

Variability in the Developmental Life History of the Genus *Gorilla*

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ABSTRACT Life history is influenced by factors both intrinsic (e.g., body and relative brain size) and extrinsic (e.g., diet, environmental instability) to organisms. In this study, we examine the prediction that energetic risk influences the life history of gorillas. Recent comparisons suggest that the more frugivorous western lowland gorilla shows increased infant dependence, and thus a slower life history, than the primarily folivorous mountain gorilla to buffer against the risk of starvation during periods of food unpredictability. We further tested this hypothesis by incorporating additional life history data from wild western lowland gorillas and captive western lowland gorillas with the assumption that the latter live under ecological conditions of energetic risk that more closely resemble those of mountain gorillas

and thus should show faster life histories than wild members of the species. Overall, we found captive western lowland and wild mountain gorillas to have faster developmental life histories than wild western lowland gorillas, weaning their infants approximately a year earlier and thus reducing interbirth intervals by a year. These results provide support that energetic risk plays an important role in determining gorilla life history. Unlike previous assertions, gorillas do not have substantially faster life histories, at least at the genus level, than other great apes. This calls for a re-evaluation of theories concerning comparative ape life history and evolution and highlights the need for data from additional populations that vary in energetic risk. *Am J Phys Anthropol* 000:000–000, 2013. © 2013 Wiley Periodicals, Inc.

Life history refers to the rate at which animals mature and reproduce with key life history traits including gestation length, interbirth interval, size and number of offspring, age at weaning and first reproduction and life span (Charnov, 1991; Stearns, 1992). Life history traits are often highly intercorrelated, resulting in general characterizations of fast or slow life history schedules (although some recent analyses demonstrate exceptions to the slow-fast continuum, e.g. Ross and Jones, 1999; Godfrey et al., 2004; Bielby et al., 2007; Borries et al., 2011; Leigh and Blomquist, 2011). For example, species with smaller body sizes and high mortality rates generally are characterized as having fast life histories whereas species with slow life histories are generally larger and have low mortality rates (Purvis et al., 2003). Other factors—including diet, patterns of non-maternal care, degree of arboreality, metabolic rate, habitat use/type, and environmental instability—can also interact to affect life history schedules (Janson and van Schaik, 1993; Ross and Jones, 1999; Kappeler et al., 2003; Godfrey et al., 2004; Harcourt and Stewart, 2007; Borries et al., 2011).

Primates have some of the slowest mammalian life histories, characterized by long gestations, the production of large neonates with slow postnatal growth rates, late ages of maturity, long life spans, and low reproductive rates (Harvey and Clutton-Brock, 1985; Harvey et al., 1987; Kappeler et al., 2003; Bielby et al., 2007). Yet considerable interspecific variation in primate life history traits exists (Lee and Kappeler, 2003). Although a number of factors likely contribute to these differences, studies have focused primarily on the role that body size, relative brain size and diet likely play. Larger body and

relative brain size generally correspond with slower primate life histories (Harvey et al., 1987; Kappeler et al., 2003). The role of diet is less well understood. In their ecological risk aversion theory, Janson and van Schaik (1993) hypothesized that frugivorous species that experience greater variability in the temporal availability of food, either from seasonal variations in quantity or quality or from high levels of intraspecific feeding competition, should experience slower life histories to reduce energetic needs and buffer against the risk of starvation. Alternatively, folivores, which are generally thought to experience lower feeding competition and to have greater access to abundant, high quality feeding resources that are temporally and spatially predictable (Leigh, 1994), are predicted to have faster life histories to minimize predation risks. Early studies of 42 species of captive anthropoids supported this hypothesis, finding faster growth rates in folivorous as compared to frugivorous

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species (Leigh, 1994). However, several subsequent datasets have not supported the ecological risk aversion hypothesis (small bodied platyrrhines: Garber and Leigh, 1997; lemurs: Godfrey et al., 2004; Asian colobines and macaques: Borries et al., 2011), perhaps because many foods of folivorous species are more seasonally constrained and/or folivores experience more feeding competition than originally realized (Koenig et al., 1997; Borries et al., 2011). Clearly, more comparative data, particularly of closely related species or populations of the same species living under different ecological conditions, would be useful in determining the relative role of energy risk on life history (Garber and Leigh, 1997; Lee and Kappeler, 2003; Breuer et al., 2009; Chapman and Rothman, 2009; Borries et al., 2011).

