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The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*)

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Abstract

Objectives: Primates have an extended period of juvenility before adulthood. Although dietary complexity plays a prominent role in hypotheses regarding the evolution of extended juvenility, the development of feeding behavior is still poorly understood. Indeed, few studies have investigated the timing and nature of feeding transitions in apes, including chimpanzees. We describe general patterns of feeding development in wild chimpanzees and evaluate predictions of the needing-to-learn hypothesis.

Materials and Methods: We analyzed 4 years of behavioral data (2010–2013) from 26 immature chimpanzees and 31 adult chimpanzees of the Kanyawara community in Kibale National Park, Uganda. Specifically, we examined milestones of nutritional independence (first consumption of solid food and cessation of suckling) as well as developmental changes in feeding time, diet composition, diet breadth, and ingestion rates.

Results: Chimpanzees first fed on solid food at 5.1 months and, on average, suckled until 4.8 years. Daily feeding time of immature individuals reached adult levels between 4 and 6 years, while diet composition showed minor changes with age. By juvenility (5–10 years), individuals had a complete adult diet breadth. Ingestion rates for five ripe fruit species remained below adult levels until juvenility but continued to show absolute increases into adolescence.

Discussion: Chimpanzees acquired adult-like patterns on all feeding measures by infancy or juvenility. These data are inconsistent with the needing-to-learn hypothesis; moreover, where delays exist, alternatives hypotheses make similar predictions but implicate physical constraints rather than learning as causal factors. We outline predictions for how future studies might distinguish between hypotheses for the evolution of extended juvenility.

KEYWORDS

extended juvenility, needing-to-learn hypothesis, nutritional independence

1 | INTRODUCTION

Primates, including humans, are characterized by extended juvenile periods compared to mammals of similar body sizes (Kappeler & Pereira, 2003; Pereira & Fairbanks, 1993; van Schaik & Isler, 2012). The function of this extended developmental period is puzzling because it necessarily imposes fitness costs by delaying reproductive maturity. The needing-to-learn hypothesis (Ross & Jones, 1999) proposes that delayed maturation in primates provides individuals with

time to acquire the skills and knowledge that are necessary to exploit a complex diet, ultimately raising lifetime fitness. Across primate species, this hypothesis predicts a positive relationship between dietary complexity and the length of the juvenile period. Additionally, within a population, the needing-to-learn hypothesis predicts that immature individuals will exhibit reduced feeding competency compared to adults.

The needing-to-learn hypothesis attempts to explain delayed maturity in nonhuman primates, but it is most supported by studies of

human populations. In small-scale foraging communities, for example, humans do not become expert hunters until adulthood (Gurven, Kaplan, & Gutierrez, 2006; Walker, Hill, Kaplan, & McMillan, 2002). However, compared to most primates, the human dietary niche is extremely skill-intensive (reviewed in Kaplan, Hill, Lancaster, & Hurtado, 2000). Comparable information on the development of feeding behavior from nonhuman primate populations is therefore needed to evaluate whether the needing-to-learn hypothesis can explain delayed maturation across primates.

To date, most studies of primate feeding development have not assessed the full developmental sequence of feeding behavior, making it difficult to identify the extent to which age-related changes exist. Instead, research has primarily focused on how immature individuals acquire adult dietary patterns and foraging behaviors (e.g., Boinski et al., 2003; Lonsdorf, 2005; reviewed in Rapaport & Brown, 2008). Although this approach has emphasized the importance of social learning, we still lack data in many species on when feeding patterns emerge. Hiraiwa-Hasegawa (1990a) suggested that immature individuals must acquire adult feeding patterns by weaning in order to survive, and indeed most studies of primate feeding development have found that individuals exhibit adult-like diets and become proficient foragers by weaning or, at a minimum, long before adulthood (e.g., *Cebus capucinus*: MacKinnon, 2006; *Eulemur fulvus*: Tarnaud, 2004; *Gorilla beringei*: Watts, 1985; *Gorilla gorilla*: Nowell & Fletcher, 2008; *Pongo abelii*: van Adrichem et al., 2006; Schuppli et al., 2016; *Pongo pygmaeus*: Schuppli et al., 2016; *Saimiri oerstedii*: Boinski & Frigaszy, 1989; *Saimiri sciureus*: Stone, 2006).

In other primate species, however, immature individuals do not become competent foragers until later in development. For example, brown capuchin monkeys (*Sapajus apella*) use extractive foraging techniques to obtain larvae that are embedded in bamboo stalks. To successfully perform this behavior, individuals must learn to locate prey. Although individuals participate in this activity at low rates as infants, they do not become fully proficient at detecting prey until subadulthood, which is at ~6 years (Gunst, Boinski, & Fragaszy, 2010). Similarly, juvenile chacma baboons (*Papio ursinus*) are less efficient foragers than adults on difficult-to-extract resources (Johnson & Bock, 2004). The reduced efficiency of juveniles does not appear to be related to feeding competition or small body size, but rather in locating food, leading to a greater amount of time spent foraging. Together, these studies indicate that certain feeding behaviors are likely to exhibit pronounced changes during development. In particular, as individuals become older, we should observe increases in diet breadth, increases in foraging efficiency, and more complex foraging techniques.

