

## RESEARCH ARTICLE



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# Variability of weaning age in mountain gorillas (*Gorilla beringei beringei*)

Martha M. Robbins  | Andrew M. Robbins

Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

**Correspondence**

Martha M. Robbins, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.  
Email: robbins@eva.mpg.de

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**Abstract**

**Objectives:** Weaning is a key life history milestone for mammals that represents both the end of nutritional investment from the perspective of mothers and the start of complete nutritional independence for the infants. The age at weaning may vary depending on ecological, social, and demographic factors experienced by the mother and infant. Bwindi mountain gorillas live in different environmental conditions and have longer interbirth intervals than their counterparts in the Virunga Volcanoes, yet other life history characteristics of this population remain less well known. We use long-term data from Bwindi Impenetrable National Park, Uganda to examine factors related to weaning age.

**Materials and methods:** We analyzed data on infants born in four mountain gorilla groups in Bwindi to quantify their age of weaning (defined as last nipple contact) and to test if the sex of offspring, parity, and dominance rank of mother influences age of weaning. We also compared the age at weaning and time to conception after resumption of mating in Bwindi and Virunga gorillas.

**Results:** Bwindi gorillas were weaned at an average age of 57.5 months. No difference was found between age of weaning for primiparous and multiparous mothers, nor did maternal dominance rank influence age of weaning, but sons were weaned at a later age than daughters. The majority of Bwindi mothers were still suckling when they resumed mating and mothers generally conceived before they weaned their previous offspring. The age of weaning was significantly later in Bwindi than in Virunga gorillas. After mothers resumed mating, the time to conceiving the next offspring was not significantly longer for Bwindi females than Virungas females (6 vs. 4 months).

**Discussion:** Later weaning age for sons than daughters is similar to findings of other studies of great apes. Bwindi mountain gorillas are weaned at approximately the same age as western gorillas and chimpanzees, which is more than a year later than Virunga mountain gorillas. The results of this study suggest that variation in ecological conditions of populations living in close geographic proximity can result in variation in life history patterns, which has implications for understanding the evolution of the unique life history patterns of humans.

**KEYWORDS**

ecological risk aversion hypothesis, gorilla, life history, weaning

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## 1 | INTRODUCTION

Weaning is considered a key life history milestone in primates and other mammals (Clutton-Brock, 1984; Lee, 1996; Trivers, 1974). It is pertinent to understanding both the evolution of species level life history patterns and variation in individual life history patterns (Lee, 1996; van Noordwijk et al., 2013). Weaning can be viewed from the perspective of both the mother and the infant, reflecting life history tradeoffs for both (Clutton-Brock, 1984; Trivers, 1974). From the point of view of the mother, weaning has implications for maternal investment in a particular offspring as well as lifetime reproductive success. For the infant, weaning signifies nutritional independence, which may be a risky time for species such as those in the order Primates with long periods of immaturity and growth. Females experience a trade-off between investing in current offspring versus future reproduction. This may result in a trade-off between growth and size of infants at weaning and faster reproductive rates (Emery Thompson et al., 2016). Humans have the capacity to wean their infants at a notably young age, which is part of the set of unusual life history traits that characterize humans, including delayed maturation and slow growth, long periods of offspring dependency, short interbirth intervals and menopause (Hawkes & Paine, 2006; Humphrey, 2010; Kuzawa & Bragg, 2012; Walker et al., 2006). Examining factors influencing the variation in weaning in extant great apes contributes to our understanding of the evolution of human life history patterns (Humphrey, 2010; Kuzawa & Bragg, 2012; Sellen, 2007).

Both ecological and social factors that influence nutritional status and mortality risks can impact the timing of life history events (Kuzawa & Bragg, 2012; Walker & Hamilton, 2008). According to the ecological risk aversion hypothesis, the risk of starvation and predation influence behavior that impact mortality rates for juvenile primates. Slower rates of body growth may reduce the risk of starvation for animals that live in more variable environments compared to those in more stable ecological conditions (Janson & van Schaik, 1993). This may also be associated with later ages at attainment of other life history milestones, such as weaning (Knott & Harwell, 2021). In contrast, the “reduced care” hypothesis predicts that mothers should terminate expensive forms of care in particularly stressful conditions (Lycett et al., 1998). Nutritional constraints and increased mortality risk imposed by increased population density may have opposite effects on life history events. Nutritional constraints may be associated with later attainment of life history milestones due to reduced daily energetic investment in growth and maturation, whereas increased mortality risk may lead to earlier termination of lower maternal investment and earlier attainment of life history events, potentially with the cost of smaller body size (Stearns, 1992; Walker & Hamilton, 2008).

