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Title

Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania:
implications for nutritional independence long before cessation of nipple contact

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Abstract

Objectives: Weaning of chimpanzees is considered to occur at 4–5-years-old with complete cessation of nipple contact and timing of reconception calculated by inter-birth interval minus gestation length. This is also the basis of “early weaning” in humans (i.e., approximately 2.5-years-old). However, recent studies of the survival of orphans and the first molar (M1) eruption in wild chimpanzees have predicted that infants move towards nutritional independence at 3-years-old. Therefore, this study aimed to investigate ontogeny of feeding behavior at around 3-years-old in wild infant chimpanzees.

Materials and Methods: I studied 19 infants aged 1–60 months in the M group in Mahale Mountains National Park, Tanzania. The total observation time was 518 hours, 25 minutes.

Results: At around 3-years-old, infant chimpanzees spent more total feeding time, and time feeding on leaves, and food physically difficult to process without food transfer from other individuals. These results suggest that infant chimpanzees significantly reduced their dependence on milk for nutrition at around 3-years-old, that is, before cessation of nipple contact.

Discussion: This study suggests that M1 eruption in wild Eastern Chimpanzees is an index of the period when infants move towards nutritional independence with a key dietary transition. This is the first study to provide behavioral evidence of the large temporal gap between nutritional independence of infants and reconception of mothers in great apes, and clarify the unique feature of human life history whereby mothers can reconceive before an infant reaches nutritional independence.
Introduction

Recent studies have attempted to reveal the unique features of human life history by comparing life history parameters, such as lifetime reproductive success, inter-birth interval, and weaning age, between primate species (Bogin, 1999; Duda and Zrzavý, 2013; Meehan and Crittenden, 2016). Researchers propose that one of the most important features of human life history is early weaning (Humphrey, 2010), supported by prepared complementary foods by the mother and allo-mothers to meet the nutritional requirements of infants (Humphrey, 2010; van Noordwijk et al., 2013a). Sellen (2001) suggested a human weaning age of approximately 2.5-years-old (ranging from 0.5 to 8 years), based on data from questionnaires about cessation of breastfeeding in 113 modern nonindustrial populations. The typical weaning age of archaeological populations estimated by recent studies using stable isotopes was approximately 2.5–3-years-old, indicating it is similar to that of modern nonindustrial populations, even though there are large variations (Tsutaya and Yoneda 2013; Tsutaya et al. 2016).

In addition, research on the distribution of barium in teeth indicated that the weaning age of Neanderthals was 1.2-years-old (Austin et al., 2013).

Conversely, the weaning age of wild non-human primates is generally estimated by complete cessation of nipple contact as a behavioral index of nursing (Machanda et al., 2015). Chimpanzees (Pan troglodytes), the species genetically closest to humans, have been observed to continue nipple contact until 4–5-years-old (e.g., Goodall, 1986). This period matches the timing of conception of the next offspring, which is calculated using the birth date of the next offspring minus gestation length (Emery Thompson et al., 2007; Emery Thompson, 2013; Lee et al., 1991). Therefore, demographic studies of chimpanzees usually assume that the age at which
infants are weaned is 4–5-years-old (Goodall, 1986; Hiraiwa-Hasegawa et al., 1984; Nishida et al., 1990).

Compared to chimpanzees (4–5-years-old), earlier weaning in humans (2.5–3-years-old) is related to other features of human life history, such as a shorter inter-birth interval and higher lifetime reproductive success (Humphrey, 2010).

However, it should be pointed out that weaning is not a simple event, but is a process that begins with the onset of solid food intake (Humphrey, 2010; Langer 2008; Lee, 1996; van Noordwijk et al., 2013a). The end of the weaning process of infants is defined as the period when infants are independent of maternal milk for nutrition (Lee, 1996). Consequently, anthropological studies have investigated the weaning age based on the termination of maternal milk provisioning (Sellen, 2007). Yet, many behavioral studies of nonhuman primates, especially those of wild populations, regard nipple contact as a good measure of actual nursing because this behavior is easy to observe, even in wild (e.g., Tarnaud, 2004). However, it is difficult to identify the end of weaning based on the complete cessation of nipple contacts for two reasons. First, some infants, including chimpanzees, suckle without receiving milk (Bădescu et al., 2016; Nishida, 1994; Tanaka, 1992). Bădescu et al. (2016) confirmed the occurrence of suckling without milk transfer (i.e. comfort nursing) by analyzing the stable isotopes in the feces of wild chimpanzees. Second, nursing might occur at night, when direct observations are not usually conducted. Using fecal stable isotopes, Reitsema (2012) suggested that Francois’ langur (Trachypithecus francoisi) nurses at night. Therefore, complete cessation of nipple contact may not be a suitable index of the period when infants become nutritionally independent of maternal milk.

