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ORIGINAL ARTICLE

Maternal lactational investment is higher for sons in chimpanzees

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Abstract

Maternal lactational investment can affect female reproductive rates and offspring survival in mammals and can be biased towards infants of one sex. We compared estimates of lactation effort among mothers, assessed as their potential milk contribution to age-specific infant diets (mother-infant differences in fecal stable nitrogen isotopes, $\delta^{15}N$), to the timing of weaning (infant age at last nursing bout) and to maternal inter-birth interval lengths for male and female infant chimpanzees (*Pan troglodytes*) at Ngogo, Uganda. Infant males had greater proportions of milk in their age-specific diets, indicated by higher mother-infant differences in $\delta^{15}N$ (Generalized Estimating Equation, GEE: $p < 0.01$). This may mean that mothers of sons showed greater lactation effort than mothers of daughters. Infant males stopped nursing at older ages than infant females (Kaplan–Meier product limit estimate, Breslow estimator: $p < 0.05$). Mothers of sons showed longer interbirth intervals than mothers of daughters (GEE: $p < 0.01$). All three measures indicated maternal lactational investment was higher for sons. Male infants may cost mothers more to ensure infant survival than female infants because males are more vulnerable and/or because maternal genetic returns on investment are greater for sons than daughters, as male philopatry means that chimpanzee mothers can have more influence on the reproductive success of sons. Chimpanzee females may trade off growth-related benefits of high lactational investment in male offspring against reduced reproductive rates.

Significance statement

Maternal investment via lactation affects the reproductive success of female mammals and their offspring and can be biased towards infants of one sex. We investigated lactational variation among wild chimpanzees in relation to infant sex using three proxies for maternal lactational investment: fecal stable nitrogen isotopes, a physiological biomarker that may provide an estimate of lactation effort; observations of nursing, which we used to establish weaning ages; and the lengths of intervals between births of surviving infants. Chimpanzee mothers biased lactational investment toward sons on all three indicators and showed reduced fecundity due to longer inter-birth intervals for mothers of sons than for mothers of daughters. These results would be expected if greater maternal investment toward sons leads to better condition and higher reproductive success for sons later in life, thus to greater inclusive fitness for mothers.

Keywords Maternal investment · Lactation · Weaning · Inter-birth intervals · Stable isotopes · Infant sex

Introduction

Age at weaning, or the length of maternal investment via lactation, is an important life history characteristic in mammals that has fitness implications for both infants and mothers (Lee et al. 1991; Lee 1997; Kennedy 2005). A wealth of studies in humans have documented the powerful survival and developmental benefits milk confers to infants through an increasingly well-understood and complex set of evolved biological pathways that include immune protection, developmental modulation, gut colonization, nutritional components, and neuro-developmental programming through the

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behavioral and psycho-social aspects of nursing interactions (Sellen 2006, 2009; Hinde and Milligan 2011). These benefits likely apply to all mammals, since lactation is a derived adaptation that has not been lost in any extant lineage (Bronson 1989). Infants likely benefit from relatively late weaning, as the immune, nutritional and developmental benefits of maternal milk improve infant health and increase body size at weaning, which can increase infant survival and may have long term benefits that improve health and reproductive success in adulthood (Clutton-Brock 1991; Lee et al. 1991; Sellen 2006, 2009; Langer 2008).

Female mammals balance the extra metabolic requirements of maintaining milk synthesis throughout the lactation period allocated to current offspring (i.e., “lactation effort”: Lee et al. 1991; Deutsch et al. 1994; van Jaarsveld et al. 1995) against their own somatic maintenance, remaining development (if they are not yet fully grown), and future reproductive investments (Trivers 1974; Clutton-Brock 1991; Hayssen 1993; Sellen 2006; Langer 2008). Litter age at weaning should be positively associated with lactation effort, thus with investment in current offspring (Lee et al. 1991; Hayssen 1993; Lee 1997; Langer 2008; Hinde and Milligan 2011). Continuing lactational investment in current infants often means that females delay their ability to conceive again (Bronson 1989); this can lengthen interbirth intervals and lower female fecundity (Lee 1997).

In theory, asymmetries in genetic relatedness drive differences in selection pressures on parents and their offspring (Trivers 1974). For mammals, natural selection should favor infants with behaviors and ontogenies that maximize the nutritional, immunological, energy-saving and care resources they obtain from their mothers by delaying weaning, while mothers are selected to distribute their resources in economically strategic ways that maximize the combined fitness effects of their own survival and that of their litters (Trivers 1974; Hayssen 1993; Lee 1997; Kennedy 2005). This can lead to weaning conflict if a mammalian mother opts for reduced lactation effort and weaning earlier than would be optimal for infants (Trivers 1974; Lee 1997; Kennedy 2005), although few data demonstrate this conclusively for any mammal. Alternatively, mothers might accrue greater fitness benefits by increasing investment (including lactation effort) in current offspring, while paying the potential cost of delaying next offspring, if the added investment increases current offspring reproductive success (Trivers and Willard 1973; Clutton-Brock 1991; Hewison and Gaillard 1999; Bercovitch 2002). Increased maternal lactational investment improves infant survival, but few data exist regarding whether increased lactational investment leads to improved reproductive success for offspring in adulthood (Clutton-Brock 1984; Lee 1987). Females clearly benefit by increasing investment in offspring who require it to survive (Clutton-Brock et al. 1985; Stinson 1985; Lindstrom 1999). Such seems to be the case when mothers of species with marked sexual dimorphism invest more resources in sons than daughters because male infants are more energetically costly (Clutton-Brock et al. 1985; Hewison and Gaillard 1999; Lindstrom 1999; e.g., gorillas, *G. beringei*: Meder 1990; Leigh and Shea 1996; Eckardt et al. 2016; Robbins and Robbins 2021; sea lions, *Zalophus* spp.: Oftedal et al. 1987; Piedrahita et al. 2014). Male offspring may also be biologically more sensitive to external stressors, such as disease or low food availability (“fragile male hypothesis”: Clutton-Brock et al. 1985; Stinson 1985; Lindstrom 1999; Wells 2000; Battles 2016). If this is the case, mothers should invest more in sons to increase their chances of survival. Females may thus make higher lactation effort for sons than daughters and wean sons relatively late, even if this lowers their fecundity, rather than distributing investment equally and in more limited amounts to current and anticipated future offspring because the increased fitness through sons offsets the reduction in fecundity. We should therefore expect variation in weaning parameters among infants of different females and even among infants of the same female.

Measuring lactation effort using stable nitrogen (δ^{15}N) isotopes

Obtaining measurements of milk transfer, and thus of lactation effort for mothers, is a formidable challenge, but meeting this challenge is key to understanding how growth, development and reproduction are linked in mammalian life history evolution (Sellen 2006). Measuring milk synthesis directly and non-invasively in the wild is not currently feasible for most mammals, but stable isotope analyses of urine and feces provide indirect means to assess aspects of diets and of when, and to what extent, infants include foods other than milk in their diets (Liden and Angerbjorn 1999; Codron et al. 2006; Oelze et al. 2011; Blumenthal et al. 2012; Reitsema et al. 2015, 2020; Bădescu et al. 2016, 2017; Loudon et al. 2016; Schoeninger et al. 2016). Several studies have used stable nitrogen isotopes in feces to calculate δ^{15}N values for infant mammals. These values reflect nitrogen in the amino acids of dietary proteins; thus, they detect an individual’s trophic position and can quantify the relative dietary contributions of maternal milk to non-milk foods in infant diets (Reitsema 2012; Bădescu et al. 2016, 2017; Reitsema et al. 2020). For infants of mammal species utilizing mostly or entirely plant-based diets, infants’ δ^{15}N values provide information about infant daily protein intake (Reitsema 2012; Bădescu et al. 2017), and thus about how much of the protein in their diets comes from milk (an animal source). Values thus provide a biomarker for weaning (Fogel et al. 1989; Katzenberg and Pfeiffer

1995; Prowse et al. 2008; Reitsema 2012; Oelze 2015; Tsutaya and Yoneda 2015; Bădescu et al. 2016, 2017). Feces of young infants are enriched in ^{15}N relative to their mothers and show higher $\delta^{15}N$ values. Infant fecal $\delta^{15}N$ values decrease progressively through infancy until they are nearly identical to their mothers when infants are completely weaned (Reitsema 2012; Tsutaya and Yoneda 2015; Bădescu et al. 2017). Decreasing $\delta^{15}N$ differences between mothers and offspring over time mean that the contribution of milk to the infant's overall diet is decreasing relative to that of non-milk foods; this helps track the progression of the weaning process.

Variation in fecal stable nitrogen isotope differences between mothers and infants may also help quantify differences in lactation effort among mothers (Reitsema 2012; Bădescu et al. 2016, 2017). For same-aged infants, lower isotopic differences between one female and her infant than between another mother-infant dyad could indicate that the first female is making less lactation effort (Bădescu et al. 2016). Milk would contribute relatively less protein than non-milk foods to the diet of the infant showing the smaller $\delta^{15}N$ difference; thus, this infant would be farther along in the weaning process and its mother would be able to divert energy to her next reproductive attempt sooner than would a female who was providing more milk to her current offspring. However, isotopic values provide relative measures of how much different foods contribute to the diet, rather than absolute measures. Decreasing $\delta^{15}N$ differences between mothers and offspring through infancy do not necessarily represent decreasing milk intake. They mean that milk is contributing relatively less to the diet and that other foods are contributing relatively more. This could happen because infants maintain milk intake while increasing the amount of non-milk food they eat per day, or because they decrease milk intake while increasing their intake of other food.