Gorillas (genus *Gorilla*) provide an excellent opportunity to further investigate the link between energy risk and life history traits. Eastern (*G. beringei*) and western (*G. gorilla*) gorillas live in a wide range of habitats that vary considerably in the distribution of vegetation and the presence/abundance of fruiting trees (Doran and McNeilage, 2001; Doran et al., 2002; Masi et al., 2009). The two best-studied subspecies—mountain and western lowland gorillas—live under significantly different ecological conditions. Mountain gorillas are specialized folivores that feed primarily on abundant, high quality herbaceous vegetation with very little seasonal variation in food quality or availability (Watts, 1984, 1988). Feeding competition is low and appears to have little impact on female reproductive success (Robbins, Steklis et al., 2007). In contrast, the diet of western lowland gorillas is less predictable in both time and space. Western lowland gorillas are seasonally frugivorous, which increases feeding costs and presumably contest competition (Doran and McNeilage, 2001; Masi et al., 2009). When fruits are not available, western lowland gorillas rely on terrestrial herbaceous vegetation, which occurs at substantially lower densities than in mountain gorilla habitat (see summary in Doran et al., 2002; Rogers et al., 2004; Masi et al., 2009). Recent studies comparing mountain and western lowland gorillas have argued that these ecological differences are responsible for several differences in social organization, behavior, brain development and life history traits observed between the species (Doran and McNeilage 2001; Robbins et al., 2004; Nowell and Fletcher, 2007; Breuer et al., 2009; McFarlin et al., 2012). In particular, studies of infant development and maternal investment have reported longer periods of infant dependency and slower physical maturation in western lowland gorillas as compared to the Virunga population of mountain gorillas (Nowell and Fletcher; 2007; Breuer et al., 2009). The authors have argued in favor of the ecological risk aversion hypotheses, suggesting that the temporally variable and widely dispersed nature of western lowland gorilla food resources requires longer investment by mothers to buffer infants against starvation risk, particularly during periods of fruit scarcity. These energetic risks may also be enhanced by larger and more variable energy costs, at least in terms of travel. Western lowland gorilla day journey lengths and home ranges are approximately two to three times those of mountain gorillas (see summary in Doran and McNeilage, 2001) and thus, not surprisingly, western lowland gorillas spend more time traveling and less time resting (Masi et al., 2009). Western lowland gorillas also show significant seasonal variation in day journey length, home range size and activity budgets whereas

mountain gorillas do not (Tutin, 1996; Watts, 1996; Remis, 1997; Doran and McNeilage, 2001; Masi et al., 2009). Thus, western lowland gorilla infants likely face a greater energetic risk of starvation from both food scarcity and increased costs related to travel.

Further testing of the hypothesis that energetic risks affect life history in gorillas requires additional data from western lowland gorillas for comparison with the relatively robust dataset on mountain gorillas. In this article, we present interbirth interval (IBI) data for a population of wild western lowland gorillas. In addition, we present data on weaning age and IBI for captive western lowland gorillas. We argue that both captive western gorillas and mountain gorillas live in environments with lower energetic risks of starvation because food is predictable in space, time, and quality. This is not to say these populations experience the same energetic costs, as we would expect travel, food processing, climbing, thermoregulation, and even digestion costs to be higher in mountain gorillas. Rather our argument is that given the predictability of their environments these populations experience lower levels of energetic risk, which should enable females to wean offspring at an earlier age with less chance of starvation. Thus we expect to see plasticity in western lowland gorilla development such that captive individuals diverge from their wild counterparts to show developmental life history trajectories that are more similar to those of wild mountain gorillas.

METHODS

Data collection on interbirth intervals and weaning

IBIs in captive western lowland gorillas. Data on IBIs were extracted from the Association of Zoos and Aquariums Gorilla Species Survival Plan© studbook. To ensure that we included only interbirth intervals that would be representative of surviving interbirth intervals in the wild (e.g., where previous infant survives until birth of next infant), we distributed questionnaires for each birth that examined the housing situation of the female, rearing of the infant, etc. This enabled us to limit our analysis to IBIs for which: (1) the female was able to get pregnant during the IBI (e.g., living with a male, not on birth control); (2) the infant was reared and weaned by its mother.

IBIs in wild western lowland gorillas. We collected data on IBIs at Mbeli Bai, a 12.9 ha forest clearing where gorillas come to feed in the south-west of the Nouabalé-Ndoki National Park, Republic of Congo (see Parnell 2002, Breuer et al., 2009 for description of site and animal identification). The gorillas are not habituated to humans and thus are observed only when they come to the bai to feed. The gorillas are observed with the help of telescopes from a 9 m high observation platform overlooking the forest clearing. Identification of gorillas is based upon features such as shape of brow-ridges, ears, nose-prints, and pelage (Parnell, 2002). Some gorillas have been observed within 1–2 days after their birth. When gorillas were first observed beyond that age, their birthdates were estimated by comparing their morphological and behavioral characteristics with

TABLE 1. Assigned weaning ages of captive western lowland gorillas

Infant	Parentage (dam \times sire)	Sex	Mother able to get pregnant	Weaning age
Olympia	Mia \times Willie B ^b	F	No	4.0
Lulu	Kuchi \times Willie B ^b	F	No	4.8
Sukari	Choomba ^b \times Willie B ^b	F	No	5.7
Kidogo	Machi \times Willie B ^b	M	No	4.2
Macy	Kudzoo \times Taz	F	No	4.1
Gunther ^a	Sukari \times Taz	M	No	5.2
			<i>Average</i>	4.6
Kazi (twin)	Kuchi \times Taz	F	Yes	3.4
Mia	Machi \times Ozoum ^b	F	Yes	3.4
Kashata	Machi \times Ozoum ^b	F	Yes	3.6
Kudzoo	Choomba ^b \times Willie B ^b	F	Yes	3.6
Kekla	Paki ^b \times Ozoum ^b	M	Yes	3.4
Kali (twin)	Kuchi \times Taz	M	Yes	4.2
Charlie	Banga ^b \times Ozoum ^b	M	Yes	4.6
Mbeli	Banga ^b \times Ozoum ^b	M	Yes	4.7
			<i>Average^c</i>	3.8

Weaning age was assigned based on last observed suckling.