An alternative index of nutritional independence in wild populations is the earliest age at which orphans with
adoptive mothers can survive without nursing. Boesch et al. (2010) reported that the earliest age of orphan chimpanzees adopted by a non-mother without nursing and surviving for more than two years in Taï, Côte d'Ivoire, was 30-months-old. In Mahale, two orphans of 37-months-old survived for more than two years without nursing, but those less than 29-months-old did not survive (Nakamura and Hosaka, 2015; Mahale Mountains Chimpanzee Research Project, unpublished data). In addition, orphans brought to sanctuaries before 2–3 years of age rarely survive (Wobber and Hare, 2011). These studies suggest that chimpanzees significantly reduce their dependence on milk for nutrition at around 3-years-old. From here on, the point at which infants considerably reduce dependence on maternal milk for nutrition is termed “nutritional independence”, based on Borries et al. (2014).

The first molar (M1) eruption coincides with the timing of weaning in many primates and, therefore, considered a “morphological landmark of independence for primates” (Smith, 1992). However, discordance between M1 eruption and weaning age is observed among the great apes (Robson and Wood, 2008), although “weaning age” is determined in this case by cessation of nipple contact, which as aforementioned may not be a suitable index. Recent studies revealed that M1 eruption in wild chimpanzees in Kanyawara, Uganda, occurs at approximately 3-years-old (30–40-months-old) (Machanda et al., 2015; Smith et al., 2013), which is similar to the earliest age of survival potential of adopted orphans (Smith et al., 2013).

Stable nitrogen isotope analysis of dentine serial sections of wild chimpanzees suggested that maternal milk transfer decreases gradually after 1–2-years-old of age (Bădescu et al., 2016; Fahy et al., 2013). However, another study suggested that maternal lactation effort remains stable throughout infancy, due to their multi-year
lactation capacity (van Noordwijk et al., 2013a). In either case, the weight and height of infants continues to increase (Hamada and Udono, 2002), requiring supplementation with food, other than milk, to meet their nutritional needs (Hinde and Milligan, 2011). As aforementioned, recent studies on orphans and M1 eruption suggest that infant chimpanzees at 3-years-old considerably reduced dependence on maternal milk earlier than the existing weaning age. If this is indeed the case, then important changes in feeding behavior of infants before and after age 3 would be expected. In non-human primates, infants move towards nutritional independence by selecting suitable solid food from a variety of options in their environment (Galef, 2009). However, before achieving nutritional independence, infants encounter several aspects of difficulty in feeding due to immaturity (Altmann, 1980). For example, infants are unable to digest food containing large quantities of fiber and secondary compounds, especially leaves, due to the immaturity of their digestive organs and small body mass (Agetsuma, 2001; Hiraiwa-Hasegawa, 1990a; Nowell and Fletcher, 2008). Since leaves are important protein sources for chimpanzees (Nishida, 2012; Takemoto, 2003), and protein in milk is necessary for development of body mass in apes (Hinde and Milligan, 2011), infants are expected to become able to feed on and digest leaves at the point when infants move towards nutritional independence. Additionally, infants cannot process and eat food that is physically difficult to process (e.g., fruits covered with a hard shell), as they lack the processing skills and physical strength (Nishida and Turner, 1996; Taniguchi, 2015). Although human infants confront similar challenges, they become nutritionally independent earlier, due to the easily digestible (and nutritionally rich) foods provided by caregivers (i.e. complementary foods) (Sellen, 2007). Infant chimpanzees can receive physically difficult food to process from other individuals; however, these items are generally less nutritionally
valuable as they are small and/or leftovers (Hiraiwa-Hasegawa, 1990c; Nishida and Turner, 1996; Silk, 1978).

Therefore, it is considered important for infant chimpanzees to be able to process and eat such food without food transfer from other individuals.

This study investigated the ontogeny of feeding behavior in wild infant chimpanzees to examine whether nutritional independence is associated with changes in infant feeding behavior. Three predictions were tested:

1. Infants spend more time feeding at around 3-years-old, to accommodate an increased need for nutrition;
2. Infants spend more time feeding on leaves at around 3-years-old, to meet the increased need for protein;
3. Infants spend more time feeding on food physically difficult to process without food transfer from other individuals, as they become able to process physically difficult food by themselves to receive adequate nourishment. This study also investigated the ontogeny of nipple contact, which is the existing index of the weaning period, to validate the consistency of weaning age with previous studies.