Fecal stable isotopes in combination with observations of nursing can help us to evaluate weaning from physiological and behavioral perspectives. In chimpanzees, fecal stable isotopes revealed the presence of comfort nursing, without milk transfer, after physiological weaning had occurred and lactation presumably ended (Bădescu et al. 2017). Thus, offspring may continue to make nipple contact even after they are nutritionally independent. Several other studies (e.g., Harlow and Harlow 1965; Martin 1984; Rajpurohit and Mohnot 1991; Reitsema 2012; Cherney et al. 2021) also illustrate that mother-infant nutritional and behavioral relationships can develop separately, despite considerable temporal overlap (Bădescu 2018). It is thus important to consider both physiological and behavioral aspects of the weaning process to understand maternal lactational investment.

Evidence for sex-biased maternal investment via lactation

Several factors affect lactation and weaning in mammals, including maternal parity, age, dominance status, the threat of infanticide, variation in food availability, and infant characteristics such as differences in nutritional demands, personality, and sex (see Clutton-Brock 1991 and Eckardt et al. 2016 for reviews). Evidence for sex-biased maternal investment via lactation is limited. When it occurs, especially among polygynandrous species and those with high sexual dimorphism, females should invest more in the offspring sex that could yield higher inclusive fitness benefits by producing more grand-offspring (Hamilton 1967; Trivers and Willard 1973; Hewison and Gaillard 1999). Iberian red deer (*Cervus elaphus hispanicus*) females with sons synthesized more milk than females with daughters and their milk contained more protein, fat, and lactose (Landete-Castillejos et al. 2005). Given that variation in reproductive success is generally greater for males than for females and that adult males in good condition should have relatively high reproductive success, higher lactation effort for sons should give greater inclusive fitness returns for mothers when effort is positively correlated with adult male condition (Hamilton 1967; Trivers and Willard 1973; Hewison and Gaillard 1999; Landete-Castillejos et al. 2005). In domestic cows (*Bos taurus*), however, females synthesized more milk for daughters, which may increase maternal inclusive fitness because greater lactational investment helps daughters begin their reproduction at earlier ages than sons (Hinde et al. 2014). Rhesus macaque (*Macaca mulatta*) mothers synthesized milk with higher energy density for sons, but produced more milk for daughters, with the result that available milk energy (the product of the milk yield and energy density) was similar for sons and daughters (Hinde 2007, 2009). Thus, while components of lactation can be geared towards infants of one sex, this does not necessarily lead to greater maternal investment in offspring of one sex over the other (Hinde 2009).

In support of the hypothesis that male offspring in highly sexually dimorphic species are energetically more costly and require greater maternal resources than female offspring, males were weaned later than females in Northern elephant seals (*Mirounga angustirostris*; weaning age: males = 27.8 days, females = 26.6 days, N = 44; Reiter et al. 1978), Galapagos fur seals (*Arctocephalus galapagoensis*; among 3-year-olds, 3 of 7 males and 0 of 19 females were still nursing; Trillmich 1986), and Antarctic fur seals (*Arctocephalus gazella*; weaning age: males = 120.2 days, N = 55, females = 116.9 days, N = 51; Lunn and Arnould 1997).

In African elephants (*Loxodonta africana*), male infants suckled more often (average across all ages: males every

37 min, females every 50 min), and mothers had longer inter-birth intervals after sons than after daughters (after male calf = 4.7 years, $N = 67$, after female calf = 4.35 years, $N = 77$; Lee and Moss 1986). Infant males were less likely to survive during stressful periods compared to females, and mothers may thus invest more heavily in males to improve their chances of survival, in line with the "fragile male" hypothesis (Lee and Moss 1986; Wells 2000; Battles 2016).

Females with extra resources may bias investment toward sons, while those with fewer may bias investment toward daughters; in theory, either can lead to higher inclusive fitness for mothers (Trivers and Willard 1973). In mountain gorillas (*Gorilla beringei beringei*), multiparous, high-ranking females, who presumably had better access to food, weaned sons later than daughters, while primiparous females weaned daughters later than sons (Eckardt et al. 2016). High-ranking females also had longer inter-birth intervals after sons than after daughters, while low-ranking females had longer inter-birth intervals after daughters than after sons (Robbins et al. 2007). Female spider monkeys (*Ateles paniscus*) invested more in males, as indicated by longer interbirth intervals following births of sons, and high-ranking females tended to bias investment toward sons (McFarland Symington 1987). Despite these and other (e.g., Boesch 1997; Lonsdorf et al. 2020) reports of maternal rank effects on differential investment as a function of offspring sex, we should not expect sex biases to be universal because female hierarchies are not universal, even among populations of the same species.

We assessed variation in maternal lactational investment in relation to infant sex in eastern chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. The duration of lactation has significant impacts on rates of offspring survival and female reproduction in chimpanzees (Boesch 1997; Thompson et al. 2012; Emery Thompson et al. 2016; Lonsdorf et al. 2020; Stanton et al. 2020). Previous research showed that sons were weaned later than daughters at Gombe in Tanzania (Lonsdorf et al. 2020) and Taï in Côte d'Ivoire (Fahy et al. 2014) and that interbirth intervals for high-ranking females at Taï were longer after the births of sons than after the births of daughters, whereas low-ranking females had longer inter-birth intervals following the births of daughters (Boesch 1997). Our investigation of variation in maternal investment at Ngogo is novel because we have data on fecal δ^{15}N, which allowed us to assess the contribution of maternal milk to infant diets and thus to estimate maternal lactation effort, along with behavioral data on nipple contact (which allowed identification of the age of behavioral weaning) and information on inter-birth intervals. Consequently, we could determine whether lactation and weaning vary systematically as a function of infant sex. We hypothesized that females at Ngogo invest more in sons; this hypothesis predicts that 1) lactational effort is greater for sons; 2) sons are weaned at later ages than daughters; and 3) inter-birth interval lengths are longer after births of sons. The Ngogo community is ideal for such a study because of its large size and because variation exists in both infant age at weaning completion (3–8 years) and in maternal lactation effort (Bădescu et al. 2016, 2017).

Methods

Study site and subjects

Behavioral and fecal data were collected over 15 months in 2013–2014 and 2018 at the Ngogo field site in Kibale National Park, Uganda. Ngogo is mostly made up of old growth forest and includes colonizing forests that were once grasslands plus areas of swamp forest, *Acanthus* bush, and anthropogenic grasslands (Lwanga 2003; Watts et al. 2012a, b). Kibale typically has two rainy seasons, from March to early June and from September to November, separated by dry periods (Chapman et al. 2005; Watts et al. 2012a, b). The Ngogo chimpanzee community is well-habituated and was the largest known at the time of observations reported here, although it had started to undergo a permanent fission by the 2018 study period (Sandel and Watts 2021). The study group included between 199 and 207 individuals, including 54 to 57 adult females, 26 to 33 adult males, 30 to 34 immature females, 33 to 42 immature males, and 40 to 53 infants. While dominance ranks between females have been documented at other chimpanzee sites (Pusey et al. 1997; Wittig and Boesch 2003; Kahlenberg et al. 2008), female dominance hierarchies at Ngogo are absent (Wakefield 2008). Decided agonistic interactions between females at Ngogo are rare, even between those dyads who associate at high rates (Wakefield 2008, 2013; Langergraber et al. 2009). We have rarely seen pant-grunts between females in thousands of hours of observations (DPW pers. observ.; this study). Chimpanzee females usually disperse into neighboring communities at sexual maturity, but some females at Ngogo have stayed in their natal group as adults (Mitani et al. 2002). Mothers in our study included five natal females, four of whom were primiparous.

The chimpanzee diet at Ngogo consists predominately of fruit, along with considerable amounts of leaves and smaller amounts of other plant parts (Watts et al. 2012a, b). The chimpanzees consume mostly C_3 plants, and their diet shows a mean δ^{15}N of 4.5 ± 1.8‰ (Carlson and Kingston 2014). Out of the thirty plant source foods eaten most often (Watts et al. 2012a), those most depleted and enriched in ^{15}N show mean δ^{15}N ratios of 1.4 ± 2.3 (SD) ‰ and 6.9 ± 0.8‰, respectively (Carlson and Kingston 2014). Chimpanzees at Ngogo rarely eat insects (Watts et al. 2012a). Mothers and infants included in this study were not seen eating insects either during focal samples or on an ad lib basis, and we have no reason to think insectivory contributed to their δ^{15}N ratios. As at all other sites for which relevant data are available, chimpanzees at Ngogo hunt and eat a variety of vertebrate prey (especially red colobus monkeys, *Piliocolobus tephrosceles*). Female chimpanzees at Ngogo hunt, but do so less often than males [e.g., females accounted for only 3% of kills 1995–2001 (Mitani and Watts 1999; Watts and Mitani 2002a, b)]. Females present at hunts often beg successfully for meat; for example, they received meat in 48% of begging events between 1995 and 2001 (Mitani and Watts 1999; Watts and Mitani 2002a, b), although usually only in small quantities. When females have meat, they typically share it with their dependent offspring (Bădescu et al. 2017). However, even for males, meat comprises only a small portion of the overall diet (Watts and Mitani 2002a, b, 2015); given that females eat less meat than males on average, meat probably has little effect on δ^{15}N ratios overall and for females in particular (Oelze et al. 2011).

We previously presented results of stable isotope analyses of feces from *P. t. schweinfurthii* at Ngogo that demonstrated this method can successfully assess infant feeding transitions including weaning, changes in the contribution of milk to non-milk food in the age-specific diets of offspring (Bădescu et al. 2017), and inter-individual variation in maternal lactation effort (Bădescu et al. 2016). The youngest chimpanzee infants were most enriched in the heavy nitrogen isotopes and showed maximum mean elevations above their mothers in δ^{15}N of 2.0‰ (permil) (Bădescu et al. 2017). To investigate differences between male and female infants in δ^{15}N values, we rely here on the same sample of fecal stable isotopes from 2013–2014 ($N=265$ mother-infant fecal sample pairs) but evaluated in a new way (i.e., in relation to infant sex), along with a new sample of feces collected in 2018 from infants and their mothers ($N=46$ mother-infant fecal sample pairs).

