011, 2014; Fahy et al., 2013; Oelze, 2016). The key advantages are that a hair strand records the dietary signature of a single individual over a long time period (several subsequent months) and hair isotopic data obtained from different individuals and species can be compared (Schwertl et al., 2005; Cerling et al., 2009; Oelze et al., 2011, 2014). In consumers, $\delta^{13}C$ values are mainly associated with the photosynthetic pathway of food plants (C_3, CAM, or C_4; DeNiro and Epstein, 1978). In forested habitats, the predominant habitat of great apes, the so called 'canopy effect' is thought to result in vertical variation in plant $\delta^{13}C$ values (van der Merwe and Medina, 1991; Graham et al., 2014). Due to the isotopic fractionation with each step in the food chain, $\delta^{15}N$ values are commonly related to the trophic level of an animal, e.g., if it can be considered herbivore, omnivore, or carnivore (Minagawa and Wada, 1984). Stable isotope ecology is based on the principle "you are what you eat," as the isotopic characteristics of the main food components are incorporated into consumers' body tissue with a predictable enrichment (indicated by Δ) caused by isotopic fractionation (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984; Kohn, 1999).

The first studies on great apes used bulk hair samples from unhabituated apes and did not control for local baseline isotopic values in the environment, as no plant samples were used for analysis (Schoeninger et al., 1999; Sponheimer et al., 2006a). Cross-site comparisons of these data are hindered as isotopic baseline values are known to differ between regions and habitats due to biotic and abiotic factors in the soil and plants (Dawson et al., 2002; Casey and Post, 2011). Thus, conclusions drawn on primate dietary behavior without controlling for isotopic baseline effects may be misleading. For example, the low $\delta^{15}N$ values in 'savanna chimpanzees' have been interpreted as legume consumption, which would cause depleted $\delta^{15}N$ values (Schoeninger et al., 1999; Sponheimer et al., 2006a). This explanation was suggested as open dry habitats are thought to commonly reveal rather high $\delta^{15}N$ values (Heaton et al., 1986). However, no vegetation samples were used to validate this assumption. We seek to show in this study that controlling for ecological isotopic characteristics at a given site is essential for data interpretation. A good example of this need is the high $\delta^{15}N$ values reported for wild bonobos from Salonga National Park, which may have been interpreted as intensive faunivory if local plant baseline values had not been considered. However, these high $\delta^{15}N$ values in bonobos were best explained by an overall ^{15}N-enriched ecosystem which was supported by the data from other sympatric herbivores (Oelze et al., 2011).

Recently, two separate attempts to compare chimpanzee stable isotope characteristics across several sites came to strikingly contradicting results. As neither study could account for plant baselines, they found different patterns between climate and chimpanzee hair isotope data (Schoeninger et al., 2016; Loudon et al., 2016). Here, we propose to systematically correct great ape hair isotope values by a standardized local plant sample set when examining inter-site isotopic variation. While $\delta^{13}C$ values in plants are mainly determined by plant physiology, forest cover (UV-radiation and air ventilation), water availability, and altitude (Tieszen, 1991; Dawson et al., 2002), $\delta^{15}N$ values mainly vary with the nitrate content of the local geological substrate and its assimilation by micro flora and fauna (Robinson et al., 1998; Martinelli et al., 1999). Thus, every location should have a unique plant isotope baseline. Recently, Crowley and colleagues (2014) suggested the calculation of a mean isotope ratio of a standardized vegetation sample (e.g., only C_3, non-leguminous plants) for each site and subsequent discussion of the deviation measured in the primate body tissue signatures from this plant baseline. This deviation from food source to consumer tissue is referred to as isotopic discrimination or fractionation (Δ) and describes the trophic enrichment from diet to tissue. In this study, we follow this suggested approach by systematically using plant baseline data in our comparison of hair isotope data from great apes.

In a recent review on primate isotope studies, Sandberg and colleagues (2012) noted that the inter-individual variation of $\delta^{13}C$ and $\delta^{15}N$ values in bonobos and chimpanzees is low. Further they state: "A significant characteristic of the chimpanzee stable isotope data is the virtual lack of variability within populations and between those living in similar environments, particularly for carbon" (Sandberg et al., 2012:980). We would argue previous analyses of bulk hair samples likely muted the isotopic variation within the growth trajectory of a given hair strand, as bulk samples represent an average of the variation within a hair sample. Moreover, most great apes feed predominantly on C_3-plant based resources. Thus, the overall isotopic variation should be within the C_3-plant range (Carlson and Kingston, 2014) and will not be as distinctive as in primates switching between C_3 and C_4-resources, such as in some baboon populations (e.g., Codron et al., 2008 and references therein). Nevertheless, isotopic variation will be detectable and indicative of differences in feeding behavior if the data can be related to a sample of local food plants (Oelze et al., 2014). For example, in an isotope study using local plant samples and sequential sections of hair samples of sympatric lowland gorillas and central chimpanzees from Gabon, Oelze and colleagues (2014) showed that there was significant intra-annual variation in hair $\delta^{13}C$ in gorillas as they seasonally shifted their dietary proportions of low canopy foliage and fruit. At the same site, temporal variation in $\delta^{15}N$ values was highly significant in chimpanzees and ranged over ~1.5‰, suggested to be a result of utilizing different fruit species (Oelze et al., 2014). These nuanced temporal patterns would not have been detected in bulk samples of ape hair. In western chimpanzees from Taï National Park, Ivory Coast, intra-individual variation was detectable even in such bulk hair samples. Here, male chimpanzees had significantly higher mean $\delta^{15}N$ values than females as they consumed meat more frequently. Males observed to be successful hunters revealed the highest $\delta^{15}N$ values in the community (Fahy et al., 2013).

Here, we present the most comprehensive $\delta^{13}C$ and $\delta^{15}N$ dataset measured to date in non-human primates. It includes all species of African apes living in different habitats ranging from evergreen forests to mosaic landscapes to savanna woodlands (see Fig. 1 and Table 1). Samples were obtained from six field sites in six African countries, including three subspecies of chimpanzees (*Pan troglodytes troglodytes*, *Pan troglodytes verus*, *Pan troglodytes schweinfurthii*), western lowland gorillas (*Gorilla gorilla gorilla*), mountain gorillas (*Gorilla beringei beringei*), and bonobos (*Pan paniscus*). This dataset is represented by 701 hair keratin isotope data from 148 hair samples and an additional collection of 189 fruit samples.