Data on feeding development are comparatively lacking for great apes, which exhibit some of the slowest developmental trajectories of all nonhuman primates (van Schaik & Isler, 2012; Watts & Pusey, 1993) and are therefore of particular interest to models of prolonged immaturity. The Sumatran orangutan (*Pongo abelii*), which has the longest immature period among great apes, frequently forages on difficult-to-extract resources (Fox, van Schaik, Sitompul, & Wright, 2004; Meulman & van Schaik, 2013; Schuppli et al., 2016). By contrast, the western

lowland gorilla (*Gorilla gorilla*) and mountain gorilla (*Gorilla beringei*) exhibit a relatively quick pace of development and have a correspondingly simple diet that consists primarily of pith and leaves (Rogers et al., 2004; Rothman, Plumptre, Dierenfeld, & Pell, 2007). Chimpanzee patterns reside between those of orangutans and gorillas; they have slow life histories (Emery Thompson, 2013a,b), a large diet breadth (Goodall, 1986; Watts, Potts, Lwanga, & Mitani, 2012), and several complex foraging behaviors (hunting: Gilby et al., 2015; Pruett et al., 2015; Watts & Mitani, 2002; nut cracking: Boesch & Boesch-Achermann, 2000; Matsuzawa, 1994; termite fishing: Goodall, 1986; Lonsdorf, 2005).

Schuppli et al. (2016) recently examined the development of feeding behavior in wild Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus wurmbii*) and found limited support for the needing-to-learn hypothesis. Although ingestion rates were delayed for difficult-to-process dietary items, basic competence was achieved shortly after weaning and long before the age of first reproduction. Nonetheless, immature orangutans in the Sumatran population reached adult feeding rates 2–3 years later than Bornean orangutans, which is consistent with the greater dietary complexity and later weaning in the former (Schuppli et al., 2016). Given the overall late age at weaning among orangutans (van Adrichem et al., 2006; van Noordwijk et al., 2013; Wich et al., 2004), this study suggests that learning requirements may be partly responsible.

To understand the extent of age-related changes in feeding behaviors across great apes, more data are needed on other species. Previous studies have investigated aspects of immature feeding behavior in wild chimpanzees, including suckling and weaning (Clark, 1977; Hiraiwa-Hasegawa, 1990b; Lonsdorf et al., 2014; Machanda et al., 2015; Matsumoto, 2017; Smith et al., 2013), feeding time (Hiraiwa-Hasegawa, 1990a; Lonsdorf et al., 2014; Matsumoto, 2017; Smith et al., 2013), diet breadth (Hiraiwa-Hasegawa, 1990a), ingestion rates (Uehara, 1990; Wrangham, 1975), food sharing (Matsumoto, 2017; Nishida & Turner, 1996; Silk, 1978, 1979), and tool use (Boesch-Achermann & Boesch, 1993; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2005). By design, most of these studies focused on one or two feeding measures. Others contained preliminary descriptions, analyzing behavior over a short duration and/or lacking comparisons to adults. These factors constrain our ability to evaluate whether the chimpanzee diet is a selective pressure on the length of the immature period. These factors also preclude a more basic understanding of the development of chimpanzee feeding behavior.

The present study has two aims. First, we characterize the development of wild chimpanzee feeding behavior using a mix of longitudinal and cross-sectional behavioral data. Specifically, we describe feeding behavior across five dietary measures: (1) *Feeding independence*: When do infants start eating solid food, and when do they cease nipple contact? (2) *Feeding time*: How much time do immature versus adult chimpanzees spend feeding each day? (3) *Diet composition*: How is feeding time distributed across different food parts (e.g. ripe fruit vs. young leaves), and does this change with age? (4) *Diet breadth*: How many unique food items do immature and adult chimpanzees eat, and to what degree do their diets overlap? (5) *Foraging efficiency*: How do

ingestion rates change throughout development, and when do chimpanzees reach adult levels of efficiency? To date, this is the largest and most complete record of wild chimpanzee feeding development.

Our second aim is to use these data to evaluate predictions of the needing-to-learn hypothesis. If the extended period of immaturity in chimpanzees functions as a time to learn how to forage effectively and exploit a complex diet, then immature chimpanzees throughout all stages of development should have a smaller diet breadth and lower ingestion rates compared to adults. Although greater time spent feeding during immaturity is often associated with reduced feeding efficiency (Janson & van Schaik, 1993), this has not been documented previously in chimpanzees (Hiraiwa-Hasegawa, 1990a; Lonsdorf et al., 2014; Smith et al., 2013), which instead show steady increases throughout infancy. It is important to note that other hypotheses for extended periods of immaturity make similar predictions as the needing-to-learn hypothesis (e.g., brain malnutrition risk: Deaner, Barton, & van Schaik, 2003; ecological risk: Janson & van Schaik, 1993), and we examine these alternatives in greater depth in the discussion.

2 | METHODS

2.1 | Study site and subjects

We conducted this study using data from the Kanyawara chimpanzee community in Kibale National Park, Uganda (*Pan troglodytes schweinfurthii*). Since 1987, the Kanyawara chimpanzees have been observed continuously by field assistants employed by the Kibale Chimpanzee Project (Wrangham, Conklin-Brittain, Chapman, & Hunt, 1991; <http://kibalechimpanzees.wordpress.com>). Except where otherwise noted, behavioral data for the current study were collected between July 2010 and December 2013. During this period, there were a total of 31 adult individuals (13 males, 18 females) and 28 immature or nonadult individuals (15 males, 13 females). We defined age classes according to commonly used criteria (Boesch & Boesch-Achermann, 2000; Goodall, 1986). Individuals under 12 months were classified as *early infants*, subjects between 1 and 5 years were classified as *late infants* (where possible, we subdivided this period into 1-year age bins), and subjects between 5 and 10 years were classified as *juveniles*. For females, *adolescence* began at 10 years and continued until the first maximal sexual swelling (Watts & Pusey, 1993). At Kanyawara, the estimated age of first swelling is 12.6 years (range: 11.1–14.5). For males, for whom sexual maturity is more difficult to measure, *adolescence* also began at 10 years but continued until they were 15 years. (Goodall, 1986). For both sexes, all individuals who were older than these cut-offs were classified as *adults*. Because the current study took place over several years, some individuals were present in more than one age class (Table 1). The chronological ages of all immature subjects were determined from birth records accurate to the nearest month, whereas the ages of adult subjects were determined from either birth records or estimates when first identified.