We defined infants as offspring aged 0 to 8 years old who did not have younger siblings and who were seen to make nipple contacts with their mothers, regardless of whether milk transfer occurred. Infancy is typically defined as ages 0 to 5 years in chimpanzees (Goodall 1986), but assigning individuals to a standardized category ignores variation in age at last nipple contact, which occurred as late as 8 years at Ngogo. However, we previously showed that infants at Ngogo are most often physiologically weaned by 4.5 years old, and while offspring can continue to make nipple contacts past this age, these are usually for comfort (without milk transfer; Bădescu et al. 2017). We estimated ages of infants from data on their first appearances and on last appearances of their mothers prior to births. Estimated ages at first sighting varied mostly from one or several days to within four weeks. We estimated birth dates of two infants to within three to four months partly based on assessments of their nutritional status and comparisons of their social and physical independence to other infants with more precise estimated ages. Data collectors could individually recognize all chimpanzees at Ngogo.

Behavioral data

From January to March 2013, September 2013 to June 2014, and January to April 2018, the lead author (IB) collected behavioral data on infants using focal sampling (Altmann 1974). During 1-h focal samples, IB recorded the frequencies and duration of all feeding bouts, including nursing. She also recorded nursing bout frequencies and durations ad libitum. Infants were considered to nurse when their faces were visible and they made nipple contact with their mothers. IB terminated focal samples if the subjects were out of view for more than 10 min. Initial selection of focal infants on a daily basis was either opportunistic or aimed at those infants for whom data were particularly needed (for instance, infants whose mothers were relatively difficult to locate). After completing a sample, IB chose another infant from among those present and subsequently aimed to cycle through all infants present in the same order for the rest of the day. Daily time spent following an individual female, or group of females, and their dependent offspring was usually between 5 and 11 h. Some follows were less than 5 h long due to the inability to find or to maintain contact with chimpanzees, or because certain mother-infant pairs left the subgroup during the follow. It was not possible to record data blind because our study involved focal animals in the field.

We included 50 infants between 2 and 8 years old (24 females and 26 males) in the behavioral analysis of nursing. We included only infants over 24 months old, as this may be the earliest age at which chimpanzee infants can be weaned and subsequently survive (Boesch et al. 2010). We divided the behavioral data for each infant into monthly increments, and noted whether infants were seen to nurse during each month. Weaned age was defined behaviorally as the first month when an infant was not seen to nurse during at least five continuous contact hours (during which ad libitum data on nursing were collected) and five focal animal sampling hours during that month and subsequent months (Tanaka 1992). Infants that contributed a weaned age to the analysis ($N=16$) had 30 days or less between observations with and without nursing. We did not include infants who were weaned prematurely due to maternal death.

The 50 infants were the offspring of 42 females. For 32 of these females, we had data on completed inter-birth intervals, which we measured by calculating the number of days from the birth date of the study infant to the birth date of the subsequent infant when the first infant survived until the second's birth. One female gave birth twice during our data collection, and she thus contributed two inter-birth interval lengths to the analysis, whereas all other females gave birth once. Thus, the sample included 33 inter-birth intervals. We also used long-term Ngogo demographic data to investigate whether individual females had longer intervals between surviving births if the first of two consecutive infants was a male than if the first infant was a female. However, we could only identify 12 females for whom we had reasonably accurate birth date data for both male-first and female-first intervals, so we regard the results as preliminary.

Fecal data and lab analyses

IB collected 311 fecal sample pairs from chimpanzee mothers and their offspring, within 10 min of defecation, with help from five field assistants from September 2013 to June 2014 and alone from January to April 2018 (Table 1). Differences in the isotopic compositions of foods eaten by chimpanzees lead to daily variation in the fecal stable isotope values from the same individuals (Reitsema 2012; Bădescu et al. 2017). To differentiate isotopic values due to nursing, most fecal samples (86%) collected from infants were matched by a sample collected from the mother on the same day. IB desiccated the fecal samples on-site using a solar food dryer, put them in vials filled with silica, and stored them in a freezer until they could be transported to Canada for further processing and analyses.

IB analyzed fecal samples collected in 2013–2014 in the Isotope Sciences Laboratory at the University of Calgary (U of C) and those collected in 2018 in the Geotop Laboratory at the Université du Québec à Montréal (UQAM). She ground and homogenized feces to a fine powder using a mortar and pestle, put them through a sieve with a 75-µm mesh, and weighed approximately 2.25 mg of each sample for analyses. Stable nitrogen analyses were conducted at U of C (for the 2013–2014 samples) using a Thermo Finnigan Delta PLUS XL stable isotope ratio mass spectrometer coupled to a Costech Elemental Analyzer in continuous flow, and at UQAM (for the 2018 samples) using a Micromass model Isoprime 100 isotope ratio mass spectrometer coupled to an Elementar Vario MicroCube elemental analyser in continuous flow. Two internal reference materials ($\delta^{15}N = -0.10 \pm 0.24$ (SE) ‰ and $+14.95 \pm 0.09$ ‰) were used to normalize the results on the AIR (IAEA-N1, IAEA-N2 & IAEA-N3) scale. A third reference material ($\delta^{15}N = -0.1 \pm 0.15$ ‰) was analyzed as an unknown to assess the precision of the normalization. We measured stable nitrogen isotopes as the permil deviation of ^{15}N:^{14}N relative to the standard AIR ($\delta^{15}N_{AIR} = [(^{15}N/^{14}N \text{ samples} \div {}^{15}N/^{14}N \text{ standard}) - 1] \times (1{,}000)$). The isotopic results are given using delta notation (δ) in permil (‰) relative to AIR. The overall analytical uncertainty was better than ± 0.2‰.

Table 1 Study subjects and fecal samples for stable isotope analysis

Sample size for stable isotope analysis				
Infant age (years)	Number of mother-infant fecal sample pairs		Number of infants	
	Female infants	Male infants	Females	Males
0–0.5	4	3	3	3
> 0.5–1	9	10	3	4
> 1–1.5	2	6	1	4
> 1.5–2	15	12	5	6
> 2–2.5	15	12	6	3
> 2.5–3	21	29	10	10
> 3–3.5	33	24	9	8
> 3.5–4	24	13	3	4
> 4–4.5	15	6	4	1
> 4.5–5	11	5	1	2
> 5–5.5	8	0	1	0
> 5.5–6	0	5	0	1
> 6–6.5	4	0	1	0
> 6.5–7	4	12	1	1
> 7–7.5	0	9	0	1
Total	311		96	

Based on the gut retention times of chimpanzees (Milton and Demment 1988), fecal stable isotope values should indicate the diets of mothers and infants one to two days prior to the collection of feces. In most cases ($N = 266$ fecal pairs or 532 total samples), fecal sample pairs from which we calculated differences in $\delta^{15}N$ between the mother and her infant were collected on the same day; this controlled for day-to-day fluctuations in solid food ingestion. We used average isotopic values from mothers of infants in the same age category to calculate the differences for the samples of infants ($N = 45$ feces) that were not matched by samples from the mother on the same day.

Our dataset of fecal samples included 50 mothers and their 60 infants (30 females and 30 males) between 0 and ≤ 7.5 years old (Table 1). Ten mothers each contributed two infants to our sample. We divided fecal samples of infants into age categories of 6-month increments. Thirty-one infants were sampled long enough to provide data to multiple age categories. Thus, the total sample size of mother-infant differences in $\delta^{15}N$ ratios included 96 infants-by-age-category (Table 1). Determining weaning ages for specific infants from the fecal stable isotope data alone is a challenge due to high day-to-day variation in fecal stable nitrogen isotope values (Reitsema 2012; Bădescu et al. 2017). Thus, we considered infants to be physiologically weaned if the mean difference between their fecal $\delta^{15}N$ values and their mothers' values was < 0.1 ‰, and physiologically not weaned if their mean $\delta^{15}N$ difference was ≥ 0.1 ‰, for at least three consecutive fecal sample pairs from each infant and its mother collected within 6 months (Bădescu et al. 2016). The age at weaning was chosen as the month of collection for the first fecal sample pair used in the sequence of samples to determine weaning age. Using these criteria, we established physiological weaning ages for four infants (two males, two females); we report these results descriptively below.

In our comparative isotopic analysis, we did not establish weaning ages for specific infants. Instead, we used two methods to categorize infants as weaned or not weaned. The first was a behavioral assessment, with infants considered weaned if they met the criterion for cessation of nursing given above. In the second, we applied the physiological weaning criteria for mother-infant $\delta^{15}N$ differences explained in the previous paragraph to fecal stable isotope values. We excluded 10 infants (comprising 14 fecal sample pairs) from the analysis of physiological weaning because they did not meet the specified criteria. Mother-infant fecal $\delta^{15}N$ differences for all infants ≤ 2 years old were automatically included in the not weaned category, because before this age, chimpanzee infants cannot be weaned and survive (Boesch et al. 2010).

Statistical analyses

We conducted three Generalized Estimating Equation (GEE) analyses (Liang and Zeger 1986) to assess the relationships between maternal lactation effort and inter-birth intervals on the one hand, and infant sex, on the other. GEEs work well with repeated measures of the same individuals and with combinations of continuous and categorical data (Liang and Zeger 1986; Ghisletta and Spini 2004; Zuur et al. 2009). GEEs also tend to be more conservative than Generalized Linear Models or Generalized Linear Mixed Models (Zuur et al. 2009). The first two GEEs evaluated how fixed effects that included infant sex (male, female), infant age (0–0.5, > 0.5–1, > 1–1.5, etc.), and maternal parity (primiparous, multiparous) were independently associated with mother-infant fecal stable nitrogen isotope ($\delta^{15}N$) differences as a continuous response variable. GEE 1 did this for infants who were not weaned, based on behavioral data, while GEE 2 repeated this analysis using the stable isotope data (GEE 2). We included infant and mother identities as the grouping structure to control for repeated measurements of the same mother-infant pairs. We set a normal error distribution and an exchangeable correlation type.

