Received: 20 October 2022 | Revised: 16 March 2023 | Accepted: 24 May 2023
DOI: 10.1002/ajpa.24792

RESEARCH ARTICLE

AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
WILEY

Comparative life history patterns of female gorillas

Martha M. Robbins[1] | Moses Akantorana[1] | Joseph Arinaitwe[2] | Thomas Breuer[3,4] | Marie Manguette[3] | Shannon McFarlin[5] | Angela Meder[6] | Richard Parnell[3] | Jack L. Richardson[5] | Claudia Stephan[3,7] | Emma J. Stokes[3] | Tara S. Stoinski[8] | Veronica Vecellio[8] | Andrew M. Robbins[1]

[1]Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[2]Uganda Wildlife Authority, Kampala, Uganda
[3]Mbeli Bai Study, Wildlife Conservation Society Congo Program, Brazzaville, Democratic Republic of the Congo
[4]World Wide Fund for Nature, Berlin, Germany
[5]Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC, USA
[6]Berggorilla Regenwald Direkthilfe, Hoevelhof, Germany
[7]Nouabalé-Ndoki Foundation, Brazzaville, Democratic Republic of the Congo
[8]Dian Fossey Gorilla Fund International, Atlanta, Georgia, USA

Correspondence
Martha M. Robbins, Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04013, Germany.
Email: robbins@eva.mpg.de

Funding information
Max Planck Society; United States Fish and Wildlife Service Great Ape Fund; Berggorilla Regenwald Direkthilfe; National Science Foundation, Grant/Award Number: BCS 1753651

Abstract

Objectives: Several theories have been proposed to explain the impact of ecological conditions on differences in life history variables within and between species. Here we compare female life history parameters of one western lowland gorilla population (*Gorilla gorilla gorilla*) and two mountain gorilla populations (*Gorilla beringei beringei*).

Materials and Methods: We compared the age of natal dispersal, age of first birth, interbirth interval, and birth rates using long-term demographic datasets from Mbeli Bai (western gorillas), Bwindi Impenetrable National Park and the Virunga Massif (mountain gorillas).

Results: The Mbeli western gorillas had the latest age at first birth, longest interbirth interval, and slowest surviving birth rate compared to the Virunga mountain gorillas. Bwindi mountain gorillas were intermediate in their life history patterns.

Discussion: These patterns are consistent with differences in feeding ecology across sites. However, it is not possible to determine the evolutionary mechanisms responsible for these differences, whether a consequence of genetic adaptation to fluctuating food supplies ("ecological risk aversion hypothesis") or phenotypic plasticity in response to the abundance of food ("energy balance hypothesis"). Our results do not seem consistent with the extrinsic mortality risks at each site, but current conditions for mountain gorillas are unlikely to match their evolutionary history. Not all traits fell along the expected fast-slow continuum, which illustrates that they can vary independently from each other ("modularity model"). Thus, the life history traits of each gorilla population may reflect a complex interplay of multiple ecological influences that are operating through both genetic adaptations and phenotypic plasticity.

KEYWORDS
female, fertility, gorilla, intrinsic mortality, life history, phenotypic plasticity

1 | INTRODUCTION

Life history theory posits that animals face energetic trade-offs in investment among growth, maintenance and reproduction (Charnov & Berrigan, 1993; Sibly & Brown, 2007; Stearns, 1992). Several theories have been proposed to explain the linkages between ecological conditions and demographic traits such as body size growth rates, age of first reproduction, reproductive rates, and adult lifespan. Extrinsic mortality risk (e.g., unavoidable mortality caused by environmental influences such as predation, low food availability, or infectious disease) may limit the benefits of investment for future reproduction (Promislow & Harvey, 1990). Species in environments with high mortality risk may attain reproductive maturity earlier, invest more heavily in reproduction earlier in life, and experience low offspring survival (Table 1). In contrast, if mortality risk is low, and all else being equal, life history theory predicts an extended developmental period and production of fewer offspring with higher survival rates (Charnov & Berrigan, 1993; Sibly & Brown, 2007).

Primates are notable for their slow growth, later age of first reproduction, longer life spans, and lower fertility compared to most other mammals of similar body size (Charnov & Berrigan, 1993; Jones, 2011). A prevalent framework for explaining the comparatively slow growth and extended juvenile period in primates is the ecological risk aversion hypothesis (ERAH; Table 1; Janson & van Schaik, 1993). While a high risk of unavoidable mortality can lead to fast juvenile growth, Janson and van Schaik (1993) proposed that variance in the energy supply can lead to selection for slower juvenile growth as a strategy to counteract the increased ecological risk of starvation. The original framework of the ERAH invokes genetic differences as a cause of inter-specific variation in juvenile growth rates, but Janson and van Schaik (1993) argue that it can be extended to explain the fast-slow continuum observed in other life history traits in primates, namely age of first reproduction, rate of reproduction, and lifespan. They suggest that differences in ecological risk may explain the slower life histories of frugivores compared to folivores because fruit availability is more variable seasonally and interannually than is availability of foods consumed by folivores (Janson & van Schaik, 1993; Leigh & Shea, 1996). Thus, these broad dietary categories have been a focus in characterizing variation in life history parameters among great apes (Leigh & Shea, 1996; Watts, 2012). However, this is likely an oversimplification and it may be more precise to directly examine the variance in caloric and nutrient intake (Knott & Harwell, 2021).

Interspecific differences in life history parameters are often attributed to genetic adaptations, whereas differences within a species are more likely to reflect phenotypic plasticity. Phenotypic plasticity is the ability of individual genotypes to have different phenotypes in response to different ecological conditions (Barrett et al., 2006; Ellis et al., 2009; Lee & Kappeler, 2003; Walker & Hamilton, 2008). Where plasticity generates novel phenotypes or combinations of traits in response to changing environmental conditions, this may facilitate genetic change via natural selection over longer time scales (Kuzawa & Bragg, 2012). Kuzawa and Bragg (2012) argue that plasticity in life history patterns are linked to nutritional sufficiency (e.g., energy intake) and extrinsic mortality (Table 1). Nutritional sufficiency refers to when energy intake meets or exceeds energy needs (Kuzawa & Bragg, 2012) and hereafter we refer to this as "energy balance" (Emery Thompson, 2017). When energy balance is positive, individuals can have faster growth, earlier reproduction, faster reproductive outputs, and larger adult body size (Kuzawa & Bragg, 2012; Walker et al., 2006). When mortality risks are high, individuals may also have faster growth, earlier reproduction and faster reproductive output, but smaller adult body sizes are predicted and have been observed in some human populations (Kuzawa & Bragg, 2012; Walker et al., 2006). Those predictions for phenotypic plasticity in response to extrinsic mortality are qualitatively similar to the extrinsic mortality risk hypothesis (above) that invokes genetic adaptation as the evolutionary mechanism (Table 1).

Gorillas, classified as two species each having two subspecies, are interesting for examining life history traits because they live in a wide range of ecological conditions (Table 2). Ecological and life history differences have primarily been reported between western gorillas (*Gorilla gorilla gorilla*) and mountain gorillas (*Gorilla beringei beringei*), as well as between the two populations of mountain gorillas in Bwindi and the Virunga Volcanoes (Breuer et al., 2009; Robbins, Gray, et al., 2009; Robbins, Stoinski, et al., 2009; Stoinski et al., 2013). Some life history data have been published for Grauer's gorillas (*Gorilla beringei beringei*) but little detailed information on their dietary intake is available (Yamagiwa et al., 2003). No life history data has been

TABLE 1 Hypotheses for life history variation.