We complied with all regulations regarding the ethical treatment of research subjects, and the Institutional Animal Care and Use

Committee of the University of New Mexico approved this research (Protocol #101117).

2.2 | Data collection

Since 2010, field assistants have conducted full-day focal follows on immature individuals, tracking individuals from the moment they leave their nest in the morning until they enter a new nest at the end of the day. When possible, field assistants followed every immature subject in the community at least once per month, choosing a new focal animal at the beginning of each day. If a new focal animal was not present, then the field assistants followed an individual that had not been recently followed. If an animal was lost during a follow, field assistants searched for them for 2 hr before beginning a new follow of a different subject. During each focal follow, one observer used focal sampling procedures (Altmann, 1974) and recorded behavior at 1-min intervals. When the focal individual was feeding (defined as solid food being swallowed), both the species and food part (e.g., ripe fruit, young leaves, and pith) were recorded. Simultaneously, a second observer recorded party composition every 15 min. To compare the behavior of immature and adult age classes, we also analyzed full-day focal follows on adults that have been collected by field assistants since 2009 in the same manner as described above. Field assistants are trained and average over 95% accuracy in interobserver reliability tests (Kibale Chimpanzee Project, unpublished data). All data are digitized and stored in a Microsoft Access relational database, which was used to extract data for the current study.

In addition to the behavioral data described above, we analyzed data from targeted observations of food ingestion rates. These data were collected in 1992–1993 as part of a study on dietary niche differentiation in primates (Conklin-Brittain, Wrangham, & Hunt, 1998; Wrangham, Conklin-Brittain, & Hunt, 1998). Observers recorded the number of food items ingested within a given time interval (max duration = 60 s). Some samples were shorter than 60 s because individuals went out of view; we only included ingestion rates that were based on at least 30 s of continuous observation and converted all samples to per minute rates. Although the complete dataset included ingestion rates on 63 plant species, we limited the dataset to items for which there were sufficient data to make comparisons across each age class. This resulted in a final dataset consisting of 321 feeding records from five commonly eaten ripe fruit species (*Ficus dawei*, *F. exasperata*, *F. natalensis*, *Mimusops bagshawei*, *Uvariopsis congensis*). Ingestion rates on each species were recorded over multiple months. During observation days, observers rotated through all individuals in the party, switching targets every 10 min. Although these data are comparatively old, these five fruits were consumed throughout the present study by all age classes. Moreover, these fruits are either figs (*Ficus* sp.), which are key fallback foods (Marshall et al., 2009; Wrangham et al., 1993), or are preferred foods in this community (*M. bagshawei* and *U. congensis*: Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996). Although chronological ages were not as well-known during this period of data collection, observers assigned individuals to general

TABLE 1 Focal follow data for immature individuals in this study

Chimp Identity	Sex	0–1 yrs	1–2 yrs	2–3 yrs	3–4 yrs	4–5 yrs	Juvenile (5–10 yrs)	Adolescent (10+ yrs)
AN	F		3	12	8	9		
AT	M							32
AZ	M						43	
BO	M						19	1
BT	M	3	6	2	4			
EU	F						19	
HT	M			2				
LE	F	12	18	4				
LL	F	2	1					
MM	F	3	6					
MN	M		1	17	6	18		
MX	M							12
NP	F							25
OB	M	6	6					
OG	M						8	25
OL	F		3	12	10	7		
OM	F						42	
QV	M			12	16	11	6	
RB	F	5						
TD	M		1					
TR	F	9	16	2				
TS	F						55	
TT	M						3	44
UK	F	2	1	5				
UN	M						34	
WC	M			15	16	15	10	
WE	F				10	13	16	
WZ	M		6					
Total Follows		42	68	83	70	73	255	139
Total Hours		332	510	654	577	620	2187	1240
Total Subjects		8	12	10	7	6	11	6

The numbers in each cell indicate the number of focal follows for each subject in each age bin.

age classes (infants, juveniles, adolescents, and adults), classifying them based on either known birth dates or body size. Individual identities, however, were not recorded.

2.3 | Data analysis

Some follows start late or end early and may not be representative of daily behavior; we therefore only analyzed focal follows that were at least 4 hr in duration (defined as in-view observation time: median

follow length = 9.1 hr, mean follow length = 8.8 hr). Between July 2010 and December 2013, there were a total of 1,654 focal follows that met this criterion (14,539 hr). Specifically, there were 730 focal follows of immature subjects (6,119 hr) and 924 focal follows of adult subjects (8,420 hr) (Table 1). Suckling behavior (i.e., nipple contact) was not recorded consistently until June 2011, so analyses involving this measure exclude all prior months. Daily feeding time showed decreases over the course of adulthood, so we limited this analysis to 559 focal

follows from prime-aged adults (<30 years). For analyses involving comparisons of ripe fruit to fibrous foods, the following food parts were included in the fibrous food category: young leaves, mature leaves, pith, bark, roots, wood, stems, and terrestrial herbaceous vegetation.

We used two milestones to describe the development of feeding independence (i.e., the process of becoming an independent forager): age at first solid food consumption and age at weaning (Sellen, 2007). For both milestones, we used operational definitions because this provided an objective way to make developmental comparisons (Lee, 1996; Smith et al., 2013). Age at first solid food was operationally defined as the first day that an individual swallowed solid food; individuals were only included if they had been observed to not feed during a focal follow in the prior 60 days. Weaning was operationally defined as the last day on which a subject was observed to suckle; individuals were only included if they were observed to not suckle during a focal follow in the subsequent 90 days. Furthermore, because these milestones are easily identified from focal follows, we expanded the sample to include data for additional subjects through May 2016 (five and two more, respectively, for first solid food and weaning).