The third GEE evaluated how infant sex and maternal parity (fixed effects) were independently associated with inter-birth intervals as a continuous response variable. We included adult female identities as the grouping structure to control for repeated measurements of the female who contributed two inter-birth intervals to the dataset. We set a normal error distribution and an unstructured correlation type.

We used a paired-sample t-test to conduct a preliminary test of the hypothesis that within-female inter-birth intervals were longer following the births of sons, after determining that the data were normally distributed. Ten of the 12 females had only single intervals following births of sons and births of daughters. One had two intervals following births of daughters and one had two intervals following births of sons. For those two females, we compared the mean of those two intervals to the length of the single interval following the birth of a son and of a daughter, respectively.

We applied a time-to-event analysis, implemented using the Kaplan–Meier (or product limit estimator) method (Kaplan and Meier 1958), to determine survival curves for nursing by male and female infants. The nursing status of infants (2 = still nursing, 1 = no longer nursing) was defined as the status variable, and age in months at the cessation of nursing (i.e., weaned age) was defined as the time variable. Sixteen infants (9 females, 7 males) met the criterion for weaning and thus contributed weaned event data. Our dataset included right-censored observations on another 34 infants who had not yet stopped nursing by the end of the observation period. We conducted log rank (Mantel 1966), Breslow (Gehan 1965; Breslow 1970), and Tarone-Ware (Tarone and Ware 1977) tests to compare the weighted difference between the observed number of events (i.e., no longer nursing) and the number of expected events at every time point and determined whether the survival distributions for nursing differed significantly between males and females. We ran statistical analyses using SPSS version 25, with alpha set at 0.05, except that of within-female inter-birth intervals, for which we used STATA version 17.

Results

Contribution of milk to the age-specific infant diet

Infants identified as behaviorally not weaned ranged in age from 0 to 7 years old (Fig. 1), and infants identified as behaviorally weaned ranged in age from > 3 to 7.5 years old (Fig. 2). The youngest infant included in the isotopic comparisons who was identified as behaviorally weaned was a female who was 3 years and 3 months old. Male infants were more enriched than their mothers in the heavy nitrogen isotope relative to female infants and their mothers ($\delta^{15}N$ mean difference ± SD = 0.67 ± 0.83 ‰ for males, $N = 127$ fecal sample pairs, and 0.30 ± 0.69 ‰ for females, $N = 155$; GEE, $p < 0.01$, Table 2 and Fig. 1).

Infants identified as physiologically not weaned also ranged in age from 0 to 7 years old (Fig. 3), and infants identified as physiologically weaned ranged in age from > 2.5 to 7.5 years old (Fig. 4). The youngest physiologically weaned infant was a female who was 2 years and 9 months old (this

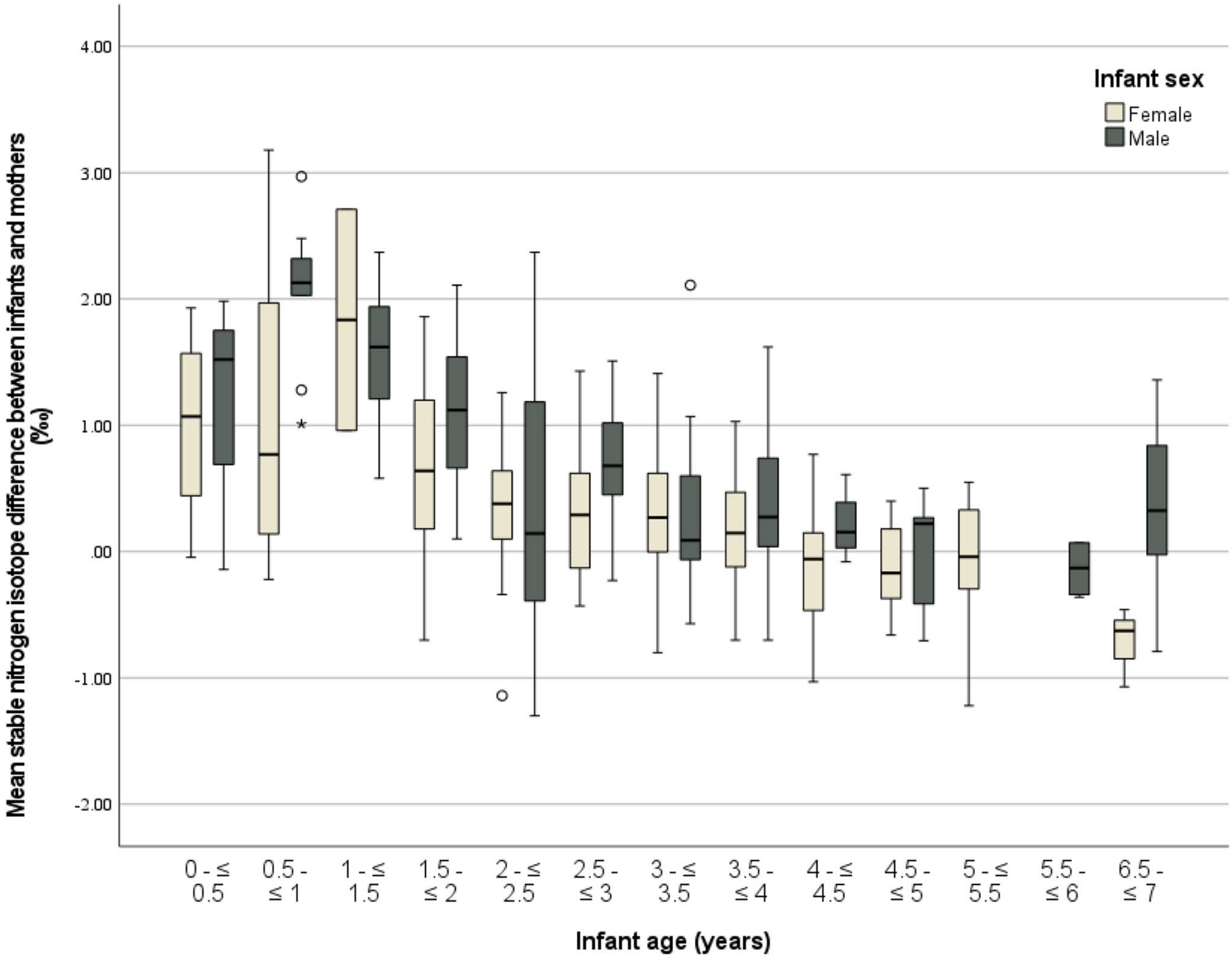

Fig. 1 Mean δ^{15}N differences between mothers and their *behaviorally not weaned* infant females ($N = 28$ individuals) and males ($N = 31$) by infant age category. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries) and highest and lowest values (whiskers) and outliers (circles; defined using Tukey's method as values between 1.5 and 3 interquartile ranges from the end of a box)

was not the female with the earliest behavioral weaning age). Male infants also were more enriched than their mothers in the heavy nitrogen isotope than were female infants (δ^{15}N mean difference ± SD = 0.77 ± 0.82 ‰ for males, $N = 111$ fecal sample pairs, and 0.52 ± 0.71 ‰ for females, $N = 100$; GEE, $p < 0.01$, Table 3 and Fig. 3). Both these analyses thus indicated that milk constituted a greater proportion of the male infant diet than the female infant diet for all age categories except ages 1 to ≤ 1.5, 2 to ≤ 2.5 and 3 to ≤ 3.5 (Figs. 1 and 3) and were consistent with the hypothesis that overall lactation effort was higher for mothers of sons than for mothers of daughters.

While all nursing infants were enriched in the heavier isotope relative to their mothers, younger infants showed relatively greater enrichment than older infants (GEE: $p < 0.001$, Tables 2, 3), consistent with the idea that milk constituted a progressively smaller relative proportion of the diet for infants as they aged. Same-age infants of primiparous and multiparous mothers were similarly enriched in the heavy nitrogen isotope ($p = 0.629$ and 0.600).