Better nutritional conditions lead to an earlier age of weaning in several species (e.g., traditional human societies (Walker et al., 2006), baboons (Altmann & Alberts, 2005; Lycett et al., 1998), vervet monkeys (Whitten & Turner, 2009), and chimpanzees (Emery Thompson et al., 2012). Primiparous mothers may wean their offspring later or have longer interbirth intervals due to the competing demands of investing in current offspring and their own continued growth or if

they face costs of feeding competition by older females (e.g., Pusey et al., 2005; Stearns, 1992). If high ranking females are in better condition and/or have access to greater resources than low ranking females, then they may be able to wean offspring earlier. Finally, primate mothers may invest more in males if they are more costly to rear or because they have greater variance in reproductive success than females (Lonsdorf et al., 2020; Robbins et al., 2007).

Weaning can be difficult to define and quantify, because milk transfer and maternal investment fluctuate over time and weaning it is not a discrete point in time (Borries et al., 2014; Lee, 1996). Behavioral criteria such as the time of last nipple contact are commonly used to quantify weaning. However, this may not be an accurate measure of offspring independence or initiation of maternal investment in the next offspring because milk ingestion rate, quantity, and quality may change over time and time spent in nipple contact is not a good measure of milk transfer (Borries et al., 2014; Hinde & Milligan, 2011; van Noordwijk et al., 2013). New approaches such as fecal stable isotope measures are being developed to provide more accurate, specific estimates of the age at weaning than is possible with only observations of wild animals (e.g., Bădescu et al., 2017). Nonetheless, Borries et al. (2014) recommend that age at last nipple contact is a good measure for observational studies of weaning. Offspring age at last nipple contact, at first postpartum ovulation, and at reconception in Pharye's leaf monkeys and orangutans were highly correlated with each other, suggesting that they were essentially measuring the same process of maternal ability to invest in the next offspring (Borries et al., 2014; van Noordwijk et al., 2018).

Among the great apes, gorillas have the fastest reproductive rates and shortest time to weaning (Eckardt et al., 2016; Knott & Harwell, 2021; Watts, 2012). Within the Virunga mountain gorilla population, social and demographic factors influenced the variability of weaning age, which likely is linked to variation in interbirth intervals. Infants of primiparous females weaned at significantly later age than infants of multiparous females (Eckardt et al., 2016), which presumably contributes to the longer interbirth interval following the birth of the first offspring than subsequent offspring (Robbins, et al., 2006). High-ranking females weaned their sons later than daughters and had longer interbirth intervals following the birth of sons (Eckardt et al., 2016; Robbins et al., 2007). Finally, infants born in one-male groups were weaned earlier than those born in multimale groups, which may be due to a higher infanticide risk in one-male groups (Eckardt et al., 2016).

Additionally, variation in the timing of weaning has been observed between the two species of gorillas. Mountain gorillas (*Gorilla beringei beringei*) of the Virunga Volcanoes were weaned at an average of 40 months of age (Eckardt et al., 2016), compared to western gorillas (*Gorilla gorilla gorilla*) at a median age of 55 months (Nowell & Fletcher, 2007). This interspecific difference was attributed to greater variability in food availability for western gorillas, following the ecological risk aversion hypothesis (Stoinski et al., 2013). Such plasticity observed thus far suggests that there may also be variation between mountain gorilla populations in Bwindi versus the Virungas.

Differences in ecology have been proposed for explaining some life history differences between the two mountain gorilla populations (Robbins et al., 2009; Robbins et al., 2019). Notably, Bwindi mountain

gorillas have an average interbirth interval of 5 years compared to only 4 years for Virunga mountain gorillas (Robbins et al., 2009). This is somewhat remarkable given the two isolated populations are only about 25 km apart, but there are broad differences in altitude and species composition of their habitat, resulting in little overlap in species comprising the majority of their diets (Ganas et al., 2004; Robbins, Nkurunungi, & McNeilage, 2006). Food availability is lower and has greater temporal variability in Bwindi than in the Virungas and Bwindi gorillas travel significantly further per day. However, no differences have been observed in food intake rates or time spent feeding and there are not strong indications of differences in energy balance (Wright et al., 2015). Nonetheless, the lower food availability and higher travel costs might affect the growth trajectories and time until independence for Bwindi gorillas. Seasonally available fruit, which is rarely eaten by Virunga gorillas, comprises about 15% of the Bwindi gorilla diet (Ostrosky & Robbins, 2020). Therefore, the variability in fruit availability in Bwindi may create greater ecological risk for immature gorillas or greater energetic costs for mothers, explaining the longer interbirth interval in Bwindi. Alternatively, the lower reproductive rate caused by the longer interbirth interval in Bwindi may be an indication that this population is closer to carrying capacity than the Virunga population and exhibiting density dependent effects of slower life histories (Eberhardt, 1977; Robbins et al., 2009; Walker & Hamilton, 2008). An examination of weaning patterns in the Bwindi mountain gorillas will help shed light on what is the cause for the difference in interbirth intervals: whether females are investing in offspring for a longer time, taking longer to conceive, or both.

