Stable Nitrogen Isotope Analysis of Dentine Serial Sections Elucidate Sex Differences in Weaning Patterns of Wild Chimpanzees (*Pan troglodytes*)

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ABSTRACT   Offspring provisioning is one of the most energetically demanding aspects of reproduction for female mammals. Variation in lactation length and weaning strategies between chimpanzees (*Pan troglodytes*), our closest living relative, and modern human societies have been reported. When and why these changes occurred is frequently debated. Our study used stable nitrogen isotope data of tooth root dentine from wild Western chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire, to quantify weaning in these chimpanzees and explore if infant sex plays a role in maternal investment. We analyzed serial sections of deciduous lateral incisor root dentine from four Taï chimpanzees to establish the $\delta^{15}N$ signal of nursing infants; we then analyzed serial sections of first permanent mandibular molar root dentine from 12 Taï chimpanzees to provide quantitative $\delta^{15}N$ data on weaning in this population. Up to 2 years of age both sexes exhibited dentine $\delta^{15}N$ values ≈2–3‰ higher than adult female Taï chimpanzees, consistent with a nursing signal. Thereafter a steady decrease in $\delta^{15}N$ values consistent with the onset, and progression, of weaning, was visible. Sex differences were also evident, where male $\delta^{15}N$ values decreased at a significantly slower rate compared to females. Confirmation of sex differences in maternal investment among Taï chimpanzees, demonstrates the viability of using isotope analysis to investigate weaning in non-human primates. Additionally, assuming that behaviors observed in the Taï chimpanzees are illustrative of the ancestral pattern, our results provide a platform to enable the trajectory of weaning in human evolution to be further explored. Am J Phys Anthropol 153:635–642, 2014.   © 2014 Wiley Periodicals, Inc.

Weaning in mammals

Attempting to understand the process of weaning requires an accurate definition of what constitutes a "weaned infant." In species where suckling ends abruptly (e.g., Japanese macaques, Hiraiwa, 1981; true seals, Oftedal et al., 1987), the complete cessation of suckling is often an appropriate definition of weaning. However when applied to species where infants continue to suckle, albeit infrequently, such as chimpanzees, while obtaining most of their energy intake independently, this definition is less appropriate. Some describe weaning in chimpanzees as a "gentle but active process" (Horvart and Kraemer, 1982) throughout the early years of the infant's life, encompassing a 2- to 4-year period of gradual weaning from the nipple (Clark, 1977). For the purpose of the present article, weaning is specifically described as a process encapsulating a series of events including the gradual termination of lactation and suckling, decreased dependency on breast milk, and increased consumption of non-milk foods (Katzenburg et al., 1996; Bogin, 1999; Humphrey, 2010).

Evolution of weaning age

The most prominent life-history trade-off involves the cost of reproduction (Stearns, 1989). Vandeleest et al.

(2012) highlight the fact that all primate mothers can choose to focus on imparting resources to current offspring and delay reproduction, or wean earlier, thereby limiting investment in current offspring, to produce other infants. In human and nonhuman primates, weaning too late can be detrimental to the mother's lifetime fitness as it delays subsequent reproduction, whereas weaning too early can have detrimental effects on the

infant in terms of mortality from increased risks of infectious and parasitic diseases (Humphrey, 2010).

Environmental differences and differing availability of complementary weaning foods may contribute to variation in weaning ages observed between modern humans and chimpanzees. In chimpanzees, maternal condition, available resources and individual dispersal patterns can play a role in when an infant is weaned. At Taï, transmission of phenological knowledge from mother to infant peaks between 3 and 5 years of age (Boesch and Boesch-Achermann, 2000) suggesting that mothers spend large amounts of time investing in the development of their infants to facilitate the infant's future independence. A major difference between humans and chimpanzees, and one of the most likely contributors to reduced weaning age in humans, involves the availability of maternal assistance via paternal care or alloparenting (Marlowe, 2001). Human females and their infants benefit from assistance and provisioning by others during weaning, whereas, in great ape societies, mothers have sole responsibility for their infant until that infant is independent. Even allowing for additional complexities in the evolution of allo-care (e.g., availability, quality, and nutritional content of supplementary foods, etc.), the facilitation of mother-infant separations that enabled allo-care, likely provided an avenue for the earlier introduction of non-milk foods in humans, thereby decreasing weaning age (Kachel et al., 2001).