2.4 | Statistical analyses

All analyses were performed in R 3.3.2 (R Core Team, 2016) using the 'lme4' package (version 1.1-12: Bates, Maecher, Bolker, & Walker, 2015) and 'multcomp' package (version 1.4-6: Hothorn, Bretz, & Westfall, 2008). We fit linear mixed models (LMM) to examine feeding time, diet composition, and diet breadth, and we fit a linear model to analyze data on ingestion rates. Details on each model are provided below. Age was the main predictor variable in all models. Late infants were subdivided into 1-year age bins, except in the models for daily diet breadth (one bin for late infants due to small sample size) and ingestion rates (one bin for all infants). Where applicable, we included "follow duration" as a continuous predictor to ensure that shorter follows, which can occur at any time during the day, were not biasing the results. Where appropriate, we included a random effect of calendar month to control for seasonal variation.

2.4.1 | Feeding time

The response variable was the percentage of observation time spent feeding on solid food; age and follow duration were included as predictor variables, and subject identity and month were included as random effects.

2.4.2 | Diet composition

The response variable was the percentage of feeding time allocated to each food part (three models total, one each for ripe fruit, young leaves, and pith); age and follow duration were included as predictor variables, and subject identity and month were included as random effects.

2.4.3 | Diet breadth

The response variable was the number of daily food items, with ripe fruit and fibrous foods coded as separate responses; age, maternal diet breadth, and food part were included as predictor variables in a three-way interaction; subject identity, maternal identity, and date were included as random effects. The random effect of date was included because each focal follow was represented twice in the dataset (once for ripe fruit items and once for fibrous food items), and the maternal diet breadth predictor matched the food part of the response variable. In addition to the model-based approach, we used paired Wilcoxon signed-rank tests to make more explicit comparisons between age classes.

2.4.4 | Ingestion rates

The response variable was the number of items ingested per minute of foraging; age and plant species were included as predictor variables. Because individual identity was not recorded, it could not be included as a random effect.

3 | RESULTS

3.1 | Feeding independence

We identified two markers of feeding independence: age at first solid food consumption and age at weaning. The earliest observation of solid food consumption was 5.1 months, but most individuals did not consume solid food until their eighth month (mean \pm s.e. = 7.9 ± 0.7 months, range = 5.1–11.1 months, $n = 9$). On average, chimpanzees suckled into their fifth year (mean \pm SE = 4.8 ± 0.7 years, range = 4.1–6.0 years, $n = 8$). The percentage of in-view observation time that individuals were observed to suckle increased with age before falling once individuals began to wean (Figure 1)

3.2 | Feeding time

We analyzed the amount of time that immature and adult individuals spent feeding on solid food as a percentage of total in-view observation time. We found steady increases in daily feeding time on solid food as individuals matured (Figure 2). Controlling for follow duration, we found a significant effect of age class (LMM, likelihood ratio test: $p < 0.0001$). Using Tukey contrasts, we found that feeding time reached adult levels around the transition from infancy to juvenility (4–5 years: $\beta = -6.22$, SE = 2.03, $z = -3.07$, $p = 0.05$; 5–6 years: $\beta = 0.82$, SE = 2.24, $z = 0.37$, $p = 1.0$). Individuals between 3 and 4 years remained significantly below adult feeding levels ($\beta = -9.43$, SE = 2.02, $z = -4.66$, $p < 0.001$).

3.3 | Diet composition

We analyzed the percentage of feeding time that immature and adult individuals spent feeding on different food parts. Specifically, using three separate models, we analyzed the proportion of feeding time that individuals ate (i) ripe fruit, (ii) young leaves, and (iii) pith, which were the three most commonly eaten food parts (overall adult diet

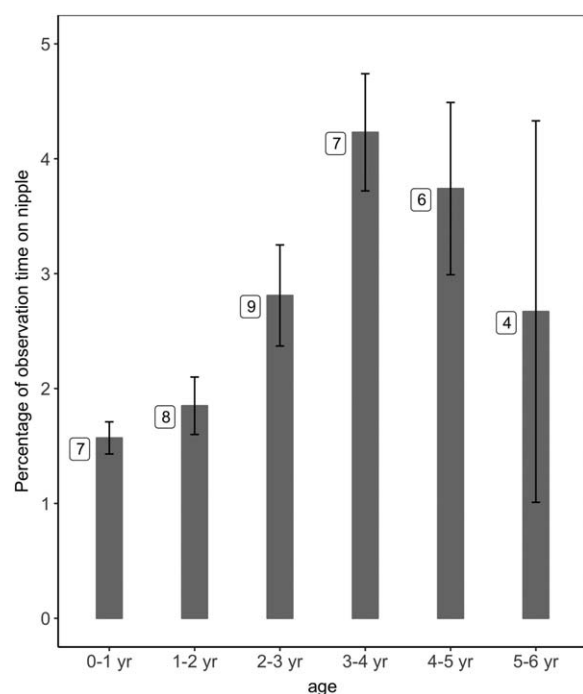


FIGURE 1 Mean \pm SE percentage of observation time that immature chimpanzees spent suckling. The numbers to the left of each bar indicate the number of subjects in the sample

composition: ripe fruit = 65.3%, young leaves = 18.7%, pith = 9.9%). Controlling for follow duration, age class had a significant effect only on the proportion of time spent eating young leaves (LMMs, likelihood ratio tests: (i) $p = 0.24$, (ii) $p = 0.04$, (iii) $p = 0.24$). Although none of the Tukey contrasts for this model were significant, the result is consistent with the raw data presented in Figure 3, which suggest that early infants may substitute young leaves in place of pith in their diet.