Hypothesis	Ecological condition	Mechanism	Age of first parturition	Interbirth intervals	Birth rates
Extrinsic mortality risk (Promislow & Harvey, 1990)	High extrinsic mortality	Genetic adaptations	Earlier	Shorter	Higher
Ecological risk aversion (Janson & van Schaik, 1993)	Highly variable food supply	Genetic adaptations	Later	Longer	Lower
Phenotypic plasticity in energy balance (Kuzawa & Bragg, 2012)	Low food availability	Phenotypic plasticity	Later	Longer	Lower
Extrinsic mortality plasticity (Kuzawa & Bragg, 2012)	High extrinsic mortality	Phenotypic plasticity	Earlier	Shorter	Higher

Note: See main text for further explanation. The ecological condition is set to worst scenario in all cases for consistency.

TABLE 2 Ecological, dietary, grouping, and dispersal patterns among gorilla populations.

	Western gorillas	Bwindi mountain gorillas	Virunga mountain gorillas
Terrestrial herbaceous vegetation density (stems per m^2)	0.2–2.3[1,2,3]	4.4–10.6[4]	8.8[5]
% Frugivory	30–35%[6,7,8]	15%[9]	<1%[5]
Day journey length	1.5–2.6 km[1,10]	1.0 km[11]	0.8 km[12]
Predation	Leopard present[13]	Leopard no longer present	Leopard no longer present
Group size	8.4 ± 4.3[14]	9.6 ± 6.4[15]	12.5 ± 9.1[16]
Nulliparous female dispersal	100%[17]	77%[18]	50%[19]
Male dispersal	100%[20]	83%[21]	50%[22]
% One male groups	95%[23]	55%[21]	60%[23]

Note: [1] Seiler & Robbins, 2020, [2] Doran-Sheehy et al., 2004, [3] Rogers et al., 2004, [4]Ganas et al., 2004, [5]Watts, 1984, [6]Doran-Sheehy et al., 2009, [7]Masi et al., 2009, [8]Robbins et al., 2022, [9]Ostrofsky & Robbins, 2020, [10]Cipolletta, 2004, [11]Seiler et al., 2018, [12]Wright et al., 2015, [13]Klailova et al., 2012, [14]Parnell, 2002, [15]Roy et al., 2014; [16]Granjon et al., 2020; [17]Manguette et al., 2020; [18]This study; [19]Robbins, Stoinski, et al., 2009; Robbins, Gray, et al., 2009; [20]Breuer et al., 2012; [21]Robbins et al., 2019; [22]Stoinski et al., 2009; [23]Robbins et al., 2016.

reported for Cross River gorillas (*Gorilla gorilla diehli*) because none is habituated and little is known about their diet (Oates et al., 2003).

Western gorillas currently may face a higher extrinsic mortality risk than mountain gorillas, but a comprehensive comparison would be difficult for several reasons. Predation by leopards (*Panthera pardus*) is a threat to western gorillas, but mountain gorillas no longer have natural predators in their habitat (Klailova et al., 2012). However, leopards were present in mountain gorilla habitat as recently as the 1950s (Schaller, 1963), so their life history patterns may still reflect predation risk avoidance strategies. One-male groups are more common for western gorillas than mountain gorillas, which is expected to create a higher risk of infanticide when the dominant male dies (Breuer et al., 2010; Robbins et al., 2013; Watts, 1989). Infanticide can occur throughout infancy, whereas the risk of predation may increase as offspring become more independent from their mothers (Breuer et al., 2010). Mountain gorillas live at higher altitudes that may increase their susceptibility to respiratory infections and thermoregulatory stress (Spelman et al., 2013; Watts, 1998). However, western gorillas are also vulnerable to respiratory disease (Grützmacher et al., 2016) and they live in a warmer climate than mountain gorillas, which may increase the risk of disease, as Gurven et al. (2016) argued for humans. Collectively, it is poorly understood how these factors may affect age-specific mortality across populations. However, recent evidence has shown differences in life expectancy at birth, which is only 14.5 years for western gorillas at Mbeli versus 19.2 years for the Virunga mountain gorillas and 19.9 years for Bwindi mountain gorillas (Colchero et al., 2021).

Ecological risk may vary among gorilla populations because of variation in the distribution, abundance, and seasonality of their main dietary items. Fruit is nearly absent from the diets of Virunga mountain gorillas, but it is important for Bwindi mountain gorillas (15% of diet) and western gorillas (35% of diet) (Doran-Sheehy et al., 2009; Masi et al., 2009; Ostrofsky & Robbins, 2020; Robbins et al., 2022; Watts, 1984; Wright et al., 2015). Fruit consumption varies between 10%–70% of feeding time per month for western gorillas (Masi et al., 2009; Robbins et al., 2022), and between 0%–70% per month for Bwindi mountain gorillas (Ostrofsky & Robbins, 2020). Those temporal variations in fruit consumption may lead to temporal changes in energy intake for western gorillas and Bwindi mountain gorillas (Masi et al., 2015; Wright et al., 2015), but there is no evidence of seasonality in energy intake for Virunga mountain gorillas (Grueter et al., 2014).

Differences in energy intake and energy expenditure may vary among gorilla populations because of the differences in food availability and distribution. The density of terrestrial herbaceous vegetation, a key food source, is the lowest in western gorilla habitat, intermediate in Bwindi, and the highest in the Virunga Volcanoes (Table 1). Correspondingly, western gorillas travel notably further per day than mountain gorillas, with Bwindi mountain gorillas traveling further than Virunga mountain gorillas (Table 1). Energy intake rates and time spent feeding were similar in both mountain gorilla populations (Wright et al., 2015). The only indication of lower energy balance for Bwindi mountain gorillas is longer daily travel distances than their Virunga counterparts, but the increase in distance traveled is unlikely to have more than a negligible effect on energy expenditure (Wright et al., 2015). A comparable analysis of energy intake has not been reported for western gorillas, and potential differences in energy expenditure due to thermoregulation and climbing have not been measured.

Despite the paucity of evidence for clear energetic differences, studies have reported marked differences in life history. Virunga mountain gorillas have the earliest age of weaning and shortest interbirth interval, with Bwindi mountain gorillas having comparable values to western gorillas (Eckardt et al., 2016; Nowell & Fletcher, 2007; Robbins, Gray, et al., 2009; Robbins & Robbins, 2021; Robbins, Stoinski, et al., 2009; Stoinski et al., 2013). Western gorillas have slower physical maturation and are considered to be adults at later ages than Virunga mountain gorillas (Breuer et al., 2009; Galbany et al., 2017). The life history differences between mountain gorillas and western gorillas have been attributed to their differences in frugivory, mainly based on the ecological risk aversion hypothesis (Breuer et al., 2009; Galbany et al., 2017). However, a recent study emphasized the potential importance of phenotypic plasticity, especially in light of faster life histories in captive versus wild western gorillas (Meder, unpublished data; Stoinski et al., 2013), ascribed to higher and more consistent food availability in captivity (Borries et al., 2022). Similarly, life history differences between the mountain gorillas at Bwindi versus the Virungas were suggested to be genetic adaptations based on differences in frugivory, and/or phylogenetic plasticity based on differences in food availability (Robbins, Gray, et al., 2009; Robbins, Stoinski, et al., 2009). While selection might have led to genetic differences between the two species of gorillas that underlie differences in life histories (different adaptations have evolved in the two species, which is also plausible, but less likely, for within-species variation in *G. beringei*), it is also plausible that any such differences between and among species result from the effects of differences in energy availability on shared, underlying genetic mechanisms (the phenotypic plasticity hypothesis). These varied interpretations highlight the need for more comprehensive comparisons of the demographic traits in each population, and more detailed discussion of how they relate to prevailing life history theories.