Here, we use 20 years of observational data on gorillas residing in four social groups of mountain gorillas in Bwindi Impenetrable National Park, Uganda to examine variation in weaning. The first aim of this paper is to quantify age of weaning in Bwindi mountain gorillas (defined as last nipple contact). Next, we examine if males are weaned later than females, if primiparous mothers wean infants later than multiparous mothers, and if higher ranking females wean their offspring earlier than lower ranking females. We did not compare age of weaning in one-male versus multimale groups because all four groups were multimale throughout the course of the study with the exception of one group being one-male for two nonconsecutive years out of the 20 years of observation (Kyagurilo Group). We correlate the age of weaning with the time that mothers resumed mating and when they conceived their next offspring. We then examine if the longer interbirth interval in Bwindi mountain gorillas is a result of a later age at weaning and/or a longer time to conception after resumption of estrus cycling in Bwindi gorillas compared to Virunga gorillas.

## 2 | METHODS

### 2.1 | Study population and field observations

This study was conducted on four habituated groups of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Demographic information was available from Bitukura Group and Oruzogo Group since 2011, with routine behavioral observations beginning in 2013.

The Kyagurilo Group was observed since August 1998, with the Mukiza Group fissioning off from that group in April 2016. Observations for this study concluded on February 1, 2020. Each group was contacted on a daily basis. The 25 infants used in the study were detected within 1–2 days of their birth and lived to at least age 30 months. We determined the date of conception by backdating 255 days from an infant's birthdate (Czekala & Sicotte, 2000).

Data were collected during focal animal sampling of the mothers for the entire study period and on the infants since January 2012 as well as on an ad libitum basis throughout the study period. Suckling was defined as nipple contact (Borries et al., 2014). Age of last nipple contact was assessed on a one/zero basis for each mother-offspring dyad to the month and not the day (Borries et al., 2014). Weaned age was quantified using the same definition as Eckardt et al. (2016) as being between the last observed suckling event (e.g., age of last nipple contact) and the following month. For example, if an offspring was last suckling at the age of 36 months, weaned age was estimated at 36.5 months. Mating behavior included mounting with pelvic thrusts, often accompanied by characteristic vocalizations (Robbins, 1999). We used the Elo rating method to calculate dominance rankings in each group using supplants and avoidance interactions among adult females (Wright et al., 2020). We used standardized dominance rankings in each group for each female at the time of birth of the infant.

### 2.2 | Statistical analyses

We used a mixed effect Cox model to compare the weaning ages for sons versus daughters (Pankratz et al., 2005). The analysis used a separate data point for each offspring that was observed since birth ( $N = 25$ ). The predictor variable was the sex of the offspring. The random effect variables were the identity of the mother and the group where the offspring was born. The response variable was the age of last observed nipple contact. Data points were censored when the last observation coincided with the death of the infant or the end of the study. We used a similar Cox model to compare the weaning ages for primiparous versus multiparous mothers and to examine the correlation between weaning age versus the dominance rank of the mother. We did not run multivariate analyses due to small sample sizes.

We ran two generalized linear mixed models (GLMMs) to compare the age when infants were weaned versus their age when their mother resumed mating (Jiang, 2007). To examine the difference between those two ages, the first GLMM used two data points for each infant. The response variable was the age of the infant. The predictor variable was the event that occurred at that age (weaning or the mother resumed mating). The random effect variables were the identity of the infant, the mother, and the group where the offspring was born. To examine the correlation between those two ages, the second GLMM used one data point for each infant. The response variable was the age of the infant when the mother resumed mating. The predictor variable was the age of weaning. The random effect variables were the identity of the mother and the group where the offspring was born. We ran a similar pair of GLMM to compare the age

when infants were weaned versus their age when their mother conceived again.

We ran a GLMM to compare the length of the mating–conception interval with the age of weaning. The test used one data point for each infant in which the weaning age and the mating–conception interval were known. The response variable was the length of the mating–conception interval. The predictor variable was the age of weaning. The random effect variables were the identity of the mother and the group where the offspring was born.