3.4 | Diet breadth

Across the main study period, adults fed on 179 food items (including 111 plant species), which were defined as unique species by food part combinations (Hiraiwa-Hasegawa, 1990a). In other words, feeding on both ripe fruit and young leaves of a single species counted as two food items. Early infants fed on 14 items, which were all part of the adult diet. Late infants, juveniles, and adolescents fed on 132, 147, and 128 items, respectively. Of these food items, 13, 20, and 14 were not part of the adult diet, respectively. Within this subset, pith and other fibrous foods were disproportionately represented; in most cases, however, these foods were eaten just once or twice (mean \pm SD = 1.42 ± 0.84 , max = 4) and often by just one or two subjects.

The differences in total diet breadth could be driven by variation in the number of focal follows and subjects across age classes; therefore, we also examined daily diet breadth. First, we used paired Wilcoxon signed-rank tests to explicitly compare the diet breadth of mothers and their offspring on days when both were observed in the same party for an entire day ($n = 95$ total). The diet breadth of mothers was significantly greater than that of their late infants (mean: 6.7 to 5.2 items; $W = 139$, $p < 0.0001$, $n = 52$ days), significantly less than that of their juvenile offspring (mean: 6.4 to 7.5 items; $W = 399$, $p = 0.01$, $n = 37$ days), and not significantly different from the diet breadth of their adolescent offspring (mean: 6.8–7.5 items; $W = 13$, $p = 0.67$, $n = 6$ days). Early infants did not feed on solid food on days when we also had a focal follow of the mother ($n = 3$ days). To determine whether specific food types were driving these effects, we analyzed the data separately for ripe fruit and fibrous foods. No differences were found in the number of ripe fruit items eaten by mothers and their offspring in any age class, except for juveniles, which ate more ripe fruits than their mothers (mean: 2.8–2.3; $W = 172$, $p = 0.01$, $n = 37$ days). All ripe fruit items eaten by juveniles but not mothers were commonly eaten by adults on

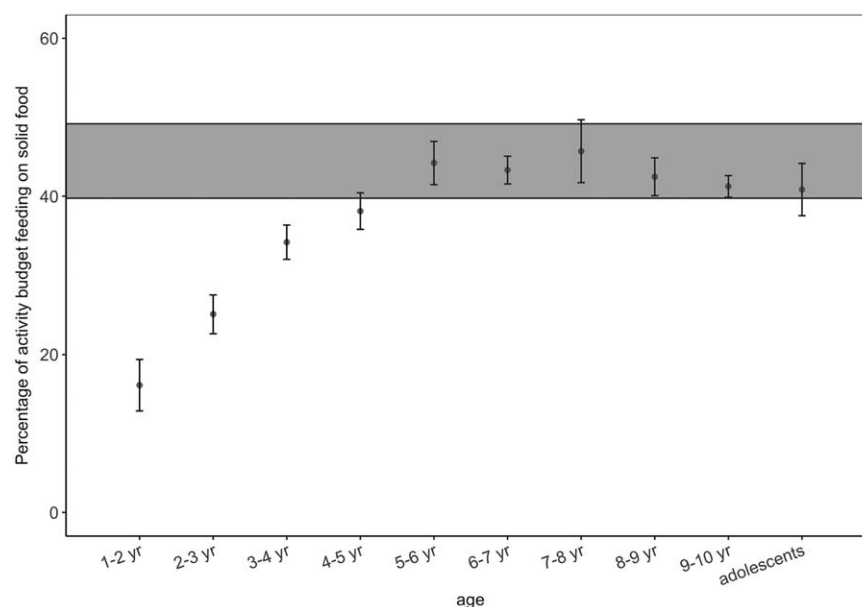


FIGURE 2 Mean \pm SE percentage of observation time that immature chimpanzees spent feeding on solid food. The gray rectangle represents the mean \pm SE of prime-aged adults (<30 years)

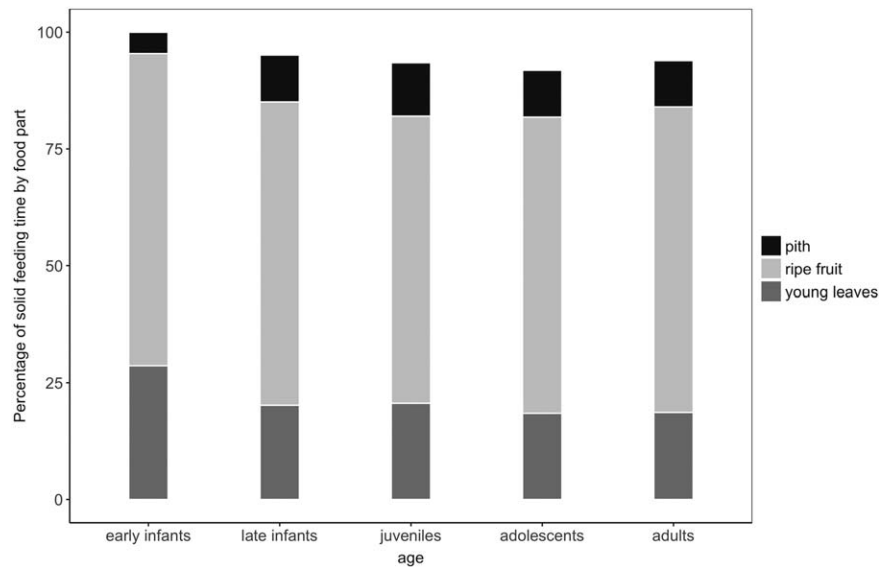


FIGURE 3 Mean percentage of feeding time spent eating ripe fruit, young leaves, and pith, the three most commonly eaten food parts in this population

other days. By contrast, the number of fibrous food items eaten was only significantly higher among mothers compared to their late infants (mean: 3.1–2.1; $W = 911.5$, $p < 0.0001$, $n = 52$ days).