Parent-offspring conflicts are predicted, especially towards the end of the period of parental investment, as the interests of the parents and the offspring increasingly diverge (Trivers, 1974). In line with this, weaning conflicts in wild chimpanzees are regular and can be quite dramatic towards the end of the suckling investment period (Goodall, 1986). For field primatologists, it is difficult to identify when and how much milk an infant chimpanzee is receiving due to limited diurnal observations, along with an inability to distinguish nutritional suckling (i.e., milk transfer) from psychological comfort suckling (i.e., no milk transfer) (Lee, 1996; Emery-Thompson et al., 2012; Reitsema, 2012). In chimpanzees, and other animals, maternal investment is generally calculated as the time between two births, known as the inter-birth interval (IBI) (Silk, 1988). The use of the IBI as a proxy for weaning in primatology is not uncommon; however, the IBI calculation includes all aspects of maternal investment, and is not restricted to time spent suckling (Boesch and Boesch-Achermann, 2000). For *Pan troglodytes*, IBI-based weaning ages range from 4.5 years at Gombe (Goodall, 1989), 5 years at Bossou (Sugiyama, 1994), 5.75 years at Taï (Boesch, 1997), 6 years at Mahale (Nishida et al., 1992) to 7.2 years at Kanyawara (McGrew et al., 1996). Reported IBIs for other great ape species also vary from 4.5 to 5 years for *Pan paniscus*, to 3.5–4.5 years for *Gorilla gorilla beringei*, with the largest reported IBIs ranging from 7.7 to 8.4 years for *Pongo pygmaeus* (review in Kennedy, 2005). Although significant variation from 2 to 5 years is reported from ethnographic studies of human "natural fertility" societies, the age ranges observed in the great apes contrast dramatically with average weaning practices in these societies where weaning generally occurs between 2 and 3 years of age (review in Kennedy, 2005).

Sex differences in maternal investment

Variation in suckling length but not inter-birth interval (IBI) has been reported for some wild chimpanzee populations; at Gombe (Clark, 1997) and Taï (Fränkl et al., unpublished data), infant nipple contact was highest during the first 6 months of life, with a steady decrease thereafter. At Mahale, Hiraiwa-Hasegawa (1990) found that while female infants suckled longer than male infants before 6 months of age, there was no significant difference detected in the IBI after a mother successfully reared a male versus a female offspring. Contrastingly, Fränkl et al. (unpublished data) reported the opposite trend at Taï during the first 6 months of life, with males observed to suckle significantly longer than females, with no sex difference observed thereafter. The social status of the mother has also been found to play a role in maternal investment at Taï, largely in conjunction with infant sex. Boesch (1997) found that dominant Taï chimpanzee mothers invested more in sons and this increased their son's survival. An analysis of IBIs at Taï (Boesch, 1997) found a combined effect of maternal rank and infant sex in that dominant female investment in sons was ~2 years longer than in daughters, and subdominant mothers invested 11 months more in daughters compared to sons.

Stable nitrogen isotope analysis

Body tissue element isotopic composition is highly influenced by food and drink consumed in life (Sealy et al., 1995; Humphrey, 2010); consequently isotopic analyses of body tissues can offer clues to aspects of diet and lifestyle in extant and extinct populations. The use of stable nitrogen ($\delta^{15}N$) isotope measurements as a proxy in the determination of weaning patterns in archaeological populations has grown substantially since it was first introduced by Fogel et al. (1989); however, its use in nonhuman primate weaning studies has, thus far, been limited. Children being breast-fed have $\delta^{15}N$ stable isotope values $\approx$2–3‰ over average adult dietary protein (Richards et al., 2002; Fuller et al., 2006). The onset of the decline in $\delta^{15}N$ values after the peak value is reached indicates that weaning has begun (Kennedy, 2005); correspondingly, an infant who is fully weaned should exhibit isotope values in line with the adults of its community/group (Herring et al., 1998). Therefore, using $\delta^{15}N$ measurements to track the weaning process in nonhuman primates offers the opportunity to obtain accurate and biologically meaningful information (Reitsema, 2012) as to the initiation of weaning, how rapid or paced the process is, and when weaning is completed.