We ran a *t* test to compare the age of weaning at Bwindi versus previously published data from the Virungas (Figure 1 of Eckardt et al., 2016). The test used one data point for each infant that was observed until it was fully weaned. The response variable was the weaning age. The predictor variable was the study site (Bwindi vs. the Virungas). We did not control for the identity of the mother or her group (or censored data points) because those details were not available for the Virungas.

Using data when mothers successfully weaned offspring, we ran a *t* test to compare the length of the interval from the resumption of mating until conception for mothers at Bwindi versus previously published data from the Virungas (Harcourt et al., 1980; Watts, 1990). The test used one data point for each infant in which the mating–conception interval was known. The response variable was the length of the interval. The predictor variable was the study site. We did not control for the identity of the mother or her group because those details were not available for the Virungas.

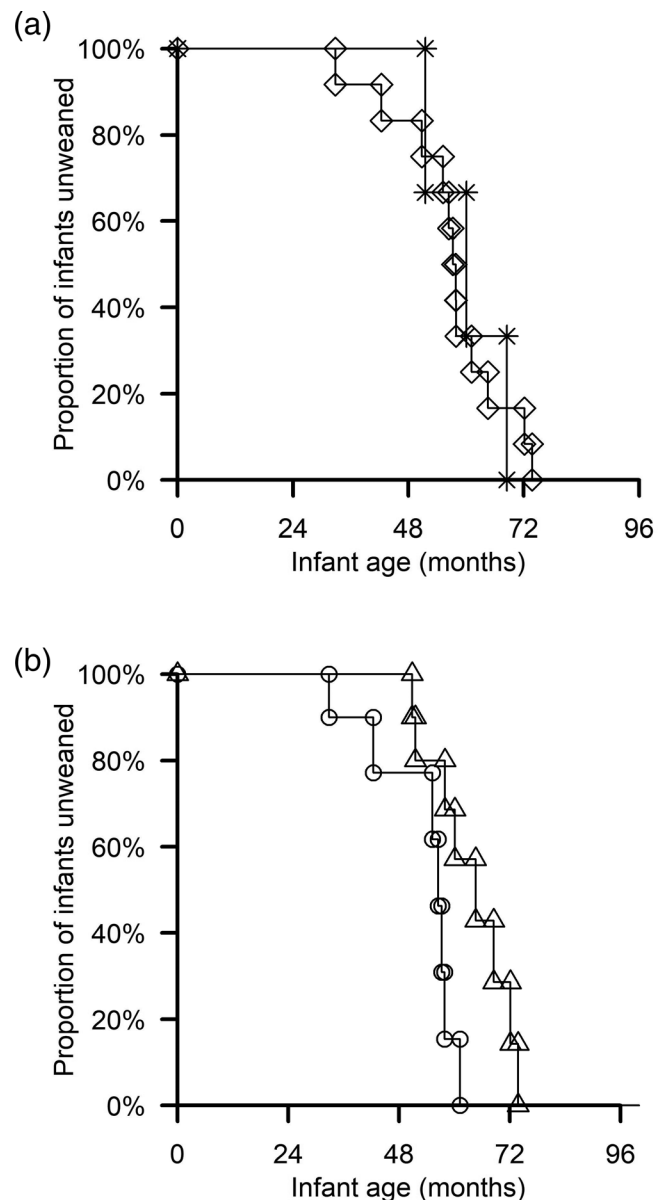
The *t* tests were run using the “*t.test*” function in R (R Core Team 2017). We used the “*coxme*” function for the Cox models, the “*lm*” function for the linear regression, and the “*lmer*” function for the GLMM. To determine the *p*-values for the GLMM, we used the “*drop1*” function to compare each full model with a reduced model in which the predictor variable had been removed.

### 3 | RESULTS

#### 3.1 | Variability of weaning in Bwindi

Of the 25 infants who survived to 30 months of age, 15 of them were weaned. The average age of weaning was  $57.5 \pm 10.7$  months for 15 infants at Bwindi (Table 1). The remaining 10 infants were between 31 and 52 months of age at the end of the study and were not yet weaned. The age of weaning was  $60.0 \pm 8.5$  months for three primiparous mothers, which is not significantly different than  $56.9 \pm 11.4$  months for 12 parous mothers (Figure 1,  $z = 0.1$ ,  $p = 0.92$ ). The age of weaning was  $62.4 \pm 8.8$  months for eight sons, which is significantly later than  $51.9 \pm 10.3$  months for seven daughters (Figure 1(b),  $z = 2.32$ ,  $p = 0.02$ ). The age of weaning was not significantly correlated with the dominance rank of the mother ( $N = 13$ ,  $z = 0.63$ ,  $p = 0.53$ ).