Here, using larger datasets than previously available, we compare female life history parameters among the Virunga mountain gorillas, Bwindi mountain gorillas, and western gorillas at Mbeli Bai in the Republic of Congo. In addition to updating the previous comparisons of interbirth intervals, we present new comparisons of the age of natal dispersal, age of first birth, and birth rates. The age at natal dispersal is not typically considered a life history variable, but it is a key life history event and it may positively correlated with the age at first reproduction (Robbins, Gray, et al., 2009; Robbins, Stoinski, et al., 2009), so it is included for future comparisons with other studies. Populations with faster maturation could have earlier ages of dispersal and first birth, while populations with faster reproductive outputs could have higher birth rates and shorter interbirth intervals. We discuss our results within the context of the hypotheses explained in Table 1.

2 | METHODS

2.1 | Study sites and data collection

Data for the Bwindi mountain gorillas were collected from April 1993 through May 2020 in Bwindi Impenetrable National Park in Uganda (Robbins et al., 2019; Robbins, Gray, et al., 2009). The demographic records include 341 individuals in 12 social units that have been habituated for research and tourism. Data for the Virunga mountain gorillas were collected by the Dian Fossey Gorilla Fund from September 1967 through December 2017 in Volcanoes National Park in Rwanda (Harcourt & Stewart, 2007; Robbins et al., 2011; Stoinski et al., 2009; Watts, 1990). Those records include 326 individuals in 39 social units that have been habituated for research. Data for western gorillas were collected at Mbeli Bai, a swampy clearing in the Nouabalé-Ndoki National Park in the Republic of Congo (Breuer et al., 2009; Manguette et al., 2019; Parnell, 2002; Stokes et al., 2003). The demographic database includes 525 gorillas in 101 social units that were observed from February 1995 through May 2020.

At Mbeli Bai, observations of the western gorillas when they entered the clearing were made from a 9 m high platform that provides almost complete visibility of the bai (Parnell, 2002). Some of those gorillas have been observed within 1–2 days after their birth, which is known because their group had just been seen without them. The gorillas do not visit the clearing every day, so birth dates were typically estimated by comparing their morphology and behavioral characteristics with other gorillas whose age was already determined (Breuer et al., 2009; Nowell & Fletcher, 2007; Parnell, 2002). The precision of those birthdates is estimated to be within a few weeks for most gorillas who were first observed as infants, up to 1–2 years for gorillas who were first observed as they approached adulthood, and ±4–10 years for adults. The mountain gorillas in Bwindi and in the Virungas were observed daily for several hours, but similar estimates of birthdates were used for individuals who were not monitored since birth (e.g., the initial composition of each group and subsequent immigrants).

2.2 | Statistical analyses

We used generalized linear mixed models (GLMM) using the “lmer” function in R version 4.0.3 to compare the age of natal transfers among the three study sites. The models contained one data point for each nulliparous female who made a natal transfer. The response variable was the age of the female, and the predictor variable was the study site. The species and social group were included as random effect variables. Dates of natal dispersal for western gorillas were estimated as the midpoint between the last observed visit of the source group and the first observed visit of the destination (Breuer et al., 2010; Stokes et al., 2003). We excluded females whose date of birth and/or natal transfer was not known to within 3 months.

We also used GLMM to compare the age of first parturition among the three study sites. The models contained one data point for each nulliparous female whose first birth was observed. The response variable was the age of the female, and the predictor variable was the study site. The species and social group were included as random effect variables. We excluded females whose date of birth and/or first parturition was not known to within 3 months.

We used GLMM to compare the length of interbirth intervals among the three study sites. The models included one data point for each interval. The response variable was the length of the interbirth interval, and the predictor variable was the study site. The species, social group, and the mother of the offspring were included as random effect variables. Interbirth intervals can be significantly shorter when an infant dies, so the analyses were limited to offspring that survived to reach age three (Robbins et al., 2007). We excluded intervals that began/ended with a birth whose date was not known to within 3 months. We also excluded intervals when the mother temporarily left the study groups, because we could have missed infants who died shortly after birth.

We used GLMM to compare infant mortality at each site. The models were run with a binomial error structure and logit link. The models included one data point for each offspring. The response variable equaled "1" if the offspring survived to reach age three, and "0" if the infant died. The predictor variable was the study site. The species, social group, and the mother of the offspring were included as random effect variables. The models excluded offspring that were born during the last 3 years of observations at each study site, because we could not determine whether those infants would survive to reach age three. Dispersal of infants is exceedingly rare (even with their mother), so all disappearances were assumed to be deaths.

We used rate-based χ^2 calculations to compare the surviving birth rates among the study sites (Altmann and Altmann, 1977). The surviving birth rate equaled the number of offspring that survived to reach age three, divided by the number of adult female-years observed. At each site, χ^2 was calculated as $(a-e)^2/e$, where "a" was the actual number of surviving births, and "e" was the expected number of surviving births. The value of "e" for each site equaled $a_T \times f_i/f_T$, where a_T was the total number of surviving births among all sites, f_i was the number of female-years at the site, and f_T was the total number of female-years among all sites. Female-years equaled the number of months that each female was observed, divided by 12. Females were considered adults starting at age eight for mountain gorillas and age 10 for western gorillas. The models excluded the last 3 years of observations at each site, because we could not fully determine whether infants would survive to reach age three.

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020), except for the rate-based χ^2 calculations, which were performed in Excel. In each case, we began with a test that compared all three study sites. If those results were significant, we performed post hoc tests to determine how each pair of sites contributed to the overall differences.

3 | RESULTS

The age of natal transfers did not vary significantly among the three study sites ($\chi^2 = 0.9$, df $= 2$, $p = 0.64$; Figure 1). The average age of natal transfers for females was 8.3 ± 1.5 ($n = 13$) in the Virungas, versus 7.9 ± 0.8 years ($n = 7$) in Bwindi and 8.6 ± 1.7 years ($n = 13$) at Mbeli.

The age of first parturition varied significantly among the three study sites ($\chi^2 = 25.5$, df $= 2$, $p < 0.001$; Figure 1). The average age of first parturition was 10.1 ± 1.7 years ($n = 56$) in the Virungas, which was not significantly different from 10.5 ± 1.3 years ($n = 10$) in Bwindi ($\chi^2 = 0.36$, df $= 1$, $p = 0.55$). The age at first parturition at Mbeli was 12.2 ± 0.6 years ($n = 7$), which was later for females in both the Virungas ($\chi^2 = 10.0$, df $= 1$, $p = 0.002$) and Bwindi ($\chi^2 = 8.9$, df $= 1$, $p = 0.003$).

The average length of interbirth intervals differed significantly among the three study sites ($N = 224$, $\chi^2 = 25.5$, df $= 2$, $p < 0.001$; Figure 1). The average length of interbirth intervals was 4.2 ± 1.2 years in the Virungas ($n = 135$), which was significantly shorter than 5.1 ± 1.3 years ($n = 35$) that survived through infancy at Bwindi ($\chi^2 = 11.1$, df $= 1$, $p < 0.001$). The interbirth intervals at Mbeli, 5.4 ± 0.9 years ($n = 54$), were longer than those in the Virungas ($\chi^2 = 21.6$, df $= 1$, $p < 0.001$), but not significantly different from Bwindi ($\chi^2 = 1.2$, df $= 1$, $p = 0.27$).