Chimpanzee dentition

Tooth root morphology preserves evidence of growth processes and can therefore provide valuable information on growth and dietary adaptation in primates (Dean and Cole, 2013). Incremental markers in root dentine enable the reconstruction of the chronology of tooth development, with growth spurts being particularly informative (Dean and Cole, 2013). In chimpanzees, the timing of the root growth spurt appears to correspond with tooth eruption at ~3.5–3.6 years of age (Kuykendall et al., 1992; Dean and Cole, 2013) which corresponds well with the M1 emergence age estimates provided by Smith and Boesch (2011). Collagen rich dentine, a major component of tooth roots, largely forms during childhood with subsequent layers of secondary and even tertiary dentine, laid down later in life (Sealy et al., 1995). As tooth dentine does not readily turnover isotopic measurements of the early primary dentine collagen reflect

the diet of an individual in their early childhood (Sealy et al., 1995; Wright and Schwarcz, 1999; Richards et al., 2002).

This study utilized nitrogen isotope data from direct dentine serial sections of deciduous and permanent teeth of wild Western chimpanzees (*Pan troglodytes verus*) from Taï National Park, Côte d'Ivoire to investigate whether isotopic evidence supports behavioral observations that weaning is a slow, continuous process in these chimpanzees and to investigate sex differences in maternal investment in this population. Additionally as each component of the weaning process is dependent on many factors (environment, infant and weanling mortality levels, reproductive demands on women (Gray, 1996), investigating weaning in our closest living relatives provides the opportunity to examine weaning as an evolutionary progression.

MATERIALS AND METHODS

Sampled individuals

The Taï chimpanzee skeletal collection is housed at the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. Identification of individual chimpanzees under behavioral observation has been systematically collected since the early 1980s (Boesch and Boesch-Achermann, 2000). Identification of cadavers sampled in this study was based on the field researchers' daily knowledge of the demography of the Taï communities and overlap with the observed disappearance of individuals. Where accuracy of such identification was reduced due to advanced decay, individuals were identified as part of an on-going genetic investigation into familial relationships at Taï by Linda Vigilant and her team at the Max Planck Institute for Evolutionary Anthropology, Departmant of Primatology, Molecular Genetics Laboratory (Vigilant et al., 2001; Boesch et al., 2006). The cause of death for most of the individuals sampled ranged from exposure to fast-acting diseases and traumatic attacks (Supporting Information Table S1), none of which are likely to affect the nitrogen isotope signals of the sampled individuals.

Sample analysis

Our sampling approach follows on from initial work by Fuller et al. (2003) and more recently by Eerkens et al. (2011). Deciduous mandibular lateral incisor root dentine from two female and two male, and permanent mandibular first molar root dentine from six female and six male, Taï chimpanzees were sequentially sectioned beginning from less than 1mm from the enamel-dentine junction (EDJ) to the root tip using a diamond-tipped burr on a hand-held drill. Depending on the length of the tooth and the completeness of the root, between six and nine samples of dentine powder were collected for each tooth. The teeth were first cleaned by air abrasion to remove any adhering particles. All sections were sampled to approximately the same average depth of 1 mm; we feel that the effects of the inherent root growth spurt on our isotope data are limited as Dean and Cole (2013) suggest that the growth spurt is confined to a small section of the tooth root, with tooth root growth rates accounted for in our age calculation (below). As these are modern samples we did not need to extract and purify the collagen to remove contaminants, as is routinely done for archaeological samples. This, coupled