**Materials and Methods**

The study periods were from January to September, 2011, from October 2012 to July 2013, and from June to August, 2015. The subjects were Eastern Chimpanzees (*Pan troglodytes schweinfurthii*) of the M group in Mahale Mountains National Park in Tanzania (6°15′ S, 29°55′ S) (Nakamura and Itoh, 2015). Individuals of the M group have been studied since 1965 and individually identified since 1980 (Hiraiwa-Hasegawa et al., 1984).

The core area of chimpanzee habitat is the west side of Mahale Mountains between 780 and 1300 m a.s.l (Nakamura et al., 2013), consisting of mosaic patches of *Erythrophleum* forest and *Pycnanthus-Xylopia* forest,
colonizing forest dominated by species such as *Senna spectabilis* and *Croton sylvaticus*, and woodland comprising *Combretum* spp., Miombo (*Brachystegia bussei*) woodland, and swamp (Itoh and Nakamura, 2015b). In general, the dry season begins in early October and the wet season in mid-May (Itoh, 2015).

Chimpanzees generally travel in fission-fusion grouping patterns to search for several species of fruits that vary seasonally (Itoh and Nakamura, 2015a; Norikoshi, 2002).

The permission to study wild chimpanzees in Mahale Mountains National Park was granted by the relevant governing bodies in Tanzania: the Tanzanian Commission for Science and Technology, the Tanzanian Wildlife Research Institute, and Tanzania National Parks (permit number 2010-215-NA-2009-26, 2011-166-ER-2006-26, 2012-409-ER-2009-26, and 2015-165-ER-2009-26).

I observed 19 infants aged 1–60 months using the focal animal sampling method (Altmann, 1974). I followed the target as far as I could, and recorded movements of infant mouths, including lip, mouth, bite, lick, and chew by continuous recording. I also recorded the target of the movement, and the start and end times. For infant mouth movements, I defined licking and/or chewing as feeding to exclude play feeding (Watts, 1985), which is not nutritionally valuable. End time of feeding was determined as the end time of licking and/or chewing. If infants started to play or travel continuously, end time was determined as the start of play or travel. I determined that feeding time continued when infants performed some mouth movements on the same target again within 30 seconds even though I was unable to observe mouth movements temporarily within 30 seconds. When the target was a plant, I recorded the plant part that was targeted, such as fruit, leaf, petiole, flower, seed, resin, pith, wood, or bark.
Nipple contact time was also recorded. If an infant transitioned from nipple contact to ventro-ventral movement with the mother while still suckling, I included the time of ventro-ventral movement as additional nipple contact time. In addition, when an infant was in ventral contact with the mother and I could not observe the mouth movements, if I was able to confirm nipple contact later (and the infant remained in ventral contact), I included the period when the infant remain in ventral contact with the mother as additional nipple contact time.

Infant chimpanzees always travel with the mother, rarely venturing far alone (Hayaki, 1988). Therefore, even if a food item is highly available in the environment, infants have little opportunity to eat it unless the mother visits the food patch. Therefore, maternal feeding time might reflect the availability of a food item for infants. I recorded the activity of the mother, including feeding and traveling by instantaneous sampling at 5-min intervals (Altmann, 1974). When the mother fed on plants, I recorded the plant parts targeted as above.

Data analysis

One severely disabled infant was excluded from the analysis (see Matsumoto et al. (2016) for details). Total observation time was 518 h, 25 min. I excluded observation time when I could not observe the mouth movements of infants. Even though the mouth movements of infants could not be observed, I include the time when there was no objects around infants’ head and infants did not have or mouth anything before, as “not feeding” time. Therefore, the total analysis time was 400 h, 45 min. I divided analysis time by individuals and by days. For example, data from different individuals on the same day were considered as independent. A total of 121 data points was analyzed. I calculated the age of infants in months by subtracting the month of the study
from the month of first observation of the infant (see Table 1 for detailed information of subject individuals).

I determined the feeding time in which the food target was shared by other individuals and/or by food transfer as feeding time with food transfer after Nishida and Turner (1996). I classified the target of feeding as difficult food for infants to process using the list of difficult food and the definition given in Nishida and Turner (1996). I excluded ant-fishing from the analysis of food physically difficult to process as previous studies have already revealed that infants over 36-months-old start to ant-fish (Nishida and Hiraiwa, 1982; Nishie, 2011). I did not observe infants feeding on meat during the current study though previous study reported that infants spent 0.6 % of their feeding time on meat (Hiraiwa-Hasegawa, 1990a).