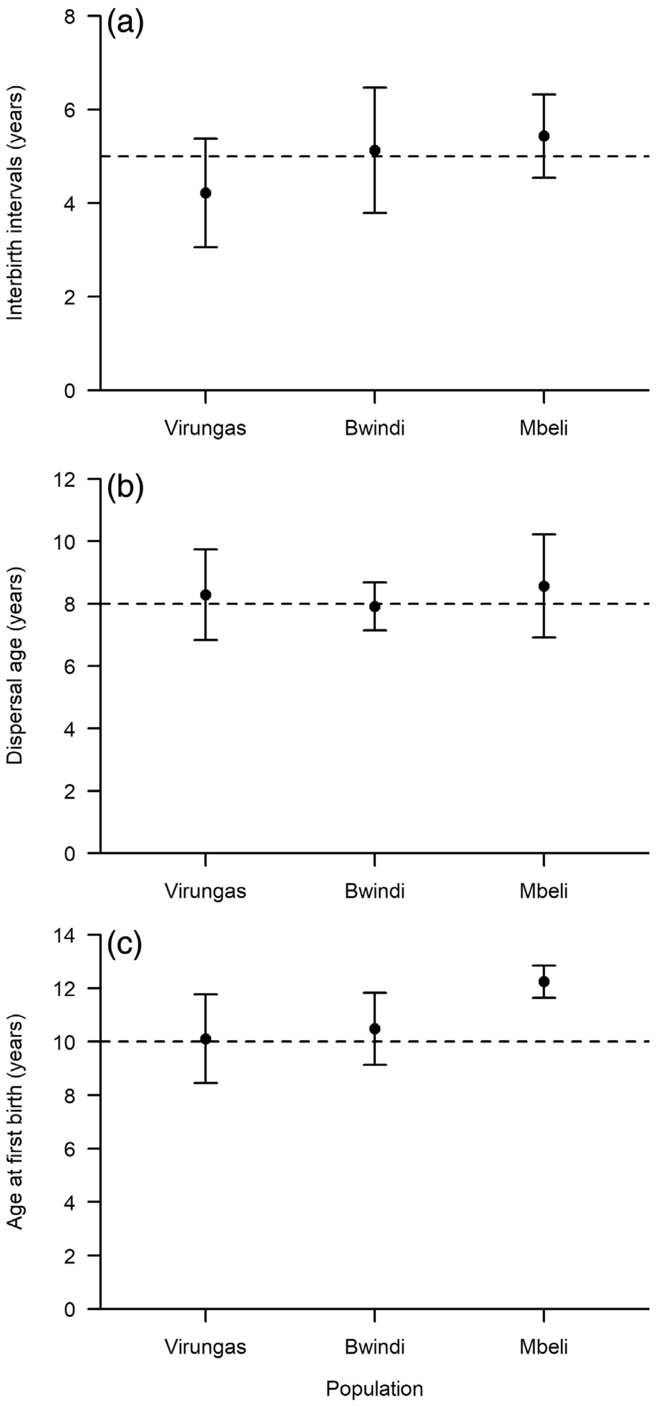

FIGURE 1 Comparisons among the three gorilla populations for (a) Interbirth interval, (b) age at nulliparous dispersal, and (c) age at first birth.

The females at the study sites showed significant differences in the rate of giving birth to offspring that survived to reach age three ($\chi^2 = 7.6$, df $= 2$, $p = 0.023$). The rate was 0.165 surviving births per adult female-year in the Virungas, versus 0.152 in Bwindi and

0.121 at Mbeli ($N = 559.8$, 1045.2, and 1142.0 adult female years, respectively). The surviving birth rate at Mbeli was significantly lower than in Bwindi ($\chi^2 = 4.4$, df $= 1$, $p = 0.035$) and the Virungas ($\chi^2 = 7.3$, df $= 1$, $p = 0.007$). The surviving birth rate at Bwindi did not differ significantly from the Virungas ($\chi^2 = 3.4$, df $= 1$, $p = 0.066$).

4 | DISCUSSION

4.1 | Life history traits

Our results generally showed the earliest maturation and fastest reproductive rates for the Virunga mountain gorillas, followed by Bwindi mountain gorillas, and then the western gorillas at Mbeli Bai (Tables 2 and 3). However, not all traits consistently varied along a fast-slow continuum. Bwindi mountain gorillas had longer interbirth intervals than Virunga mountain gorillas, which is consistent with a later age of weaning in Bwindi (Robbins & Robbins, 2021). However, the two populations shared a similar age at natal transfer, age at first birth and surviving birth rate (Figure 1). The Mbeli western gorillas had a later age at first birth and lower surviving birth rate than both mountain gorilla populations, but the interbirth interval for Mbeli was not different from Bwindi and it was longer than for the Virunga mountain gorillas. The age of natal transfers is the only trait that did not vary significantly among all three sites. Those results suggest that there is more variation in traits that require meeting a threshold of energetic, physiological, or physical condition such as the age at first birth, interbirth intervals, and surviving birth rates. The lack of consistent patterns among the three populations for all life history variables examined lend support to the concept of "life history modes," which postulates that life history variables are dissociable and may respond to selection independently of each other as opposed to a "fast versus slow continuum" of life history traits, (Borries et al., 2011; Leigh & Bernstein, 2006).

4.2 | Life history hypotheses

According to the extrinsic mortality risk hypothesis (Table 1), individuals with a higher extrinsic mortality risk are expected to have earlier maturation and faster reproductive rates than those with lower extrinsic mortality risk (Charnov & Berrigan, 1993; Kuzawa & Bragg, 2012; Promislow & Harvey, 1990). From that perspective, our results would suggest that the extrinsic mortality risk has been highest in the Virungas, followed by Bwindi, and then Mbeli. Those expectations contrast with evidence that western gorillas may currently have a higher extrinsic mortality risk than mountain gorillas (Colchero et al., 2021). The apparent discrepancy does not necessarily conflict with the extrinsic mortality risk hypothesis, however, because the current ecological conditions may not be representative of the evolutionary history of each population. Hypothetically, this caveat could apply to many evaluations of primate evolution, but it seems especially relevant in this case because leopards were reported in the mountain gorilla habitats until just a few decades ago (Schaller, 1963). Similarly, it has been proposed that multimale groups are a moderately recent development in the evolutionary history of mountain gorillas because they do not have other traits typically associated with a multimale social structure in other species, such as large testes, long estrous periods, or exaggerated female sexual swellings (Harcourt, 1995; Robbins, 2003). In addition to the absence of traits that we might expect from an evolutionary history in which formation of multi-male groups was typical, life history traits may also not fully reflect the corresponding decline in infanticide risk for multimale mountain gorilla groups and its impact on extrinsic mortality rates (see introduction; Breuer et al., 2010; Robbins et al., 2013; Watts, 1989; see also Caillaud et al., 2020). Regardless, our results also do not seem consistent with the extrinsic risk hypotheses (Table 1).

According to the ecological risk aversion hypothesis, populations with a higher variation in energy supply are expected to have later maturation and slower reproductive rates (Janson & van Schaik, 1993). Support for the ecological risk aversion hypothesis has

TABLE 3 Mean values for female life history patterns of great apes.

	Virunga mountain gorilla	Bwindi mountain gorilla	Mbeli western gorilla	Bonobo[1]	Chimpanzee	Orangutan
Age at weaning	3.3[2]	4.5[3]	4.6[4]	Not available	4–6[5,6,7,8]	6.5[9]
Age of natal transfer	8.3	7.9	8.6	7–9	11–11.5[10,11]	Female philopatry
Age at first birth	10.1	10.5	12.2	13–14.5	13–14.5[10,11,12]	15[13]
Interbirth interval	4.2	5.1	5.4	4.8	5.0–6.6[10,11,12,14,15]	7.6[13]
Surviving birth rate	0.165	0.152	0.121	Not available	Not available	Not available
Female life expectancy at birth	19.2[16]	19.9[16]	14.5[16]	Not available	7.5 (Tai)[16] 15.0 (Gombe)[16] 16.2 (Kanyawara)[16] 24.0 (Budongo)[16]	28.8[17]

Note: The values are given in years, except for the surviving birth rate, which equaled the number of offspring that survived to reach age three, divided by the number of adult female-years observed. Values for gorilla populations represent results from the current study, except where noted.