with our requirement for nitrogen isotope data alone, enabled us to use much smaller samples than are usually taken for dentine isotope measurements (Wright and Schwarcz, 1999; Fuller et al., 2003). We sectioned only dentine roots from the EDJ, rather than the entire dentine length, as research suggests that the root growth at this junction corresponds to 1.7 years (Anemone et al., 1991). While extending dentine sectioning above the neonatal line can render isotopic data on fetal life (Burt and Garvie-Lok, 2013), our study focused on the isotope signal of weaning. Therefore, given the confirmation of a lack of weaning prior to 2 years from our deciduous dentition, we felt that sampling the entire root length was unnecessarily destructive. Each dentine powder sample (average weight 4 mg) was weighed into tin capsules for direct dentine $\delta^{15}N$ isotope ratio mass spectrometry (IRMS) analysis. Isotopic measurements were done using a Flash EA 2112 coupled to a DeltaXP mass spectrometer (Thermo-Finnegan®, Bremen, Germany) at the Max Planck-Institute for Evolutionary Anthropology. The analytical precision, calculated from repeated analysis of internal and international standards, was better than $0.2‰$ (1σ) $\delta^{15}N$. As carbon in untreated dentine powder can come from multiple sources (in addition to collagen) we did not measure the carbon isotope values of the powder. In future studies carbon isotope analysis of these specimens may also provide an insight into weaning behavior if collagen is extracted and isolated through chemical pretreatment procedures. In this study we were not able to do this, as the resulting collagen extract would have been too small for the instrumentation to make accurate carbon isotopic measurements. Therefore we have not included carbon isotope measurements in this study.

Age calculation from dentine serial sections

No data exists on age at eruption and emergence patterns of deciduous teeth in chimpanzees, however Stack (1967) found that, in modern humans, deciduous teeth form quickly and have high extension rates of up to 19 μm/day with no obvious growth spurts. Data from modern humans indicates that deciduous mandibular lateral incisors begin growing *in utero* and are fully erupted between 1.5 and 2 years of age (AlQuahtani et al., 2010). We used this modern human data for our study as growth rate data on deciduous chimpanzee dentine are unknown. Permanent first molars begin growing at birth at the EDJ (Eerkens et al., 2011); root formation begins as the calcification of the crown reaches completion (Anemone et al., 1991). Molar teeth in *Pan* have similar root lengths (Dean and Vesey, 2008) to humans averaging 11–13 mm in length when fully formed (Gleiser and Hunt, 1955). To determine the age represented by each permanent serial dentine sample it was necessary to calculate the timing of root growth for each individual M1. The method used to assign an age-at-section stage for which our isotope values are representative of is an extension of that used by Eerkens et al. (2011). As our samples were taken from the EDJ to the root tip, it was necessary to calculate our start age for dentine growth at the EDJ. Anemone et al. (1991) proposed that M1 roots in *Pan troglodytes* begin developing at ~24 months. This was further refined in by Anemone et al. (1996) who, in an extension of the eight stages of chimpanzee molar development proposed by Demirjian (1986), found that stage D reflects the last stage of

crown development and the initiation of root development; the mean age assigned to this stage is 1.71 years (20.55 months). Dean (2010) showed that growth rates vary between individuals therefore *P. troglodytes* permanent mandibular M1 root growth extension rates were extrapolated from Dean and Vesey (2008) who presented average root extension rates (μm) [with standard deviation (SD)] from 200 to 10,000 μm of M1 root length. For the purpose of our study, these data were converted to yearly data (the extension rate data given for 200, 500, and 1,000 μm was averaged to give an extension rate for the first 1 mm of root length from the EDJ). These data were then used to calculate the age (±SD) represented by each of our permanent dentine serial samples. To determine the length of time (yrs) covered by the serial sections in each individual tooth, the distance (mm) of each measurement from the EDJ was divided by the chimpanzee root growth extension rate (Dean and Vesey, 2008) for that section to give mm per year. Using the start age of 1.71 years suggested by Anemone et al. (1996) the root length growth rate per year was added to this start age to give a representative age estimate for each serial section (refer to Supporting Information Table S3 for sample calculation).