Behavioral weaning age

The mean and median ages at which infants of both sexes combined were behaviorally weaned were 58.1 ± 17.3 (SD) months old and 53.5 months old, respectively. The mean and median values for males ($N = 7$) were 67.6 ± 17.1 months and 69 months (range = 43–96 months), respectively; those for females ($N = 9$) were 50.8 ± 13.5 months and 44 months (range = 39–82 months). Kaplan–Meier product limit estimates for the nursing survival distributions of female and male chimpanzee infants were significantly different: the last

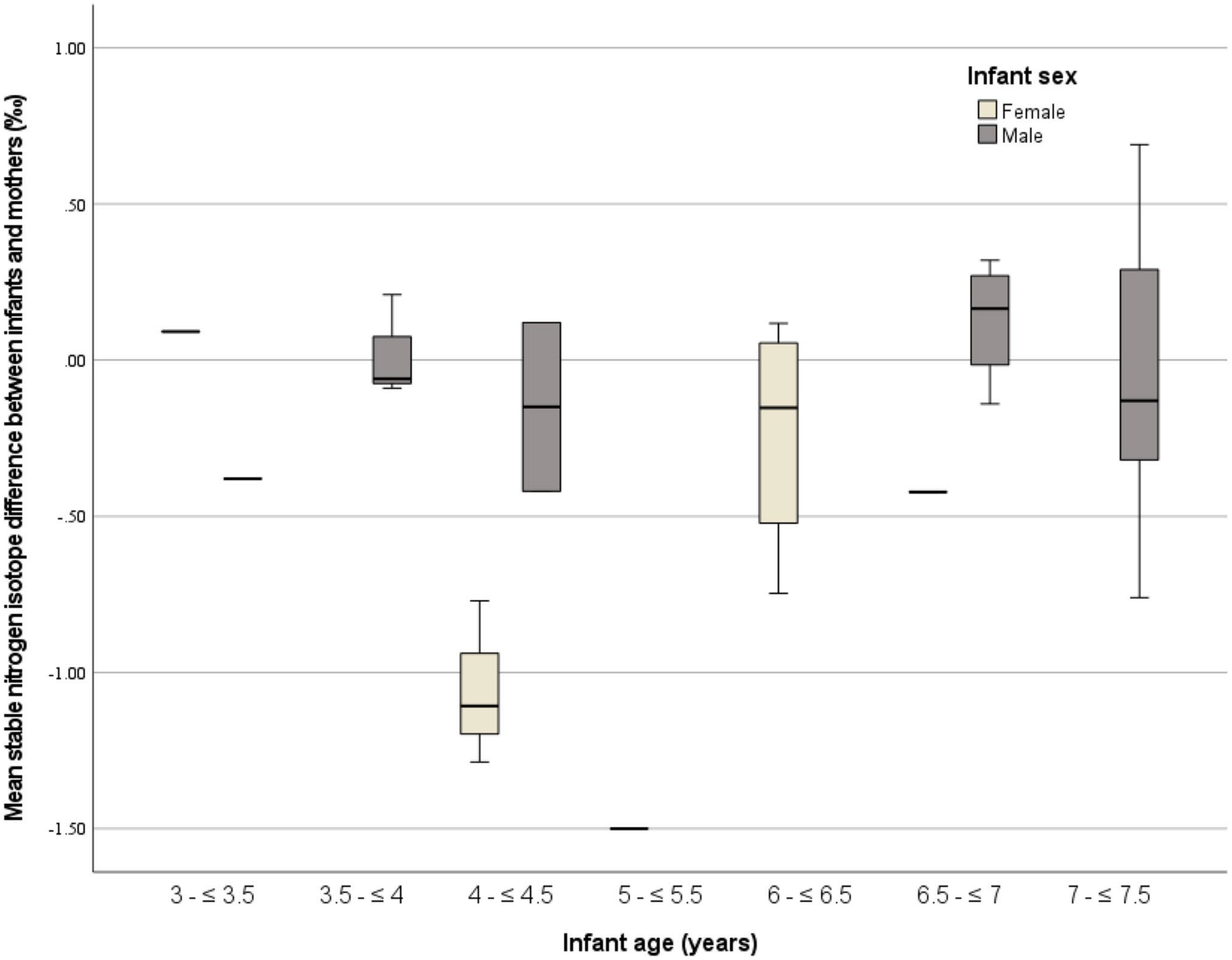

Fig. 2 Mean δ^{15}N differences between mothers and their *behaviorally weaned* infant females ($N = 6$ individuals) and males ($N = 3$) by infant age category. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries), highest and lowest values (whiskers) and outliers (circles; defined using Tukey's method as values between 1.5 and 3 interquartile ranges from the end of a box)

Table 2 Generalized estimating equation results for the associations between infant sex and age, and maternal parity (fixed effects) with mother-infant fecal δ^{15}N differences as a continuous response variable, including infants 0 to ≤ 7 who were not yet behaviorally weaned, as determined from observations of nursing ($N = 58$ infants, 48 mothers, 282 fecal sample pairs)

Test variable	*B*	Wald 95% confidence intervals		Wald's χ^2 (df = 1)	Standard error	*P*
		Lower	Upper			
Infant sex	0.306	0.092	0.521	7.823	0.109	**0.005**
Infant age category	-0.301	-0.410	-0.192	29.456	0.056	**0.000**
Maternal parity	-0.053	-0.266	0.161	0.234	0.109	0.629

nursing bouts of infant males were at older ages than the last nursing bouts of infant females (Breslow, Generalized Wilcoxon: $p < 0.05$, Fig. 5 and Table 4). This indicates that infant males were behaviorally weaned at older ages than infant females.

Inter-birth intervals

The mean (SD) and median inter-birth intervals ($N = 33$) among all the females in this study were 65.5 ± 15.7 months and 64.2 months, respectively. Mothers

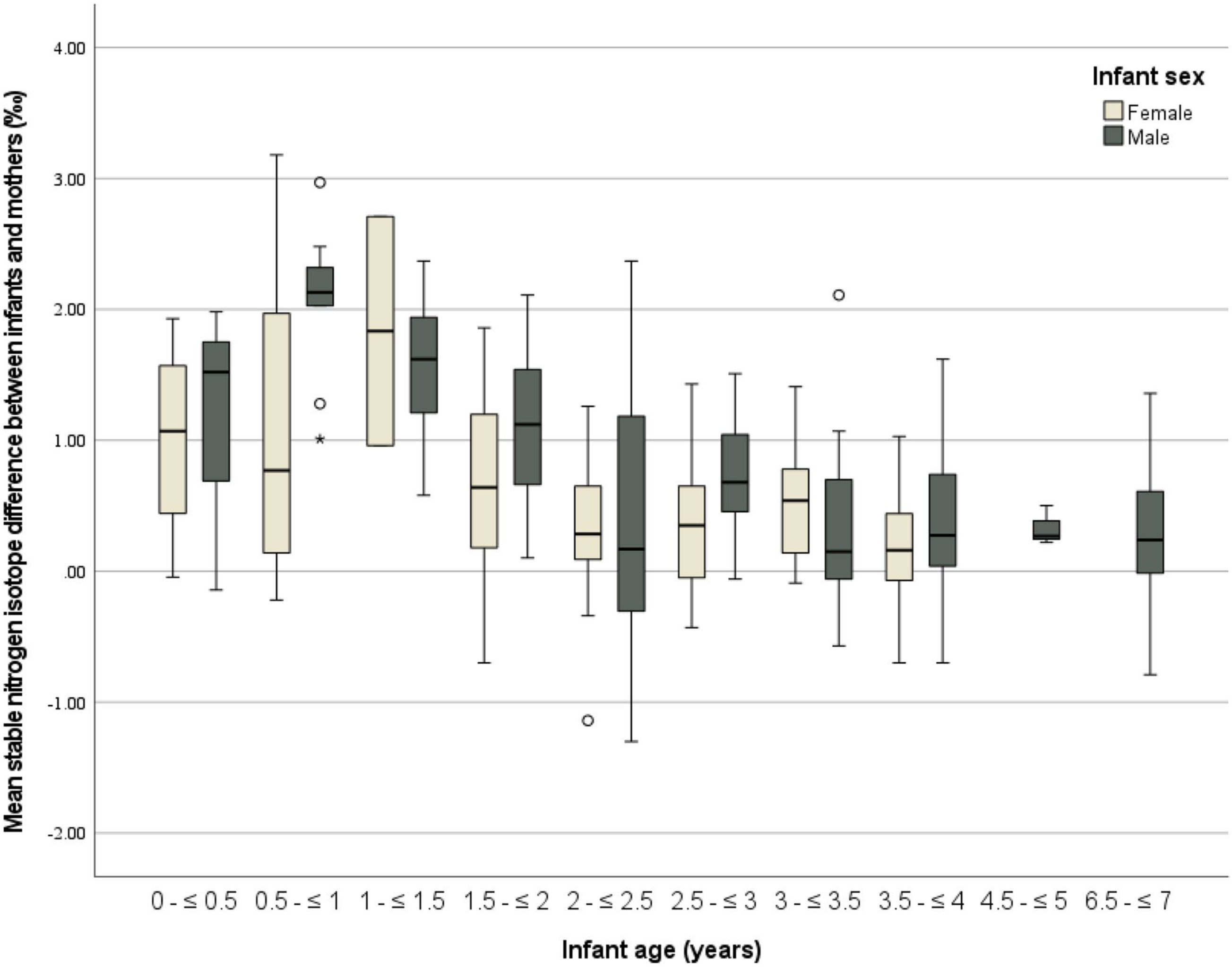

Fig. 3 Mean δ^{15}N differences between mothers and their *physiologically not weaned* infant females ($N = 20$ individuals) and males ($N = 25$) by infant age category. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries), highest and lowest values (whiskers) and outliers (circles; defined using Tukey's method as values between 1.5 and 3 interquartile ranges from the end of a box)

with male infants had longer intervals (mean ± SD = 74.7 ± 11.8 months, median = 74.5 months; $n = 15$) than mothers with female infants (mean ± SD = 57.8 ± 14.2 months, median = 52.3 months, $n = 18$; GEE: $p < 0.01$, Table 5 and Fig. 6). Whether mothers were primiparous or multiparous did not significantly predict inter-birth interval lengths ($p = 0.944$).

Analysis of within-female inter-birth intervals yielded results that were in the same direction. The mean interval following the births of sons was 62.3 ± 10.6 months (95% CI = 55.6–69.1 months) and that following the births of daughters was 59.5 ± 11.5 months (95% CI = 52.0−67.1 months). However, the difference was not significant by conventional standards (df = 11, $t = 1.21$, $p = 0.127$) and the effect size was small (point biserial correlation = 0.129, 95% CI = -0.280–0.480), although the small sample size meant that the test had low power (1-tailed power = 0.112).