[1]Furuichi, 1989; [2]Eckardt et al., 2016; [3]Robbins & Robbins, 2021; [4]Nowell & Fletcher, 2007; [5]Lonsdorf et al., 2020; [6]Matsumoto, 2017; [7]Bray et al., 2018; [8]Bădescu et al., 2017; [9]van Noordwijk et al., 2013; [10]Nishida et al., 2003; [11]Wittig & Boesch, 2019; [12]Wallis, 1997; [13]van Noordwijk et al., 2018; [14]Reynolds, 2005; [15]Sugiyama, 2004; [16]Colchero et al., 2021; [17]Wich et al., 2004.

been found in studies of gibbons (Reichard & Barelli, 2008) and sifaka (Ravosa et al., 1993). Our results would suggest that the variance in energy supply has been highest for western gorillas at Mbeli, followed by mountain gorillas in Bwindi and then those in the Virungas. Those expectations are consistent with the differences in frugivory among the three populations, which has been used as a proxy for the variance in energy supply for gorillas and other primates, but broad food categories may not reflect energy intake (Knott & Harwell, 2021). Further study is needed to more precisely quantify the variation in food availability for gorillas, particularly because the availability of one of the main food sources for western gorillas (tree leaves) has not been quantified at any site. Using endocrine measures, such as C-peptides, to measure energy balance would be a valuable way to avoid the complexities of measuring energy intake via dietary studies and the energetic costs of thermoregulation and climbing (e.g., Grueter et al., 2014).

The energy balance hypothesis is similar in its predictions to the ERAH, but it invokes phenotypic plasticity as the mechanism, whereas the ERAH invokes genetic adaptations as a way to overcome limitations in phenotypic plasticity and it does not preclude existence of any phenotypic plasticity (Table 1). According to this hypothesis, animals are expected to have earlier maturation and faster reproductive rates when they have a greater net energy balance (Kuzawa & Bragg, 2012). From that perspective, we suggest that the energy balance has been highest in the Virungas, followed by Bwindi, and then Mbeli. Those results are consistent with the availability of the most reliable food for gorillas at all sites (terrestrial herbaceous vegetation), as well as the variation in their daily travel distances. To further illustrate the potential for phenotypic plasticity, we ran post hoc *t*-tests to compare the interbirth intervals and age of first parturition between captive western gorillas (A. Meder, unpublished data; females were not on contraception and they resided with a suitable male who was not the silverback of the group where they grew up) versus the wild western gorillas at Mbeli. The average length of interbirth intervals was 4.7 ± 1.8 years ($n = 74$) for captive western gorillas (similar to values in Stoinski et al., 2013; which is significantly less than 5.4 ± 0.9 years [$n = 54$] at Mbeli [$t = 3.2$, df = 112.7, $p = 0.002$]). The average age of first parturition was 8.2 ± 1.2 years among 27 female captive western gorillas, which is significantly earlier than 12.2 ± 0.6 years among seven females at Mbeli ($t = 12.8$, df = 19.7, $p < 0.001$). Those results would suggest that captive western gorillas can more easily maintain a neutral or positive energy balance than wild western gorillsa at Mbeli. The age of first parturition for captive western gorillas was even earlier than the Virunga mountain gorillas (10.1 ± 1.7 years, $n = 56$; $t = 6.1$, df = 69.2, $p < 0.001$). There are no mountain gorillas in captivity so it is unclear whether the life histories of the two species would differ from each other under optimal conditions. Similarly, some of the strongest support for the energy balance hypothesis are cases of accelerated reproductive schedules of animals consuming supplemental food compared to those foraging solely in the wild (e.g., Altmann & Alberts, 2005; Borries et al., 2011). In addition to the life history traits that we have examined, energy balance has also been linked to physical ontogeny, growth rates, and variation in adult body size in humans and baboons (Antón et al., 2016; Leigh & Bernstein, 2006; Walker et al., 2006).

4.3 | Great apes and human evolution

Studies examining the evolution of life history patterns of great apes have mainly focused on the role of food availability and seasonality (e.g., Knott & Harwell, 2021; Leigh & Shea, 1996; Watts, 2012). Orangutans face the most uncertainty in food availability and have the "slowest" life history patterns, mountain gorillas have the most stable food supply and the "fastest" life history patterns, and those of chimpanzees and bonobos are intermediate (Table 3; Emery Thompson, 2013; Knott & Harwell, 2021; van Noordwijk et al., 2018; Watts, 2012). Surprisingly, some life history parameters for western gorillas are closer to chimpanzees than to the Virunga mountain gorillas (Table 3). Western gorilla females disperse from their natal groups and have their first offspring a year earlier than chimpanzees, but they appear to have similar interbirth intervals. Western gorillas consume less fruit and more terrestrial herbaceous vegetation than chimpanzees (Head et al., 2011; Morgan & Sanz, 2006), but the diet of western gorillas is closer to chimpanzees than to the Virunga mountain gorillas (Lodwick & Salmi, 2019; Rothman et al., 2007; Wrangham et al., 1998). However, such between species comparisons should also factor in adult body size, brain size, and growth rates from wild populations.

Like gorillas, chimpanzees and orangutans live in environmentally heterogeneous habitats (Kalan et al., 2020; Vogel et al., 2015), yet few studies have examined inter-population variability in their life history patterns. Variability in reproductive rates of chimpanzees is believed to be linked to differences in environmental conditions within and between populations (Emery Thompson, 2013; Walker et al., 2018; Wittig & Boesch, 2019). No differences in reproductive parameters were observed among orangutan populations, however, despite variation in ecological conditions (van Noordwijk et al., 2018). Food availability and extrinsic mortality risk may influence fertility parameters and survivorship in a complex fashion (Barrett et al., 2006; Ellis et al., 2009; Walker & Hamilton, 2008).

5 | CONCLUSION

This study of mountain gorillas and western gorillas has highlighted the potential roles of both genetic adaptations and phenotypic plasticity by examining the differences in ecological conditions and life history patterns both between species and within species. Our results showed greater similarity between the two populations of mountain gorillas than we observed between mountain gorillas versus western gorillas. Those results may not only reflect that mountain gorillas have greater environmental similarity with each other compared to western gorillas, but also a shorter time of genetic isolation. The Virunga and Bwindi populations split about 5000 years ago (Roy et al., 2014), whereas the western and eastern species of gorillas split roughly 1.2 to 3 MYA, with some gene flow continued until as recently as 80,000 to 200,000 years ago (Xue et al., 2015).

Based on the current ecological conditions for each gorilla population, the detailed differences in life history traits seem more consistent with the ecological risk aversion and energy balance hypotheses than the extrinsic mortality risk hypotheses (Charnov & Berrigan, 1993; Janson & van Schaik, 1993; Kuzawa & Bragg, 2012). Interestingly, not all life history traits vary in the same way across gorilla populations, suggesting that age at first birth, interbirth interval, and surviving birth rate may be dissociated in their response to variation in ecological conditions. When interpreting these findings, however, any conclusions about genetic adaptations must be considered tentative, because the current ecological conditions may not reflect the evolutionary history of each species (especially mountain gorillas). Moreover, the consequences of phenotypic plasticity and genetic adaptation may be difficult to distinguish in the absence of genetic data, as the two mechanisms may also be related. Multiple hypotheses may be relevant simultaneously, and their relative importance can be difficult to discern for closely related populations (Borries et al., 2022; Ellis et al., 2009). Thus, the life history traits of each gorilla population may reflect a complex interplay of multiple ecological influences that are operating through genetic adaptations as well as phenotypic plasticity.

AUTHOR CONTRIBUTIONS

Martha Robbins: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal). **Moses Akantorana:** Data curation (equal). **Joseph Arinaitwe:** Data curation (equal). **Thomas Breuer:** Data curation (equal). **Marie Manguette:** Data curation (equal). **Shannon McFarlin:** Investigation (equal). **Angela Meder:** Data curation (equal). **Richard Parnell:** Data curation (equal). **Jack L. Richardson:** Data curation (equal). **Claudia Stephan:** Data curation (equal). **Emma J. Stokes:** Data curation (equal). **Tara S. Stoinski:** Data curation (equal); funding acquisition (equal). **Veronica Vecellio:** Data curation (equal). **Andrew M. Robbins:** Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal).