Statistical analysis

To test for the effects of weaning age on isotope levels, we ran a linear mixed effects model with Gaussian error structure and identity link function; to do this we used the lmer function of the R package lme4 (Bates et al., 2012). The full model included the fixed effects age and sex, and their interaction, with sex as a control predictor. The identity of the individual as a random intercept term and age as a random slopes term within subjects were included to control for individual variation ($n = 97$, number of individuals = 12). The significance of the full model compared to the null model (excluding age) was established using a likelihood ratio test (Forstmeier and Schielzeth, 2011) minus age and its interaction but including all other terms used in the full model. We verified the assumptions of normally distributed and homogeneous residuals by visually inspecting a histogram of the residuals, as well as the residuals plotted against fitted values; there were no deviations from these assumptions. Variance Inflation Factors (VIF, Field, 2005) were calculated using the function *vif* of the R-package car (Fox and Weisberg, 2011). The VIFs were derived from a standard linear model excluding both random effects and did not indicate the presence of collinearity (maximum VIF = 1.000). We checked for model stability by excluding individuals sequentially from the data set, running the full model and comparing the results with those from the original model. No obvious differences led us to conclude that there were no influential individuals, indicating model stability. *P* values for individual effects were derived using the Markov Chain Monte Carlo (MCMC) sampling method (Baayen, 2008) using the package language R (Baayen, 2011).

RESULTS

To identify a nursing signal (necessary to identify a subsequent weaning signal), we examined the pattern of dentine δ^{15}N in deciduous lower lateral incisors. Deciduous incisor root dentine δ^{15}N values are reflective of a period of almost exclusive suckling during the first 2 years of life. Our results exhibited constant dentine δ^{15}N

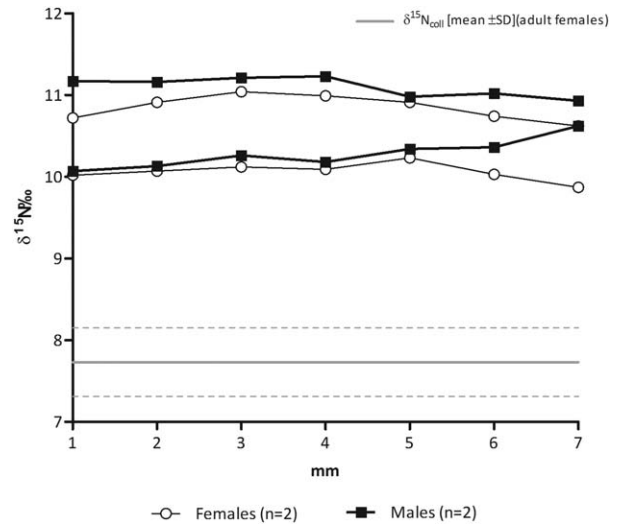**Fig. 1.** Dentine serial section δ^{15}N data of deciduous lower lateral incisors of Taï infants: dentine δ^{15}N data indicates enriched and relatively consistent levels of protein in the Taï infant diet for the first 2 years of life. *mm = distance from the EDJ.

enrichment with values ≈2–3‰ higher than the average δ^{15}N of adult female Taï chimpanzees (7.7‰ ± 0.4‰, data from Fahy et al., 2013) consistent with a nursing signal. No sex or maternal rank differences are observable and there is no evidence that weaning commences prior to 2 years of age (Fig. 1).

Our permanent dentine δ^{15}N data suggests that weaning is a dynamic process, beginning from ∼1.7 years of age (see Materials and Methods), rather than an abrupt event at Taï. Overall there was a significant effect of advancing age on dentine δ^{15}N values (full-null model comparison: $\chi^2 = 34.99$, df = 2, $P < 0.001$) consistent with the commencement, and progression, of weaning. Initially males and females exhibited similar dentine δ^{15}N values of 10–11‰. Subsequently, male dentine δ^{15}N values decreased at a significantly slower rate (test of interaction: pMCMC = 0.006) compared to females (Fig. 2). We determine the weaning process complete when an infant δ^{15}N falls within the collagen δ^{15}N range observed for the adult females in the community. Even with inherent individual variation, and the statistical error, our results indicate that females complete the weaning process earlier than males, falling within the δ^{15}N range of adult females in the community up to 6 months earlier than male infants (Fig. 3A,B). However, given the uncertainty currently inherent in dentine growth rates in chimpanzees, assigning specific age at weaning differences between males and females is not yet possible.