Continuous feeding time and nipple contact time were converted to scan points at 1-min intervals. Using maternal data of scan points at 5-min intervals, I calculated the indexes as follows: maternal feeding time ratio = no. of scan points for feeding/no. of total scan points; maternal traveling time ratio = no. of scan points for traveling/no. of total scan points; maternal leaf feeding time ratio = no. of scan points for feeding on leaves/no. of total scan points; maternal time ratio for feeding on food difficult to process = no. of scan points for feeding on food difficult for infants to process /no. of total scan points.

Statistical analysis

I used Generalized Additive Mixed Models (GAMMs) to examine the influence of developmental changes (age in months) on each feeding time and nipple contact time, as GAMMs fits smooth functions to non-linear
data and uses random effects for repeated measures on the same subject. GAMMs have been used in previous studies of ontogeny of behavior (e.g., chimpanzee development in Gombe; Lonsdorf et al., 2014). I used the gam4 package (Wood and Scheipl, 2015) in R 3.1.2 (R Core Team, 2015) and tested predictions by constructing GAMMs with a binomial error distribution and a logit link function. I used Akaike’s information criterion for model selection (Burnham and Anderson, 2002), and selected the model with the smallest AIC value and examined the model(s) that had a ΔAIC (AIC value difference from the best model) of <2 (Burnham and Anderson, 2004). I checked multi-collinearity between explanatory variables using the DAAG package (Maindonald et al., 2015). The variance inflation factors (VIF) were sufficiently low among variables of each model (VIF <2).

Response variables and explanatory variables for each model are detailed below. Maternal feeding time ratio (on all food items, leaves, and food physically difficult to process for infants) was included as an explanatory variable for the index of availability of food items to infants. In addition, maternal traveling time ratio was also added as an explanatory variable as the index of travel distance during the observation time.

(A) Nipple contact I used nipple contact time/total observation time of an infant as the response variable; age in months (fit smooth function), maternal feeding time ratio, and maternal traveling time ratio as the explanatory variables; and infant ID as random effects.

(B-1) Total feeding time I verified prediction (1), using feeding time/total observation time of an infant as the response variable; age in months (fit smooth function), maternal feeding time ratio, and maternal traveling time...
ratio as explanatory variables; and infant ID as random effects.

(B-2) Feeding time on leaves I verified prediction (2), using feeding time on leaves/total observation time of an infant as the response variable; age in months (fit smooth function), maternal leaf feeding time ratio, and maternal traveling time ratio as explanatory variables; and infant ID as random effects.

(B-3) Food transfer I verified prediction (3) using feeding time on food physically difficult to process with food transfer/total feeding time on food physically difficult to process as the response variable; age in months (fit smooth function), maternal time ratio for feeding on food physically difficult to process, and maternal traveling time ratio as the explanatory variables; and infant ID as random effects.

When the influence of age in months on each response variable changed significantly, I estimated age in months to determine and evaluate the developmental change points. The number and value of the change points was determined by assuming smoothing splines as a combination of linear expressions (Crawley, 2005). Estimated change points are shown in Figure 2. The actual change points cannot be directly determined as smoothing splines cannot be differentiated; therefore, I analyzed the actual change points using generalized linear mix models (GLMMs). I used age and “age - age at the estimated change point” as explanatory variables in each model. This meant that summing of linear expressions, which change the coefficient at the point of estimated change point, approximates the smoothing spline (Crawley, 2005). I detected the actual change point ±3 months of the estimated change point, which showed the smallest AIC using GLMMs with a binomial error distribution and a logit link function. When there were multiple estimated change points, I examined the combination of change points that produced the smallest AIC in each model. I used the glmmML package
Results

Figure 1 [A] shows the ontogeny of nipple contact time. In the best model, age in months significantly affected nipple contact time ratio (P < 0.001). The effect of maternal feeding time ratio was negative (P < 0.01) and maternal traveling time ratio was non-significant (P > 0.1) (see Table 2 for details).

Table 2 here.

Figure 1 here.

Figure 2 [A] shows smoothing splines of age in months and the estimated change points in nipple contact time. An actual change point in nipple contact was detected at 48-months-old in the GLMMs analysis. Nipple contact time decreased gradually before 48-months-old, and started rapidly decreasing after 48 months. This trend matched well with the weaning age using the conventional definition (cessation of nipple contact). An obvious developmental change in nipple contact time, especially around 36-months-old, was not detected.

Figure 2 here.