ACKNOWLEDGMENTS

Funding for this project was provided by Max Planck Society.

For data collected in Bwindi, we thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology for permission and support in Bwindi Impenetrable National Park. We also thank the International Gorilla Conservation Programme, the Mountain Gorilla Veterinary Program, and Conservation through Public Health for their assistance with the “Gorilla ID and Demography” project. Funding for the Bwindi data collection was provided by Max Planck Society, the United States Fish and Wildlife Service Great Ape Fund, Berggorilla Regenwald Direkthilfe, and the National Science Foundation (BCS 1753651).

The Dian Fossey Gorilla Fund gratefully acknowledges the Rwandan government and national park authorities for their long-term commitment to gorilla conservation. The Fossey Fund is indebted to the many Karisoke field assistants and researchers for their work in collecting demographic data over the past 50 years. Without their tireless effort and commitment to the gorillas, these data would not be possible. Finally, we thank the public and private agencies, foundations and individuals that have provided support to the organization over the last five decades.

In the Republic of Congo, we are grateful to the Ministère de l'Economie Forestière, the Agence Congolaise de la Faune et des Aires Protégées (ACFAP), and to the Institut en Recherche Forestière within the Ministère de la Recherche Scientifique et de l'Innovation Technologique for permission to work in the Nouabalé-Ndoki National Park. Particular thanks go to all research assistants and guides for their invaluable help throughout data collection. We also thank Milou Groenenberg for her contribution to the data set and management of Mbeli Bai. The current research received funding from US Fish and Wildlife Service, the European Union, USAID's Central Africa Forest Ecosystems Conservation Project, Fondation Tri-National de la Sangha, Columbus Zoo and Aquarium, Cincinnati Zoo and Botanical Garden, Woodland Park Zoo, Riverbanks Zoo and Garden, Dublin Zoo, Dutch Gorilla Foundation, Koeln Zoo, and JRS Biodiversity Foundation. Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

Data are available in Supplementary Materials.

ORCID

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

REFERENCES

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: Ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, *57*, 490–501.

Antón, S. C., Taboada, H. G., Middleton, E. R., Rainwater, C. W., Taylor, A. B., Turner, T. R., Turnquist, J. E., Weinstein, K. J., & Williams, S. A. (2016). Morphological variation in *Homo erectus* and the origins of developmental plasticity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150236.

Altmann, S. A., & Altmann, J. (1977). Analysis of rates of behaviour. *Animal Behaviour*, *25*, 364–372.

Bădescu, I., Katzenberg, M. A., Watts, D. P., & Sellen, D. W. (2017). A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. *American Journal of Physical Anthropology*, *162*(2), 285–299.

Barrett, L., Henzi, S. P., & Lycett, J. E. (2006). Whose life is it anyway? Maternal investment, developmental trajectories, and life history strategies in baboons. In *Reproduction and fitness in baboons: Behavioral, ecological, and life history perspectives*. Springer.

Borries, C., Lodwick, J. L., Salmi, R., & Koenig, A. (2022). Phenotypic plasticity rather than ecological risk aversion or folivory can explain variation in gorilla life history. *Frontiers in Ecology and Evolution*, *10*, 873557.

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., & Koenig, A. (2011). Primate life histories and dietary adaptations: A comparison of Asian colobines and Macaques. *American Journal of Physical Anthropology*, *144*(2), 286–299.

Bray, J., Emery Thompson, M., Muller, M. N., Wrangham, R. W., & Machanda, Z. P. (2018). The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). *American Journal of Physical Anthropology*, *165*, 34–46.

Breuer, T., Hockemba, M. B.-N., Olejniczak, C., Parnell, R. J., & Stokes, E. J. (2009). Physical maturation, life-history classes and age estimates of free-ranging western gorillas-insights from Mbeli Bai, Republic of Congo. *American Journal of Primatology*, *71*, 106–119.

Breuer, T., Robbins, A. M., Olejniczak, C., Parnell, R. J., Stokes, E. J., & Robbins, M. M. (2010). Variance in the male reproductive success of western gorillas: Acquiring females is just the beginning. *Behavioral Ecology and Sociobiology*, *64*, 515–528.

Breuer, T., Robbins, A. M., Boesch, C., & Robbins, M. M. (2012). Phenotypic correlates of male reproductive success in western gorillas. *Journal of Human Evolution*, *62*, 466–472.

Caillaud, D., Eckardt, W., Vecellio, V., Ndagijimana, F., Mucyo, J.-P., Hirwa, J. P., & Stoinski, T. (2020). Violent encounters between social units hinder the growth of a high-density mountain gorilla population. *Science Advances*, *6*, eaba0724.

Charnov, E., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? *Evolutionary Anthropology*, *1*, 191–194.

Cipolletta, C. (2004). Effects of group dynamics and diet on the ranging patterns of a western gorilla group (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. *American Journal of Primatology*, *64*(2), 193–205.

Colchero, F., Aburto, J. M., Archie, E. A., Boesch, C., Breuer, T., Campos, F. A., Collins, A., Conde, D. A., Cords, M., Crockford, C., Thompson, M. E., Fedigan, L. M., Fichtel, C., Groenenberg, M., Hobaiter, C., Kappeler, P. M., Lawler, R. R., Lewis, R. J., Machanda, Z. P., … Alberts, S. C. (2021). The long lives of primates and the 'invariant rate of ageing' hypothesis. *Nature Communications*, *12*, 3666.

Doran-Sheehy, D. M., Greer, D., Mongo, P., & Schwindt, D. (2004). Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology*, *64*, 207–222.

Doran-Sheehy, D. M., Mongo, P., Lodwick, J., & Conklin-Brittain, N. L. (2009). Male and female western gorilla diet: Preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. *American Journal of Physical Anthropology*, *140*, 727–738.

Eckardt, W., Fawcett, K., & Fletcher, A. W. (2016). Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): Influential factors. *Behavioral Ecology and Sociobiology*, *70*, 493–507.

Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental dimensions of environmental risk: The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. *Human Nature*, *20*, 204–268.

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology*, *75*, 22–237.

Emery Thompson, M. (2017). Energetics of feeding, social behavior, and life history in non-human primates. *Hormones and Behavior*, *91*, 84–96.

Furuichi, T. (1989). Social interactions and the life history of female Pan paniscus in Wamba, Zaire. *International journal of Primatology*, *10*, 173–197.

Galbany, J., Abavandimwe, D., Vakiener, M., Eckardt, W., Mudakikwa, A., Ndagijimana, F., Stoinski, T. S., & McFarlin, S. C. (2017). Body growth and life history in wild mountain gorillas (*Gorilla beringei beringei*) from Volcanoes National Park, Rwanda. *American Journal of Physical Anthropology*, *163*, 570–590.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A., & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, *25*, 1043–1072.

Granjon, A. C., Robbins, M. M., Arinaitwe, J., Cranfield, M. R., Eckardt, W., Mburanumwe, I., Musana, A., Robbins, A. M., Roy, J., Sollmann, R., Vigilant, L., & Hickey, J. R. (2020). Estimating abundance and growth rates in a wild mountain gorilla population. *Animal Conservation*, 23a.12559.

Grueter, C. C., Deschner, T., Behringer, V., Fawcett, K., & Robbins, M. M. (2014). Socioecological correlates of energy balance using urinary C-peptide measurements in wild female mountain gorillas. *Physiology & Behavior*, *127*, 13–19.