Weaning of two of the 15 individuals was due to the dispersal or death of their mother. The only case in which the mother had either died or dispersed (fate unknown) prior to the average age of weaning was the second shortest time of weaning (MHZ at



**FIGURE 1** (a) Cox regression plots showing the proportion of infants still suckling according to a. parity of mother age (months). Stars represent offspring of primiparous mothers and diamonds represent offspring of multiparous mothers. (b) Sex of offspring. Circles represent daughters and triangles represent sons

42.4 months). Following the disappearance of her mother in June 2018, the orphan's play activity declined sharply, she appeared lethargic and depressed, and she spent most of her time in close proximity to her subadult sister. They both separated from the group following an intergroup encounter in April 2019. Her subadult sister returned to the group 2 weeks later, but MHZ did not. MHZ was spotted alone in June 2019, in a very weak state and presumably died shortly afterward. The only other case of suckling terminated due to the mother dispersing occurred when a male was 72 months of age (GG). He had been observed suckling routinely prior to his mother's departure.

**TABLE 1** Age at weaning, age of infant when mother resumed mating, and age of infant when next offspring was conceived (in months). Infants that did not survive are not listed so some time periods between birthdates of infants by the same mother are not representative of the interbirth intervals. Parity: primi = primiparous, multi = multiparous. Standardized dominance rank was not available for two females (n/a)

Name	Group	Birthdate	Sex	Mother	Parity	Age at Weaning	Age of Infant when Mother Resumed Mating	Age of infant when Next Offspring was Conceived
MB	Kyagurilo	6-Nov-2011	female	KR	Multiparous	32,82		28,65
MHZ	Oruzogo	18-Sep-2014	female	KKB	Multiparous	42,41	41,40	mother disappeared
RG	Bitukura	4-Feb-2011	male	BT	Multiparous	50,83		47,84
KA	Kyagurilo	16-Sep-2002	male	TN	Primiparous	51,52	44,48	51,22
BB	Kyagurilo	5-Feb-2000	female	ST	Multiparous	55,23	49,25	53,72
ZA	Kyagurilo	18-Dec-2010	female	BY	Multiparous	56,44	60,45	mother transferred
TD	Kyagurilo	22-Sep-2005	female	BY	Multiparous	57,26	50,30	54,51
TV	Kyagurilo	5-Jul-2013	female	JN	Multiparous	57,86	48,89	58,51
HP	Kyagurilo	1-Sep-2005	male	MG	Multiparous	57,95	46,72	55,95
MK	Kyagurilo	29-Nov-1999	male	MG	Primiparous	60,09	54,83	60,75
NL	Kyagurilo	28-Dec-2011	female	MG	Multiparous	61,17	none	none
BR	Kyagurilo	15-Sep-2011	male	TN	Multiparous	64,59	51,55	60,25
KY	Kyagurilo	16-Jun-2011	male	TW	Primiparous	68,50	56,51	63,18
GG	Kyagurilo	31-Dec-2010	male	ST	Multiparous	72,15	63,01	mother transferred
KT	Bitukura	7-Apr-2013	male	RH	Multiparous	73,79	64,82	none

Another notable case is when a 22-month-old infant (TV) survived a 10-day separation from her mother, following an intergroup interaction. During this time, the infant was carried by two blackbacks and the dominant silverback, rested in physical contact regularly with the dominant silverback, and was observed feeding. Upon the mother's return to the group, regular suckling resumed. On the opposite end of the spectrum, a male infant (RG) was weaned at 50.8 months of age, 5 months prior to the birth of a younger sibling. RG resumed suckling when NG was 3 months old and continued to do so for the next 21 months.

Two cases of allo-nursing were observed by a primiparous female (JN). When her infant was 5 months old, she nursed a 24-month-old infant for 1 min (after initially pushing the infant away) and when her infant was 8 months old, she nursed a 39-month-old infant for 90 s.

### 3.2 | Weaning and resumption of mating

Infants had an average age of  $50.4 \pm 9.5$  months when their mother resumed mating, which is significantly less than the age of those infants when they were weaned ( $N = 14$ ;  $LRT = 17.6$ ,  $df = 1$ ,  $p < 0.001$ ). In 13 of those 14 cases (93%), mothers resumed mating before weaning their offspring. The infant's age when the mother resumed mating had a significant positive correlation with the age of weaning (coefficient = 1.1,  $LRT = 25.5$ ,  $df = 1$ ,  $p < 0.001$ , Figure 2). Thus, weaning typically occurred earlier for mothers who had resumed mating earlier.