DISCUSSION

Suckling in Taï chimpanzees

While chimpanzee behavioral studies from Mahale (Hiraiwa-Hasegawa, 1990) and Taï (Fränkl et al., unpublished data) have report sex differences in suckling length between males and females before 6 months of age, our isotope data from deciduous dentine of Taï chimpanzees provides no evidence of this sex difference and, in fact, shows no evidence of weaning prior to 2 years of age (Fig. 1). Slight variation in deciduous
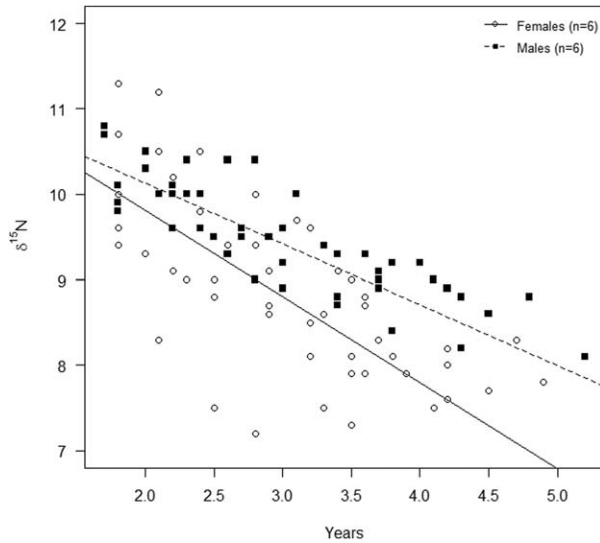
Fig. 2. Dentine $\delta^{15}N$ data as a function of age for all individuals, separated by sex: at the start of the weaning process (~2 years of age) males and females had similar dentine $\delta^{15}N$ values of 10–11‰; however as the weaning process progresses with advancing age differences in between males and females become apparent with male dentine $\delta^{15}N$ values decreasing at a significantly (pMCMC = 0.006) slower pace compared to females.

dentine $\delta^{15}N$ values between individuals may be explained by referring to previous isotope work at Taï by Fahy et al. (2013) who found significant individual variation in collagen $\delta^{15}N$ values of the adult females. Therefore variation observed in the deciduous dentine $\delta^{15}N$ values between individual infants may be due to general underlying maternal variation and not sex-related differences in infant milk intake. While no sex difference was evident in milk consumption prior to 2 years of age in Taï chimpanzee infants, our permanent molar dentine $\delta^{15}N$ data demonstrates that weaning at Taï is a slow, continuous progress commencing around 2 years of age with a steady decline in dentine $\delta^{15}N$ values evident in all individuals (Fig. 2).

Differences in maternal investment in chimpanzees

Differing fitness and reproductive success returns lead to different costs and benefits which primarily influence the amount of parental investment in one sex over the other (Clark, 1978; Silk, 1983; Clutton-Brock, 1991) meaning that mothers may need to alter lactation strategies across a series of pregnancies, depending on the sex of the infant (Lee, 1996). Clutton-Brock et al. (1986, 1988) found that high levels of maternal investment in male offspring led to improved survivorship, faster growth and high reproductive success in these males. The parental investment hypothesis (Trivers and Willard, 1973) predicts that investment should be higher in the offspring whose biological sex promises the most return under the prevailing conditions (Boesch and Boesch-Achermann, 2000). For example, Trivers and Willard (1973) stated that if a mother can increase her son's ability to obtain more mates, and therefore increase his reproductive output, she should invest more in sons. However, if a mother's investment cannot