Figure 1 [B-1] shows the ontogeny of total feeding time. In the best model, age in months significantly affected feeding time ratio (P < 0.001). The effect of maternal feeding and traveling time ratio was positive and negative, respectively (both P < 0.01) (see Table 2 for details). Change points in feeding times were detected at 10, 38, and 44-months-old (Fig. 2 [B-1]). Feeding time increased gradually before 3-years-old and increased more rapidly after 3-years-old.
Figure 1 [B-2] shows the ontogeny of feeding time on leaves. In the best model, age in months significantly affected feeding time ratio ($P < 0.001$). The effect of maternal leaf feeding and traveling time ratio was positive and negative, respectively (both $P < 0.01$) (see Table 2 for details). Change points in feeding times on leaves were detected at 10, 29, and 36-months-old (Fig. 2 [B-2]). Infants between 29 and 36-months-old significantly increased feeding time on leaves.

Figure 1 [B-3] shows the ontogeny of feeding time on food physically difficult to process with food transfer in total feeding time on food physically difficult to process (food transfer ratio). In the best model, age in months significantly affected food transfer ratio ($P < 0.001$). The effect of maternal time ratio for feeding on difficult food to process was positive ($P < 0.01$) but maternal traveling time ratio was non-significant ($P > 0.5$) (see Table 2 for details). Change points in food transfer ratio were detected at 11 and 30-months-old (Fig. 2 [B-3]). Infants over 30-months-old started to decrease food transfer ratio. Infants around 3-years-old showed a significant decrease in food transfer ratio.

Discussion

The results supported the predictions (1), (2), and (3), and were consistent with the results of previous studies that conclude a weaning age at 4–5-years-old using nipple contact as an index (Hiraiwa-Hasegawa, 1990b; Matsumoto and Hayaki, 2015). However, major changes in feeding behavior at around 3-years-old confirmed that infant chimpanzees significantly moved towards nutritional independence earlier than the “weaning age” determined by the current index. Therefore, this study suggested that nutritional independence (i.e.,
physiological weaning), when infants significantly reduce their dependence on maternal milk for nutrition, occurs at 3-years-old, whereas nipple contact ceases at 4–5-years-old. This temporal gap between nutritional independence and weaning age based on the cessation of nipple contact was also detected by a staple isotopic analysis of chimpanzee feces in Ngogo, Uganda. However, age differed among groups (i.e., nutritional independence and weaning age were at 4-years-old and 6 years old, respectively, in Ngogo) (Bădescu et al., 2016).

A change point at 38-months-old was observed in ontogeny of feeding time. The smoothing spline of age in months showed that feeding time increased gradually before 38-months-old and more rapidly after 38-months-old. In other words, developmental changes in feeding time between the other two change points, i.e., 1–4-years-old, did not increase linearly. This developmental change in feeding time at around 3-years-old was seen in previous studies of development of chimpanzees at other field sites, such as Kibale (Smith et al., 2013) and Gombe, Tanzania (Lonsdorf et al., 2014). Most infants over 36-months-old were able to ant-fish (Nishida and Hiraiwa, 1982; Nishie, 2011). This shift would reflect the developmental changes in total feeding time at around 3-years-old. Although infants younger than 29-months-old spent little time feeding on leaves, those aged 29–36 months drastically increased their feeding time on leaves. Maturation of digestive organs and increasing body mass may enable infants to eat more leaves, which contain much fiber and secondary compounds (Agetsuma, 2001; Nowell and Fletcher, 2008). Hiriwa-Hasegawa (1990a) showed that infant chimpanzees spend more time than adults feeding on young leaves that contain relatively lower fiber and secondary compounds. However, changes
in the types of leaves targeted by infants were not investigated here, as it was not possible to discriminate leaf type. This study showed that drastic changes in feeding time on leaves between 29- and 36-months-old occurred just before the period when infants are assumed to move towards nutritional independence. Leaves provide a protein-rich diet (Nishida, 2012), and infant chimpanzees could compensate for the need of protein and be nutritionally independent after 36-months-old.