Comparison of physiological and behavioral weaning ages

We established physiological weaning ages for four infants. Male CL was weaned at 50 months, male GU was weaned at 85 months, female KA was weaned at 39 months, and female SS was weaned at 49 months. Thus, based on the stable isotope data, the males were weaned at a mean of 67.5 months, and the females were weaned at a mean of 44 months. Behavioral weaning age for the males were 50 months for CL, the month when physiological data also indicated he was weaned, and 83 months for GU, two months earlier than physiological data indicated he was weaned. Female KA was

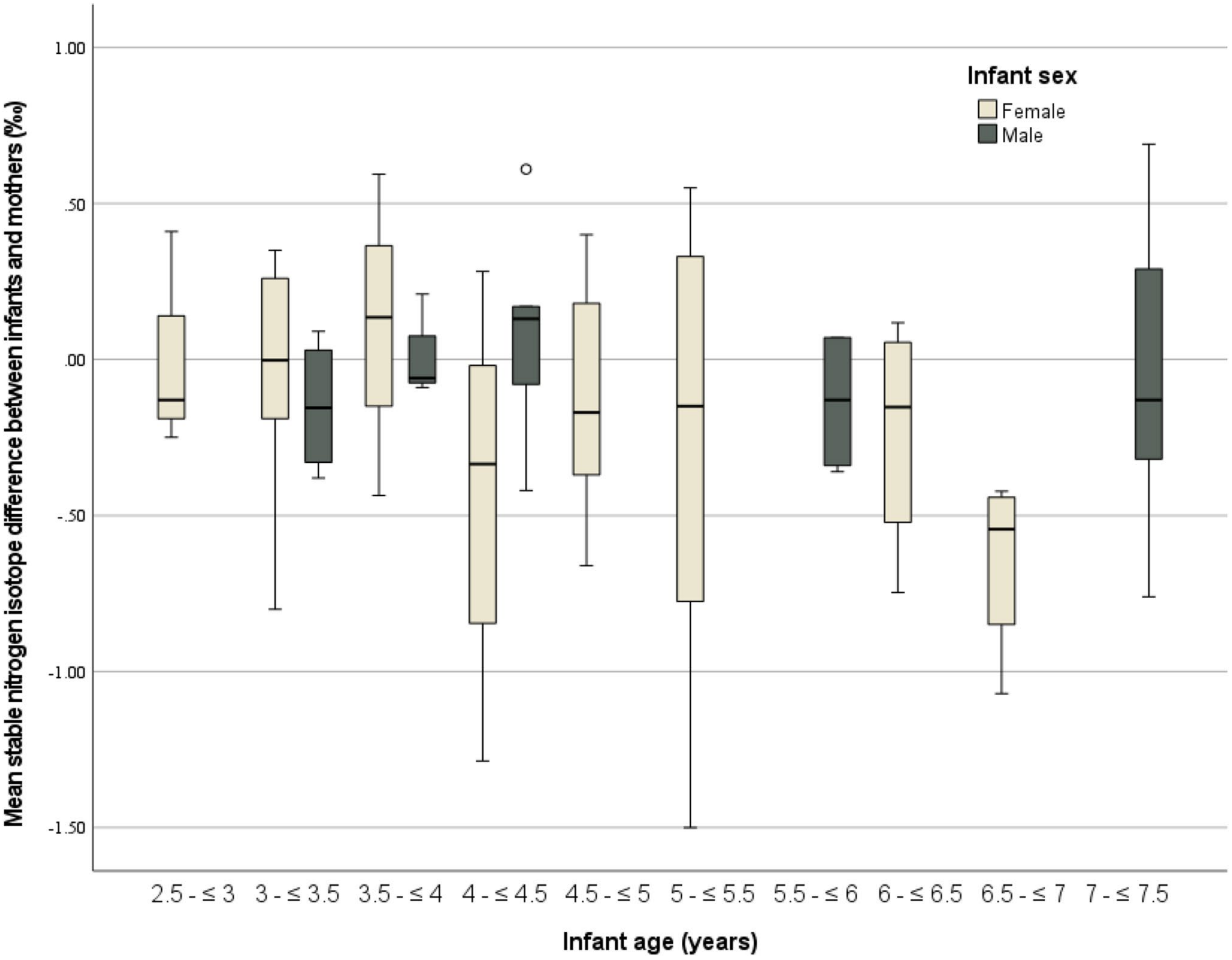

Fig. 4 Mean δ^{15}N differences between mothers and their *physiologically weaned* infant females ($N=9$ individuals) and males ($N=4$) by infant age category. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries), highest and lowest values (whiskers) and outliers (circles; defined using Tukey's method as values between 1.5 and 3 interquartile ranges from the end of a box)

Table 3 Generalized estimating equation results for the associations between infant sex and age, and maternal parity (fixed effects) with mother-infant fecal δ^{15}N differences as a continuous response variable, including infants 0 to ≤ 7 who were not yet physiologically weaned, as determined from the stable nitrogen isotope values ($N=44$ infants, 37 mothers, 211 fecal sample pairs)

Test variable	*B*	Wald 95% confidence intervals		Wald's χ^2 (df = 1)	Standard error	*P*
		Lower	Upper			
Infant sex	0.338	0.084	0.593	6.783	0.130	**0.009**
Infant age category	-0.285	-0.423	-0.147	16.410	0.070	**0.000**
Maternal parity	-0.067	-0.316	0.183	0.275	0.127	0.600

still nursing at 37 months, when behavioral data collection ended, although the physiological assessment indicated she was weaned two months later. Female SS was still nursing at 49 months, when behavioral data collection ended, even though isotopic data indicated she was weaned at this age.

Discussion

Our results collectively indicate that chimpanzee females invest more heavily via lactation in sons than in daughters,

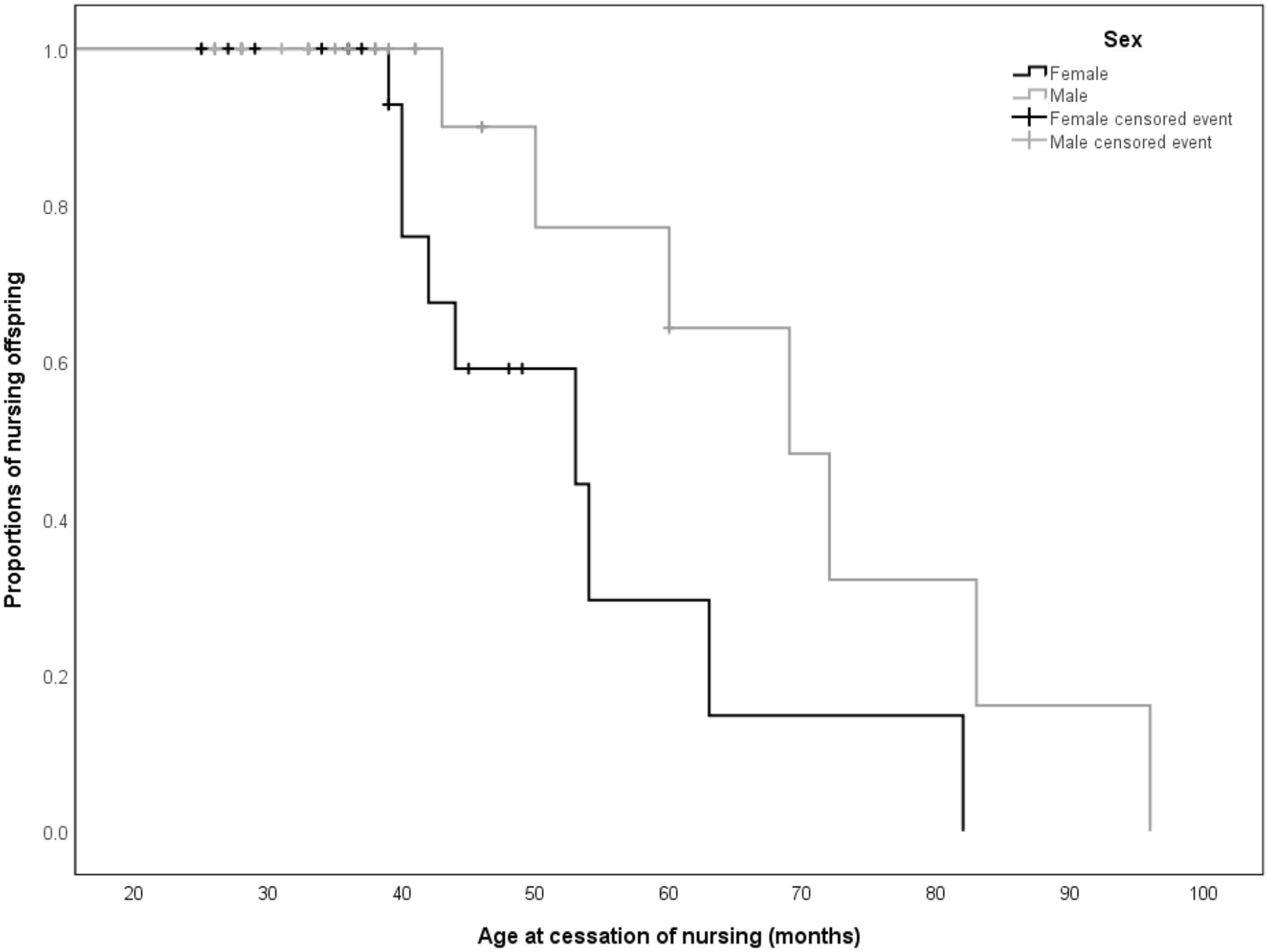

Fig. 5 Kaplan–Meier product limit estimate for nursing survival showing the proportion of offspring still nursing by the end of the study, by infant sex. Plot includes right-censored observations, as we included infants who did not yet stop nursing by the end of the study

Table 4 Statistical tests comparing the differences in the survival distribution for nursing in male ($N=26$) versus female ($N=24$) chimpanzee infants