Infants had an average age of  $53.5 \pm 9.9$  months when their mother conceived again, which is significantly less than the age of those infants when they were weaned ( $N = 10$ ;  $LRT = 8.0$ ,  $df = 1$ ,  $p = 0.0046$ ). Thus, mothers generally conceived their next offspring before they weaned their previous offspring. The infant's age when the mother conceived her next offspring had a significant positive correlation with the age of weaning (coefficient = 0.96,  $N = 10$ ,  $LRT = 31.0$ ,  $df = 1$ ,  $p < 0.001$ , Figure 2(b)). Thus, weaning typically occurred earlier for mothers who had conceived their next offspring earlier.

When mothers successfully weaned an infant, they conceived an average of  $5.9 \pm 3.0$  months after they had resumed mating. The interval between the resumption of mating and conception was significantly correlated with the age of weaning (coefficient = 0.23,  $N = 10$ ,  $LRT = 7.5$ ,  $df = 1$ ,  $p = 0.006$ ).

### 3.3 | Comparison with the Virunga mountain gorillas

The average age of weaning at Bwindi is significantly later than  $40.9 \pm 8.1$  months for 34 infants in the Virungas ( $t$  test:  $t = 5.4$ ,  $df = 21.4$ ,  $p < 0.001$ ). Only one (MB) of the 15 infants in Bwindi was weaned at an age younger than the average age in the Virungas. The interval between the resumption of mating and conception at Bwindi is not significantly different from the Virungas ( $3.9 \pm 2.6$  months,  $t$  test:  $t = 1.7$ ,  $df = 16.4$ ,  $p = 0.10$ ).

## 4 | DISCUSSION

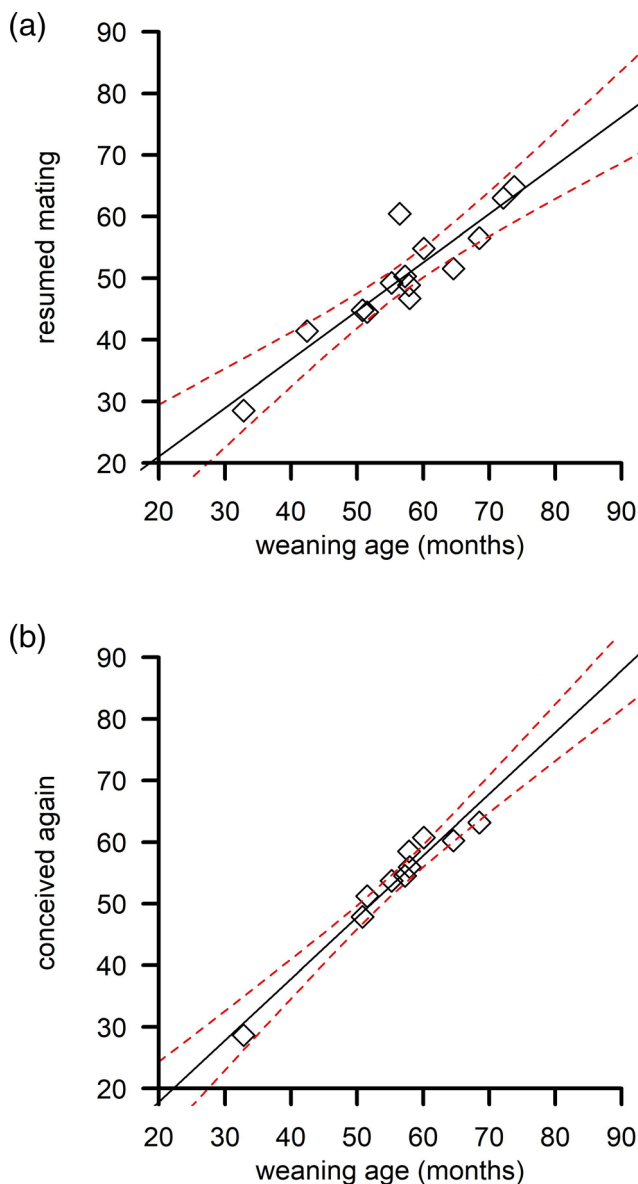
### 4.1 | Variability of weaning within Bwindi

The average age at weaning was 4.8 years, yet varied from 2.7 to 6.2 years in Bwindi mountain gorillas. Gorillas at the average age of weaning spent comparable amount of time feeding as adults (Ostrowsky & Robbins, 2020), suggesting they had reached adult competency in foraging behavior by the time they were weaned.