Infant chimpanzees older than 30-months tended to spend more time feeding on food difficult to process without food transfer; however, this time drastically decreased by the age of 36 months. Previous studies suggested that food gained by food transfer has low nutritional value (Hiraiwa-Hasegawa, 1990c; Nishida and Turner, 1996; Silk, 1978). Therefore, it is possible that infants older than 30-months-old can eat food physically difficult to process without food transfer as part of the move towards nutritional independence. In particular, fruits of *Saba comorensis*, which are a “top-ranking food item” that chimpanzees of the M group spend about 20% of their annual feeding time (Itoh, 2004), has a hard shell and is classified as “difficult food to process” (Nishida and Turner, 1996). These fruits are highly available from August to January (Itoh and Muramatsu, 2015), and although this period is limited, it is important for infants to be able to eat *S. comorensis* fruits by themselves to achieve nutritional independence. The observation that infant chimpanzees can process *S. comorensis* fruits well after 3-years-old concurs with the finding of a previous study on manual skills for processing fruits of *S. comorensis* (Corp and Byrne, 2002). In addition to this fruit, Nishida (1991) classified other “Major Food” and “Important Food” of chimpanzees of the M group. In this list, the piths of many species of terrestrial herbaceous vegetation (THV) (e.g., *Pennisetum purpureum*) are classified as food that is difficult
for infants to process (Nishida and Turner, 1996), but are available almost year-round (Itoh et al., 2015). Thus, the ability of infants to eat THV piths year-round might contribute to nutritional independence.

Change points between 10–12-months-old were observed in ontogeny of feeding time (Fig. 2 B-1), feeding time on leaves (Fig. 2 B-2), and feeding time on difficult food with food transfer (Fig. 2 B-3). This period concurred with the completion of the eruption of deciduous teeth (Nissen and Riesen, 1945). Infants spent up to 15% of their time on feeding on solid foods at this change point. The current study did not investigate the period when infants start to eat, because of a lack of data on infants under 5-months-old. However, a previous study on chimpanzees in Mahale suggested that 5-months-old infant chimpanzees begin to eat for a short period of time (Hiraiwa-Hasegawa, 1990a). The subsequent completion of the eruption of deciduous teeth might allow infants to eat for relatively longer amounts of time. A further change point at 44-months-old was found in developmental changes in total feeding time. This period matched the time at which M1 reached functional occlusion (Machanda et al., 2015). At this change point, total feeding time ratio reached a maximum and was almost the same as that of adults (40% of daily activity time) (Hiraiwa-Hasegawa, 1990a). This result concurs with the previous studies in other field sites, such as Kibale (Smith et al., 2013) and Gombe (Lonsdorf et al., 2014). Additionally, total feeding time appeared to decrease just before 60-months-old. This phenomenon might be caused by the shortening of food processing time. However, it was not possible to conclude whether feeding time decreased just before 60-months-old in the current study because the 95% confidence interval was relatively wide at this time point.

M1 eruption is considered an important indicator of the weaning period in many primates (Smith, 1992),
although not in apes (Robson and Wood, 2008). Smith et al. (2013) suggested that “M1 emergence in eastern chimpanzees may relate to a key dietary transition around age 3”. The detailed behavioral data in this study supported this suggestion. Therefore, M1 eruption in chimpanzees may be an index of the period when infants move towards nutritional independence via a dietary transition.

The period when mothers stop nutritional investment (nursing) to the current infant and begin to invest in the next infant (resume menstrual cycling and reconception) is a definition of the weaning age that assumes conflict between mother and infant (Trivers, 1974). The main index of the weaning age in this assumption can be calculated by subtracting gestational length from inter-birth interval (Lee et al., 1991). The weaning age of chimpanzees using this index gives the same age (4–5-years-old) as the conventional cessation of nipple contact, therefore, these two definitions and indexes have yet to be clearly distinguished from each other. However, Emery Thompson et al. (2012) pointed out that the majority of mothers reduce their energetic investment to the infant (including milk transfer, carrying on the infant, and so on) long before the resumption of menstrual cycling and conception of the next offspring. The current study supported the prediction that infants move towards nutritional independence at around 3-years-old. This period partially matches the period when mothers reduce energetic investment (Emery Thompson et al., 2012), and these results highlight the temporal gap between significant reduction in energetic investment to the infant and existing weaning age (4–5-years-old).

Bădescu et al. (2016) indicated this temporal gap between the nutritional independence of infants and the reconception of chimpanzee mothers in Ngogo using fecal stable isotopes. Future studies should investigate the actual amount of milk intake proportional to solid food intake by using stable isotopes at Mahale to reveal the
relationship with the behavioral change point suggested by the current study.

This temporal gap between nutritional independence of infants and reconception of mothers has been observed in other great apes. For example, orangutans have the longest inter-birth interval in primates, with a weaning age based on cessation of nipple contact at 6–7-years-old (Humphrey, 2010; van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2013b). However, Sumatran orangutans (Pongo abelii) showed drastic developmental changes in locomotive ability and started to feed separately from the mother at 3-years-old (van Noordwijk and van Schaik, 2005). In addition, Bornean orangutans (P. pygmaeus) at 4–5-years-old significantly reduced feeding time in the same patch as the mother. The ratio of food transfer during maternal feeding bouts on difficult food also decreased considerably during this period (Jaeggi et al., 2008). Therefore, this period was also regarded as weaning age (Jaeggi et al., 2010). In mountain gorillas (Gorilla beringei beringei), weaning age, assessed by the complete cessation of nipple contact, matches the timing of conception of the next offspring (3.4-years-old on average) (Stoinski et al., 2013). However, Watts (1985) reported that infants at around 2-years-old can eat plant foods similar to that of older group members and that infants by the end of their third year can eat all adult foods, including food difficult to process. These studies imply a temporal gap between nutritional independence and conception of the next offspring in apes, as suggested for chimpanzees in this study.