	Chi-square (df = 1)	*P*
Log Rank (Mantel-Cox)	4.289	**0.038**
Breslow (Generalized Wilcoxon)	4.341	**0.037**
Tarone-Ware	4.496	**0.034**

which supports the hypothesis. Physiological biomarker data revealed that sons had greater proportions of milk in their diets than daughters, which indicated that mothers could have made greater lactation effort for sons, and that sons were weaned at later ages than daughters. Variation in age at weaning had reproductive implications for adult females. Data on inter-birth intervals showed that mothers of sons experienced more delayed fecundity than mothers of daughters. That results of statistical analyses

Table 5 Generalized estimating equation results for associations between infant sex and maternal parity (fixed effects) with inter-birth interval lengths of mothers as a continuous response variable

Test variable	*B*	Wald 95% confidence intervals		Wald's χ^2 (df = 1)	Standard error	*P*
		Lower	Upper			
Infant sex	479.52	176.51	782.52	9.62	154.60	**0.002**
Maternal parity	45.68	-274.47	365.83	0.08	163.35	0.780

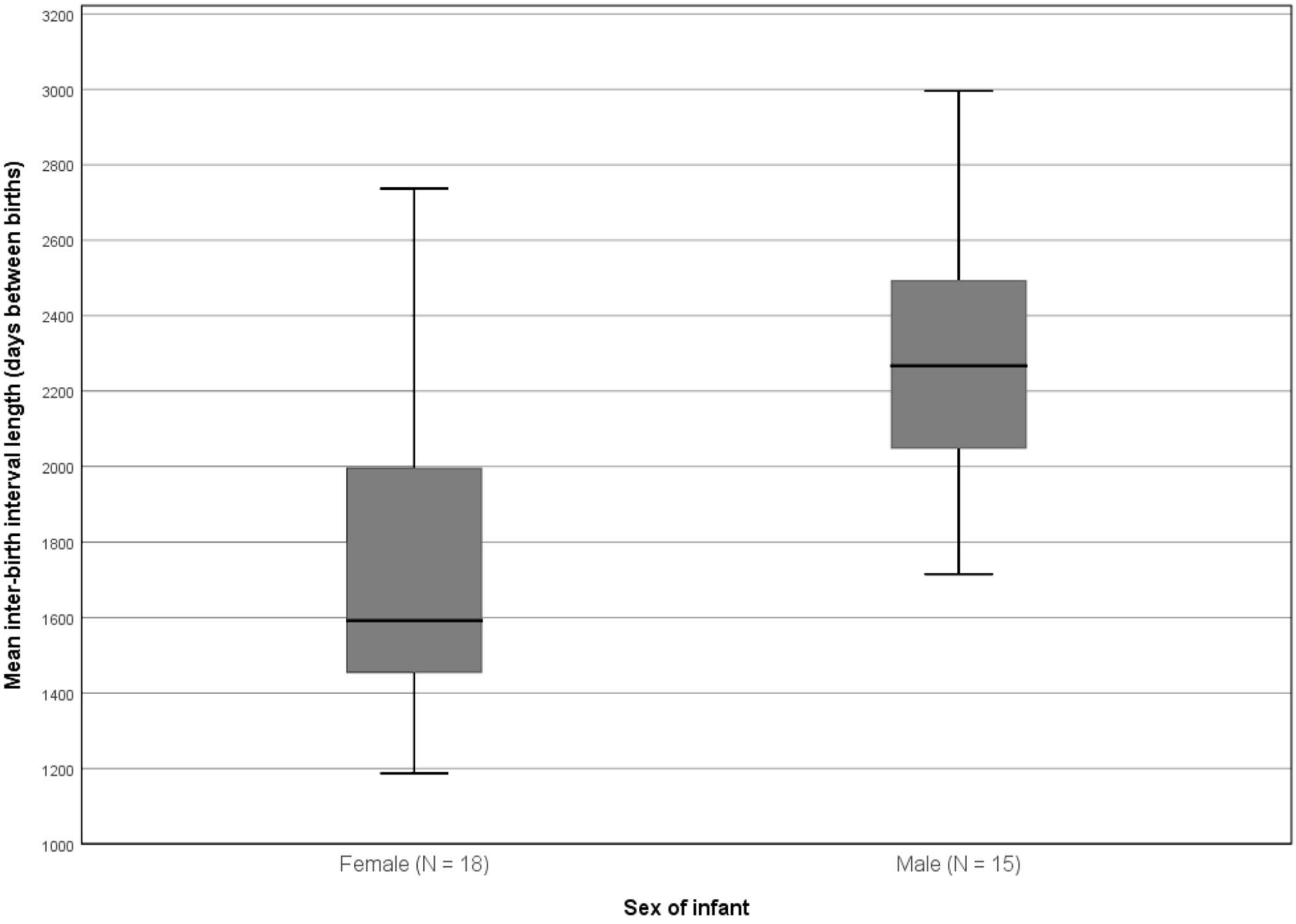

Fig. 6 Inter-birth interval lengths of mothers with sons compared to mothers with daughters (N = 33 mother-infant dyads). Inter-birth interval lengths were the number of days from the birth of the study infant to the birth of their next sibling. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries), and highest and lowest values (whiskers)

of demographic, behavioral, physiological data were in the same direction lends support to the argument that this is a true pattern. Our results are in line with previous studies that found evidence for higher maternal investment in sons for chimpanzees at Taï (Boesch 1997; Fahy et al. 2014) and Gombe (Lonsdorf et al. 2020); in other nonhuman primates (spider monkeys, *A. paniscus*: McFarland Symington 1987; mountain gorillas, *G. beringei*: Robbins et al. 2007; Eckardt et al. 2016; Robbins and Robbins 2021); and in other mammals (African elephants, *L. africana*: Lee and Moss 1986; seals, *M. angustirostris*: Reiter et al. 1978, *Arctocephalus* spp.: Trillmich 1986; Lunn and Arnould 1997; Iberian deer, *C. e. hispanicus*: Landete-Castillejos et al. 2005).

As assessed by isotopic data, the divergence in dependence on maternal milk between male and female infants was clearest early in infancy (≤ 1 year old, > 1.5 to 2 years old) and late in infancy (> 3.5 years old), when males continued relying on milk while many females were weaned (Figs. 1 and 3; when infants > 5 years old were removed from the analyses, results did not change: Supplementary Information). At some ages, however, infant females relied on milk more than males, and overlap between the mother-infant stable nitrogen isotope differences of male and female infants was considerable for all age categories. Thus, while analyses indicated that infant males relied on milk more than females overall, these results should be interpreted with caution as indications of potentially real effects that warrant further investigation to validate and replicate. Similarly, and consistent with an evolutionary conceptual framework in which infant sex is not expected to be the sole driver of maternal investment, the range of observed weaning ages and female interbirth intervals overlapped, which indicated that some sons were weaned earlier than most daughters and that some mothers of sons had shorter inter-birth intervals than most mothers of daughters. This suggests that other variables, including maternal, ecological, or social factors not measured here, also influenced developmental trajectories. For example, infant carrying is presumably the second most energetically expensive form of maternal investment in most primates (Altmann and Samuels 1992); we do not have data on age-independent variation in the time mothers carried infants, and thus cannot assess its possible contribution to variation in inter-birth intervals. Relatively long inter-birth intervals could result from poor maternal condition, as seems to be the case for olive baboons, *Papio anubis* (Patterson et al. 2021). However, no obvious reason exists why mothers with daughters would consistently be in poorer condition than mothers with sons. Also, Ngogo provides relatively favorable energetic conditions for chimpanzees, as indicated by data on feeding ecology (Potts et al. 2011; Watts et al. 2012a, b) and C-peptide data (Emery Thompson et al. 2009). Higher mortality of first-born than later-born infants at Ngogo (Wood et al. 2017) is likely to be an effect of maternal condition that results from trade-offs that primiparas face between investing in their own growth versus maternal investment, but we found no effect of parity on weaning ages.

Male infants might have relied more on milk than non-milk foods than same-aged females because they ingested less solid food. If so, this could explain the higher mother-infant $\delta^{15}N$ differences for males, because even if absolute milk intake was similar between the sexes, milk would still have contributed a greater proportion of the male infant diet relative to non-milk food. Infant solid food intake data at Ngogo are needed to resolve this issue. At Gombe, there were no differences in the amount of time that male and female infant chimpanzees spent feeding on solid foods up to 5 years of age (Lonsdorf et al. 2014). It may thus be that the higher mother-infant $\delta^{15}N$ differences we found for infant males at Ngogo were due to chimpanzee mothers of sons synthesizing more milk, on average, than mothers of daughters. Also, the $\delta^{15}N$ differences we obtained probably did not occur because mothers and infants ate different solid foods. Dependent chimpanzee offspring usually foraged at the same time and on the same foods as their mothers, and mothers always shared foods that were difficult to access or extract (Badescu et al. 2017, 2020).

Stable nitrogen isotope ratios primarily reflect the protein component of milk. We therefore cannot exclude the possibility that total energetic lactational investment was similar for mothers of sons and daughters, but mothers of daughters made milk lower in protein and richer in fats and/or sugars compared to mothers of sons. Differences in maternal milk compositions for sons and daughters have been documented in some species (Landete-Castillejos et al. 2005; Hinde 2007, 2009). Nevertheless, our findings that infant males are weaned later than infant females and that mothers of sons have longer IBIs are strong indications of higher total lactational costs of raising males.