To control for repeated observations of individuals, we also fit a linear mixed model to these data. On the basis of the above results, which indicated that immature individuals had as large of a diet as their mothers by juvenility, we lumped juveniles and adolescents together to evaluate whether late infants exhibited a smaller diet breadth. As

shown in the plot of the three-way interaction (Figure 4), maternal diet breadth was a good predictor of ripe fruit diet breadth across age classes, indicating similar numbers of ripe fruit items in their diets. However, maternal diet breadth was not as good of a predictor of late infant diet breadth for fibrous foods as it was for juveniles and adolescents, indicating that mothers and their infants fed on different numbers of fibrous foods. This result matches the paired Wilcoxon signed-rank tests.

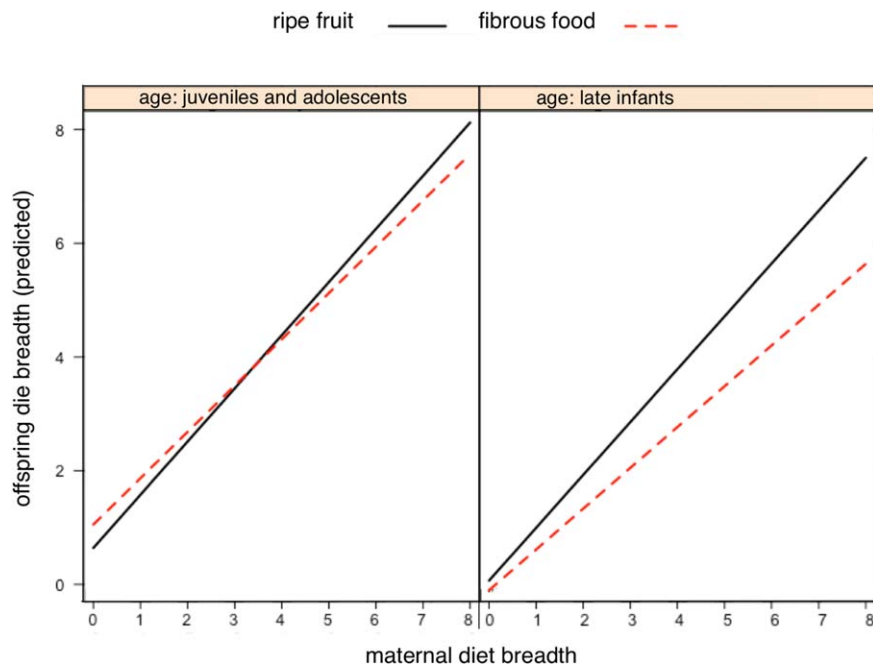


FIGURE 4 The effect of the three-way interaction between age class, maternal daily diet breadth, and food part on offspring daily diet breadth. Diet breadth represents the number of unique species within each food part (ripe fruit vs. fibrous food). The x- and y-axes indicate the daily diet breadth of the mother and the predicted diet breadth of the offspring, based on the linear mixed model. For late infants only, maternal diet breadth was not as good of a predictor of the number of fibrous food items in the offspring's diet as it was for ripe fruit items

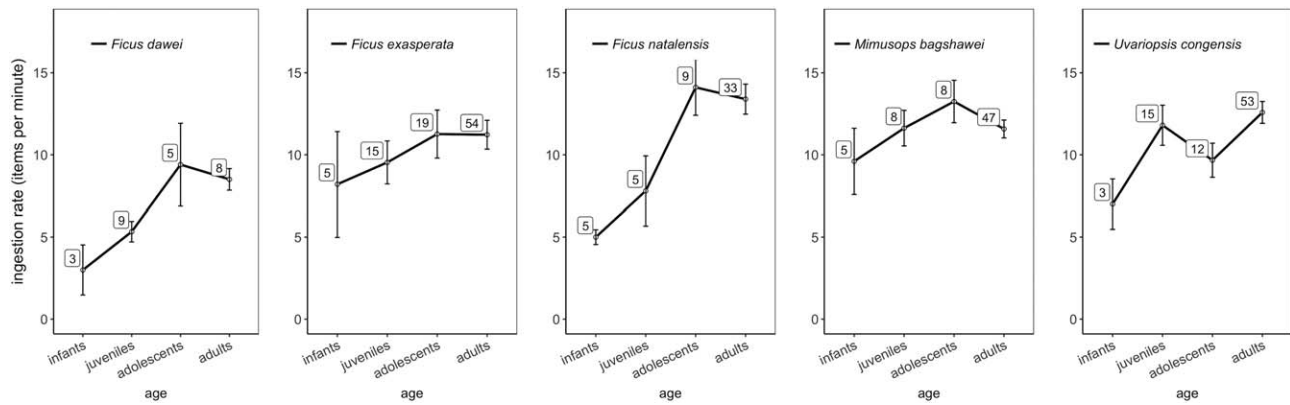


FIGURE 5 Mean \pm SE ingestion rates, defined as the number of items ingested per minute of foraging, across five different ripe fruit species. The numbers to the top-left of each point indicate the number of rates in the sample

3.5 | Foraging efficiency

We fit a linear model to test whether age class predicted differences in ripe fruit ingestion rates, controlling for food species (*F. dawei*, *F. exasperata*, *F. natalensis*, *M. bagshawei*, *U. congensis*). Overall, we found increases over developmental time across all food items (Figure 5). Specifically, infants showed significantly lower ingestion rates than adults ($\beta = -4.72$, $SE = 1.15$, $t = -4.08$, $p < 0.001$), whereas juvenile ingestion rates were lower but not significantly different from adults ($\beta = -1.72$, $SE = 0.79$, $t = -2.17$, $p = 0.13$). Adolescent ingestion rates were closest to those of adults and not significantly different ($\beta = -0.13$, $SE = 0.78$, $t = 0.17$, $p = 1.0$).