increase her sons' success, she should focus her attention and investment in her daughters who have limited but more certain, reproductive outputs. Additionally, the social status of the mother has also been found to play a role in maternal investment, largely in conjunction with infant sex. Boesch (1997) found that IBI length at Taï was not dependent on maternal rank or infant sex when considered alone, although a combined effect was visible. In our study, a slight bias towards infants with high-ranking mothers in our sample meant that corroborating the findings of Boesch (1997) in terms of a combined effect of maternal rank and infant sex differences in weaning behavior was not possible. However, in contrast to Boesch (1997) we did find a significant effect of infant sex alone on weaning behavior between male and female Taï chimpanzees (Fig. 2). No isotopic study of weaning is currently available for another wild chimpanzee population; however a recent study from Mahale by Nakamura et al. (2013) found that orphaned chimpanzee sons die younger than expected even if they lose their mothers after weaning, suggesting that maternal investment in sons at Mahale is often vital to their survival.

Weaning in Taï chimpanzees

As previously stated, in chimpanzees, earlier weaning seen in females and later weaning in males suggests that mothers may invest more in nonemigrating males as this can influence their own future success and status in the community (Trivers, 1972; Trivers and Willard, 1973). At Taï both sexes appear to commence the weaning processes at a similar age, however our dentine $\delta^{15}N$ data indicates that the weaning processes is significantly faster in females, with females appearing to be fully weaned 6 months or longer compared to males (Fig. 3A,B). Research suggests that differences in growth rates between males and females may lead to corresponding differences in nitrogen isotope fractionation (Schoeller, 1999). However, while Gavan (1953) found that, in captivity, female chimpanzees grow faster than males in the late infant-early juvenile period, this acceleration is seemingly not apparent in the wild and many studies agree that skeletal growth in captive primates is faster than their wild counterparts (Matsuzawa et al., 1990; Kimura and Hamada, 1996). Conversely, skeletal sex differences generally do not manifest themselves until the age of sexual maturation, which is later than weaning age in most great apes (Nowak, 1999). Therefore, we feel it is unlikely that nitrogen isotope fractionation differences occurring from sex-specific growth rates account for the differences observed in our data, and a more parsimonious explanation is differences in maternal investment between male and female infants.