In comparing physiological and behavioral assessments of weaning for the four infants for whom we could determine weaning ages isotopically, we found that behavioral and physiological weaning ages matched exactly for one male, but the second was not observed nursing during the two months before he was physiologically weaned. This disparity could have occurred because he was only night-time nursing for the last few months before he stopped drinking milk. If so, he was the only infant in our dataset who exhibited night-time nutritive nursing despite being identified as behaviorally weaned. We could only assess whether physiological and behavioral weaning ages matched for one of two females. This infant nursed during the month that she was physiologically weaned, which indicated that she was comfort nursing without milk transfer, a pattern described among several of our study infants (Bădescu et al. 2017). Because the sample of infants for whom we could establish weaning ages isotopically was so small, we could not conclusively say whether males were physiologically weaned later than females. However, this seems to be a strong possibility given that physiological weaning occurred an average of 23.5 months later for the two males than the two females for whom we had firm data.

Mothers may be under direct selective pressures to invest more in sons because infant males require greater maternal investment to survive. Infant males could also be more demanding of maternal investment and may solicit greater lactation effort from their mothers than infant females. In some highly sexually dimorphic species, infant growth is faster in males than females, and males therefore require more lactation effort (e.g., mountain gorillas, *G. beringei*: Eckardt et al. 2016; western gorillas, *G.* gorilla: Meder 1990; Leigh and Shea 1996; California sea lion, *Zalophus californianus*: Oftedal et al. 1987; Galápagos sea lion, *Zalophus wollebaeki*: Piedrahita et al. 2014). However, chimpanzee body mass dimorphism is moderate, and while growth data are not available for wild chimpanzee infants younger than 3 years old, the absence of sex differences in body mass at age 3 at Kasekela (Pusey et al. 2005) and the similarity of male and female growth trajectories there and at Kanyawara (Emery Thompson et al. 2016) imply that no consistent sex difference in infant growth exists. Second, male offspring may be biologically less resilient and more sensitive and may therefore be less buffered in the face of hardship than female offspring ("fragile male hypothesis": Clutton-Brock et al. 1985; Stinson 1985; Lindstrom 1999; Wells 2000; Battles 2016). Higher infant mortality rates for males than females have been demonstrated in several mammals including Galápagos sea lions, *Z. wollebaeki* (Kraus et al. 2013), red deer, *Cervus elaphus* (Clutton-Brock et al. 1985), and humans, *Homo sapiens* (Kraemer 2000), as expected under this hypothesis. Infant mortality at Ngogo is substantial and resembles that at other chimpanzee research sites, but whether a sex difference exists is unclear because mortality is highest for very young infants, for whom determining sex is difficult (Wood et al. 2017). At Gombe, immature male chimpanzees between 10 and 15 years of age (but not at younger ages) showed higher mortality than females after maternal loss (Stanton et al. 2020); this suggests that early life mortality in chimpanzees is higher for males. Male offspring could suffer injuries more often, given that (as in other nonhuman primates), they spend more time in social play and engage in rough and tumble play more than females (Owens 1975; Forster and Cords 2005; Lonsdorf et al. 2014). Chimpanzee mothers may therefore face selective pressure to provide high maternal investment in sons, via higher lactation effort and longer lactation length, to increase the probability that sons survive, especially during times of food scarcity or infectious disease epidemics (Clutton-Brock et al. 1985; Stinson 1985; Lindstrom 1999; Wells 2000; Battles 2016). However, food scarcity probably did not affect the differential maternal investment of infants in our study, as noted above. Also, none of our study infants suffered major injuries during data collection. A respiratory virus outbreak at Ngogo in 2016–2017 led to a spike in infant mortality (Negrey et al. 2019), but we cannot assess whether a sex bias in mortality occurred because some young infants died before observers had been able to ascertain their sex.

Female chimpanzees may stand to gain greater inclusive fitness by investing more in sons than in daughters. Female mammals generally produce a limited number of offspring in their lifetimes, whereas males can theoretically produce few or no offspring, or many, depending on their condition and access to fertile females (Trivers 1972). Especially when conditions are good, such as when food availability is high, maximum potential reproductive output is much higher for males than for females (Trivers and Willard 1973; Bercovitch 2002). Similarly, mothers in good condition are predicted to bias investment towards offspring of the sex that is most likely to benefit from the increased maternal contribution (Trivers and Willard 1973; Bercovitch 2002). In male philopatric species, sons are more likely to benefit from the added maternal investment under good conditions than are daughters. At Taï, females identified as high-ranking, who were presumably in better condition than lower-ranking females because of better access to high quality resources, had longer inter-birth intervals following births of sons than births of daughters. Boesch (1997) argued that this showed they invested more via lactation in sons. In contrast, low-ranking females, who were presumably in worse condition, had longer inter-birth intervals after producing daughters and apparently made more lactational investment in daughters than sons (Boesch 1997). Compared to other chimpanzee research sites, food abundance at Ngogo is high and feeding competition is low (Potts et al. 2009, 2011, 2020), and female energetic condition there is probably generally good (Potts et al. 2011; Potts 2013), which helps explain why females do not form dominance hierarchies there (Wakefield 2008). All mothers in this favorable ecological context could benefit from investing more heavily in sons because the potential for high reproductive success, and hence greater inclusive fitness for the mothers, is higher for males than for females (Trivers and Willard 1973; Bercovitch 2002). However, how well the Trivers and Willard (1973) hypothesis applies to chimpanzees is still unclear. Moreover, the relatively high gregariousness of Ngogo females and relatively low variation in fruit abundance there argue against competition effects on female fecundity like those proposed for Gombe (Pusey et al. 1997) and Kanyawara (Kahlenberg et al. 2008). As Riedel et al. (2011) argue, chimpanzee socioecological circumstances are not universally the same, and care should be taken before generalizing findings from any one community to the species level.

Compared to other long-term research sites, reproductive skew among males at Ngogo is low and mean male reproductive success is high (Langergraber et al. 2017). Prior to the permanent community fission, all Ngogo males gained long-term reproductive benefits from participating in cooperative territory defense (Langergraber et al. 2017). Thus, females at Ngogo, in favorable ecological circumstances that allow a large community with many males who can do well in intergroup competition, could benefit from investing more heavily in sons because success in intergroup competition increases mean male reproductive success (Potts et al. 2009, 2011, 2020; Langergraber et al. 2017).

In contrast, daughters might benefit from relatively early nutritional independence. This could facilitate social independence, which is important because most chimpanzee females must establish social relationships with strangers in their new communities. In ursine red howler monkeys (*Alouatta arctoidea*), females who emigrated from natal groups were weaned faster than those who stayed in their natal groups (Crockett and Rudran 1987), which suggests that early weaning provides benefits associated with dispersal. However, the benefits of faster development for female chimpanzees, if any, are unclear, especially because juvenile and young adolescent females at Gombe associated more closely, not less, with their mothers than males did (Pusey 1983, 1990). Thus, it seems unlikely that chimpanzee females acquire social competence faster than males.

Whether early maternal investment in sons influences the sons' reproductive success in chimpanzees is unclear, partly because we do not have data on infant and juvenile growth. Bonobos (*Pan paniscus*) are also male philopatric, and female bonobos can influence the mating opportunities, rank, and reproductive success of their sons after weaning. Such influence seems mostly due to the effect of mother-adult son alliances on male-male competition (Surbeck et al. 2011, 2019). Female chimpanzees rarely intervene in contests between adult males and do not directly influence their adult sons' dominance ranks (Surbeck et al. 2019). Whether early maternal investment influences adult male chimpanzee competitive ability is unknown. At Taï, the presence of mothers was positively associated with post-weaning growth, although this applied to both offspring sexes (Samuni et al. 2020). Likewise, association between mothers and sons before maturity, but after weaning, was positively associated with male reproductive success (Crockford et al. 2020), but causality, if any, was unclear. Any causal influence is likely to act via early growth and nutrition provided by maternal milk, as happens in bighorn sheep (Festa-Bianchet et al. 2000). Adult body size presumably influences male dominance ranks in chimpanzees, and male rank and reproductive success are positively correlated (Wroblewski et al. 2009; Langergraber et al. 2013). If adult body size is also positively associated with early growth and size at weaning, high lactational investment for male offspring could indeed bring fitness payoffs (Clutton-Brock et al. 1984; Clutton-Brock 1991; Lee et al. 1991). Differential maternal investment in sons by chimpanzee females in our study may translate into better condition for male offspring later in life, which could lead to higher male reproductive success and greater inclusive fitness for mothers. Cross-sectional data showing longer inter-birth intervals following births of sons than births of daughters imply that females trade off any growth-related benefits of high lactational investment in males against reduced reproductive rates, as Emery Thompson et al. (2016) argued for chimpanzees at Kanyawara. Continued documentation of within-female variation in inter-birth intervals as a function of offspring sex will help address this issue.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03153-1.

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Author contribution IB co-designed the study, collected the behavioral and fecal data, conducted stable isotope analyses, and conceived and wrote the manuscript. DPW provided access to the field site and fieldwork resources and contributed to the analysis, interpretation and drafting of the manuscript. MAK supervised stable isotope analyses and contributed to the analysis, interpretation and drafting of the manuscript. DWS co-designed the study, supervised the project, and contributed to the theoretical framework, analysis, interpretation and drafting of the manuscript.

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Data availability Data associated with this paper are available in Supplementary Information.

Code availability Not applicable.

Declarations

Ethics approval All components of the data collection and analyses were approved by the Uganda Wildlife Authority (UWA), Uganda National Council for Science and Technology (UNCST), the University of Toronto's Office of Research Ethics and Environmental Health and Safety, and the Université de Montréal's Comité de déontologie de l'expérimentation sur les animaux (CDEA). Permits to export faecal samples were granted by UWA and UNCST. Permits to import faecal samples were granted by Public Health Agency of Canada, Pathogen Regulation Directorate in 2014, and by the Canadian Food Inspection Agency (CFIA) and the Canadian Wildlife Service, CITES in 2018.

Consent for publication Not applicable.

Conflicts of interest The authors declare no competing interests.

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