We found that sons were weaned at significantly later ages than daughters, which suggests that mothers invest more in sons than daughters. Similar results were reported for the Virunga mountain

gorillas and for chimpanzees at Gombe (Eckardt et al., 2016) (Lonsdorf et al., 2019). However, given that observations of suckling alone are a relatively crude measure of energy transfer, in the absence of measures of quality and quantity of milk transfer, these results may not be truly indicative of a difference in maternal investment to sons versus daughters. It may be beneficial for mothers to invest more in male infants than females because male–male competition in mountain gorillas is high and male body size correlates positively with dominance rank (Wright et al., 2019).

The age of weaning was not significantly different for primiparous mothers versus multiparous mothers, and it was not significantly correlated with the dominance rank of the mother. In contrast with our results, weaning was significantly later for primiparous mothers than multiparous mothers among the Virunga mountain gorillas, and dominance rank of the mother had a significant interaction with the offspring sex (Eckardt et al., 2016). The statistical power of our analyses may have been too limited by small sample sizes, which were also evoked to explain the lack of a significant difference between primiparous and multiparous chimpanzees at Gombe (Lonsdorf et al., 2019). We observed one case of a female suckling her juvenile son for a year after the birth of her next infant, which has also been observed in Ngogo chimpanzees (Bădescu et al., 2017), showing the variability possible in duration of suckling behavior.



**FIGURE 2** (a) Correlation between age at weaning and age of the infant when the mother resumed mating (months). (b) Correlation between age at weaning and the age of the infant when the mother conceived again (months). Dashed lines indicate the 95% confidence intervals

### 4.2 | Weaning and resumption of matings and conceiving the next offspring

Resumption of mating and conceiving the next offspring while still suckling occurred in nearly all the cases of mothers who weaned offspring in this study. This is similar to findings of other species including Phayre's leaf monkeys (Borries et al., 2014), chimpanzees (Smith et al., 2013) and orangutans (van Noordwijk et al., 2013, 2018). Age of weaning at Bwindi was positively correlated with the infant's age when the mother resumed mating and when the mother conceived again (Figure 2). These results suggest that females needed to attain a certain level of energy gain before they resumed ovulating as observed in chimpanzees (Emery Thompson et al., 2012). The age of conception was estimated directly from the length of the interbirth interval, so our results are comparable to a correlation between weaning age and interbirth interval in the Virungas. Such results suggest that the length of IBI is generally a reliable indicator of weaning age (Eckardt et al., 2016).

To fully understand the energetic costs of lactation from birth to weaning of an infant and gestation of the next infant, studies are needed that examine changes in suckling rates and food intake over time (e.g., Bray et al., 2018; van Noordwijk et al., 2013), energy balance of the mothers (Emery Thompson et al., 2012), as well as specific measures of milk transfer such as those using stable isotopes (Bădescu et al., 2017; Smith et al., 2017) and milk quality (Hinde & Milligan, 2011). Based on stable isotope measurements, chimpanzees at Ngogo, Uganda were weaned at approximately 4–4.5 years of age, yet continued nipple contact, or “comfort nursing,” for an additional

1–2 years, implying that suckling behavior may be a misleading measure of milk transfer (Bădescu et al., 2017). Further studies on changes in suckling behavior and diet acquisition as well as the use of stable isotopes in gorillas are needed to better understand the patterns of energy balance in female gorillas.

Nonetheless, based on observations of suckling, our findings that the gorillas resume mating and conceive prior to weaning offspring stresses the seemingly nonstop energy transfer to current and then future offspring as females seek to maximize reproductive success (e.g., van Noordwijk et al., 2013). Humans apparently have taken this a step further by having other family members assist in infant carrying and provisioning infants, enabling women to wean their current and conceive their next offspring at very short intervals (Walker et al., 2006).

### 4.3 | Later age of weaning and longer time to conception in Bwindi than the Virungas

The age of weaning was significantly later in Bwindi mountain gorillas than in their counterparts in the Virunga Volcanoes (4.5 vs. 3.3 years). Furthermore, after they resumed mating, mothers took longer to conceive at Bwindi than they did in the Virungas (6 vs. 4 months), but the difference was not statistically significant. Together, these two components contribute to the significantly longer interbirth interval in Bwindi than in the Virungas (Robbins et al., 2009). One potential caveat is that the nearly all of the Bwindi data comes from multimale groups, and the Virungas mountain gorillas had later weaning in multimale groups than one-male groups (Eckardt et al., 2016). This difference was attributed to the risk of infanticide being greater in one-male groups, leading to earlier weaning as a means to reduce this greater mortality risk (Eckardt et al., 2016). However, no difference was found in the interbirth intervals of infants born in one-male and multimale groups in Bwindi (Robbins et al., 2009). Also, the risk of infanticide would not explain the longer time needed to conceive the next offspring. A comparison of mortality risk as all ages are needed to further test the mortality risk hypothesis, but it is difficult to obtain in such long-lived animals.