4 | DISCUSSION

4.1 | General feeding patterns

The first aim of this study was to provide a comprehensive account of chimpanzee feeding development. In the Kanyawara chimpanzee community, most feeding behaviors developed quickly and reached adult levels long before adulthood. Specifically, we found that most dietary patterns of immature chimpanzees matched those of adults either before or near weaning. Although early infants (<12 months) displayed minor differences in diet composition compared to adults, late infants (1–5 years) matched adults in the percentage of solid feeding time allocated to ripe fruit, young leaves, and pith, the three most commonly eaten food parts in this community. With respect to daily time spent feeding on solid food, immature chimpanzees exhibited steady increases with age and reached adult levels between 4 and 6 years, around the mean age of weaning. These results are unsurprising; given that infants travel with their mothers to feeding sites, the acquisition of these feeding patterns can be explained by covefeeding with the mother. Consistent with our data, prior studies also show steady increases in daily feeding time throughout infancy (Mahale: Hiraiwa-Hasegawa, 1990a; Matsumoto, 2017; Gombe: Lonsdorf et al., 2014). Likewise, Hiraiwa-Hasegawa (1990a) found that late infant diets at Mahale matched those of adults

in terms of the percentage of feeding time allocated to different food parts, while noting that infants ate fewer leaf items than their mothers.

As for feeding independence, we documented a long period of transitional feeding between the first instance of solid food ingestion and complete cessation of suckling. Infant chimpanzees at Kanyawara did not feed on solid foods until 5.1 months, which is comparable to the populations of Mahale and Gombe, where infants fed on solid food starting at 4 and <6 months, respectively (Hiraiwa-Hasegawa, 1990a; Lonsdorf et al., 2014). The range of weaning ages in the Kanyawara population (4.1–6.0 years) was also similar to previous studies (e.g., Clark, 1977: 4.2–7.2 years). However, there is substantial variation among studies in the amount of suckling time observed across infancy; studies have found that time spent suckling decreases (Clark, 1977; Matsumoto, 2017), decreases then increases (Hiraiwa-Hasegawa, 1990b), or increases then decreases (this study). One study found no change in suckling time with age (Lonsdorf et al., 2014). The immense variability across studies in suckling behavior likely reflects its inconspicuous nature, particularly for young infants that cling exclusively to their mothers' chests (the reverse is also true: suckling is highly conspicuous for older infants that rarely spend time on their mothers' chests). Moreover, behavioral studies are limited in other ways; they cannot detect the volume of ingested milk or observe suckling that occurs at night or in nests. Fecal stable isotope studies will hopefully clarify these patterns (Reitsema, 2012). For example, Bădescu et al. (2016) recently analyzed fecal isotopes to evaluate feeding transitions in chimpanzees at Ngogo in Kibale National Park. Bădescu and colleagues found that the amount of milk in infant diets gradually decreased from ~1 year onward, ultimately ceasing between 4 and 4.5 years. These data suggest that milk intake generally declines with age and that suckling behavior at later ages reflects comfort nursing. This study also suggested that feeding on solid food might begin by as early as 2–5 months after birth, which would be an earlier start to solid feeding than observational studies have found.

Two feeding behaviors in our study exhibited greater developmental delays. First, the daily diet breadth of immature chimpanzees remained lower than that of their mothers until juvenility (5–10 years). This effect was driven by food part: late infants ate the same number

of ripe fruit food items as their mothers, but they fed on fewer fibrous foods. By contrast, juveniles ate the same number of fibrous food items. Second, ingestion rates across five commonly eaten ripe fruit species remained significantly below adult levels until juvenility, at which point ingestion rates were lower but not significantly different from those of adults. By adolescence, ingestion rates of immature individuals were fully comparable to those of adults. Although this dataset is limited to a set of five ripe fruit species for which sufficient data were available, immature chimpanzees appear to reach adult ingestion rates as early as juvenility and by adolescence at the latest.

4.2 | Needing-to-learn hypothesis

The second aim of this study was to evaluate the needing-to-learn hypothesis (Ross & Jones, 1999), which predicts that immature chimpanzees should have a smaller diet breadth and lower ingestion rates compared to adults. Although mothers and their late infants exhibited differences in their daily diet breadth (driven by fewer fibrous foods in the infant diet), a complete adult diet breadth was acquired during juvenility. This delay is unlikely to be accounted for by learning since fibrous foods, particularly young leaves and pith, are typically cognitively simple to acquire (Gibson, 1986; Milton, 1981a; but see Byrne & Byrne, 1993; Corp & Byrne, 2002). Instead, delays in dental development (Machanda et al., 2015; Smith et al., 2013), which restrict an individual's ability to efficiently chew fibrous foods, better explain both this pattern and the greater emphasis on young leaves over pith in the first year of life. We should note that although the mean absolute difference in the daily number of fibrous food items eaten by mothers and late infants was just one item, this represents one-third of the fibrous food items in the mothers' diets.

Additionally, immature ingestion rates were not significantly different from those of adults by juvenility, although they continued to show absolute gains into adolescence. Individuals thus appear to reach adult ingestion rates before becoming physically mature; this result is inconsistent with the needing-to-learn hypothesis but should be viewed as preliminary given the limited number of food species and food parts included in this study. Furthermore, ingestion rates, a standard measure of foraging proficiency across multiple primate species (Nakagawa, 2009), are influenced by factors aside from learning. Thus, even if ingestion rates on other food items were to exhibit longer delays, alternative hypotheses for the evolution of prolonged immaturity make nearly identical predictions as the needing-to-learn hypothesis. For example, the ecological risk (Janson & van Schaik, 1993) and brain malnutrition risk (Deaner et al., 2003) hypotheses propose that long developmental periods are a consequence of slow somatic and brain growth, respectively. By growing slowly, individuals limit their daily energy requirements and minimize the risk of starvation or brain damage. Delays in foraging efficiency could thus be caused by delays in factors that covary with body size, including strength (Fragaszy & Boinski, 1995; Gibson, 1986), gape width or mouth volume (Milton, 1981b), and gut size (Demment & Van Soest, 1985; Milton, 1981b). Lower ingestion rates among young chimpanzees could also result from intra-group feeding competition if individuals are forced to forage in less-

preferred locations (Janson & van Schaik, 1993). Delays in dental development could result in lower ingestion rates as well (Kay & Sheine, 1979; Machanda et al., 2015).