CONCLUSION

Accurately estimating weaning patterns in non-human primates allows for comparison between primate populations in terms of identifying differences in maternal investment and offspring dependence (Galdikas and Wood, 1990). It also enables a more accurate study of evolutionary life history patterns. Our dentine $\delta^{15}N$ isotope data suggests the weaning process at Taï commences at ~2 years, and, on average, females are weaned earlier than males who exhibit a slower progression and longer lactation times. Consequently, confirmation, using nitrogen isotopes, of differences in maternal investment between males and females in Taï chimpanzees,
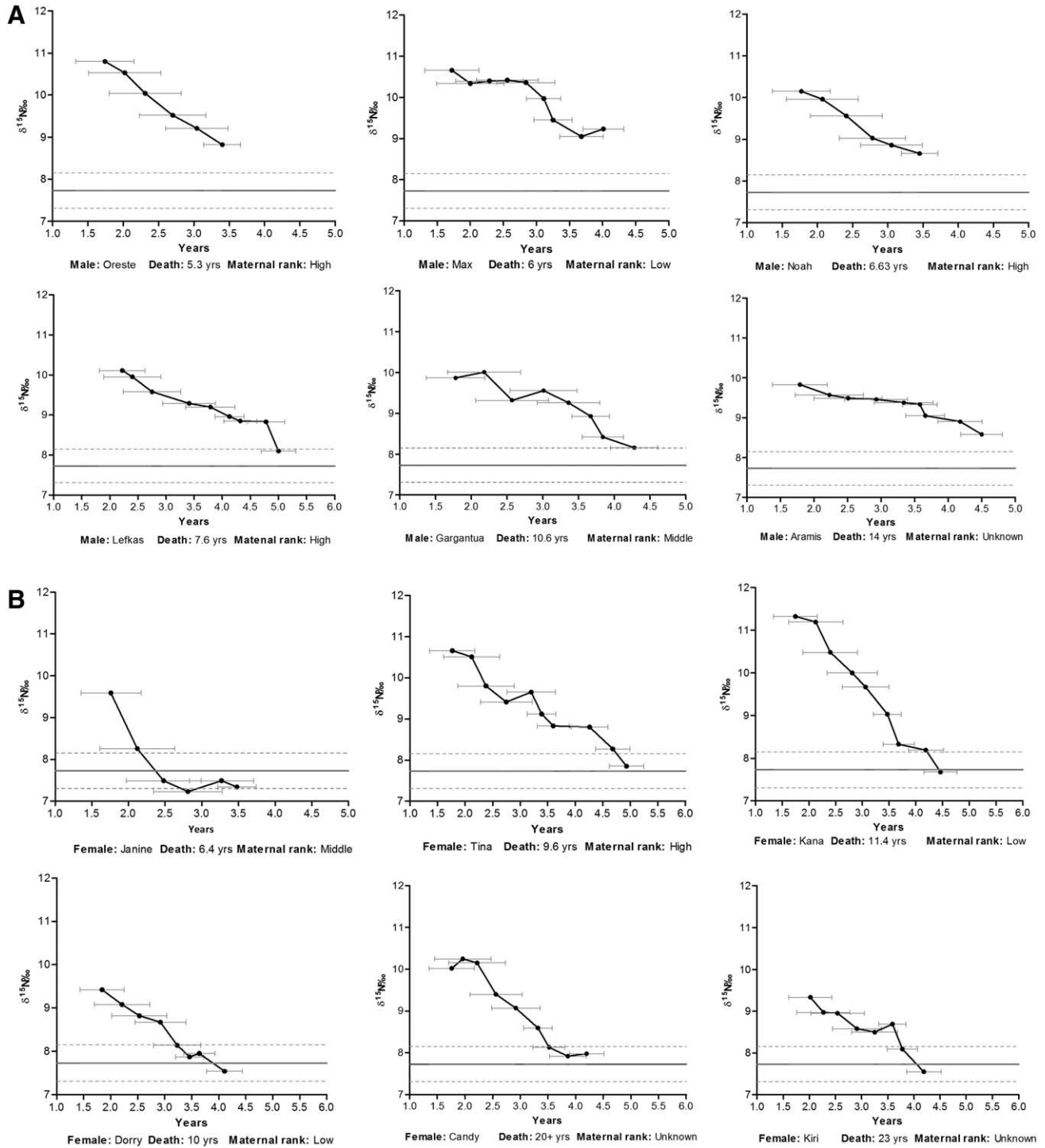
Fig. 3. A—Male Taï chimpanzee serial section dentine δ^{15}N data: the weaning process in males is significantly slower compared to their female counterparts with male Taï infants appearing to take much longer to reach the adult female community nitrogen level compared to females. Error bars are representative of standard deviation values of the initial chimpanzee M1 extension rate data extrapolated from Dean and Vesey (2008). *Oreste and Noah do not have sufficient sectional data to conclusively infer this and so this comparison relates only to the remaining four males sampled. **B**—Female Taï chimpanzee serial section dentine δ^{15}N data: females at Taï appear to have a more rapid weaning process reaching the adult female community average earlier than their male counterparts. Error bars are representative of standard deviation values of the initial chimpanzee M1 extension rate data extrapolated from Dean and Vesey (2008). In all cases there was a 1.5- to 2-mm portion extending from the last section to the root tip that was not sampled, when age error rates are included, this accounts for much of the differences in the age at final sample section and age at death/end of tooth root growth of the individuals.

demonstrates the viability of using stable isotope analysis to investigate weaning in nonhuman primate populations. Additionally, assuming that behaviors observed in the Taï chimpanzees are illustrative of the ancestral pattern, our results provide a platform to enable the trajectory of weaning in human evolution to be further elucidated. Further studies utilizing noninvasive samples such as hair keratin would enable this technique to be employed in the investigation of weaning patterns in both habituated and unhabituated nonhuman primate populations, and enable a more complete picture of the evolutionary progression of weaning to be made.

ACKNOWLEDGMENTS

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