Grützmacher, K. S., Köndgen, S., Keil, V., Todd, A., Feistner, A., Herbinger, I., Petrzelkova, K., Fuh, T., Leendertz, S. A., Calvignac-Spencer, S., & Leendertz, F. H. (2016). Codetection of respiratory syncytial virus in habituated wild western lowland gorillas and humans during a respiratory disease outbreak. *EcoHealth*, *13*, 499–510.

Gurven, M. D., Trumble, B. C., Stieglitz, J., Yetish, G., Cummings, D., Blackwell, A. D., Beheim, B., Kaplan, H. S., & Pontzer, H. (2016). High resting metabolic rate among Amazonian forager-horticulturalists experiencing high pathogen burden. *American Journal of Physical Anthropology*, *161*(3), 414–425.

Harcourt, A. H. (1995). Sexual selection and sperm competition in primates: what are male genitalia good for? *Evolutionary Anthropology*, *4*, 121–129.

Harcourt, A. H., & Stewart, K. J. (2007). *Gorilla society: Conflict, compromise, and cooperation between the sexes*. University of Chicago Press.

Head, J. S., Boesch, C., Makaga, L., & Robbins, M. M. (2011). Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology*, *32*, 755–775.

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: Slow and steady wins the race. In *Juvenile primates: Life history, development, and behavior* (pp. 57–74). Oxford University Press.

Jones, J. H. (2011). Primates and the evolution of long, slow life histories. *Current Biology*, *21*, R708–R717.

Kalan, A. K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C. D., Abwe, E. E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E. A., Bailey, E., Bessone, M., Brazzola, G., Buh, V. E., Chancellor, R., Cohen, H., Coupland, C., … Kühl, H. S. (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature Communications*, *11*, 4451.

Klailova, M., Casanova, C., Henschel, P., Lee, P., Rovero, F., & Todd, A. (2012). Non-human predator interactions with wild great apes in Africa and the use of camera traps to study their dynamics. *Folia Primatologica*, *83*, 312–328.

Knott, C. D., & Harwell, F. (2021). Ecological risk and the evolution of great ape life histories. In *Chimpanzees in context: A comparative perspective on chimpanzee behavior, cognition, conservation and welfare*. University of Chicago Press.

Kuzawa, C. W., & Bragg, J. M. (2012). Plasticity in human life history strategy: Implications for contemporary human variation and the evolution of genus *Homo*. *Current Anthropology*, *53*(S6), S369–S382.

Lee, P., & Kappeler, P. M. (2003). Socioecological correlates of phenotypic plasticity of primate life histories. In *Primate life histories and socioecology* (pp. 41–65). University of Chicago Press.

Leigh, S., & Bernstein, R. (2006). Ontogeny, life history, and maternal investment in baboons. In *Reproduction and fitness in babbons* (pp. 225–256). Springer Press.

Leigh, S., & Shea, B. (1996). Ontogeny of body size variation in African apes. *American Journal of Physical Anthropology*, *99*, 43–65.

Lodwick, J. L., & Salmi, R. (2019). Nutritional composition of the diet of the western gorilla (*Gorilla gorilla*): Interspecific variation in diet quality. *American Journal of Primatology*, *81*, e23044.

Lonsdorf, E. V., Stanton, M. A., Pusey, A. E., & Murray, C. M. (2020). Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. *American Journal of Physical Anthropology*, *171*, 419–429.

Manguette, M. L., Robbins, A. M., Breuer, T., Stokes, E. J., Parnell, R. J., & Robbins, M. M. (2019). Intersexual conflict influences female reproductive success in a female-dispersing primate. *Behavioral Ecology and Sociobiology*, *73*, 118.

Manguette, M. L., Robbins, A. M., Breuer, T., Stokes, E. J., Parnell, R. J., & Robbins, M. M. (2020). Female dispersal patterns influenced by male tenure duration and group size in western lowland gorillas. *Behavioral Ecology and Sociobiology*, *74*, 81.

Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western Lowland Gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *American Journal of Primatology*, *71*, 91–100.

Masi, S., Mundry, R., Ortmann, S., Cipolletta, C., Boitani, L., & Robbins, M. M. (2015). The influence of seasonal frugivory on nutrient and energy intake in wild western gorillas. *PLoS One*, *10*, e0129254.

Matsumoto, T. (2017). Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact. *American Journal of Physical Anthropology*, *163*, 356–366.

Morgan, D., & Sanz, C. (2006). Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 97–122). Cambridge University Press.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., & Hosaka, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, *59*, 99–121.

Nowell, A. A., & Fletcher, A. W. (2007). Development of Independence from the Mother in Gorilla gorilla gorilla. *International Journal of Primatology*, *28*(2), 441–455.

Oates, J. F., McFarland, K. L., Groves, J. L., Bergl, R. A., Linder, J. M., & Disotell, T. R. (2003). The Cross River gorilla: Natural history and status of a neglected and critically endangered subspecies. In A. B. Taylor & M. L. Goldsmith (Eds.), *Gorilla biology: A multidisciplinary approach* (pp. 472–497). Cambridge University Press.

Ostrofsky, K. R., & Robbins, M. M. (2020). Fruit-feeding and activity patterns of mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda. *American Journal of Physical Anthropology*, *173*, 3–20.

Parnell, R. J. (2002). Group size and structure in western lowland gorillas (Gorilla gorilla gorilla) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, *56*, 193–206.

Promislow, D., & Harvey, P. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of Zoology*, *220*, 417–438.

R Core Team. (2020). R: A language and environment for statistical computing.Vienna: R Foundation for Statistical Computing. https://www.Rproject.org

Ravosa, M. J., Meyers, D. M., & Glander, K. E. (1993). Relative growth of the limbs and trunk in sifakas: Heterochronic, ecological, and functional considerations. *American Journal of Physical Anthropology*, *92*, 499–520.

Reichard, U. H., & Barelli, C. (2008). Life history and reproductive strategies of Khao Yai Hylobates lar: Implications for social evolution in apes. *International Journal of Primatology*, *29*, 823–844.

Reynolds, V. (2005). *The chimpanzees of Budongo Forest: Ecology, behaviour, and conservation*. Oxford University Press.

Robbins, A. M., Gray, M., Basabose, A., Uwingeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2013). Impact of male infanticide on the social structure of mountain gorillas. *PLoS One*, *8*(11), e78256.

Robbins, A. M., Gray, M., Breuer, T., Manguette, M., Stokes, E., Uwingeli, P., Mburanumwe, I., Kagoda, E., & Robbins, M. M. (2016). Mothers may shape the variations in social organization among gorillas. *Royal Society Open Science*, *3*, 160533.

Robbins, A. M., Stoinski, T. S., Fawcett, K. A., & Robbins, M. M. (2009). Does dispersal cause reproductive delays in female mountain gorillas? *Behaviour*, *146*, 525–549.

Robbins, M. M., Akantorana, M., Arinaitwe, J., Kabano, P., Kayijamahe, C., Gray, M., Guschanski, K., Richardson, J., Roy, J., Tindimwebwa, V., Vigilant, L., & Robbins, A. M. (2019). Dispersal and reproductive careers of male mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Primates*, *60*, 133–142.

Robbins, M. M., Gray, M., Fawcett, K. A., Nutter, F. B., Uwingeli, P., Mburanumwe, I., Kagoda, E., Basabose, A., Stoinski, T. S., Cranfield, M. R., Byamukama, J., Spelman, L. H., & Robbins, A. M. (2011). Extreme conservation leads to recovery of the Virunga mountain gorillas. *PLoS One*, *6*, e19788.

Robbins, M. M., Gray, M., Kagoda, E., & Robbins, A. M. (2009). Population dynamics of the Bwindi mountain gorillas. *Biological Conservation*, *142*, 2886–2895.