Bwindi gorillas may have a later age at weaning than the Virunga gorillas if there is lower overall food availability leading to lower energy balance and/or if seasonality in food resources leads to greater unpredictability in energy balance (ecological risk aversion hypothesis; Janson & van Schaik, 1993). The Virunga gorillas live in an environment with extremely high food availability with no or little seasonality (Watts, 1984; Wright et al., 2015). Bwindi gorillas consume more seasonally available fruit than the Virunga gorillas (Ostrosky & Robbins, 2020), which coupled with later weaning provides support for the ecological risk hypothesis. However, they also experience a lower overall availability of the foods that comprise the majority of their diet, yet no strong signs of a difference in energy balance (Wright et al., 2015). Combined, these factors make it difficult to speculate if it is differences in overall availability and/or seasonal predictability of food resources that may be driving these differences.

**TABLE 2** Comparison of weaning age in wild great apes. All studies defined age at weaning as the cessation of suckling except Bădescu et al. (2017) at Ngogo, which used stable isotopes

Species	Site	Weaning age (mean and range in years)
<i>Gorilla beringei beringei</i> <sup>a</sup>	Virungas	3.3 (2–4.75)
<i>Gorilla beringei beringei</i> <sup>b</sup>	Bwindi	4.5 (2.7–6.2)
<i>Gorilla gorilla gorilla</i> <sup>c</sup>	Mbeli Bai	4.6
<i>Pan troglodytes</i> <sup>d</sup>	Gombe	4.7 (2.8–8.0)
<i>Pan troglodytes</i> <sup>e</sup>	Mahale	4–5
<i>Pan troglodytes</i> <sup>f</sup>	Kanyawara	4.1–6
<i>Pan troglodytes</i> <sup>g</sup>	Ngogo	4–4.5
<i>Pongo pygmaeus wurmbii</i> <sup>h</sup>	Tuanan	6.5 (5.8–7.5)

<sup>a</sup>Eckardt et al. (2016).

<sup>b</sup>This study.

<sup>c</sup>Nowell and Fletcher (2007).

<sup>d</sup>Lonsdorf et al. (2019).

<sup>e</sup>Matsumoto (2017).

<sup>f</sup>Bray et al. (2018).

<sup>g</sup>Bădescu et al. (2017).

<sup>h</sup>van Noordwijk et al. (2013).

### 4.4 | Comparisons with other apes

Bwindi mountain gorillas are weaned at approximately the same age as western gorillas (Nowell & Fletcher, 2007; Table 1). Those values from western gorillas may be underestimated since they based on observations of gorillas in a forest clearing in which they predominantly feed and reflect a small proportion of daytime activities (Nowell & Fletcher, 2007). Additional data from sites with habituated western gorillas that are observed throughout the day are needed to make better comparisons among populations and species.

The similarity in weaning age for Bwindi mountain gorillas and western gorillas suggest that the Virungas gorillas are more the exception than the rule, regarding statements that gorillas are weaned at the earliest age of any great ape (Table 2). In fact, the age of weaning for Bwindi mountain gorillas and western gorillas overlap with those for chimpanzees, but is still notably shorter than the late age of weaning in orangutans (Table 2). This would fit with the hypothesis that ecological variability and/or low food availability would lead to later age at weaning and longer interbirth intervals, and slower life histories among great apes, with Virunga mountain gorillas being at one end of the continuum, orangutans at the other end, and Bwindi mountain gorillas, western gorillas, and chimpanzees along the middle (Knott & Harwell, 2021.; Watts, 2012). Comparisons of other life history traits among gorilla populations and great ape species are needed to provide further support to these predictions. Examining the causes and consequences of variability in life history patterns within and between populations of extant great apes contributes to our understanding of the unique life history patterns of humans, with our slow development and longevity, yet early weaning and short interbirth intervals (Humphrey, 2010; Walker et al., 2006).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

**Martha M. Robbins:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration. **Andrew M. Robbins:** Data curation; formal analysis; investigation; methodology.

## DATA AVAILABILITY REQUEST

Data are available on request to the authors.

## ORCID

Martha M. Robbins  <https://orcid.org/0000-0002-6037-7542>

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