In other non-ape primates, Tanaka (1992) suggested that mothers of Japanese macaques (Macaca fuscata) reduce milk transfer at 6-months-old, and can resume menstrual cycling and reconceive at the same time when in good nutritional condition. Sixty-five percent of the multiparous females give birth at an interval of one year in a provisioned group (Koyama et al., 1992). Similarly, studies in patas monkeys (Erythrocebus patas)
suggested that infants may move towards nutritional independence at 7-months-old (Chism, 1986), and that twenty-five of 33 inter-birth intervals (approximately 75%) in wild are one-year long (Nakagawa et al., 2003).

Additionally, Borries et al. (2014) suggested that the earliest age at which orphans can survive without nursing (the timing of nutritional independence) in wild Phayre’s leaf monkeys (*Trachypithecus phayrei*) matches the timing of conception of the next offspring. Twenty-five of 35 timings of reconception (about 70%) were shorter than or consistent with the age of nutritional independence of infants (Borries et al., 2014). Furthermore, Altmann (1980) researched wild yellow baboons (*Papio cynocephalus*), and suggested that infants at 12-months-old were independent and perhaps could survive without the mother. This age matches the timing of resumption of menstrual cycling of mothers (mean: 12–12.5, n = 20, range: 6–16), who take about four months to conceive the next offspring (Altmann et al., 1977). Therefore, these studies of non-ape primates imply that there is no or a very small gap between nutritional independence and the timing of conception of the next offspring.

In chimpanzees in Mahale, the shortest inter-birth interval after surviving offspring (3.7 years; Emery Thompson, 2013) minus gestation length (approximately 0.6 years; Tutin and McGinnis, 1981) gives a shortest reconception period of about three years. However, this is very rare as the average inter-birth intervals following surviving male and female infants in Mahale are 6.19 years (n = 9, sd = 1.03) and 5.18 years (n = 14, sd = 0.65), respectively (Nakamura, 2015). Therefore, the large temporal gap between nutritional independence and conception of the next offspring, may be a unique feature of the life history of chimpanzees (and great apes in general). As aforementioned, this is rarely considered in chimpanzee studies because of the temporal accord
between cessation of nipple contact and the timing of conception of the next offspring. This study highlighted the large gap between nutritional independence and existing weaning age and clarified the unique feature of early weaning in humans (Humphrey, 2010). The results showed that infants significantly changed their feeding behavior at 3-years-old, long before cessation of nipple contact and the timing of conception of the next offspring. Furthermore, results supported the suggestion by Emery Thompson et al. (2012) that inter-birth interval in chimpanzees is much longer than in other primates as females need to sustain a positive energy balance and recover their physical condition after significant reduction of milk production, rather than the direct expense of milk production itself. Future behavioral studies should investigate the meaning of this gap from the standpoint of infants, which might continue receiving some investments from the mother other than maternal milk (e.g., sharing a bed, learning social behaviors, or sharing a food patch) (Matsumoto and Hayaki, 2015; Nakamura et al., 2014). In contrast to chimpanzees and other great apes, a unique feature of humans is that mothers may start to invest in the next offspring “before” nutritional independence of infants (Bogin, 1999). This study highlighted the importance of specially prepared complementary foods for human infants (van Noordwijk et al., 2013a) and/or provisioning and cooperative breeding by allomothers (Hrdy, 2016) for human mothers to conceive the next offspring much earlier than great apes do.