The fact that multiple hypotheses make similar predictions poses a challenge to our ability to understand the evolution of prolonged immaturity. To distinguish between the needing-to-learn hypothesis and alternatives, we recommend more refined studies of feeding behavior in chimpanzees that can test non-overlapping predictions. Generally, these hypotheses can be distinguished by whether they implicate learning or physical constraints. In terms of ingestion rates, the needing-to-learn hypothesis predicts that immature individuals will exhibit greater delays on foods that require more processing or else that are difficult to handle (e.g., Eadie, 2015), both between and within general food categories such as ripe fruit, leaves, and pith.

However, if slow growth rates result in physical constraints, we can make several alternative predictions. (i) If gut size constrains ingestion rates, individuals should forage more efficiently at the start compared to the end of a bout, and when the duration since the previous foraging bout is longer. (ii) If physical strength constrains ingestion rates, we should observe delays on foods that require more force to open. Additionally, ingestion rates should be consistently low throughout a bout, based on an individual's body size. (iii) If intragroup feeding competition limits ingestion rates, we should expect immature chimpanzees to forage in less-preferred locations within a feeding tree when in large groups. This effect should not be observed with food items where group foraging is dispersed (e.g., fruit groves). Conversely, young chimpanzees should forage more efficiently when in family groups. (iv) If gape width or mouth volume is a constraint, we should expect delays when individual fruits are large but otherwise easy to access. (v) Lastly, if dental development limits ingestion rates, we should expect delays in foods that are difficult to chew, especially fibrous foods such as pith and mature leaves. We should also expect variation within food categories according to their mechanical properties (Chapman, Rothman, & Lambert, 2012; Norconk, Wright, Conklin-Brittain, & Vinyard, 2009).

Chimpanzees exhibit a number of more difficult foraging behaviors, such as termite fishing (Goodall, 1986; Lonsdorf, 2005), nut cracking (Boesch & Boesch-Achermann, 2000; Matsuzawa, 1994), and hunting (Gilby et al., 2015; Pruett et al., 2015; Watts & Mitani, 2002). Immature individuals spend substantial amounts of time observing the tool use of others and practicing (e.g., Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2005). Additionally, the probability that a male participates in a hunt peaks in their mid-20s, and kill probability also does not peak until adulthood (Gilby et al., 2015). However, in contrast to human hunter-gatherer societies, where skill-intensive foraging activities are widespread and essential to the diet (Kaplan et al., 2000), skill-intensive activities represent only a small percentage of a chimpanzee's caloric intake (Goodall, 1986; Mitani & Watts, 1999; but see Pruett, 2006). It therefore seems unlikely that these foods would exert substantial selective pressure on the duration of immaturity in this species. Similarly, delayed maturation could help in learning the location and seasonality of food resources (Menzel, 1997; Milton, 1981a; optimal

foraging theory suggests that travel time between patches is a key component of foraging efficiency (Charnov, 1976). However, given that females typically disperse upon reaching sexual maturity (Pusey & Schroepfer-Walker, 2013), and that adult males are highly gregarious (Goodall, 1986; Pepper, Mitani, & Watts, 1999) and can rely on others' knowledge, this is also unlikely to explain the prolonged immature period in chimpanzees.

From a comparative perspective, great apes provide mixed support for the needing-to-learn hypothesis. Within species, the hypothesis predicts that immature individuals will exhibit reduced feeding competency compared to adults. Like chimpanzees, though, individuals attain adult feeding patterns long before adulthood in both orangutans (Schuppli et al., 2016) and gorillas (Nowell & Fletcher, 2008; Watts, 1985). However, across species, the needing-to-learn hypothesis predicts a positive relationship between dietary complexity and the length of the immature period. And, consistent with each species' dietary complexity, Sumatran orangutans exhibit the longest developmental delays, followed by Bornean orangutans, chimpanzees, and gorillas. Developmental data on feeding are not yet available in bonobos (*Pan paniscus*). Although more research is therefore necessary to explain delayed immaturity in great apes, they do exhibit distinct feeding patterns from humans, which have an extra developmental stage (childhood) in which individuals are dependent on others for energetic and nutritional support even after weaning (Bogin, 1997). Additionally, human foragers do not reach peak efficiency until adulthood (Gurven et al., 2006; Walker et al., 2002), which contrasts with the feeding patterns observed in great apes.

5 | CONCLUSIONS

This study provides a comprehensive account of chimpanzee feeding development across multiple measures. Most feeding behaviors were acquired early in development, although immature chimpanzees did not exhibit a complete adult feeding pattern until juvenility (5–10 years). Together, these patterns do not support the standard predictions of the needing-to-learn hypothesis; moreover, observed developmental delays can also be explained by physical constraints that covary with body size. Instead, these results are most consistent with the hypothesis that adult feeding patterns need to be in place around the time of weaning, when individuals become responsible for all their caloric and nutritional requirements. The need to learn feeding behavior therefore does not appear to have increased the length of the immature period in chimpanzees. However, further study of feeding development, in combination with developmental work in chimpanzees on dental eruption (Machanda et al., 2015; Smith et al., 2013), mortality rates (Muller & Wrangham, 2013), and body growth (Emery Thompson, Muller, & Wrangham, 2012), is needed to clarify both patterns of chimpanzee life history and the function of prolonged immature periods more broadly.

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