Robbins, M. M., Ortmann, S., & Seiler, N. (2022). Dietary variability of western gorillas (*Gorilla gorilla gorilla*). *PLoS One*, *17*, e0271576.

Robbins, M. M., & Robbins, A. M. (2021). Variability of weaning age in mountain gorillas (*Gorilla beringei beringei*). *American Journal of Physical Anthropology*, *174*, 776–784.

Robbins, M. M., Robbins, A. M., Gerald-Steklis, N., & Steklis, H. D. (2007). Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*). *Behavioral Ecology and Sociobiology*, *61*, 919–931.

Robbins, M. M. (2003). Behavioral aspects of sexual selection in mountain gorillas. In C. L. Jones (Ed.), *Sexual Selection & Reproductive Competition in Primates: New Perspectives and Directions* (pp. 477–501). American Society of Primatologists.

Robbins, M. M., Ortmann, S., & Seiler, N. (2022). Dietary variability of western gorillas (Gorilla gorilla gorilla). *Plos One*, *17*, e0271576.

Rogers, M. E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., Mcfarland, K., Nishihara, T., Remis, M., & Tutin, C. E. G. (2004). Western gorilla diet: A synthesis from six sites. *American Journal of Primatology*, *64*, 173–192.

Rothman, J. M., Plumptre, A. J., Dierenfeld, E. S., & Pell, A. N. (2007). Nutritional composition of the diet of the gorilla (*Gorilla beringei*): A comparison between two montane habitats. *Journal of Tropical Ecology*, *23*, 673–682.

Roy, J., Arandjelovic, M., Bradley, B. J., Guschanski, K., Stephens, C. R., Bucknell, D., Cirhuza, H., Kusamba, C., Kyungu, J. C., Smith, V., Robbins, M. M., & Vigilant, L. (2014). Recent divergences and size decreases of eastern gorilla populations. *Biology Letters*, *10*, 20140811.

Schaller, G. (1963). *The mountain gorilla: Ecology and behavior*. University of Chicago Press.

Seiler, N., Boesch, C., Ortmann, S., Mundry, R., & Robbins, M. M. (2018). Ecological and social influences on space use behavior in a large nonterritorial mammal. *American Journal of Primatology*, *80*, e22754.

Seiler, N., & Robbins, M. M. (2020). Ecological correlates of space use patterns in wild western lowland gorillas. *American Journal of Primatology*, *82*, e23168.

Sibly, R. M., & Brown, J. H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences*, *104*, 17707–17712.

Spelman, L. H., Gilardi, K. V. K., Lukasik-Braum, M., Kinani, J.-F., Nyirakaragire, E., Lowenstine, L. J., & Cranfield, M. R. (2013). Respiratory disease in mountain gorillas (*Gorilla beringei beringei)* in Rwanda, 1990–2010: Outbreaks, clinical course, and medical management. *Journal of Zoo and Wildlife Medicine*, *44*, 1027–1035.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Stoinski, T. S., Perdue, B., Breuer, T., & Hoff, M. P. (2013). Variability in the developmental life history of the genus *Gorilla*: Gorilla developmental life history. *American Journal of Physical Anthropology*, *152*, 165–172.

Stoinski, T. S., Vecellio, V., Ngaboyamahina, T., Ndagijimana, F., Rosenbaum, S., & Fawcett, K. A. (2009). Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*. *Animal Behaviour*, *77*, 1155–1164.

Stokes, E. J., Parnell, R. J., & Olejniczak, C. (2003). Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology*, *54*, 329–339.

Sugiyama, Y. (2004). Demography and life history parameters of chimpanzees at Boussou., Guinea. *American Journal of Physical Anthropology*, *124*, 154–165.

van Noordwijk, M. A., Utami Atmoko, S. S., Knott, C. D., Kuze, N., Morrogh-Bernard, H. C., Oram, F., Schuppli, C., van Schaik, C. P., & Willems, E. P. (2018). The slow ape: High infant survival and long interbirth intervals in wild orangutans. *Journal of Human Evolution*, *125*, 38–49.

van Noordwijk, M. A., Willems, E. P., Utami Atmoko, S. S., Kuzawa, C. W., & van Schaik, C. P. (2013). Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behavioral Ecology and Sociobiology*, *67*, 805–814.

Vogel, E. R., Harrison, M. E., Zulfa, A., Bransford, T. D., Alavi, S. E., Husson, S., Morrogh-Bernard, H., Santiano, Firtsman, T., Utami-Atmoko, S. S., van Noordwijk, M. A., & Farida, W. R. (2015). Nutritional differences between two orangutan habitats: Implications for population density. *PLoS One*, *10*, e0138612.

Walker, K. K., Walker, C. S., Goodall, J., & Pusey, A. E. (2018). Maturation is prolonged and variable in female chimpanzees. *Journal of Human Evolution*, *114*, 131–140.

Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., Djurovic, G., Hames, R., Hurtado, A. M., Kaplan, H., Kramer, K., Oliver, W. J., Valeggia, C., & Yamauchi, T. (2006). Growth rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology*, *18*, 295–311.

Walker, R. S., & Hamilton, M. J. (2008). Life-history consequences of density dependence and the evolution of human body size. *Current Anthropology*, *49*, 8.

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, *109*, 297–307.

Watts, D. P. (1984). Composition and variability of mountain gorilla diets in the Central Virungas. *American Journal of Primatology*, *7*, 323–356.

Watts, D. P. (1989). Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. *Ethology*, *81*, 1–18.

Watts, D. P. (1990). Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zoo Biology*, *9*, 185–200.

Watts, D. P. (1998). Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). *International Journal of Primatology*, *19*, 929–948.

Watts, D. P. (2012). The apes: Taxonomy, biogeography, life histories, and behavioral ecology. In *The evolution of primate societies* (pp. 113–142). University of Chicago Press.

Wich, S. A., Utami-Atmoko, S. S., Setia, T. M., Rijksen, H. D., Schürmann, C., van Hooff, J. A. R. A. M., & van Schaik, C. P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution*, *47*(6), 385–398.

Wittig, R., & Boesch, C. (2019). Demography and life history of five chimpanzee communities in Tai National Park. In *The chimpanzees of the Taï forest: 40 years of research*. Cambridge University Press.

Wrangham, R., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance I. Antifeedants. *International Journal of Primatology*, *19*, 949–970.

Wright, E., Grueter, C. C., Seiler, N., Abavandimwe, D., Stoinski, T. S., Ortmann, S., & Robbins, M. M. (2015). Energetic responses to variation in food availability in the two mountain gorilla populations (*Gorilla beringei beringei*). *American Journal of Physical Anthropology*, *158*, 487–500.

Xue, Y., Prado-Martinez, J., Sudmant, P. H., Narasimhan, V., Ayub, Q., Szpak, M., Frandsen, P., Chen, Y., Yngvadottir, B., Cooper, D. N., de Manuel, M., Hernandez-Rodriguez, J., Lobon, I., Siegismund, H. R., Pagani, L., Quail, M. A., Hvilsom, C., Mudakikwa, A., Eichler, E. E., … Scally, A. (2015). Mountain gorilla genomes reveal the impact of long-term population decline and inbreeding. *Science*, *348*, 242–245.

Yamagiwa, J., Kahekwa, J., & Basabose, A. K. (2003). Intra-specific variation in social organization of gorillas: Implications for their social evolution. *Primates*, *44*, 359–369.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Robbins, M. M., Akantorana, M., Arinaitwe, J., Breuer, T., Manguette, M., McFarlin, S., Meder, A., Parnell, R., Richardson, J. L., Stephan, C., Stokes, E. J., Stoinski, T. S., Vecellio, V., & Robbins, A. M. (2023). Comparative life history patterns of female gorillas. *American Journal of Biological Anthropology*, *181*(4), 564–574. https://doi.org/10.1002/ajpa.24792