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### Table 1. Individuals in this study

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>No. of scan points</th>
<th>No. of observation days</th>
<th>Age in months</th>
<th>Sex</th>
<th>Mother</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asahi</td>
<td>AH</td>
<td>1115</td>
<td>7</td>
<td>14–47</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Ayu</td>
<td>AY</td>
<td>2446</td>
<td>11</td>
<td>9–37</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Cissy</td>
<td>CI</td>
<td>1985</td>
<td>9</td>
<td>36–58</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td></td>
<td>CY14</td>
<td>175</td>
<td>2</td>
<td>13</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Figaro</td>
<td>FG</td>
<td>2781</td>
<td>14</td>
<td>12–42</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Iris</td>
<td>IR</td>
<td>1174</td>
<td>7</td>
<td>18–42</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td></td>
<td>JJ13</td>
<td>257</td>
<td>1</td>
<td>23</td>
<td>♂️</td>
<td>Primipara</td>
</tr>
<tr>
<td>Omali</td>
<td>OL</td>
<td>1036</td>
<td>8</td>
<td>6–28</td>
<td>♂️</td>
<td>Primipara</td>
</tr>
<tr>
<td></td>
<td>PF14</td>
<td>304</td>
<td>2</td>
<td>14</td>
<td>♂️</td>
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<tr>
<td></td>
<td>QA13</td>
<td>710</td>
<td>3</td>
<td>29–31</td>
<td>♂️</td>
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<tr>
<td>Quilt</td>
<td>QL</td>
<td>266</td>
<td>1</td>
<td>50</td>
<td>♂️</td>
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<tr>
<td>Shinji</td>
<td>SJ</td>
<td>1518</td>
<td>8</td>
<td>13–43</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Teto</td>
<td>TO</td>
<td>2573</td>
<td>12</td>
<td>34–59</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td></td>
<td>TZ09²</td>
<td>2309</td>
<td>10</td>
<td>16–23</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
<tr>
<td>Upepo</td>
<td>UP</td>
<td>3193</td>
<td>16</td>
<td>9–37</td>
<td>♂️</td>
<td>Primipara</td>
</tr>
<tr>
<td>Xyla</td>
<td>XL</td>
<td>1555</td>
<td>7</td>
<td>1–32</td>
<td>♂️</td>
<td>Primipara</td>
</tr>
<tr>
<td>Zorufa</td>
<td>ZF</td>
<td>374</td>
<td>2</td>
<td>44–48</td>
<td>♂️</td>
<td>Multipara</td>
</tr>
</tbody>
</table>
Researchers at Mahale do not name infants under 3-years-old because of high infant mortality, therefore, I used the mothers’ abbreviation, plus the latter two digits of the birth years to label unnamed infants.

TZ09 died before 3-years-old.

For individuals with multiple datasets from different seasons (years), the age range of the individual is shown.
### Table 2. Parameter estimates, AIC, and ΔAIC values for models

<table>
<thead>
<tr>
<th>Order</th>
<th>AIC (ΔAIC)</th>
<th>P value</th>
<th>Parameter estimates</th>
<th>Parameter estimates</th>
<th>Parameter estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Age in months&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Intercept</td>
<td>Feeding time ratio of mother</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(A) Number of Nipple contact</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>774.2 (0.0)</td>
<td>&lt;0.001</td>
<td>-2.9±0.2</td>
<td>-0.9±0.3</td>
<td>-0.6±0.4</td>
</tr>
<tr>
<td>2</td>
<td>774.6 (0.4)</td>
<td>&lt;0.001</td>
<td>-3.0±0.2</td>
<td>-0.9±0.3</td>
<td>—</td>
</tr>
<tr>
<td>(B-1) Number of Feeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1128.1 (0.0)</td>
<td>&lt;0.001</td>
<td>-2.2±0.1</td>
<td>2.4±0.1</td>
<td>-0.4±0.2</td>
</tr>
<tr>
<td>2</td>
<td>1129.3 (1.2)</td>
<td>&lt;0.001</td>
<td>-2.3±0.1</td>
<td>2.4±0.1</td>
<td>—</td>
</tr>
<tr>
<td>(B-2) Number of Feeding on leaves</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>752.8 (0.0)</td>
<td>&lt;0.001</td>
<td>-4.2±0.2</td>
<td>9.9±0.8</td>
<td>-2.7±0.7</td>
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<tr>
<td>2</td>
<td>754.6 (1.8)</td>
<td>&lt;0.001</td>
<td>-2.3±0.1</td>
<td>2.4±0.1</td>
<td>—</td>
</tr>
<tr>
<td>(B-3) Number of food transfer in feeding on difficult food</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>983.6 (0.0)</td>
<td>&lt;0.001</td>
<td>-1.3±0.5</td>
<td>4.6±1.5</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>985.4 (1.8)</td>
<td>&lt;0.001</td>
<td>-1.4±0.5</td>
<td>4.6±1.5</td>
<td>0.1±1.1</td>
</tr>
</tbody>
</table>

2 The best model is in bold.

3 As ‘Age in months’ is smoothed for modeling, the coefficient could not be evaluated.
Figure 1
Figure 2

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