^a Still nursing at very low rates at end of data collection and so not included in calculation of weaning age.

^b Represent wild caught individuals. Remaining parents are first generation born in captivity.

^c Value calculated with each female contributing a single data point.

other gorillas where age was already determined (Parnell, 2002; Nowell and Fletcher, 2007; Breuer et al., 2009).

Wild western lowland gorilla IBIs were calculated for surviving interbirth intervals, as was done for the captive data and previously in mountain gorillas (Robbins et al., 2006; Robbins et al., 2007a,b). However, for both these latter populations, females are observed daily and thus all births are captured. Alternatively, in the bai setting, there are gaps in observation time between bai visits, creating the potential for a birth to be missed if it occurs and the infant then dies during a gap period. Because this could lead to overestimations of IBIs, we also examined IBIs in conjunction with nursing data, as females generally wean infants before their next parturition. We removed any IBIs where the time difference between the last observed nursing bout for the first infant, which defined weaning (Breuer et al., 2009), and next recorded birth was greater than two gestation lengths (gestation length of 256 days; Harvey et al., 1987).

Weaning age of captive western lowland gorillas. Age at last observed suckling has been used to determine weaning age for both mountain (Stewart, 1981; Fletcher, 1994, 2001) and western lowland gorillas (Nowell and Fletcher, 2007; Breuer et al., 2009). This methodology was also used to determine weaning for 14 infants born at Zoo Atlanta. All infants born at Zoo Atlanta are part of a longitudinal study and thus are observed from birth until death or departure from the zoo. For this analysis, we included data up until six years of age (or current age if less than six years; see Table 1), as nursing has not been observed past this age. Behavioral observations on nursing patterns were conducted one to two times per week between March 1989 and August 2011 using focal animal sampling (Altmann, 1974). Data from year one of an infant's life were collected using a mother-infant ethogram (30-minute observation period). Data from years two through six were collected using a broader gorilla ethogram (10-minute observation period; see Hoff et al., 1994 for description of ethogram) but

with maternal-infant interactions still recorded. Observations occurred while mother-infant dyads were in their groups in outdoor enclosures, usually between the hours of 1000 and 1400. Enclosures ranged in size from 1,445 sq m to 2,725 sq m (see Stoinski et al., 2001 for description of enclosures). Infants were born into one of three groups, which ranged in size and membership over the course of the study but were no smaller than five and no larger than nine individuals. Parentage information on infants is provided in Table 1.

Data analysis

IBI data. Because a previous study found gorilla interbirth intervals to vary as a function of infant sex and maternal rank (Robbins et al., 2007), we examined all sex ratios to ensure there was not a bias in one dataset towards longer IBIs simply as a function of differences in the underlying sex ratio. All sex ratios approximated 50/50: wild western lowland (6 females, 8 males); captive western lowland gorilla (30 females, 34 males); mountain gorilla (47 females, 44 males).

Weaning data. We were able to assign an age of weaning for 13 captive individuals; one individual was still nursing at the end of the study, and his data were not included in the analysis but are included in Table 1.

Eight of the captive mother-infant dyads lived in groups consisting of a single silverback, multiple females and nonadult offspring; six mothers lived without a male at the approximate age of infant weaning or were on birth control and thus could not become pregnant. We predicted these latter individuals would have later weaning ages than their counterparts whose mothers could become pregnant. A one-tailed Wilcoxon-Mann-Whitney U test was used to compare age of weaning in the two subsets to see if a female's ability to become pregnant influenced weaning age. When comparing weaning age across the three gorilla populations, we used two-tailed Kruskal-Wallis tests followed by Wilcoxon-Mann-Whitney U post hoc tests to identify which populations differed from each other.

TABLE 2. Interbirth interval data for Mbeli Bai

Name of Mother	IBI (years)	Time between last observed suckling and next birth (years)
<i>Alberta</i>	5.0	2.0
Bessie	4.7	0.8
Eleanor	5.0	1.0
Fulani	4.8	0.7
Hilary	4.5	na
<i>Jakala</i>	7.6	1.8
Jewel	7.4	na
Jodie	5.4	na
Khoisan	4.8	0.7
Leah	5.2	1.3
<i>Matkah</i>	7.6	1.7
Misty	4.3	na
<i>Motaba</i>	8.2	3.0
Nagaira	9.0	2.9
Niari	5.8	na
Pansy	6.1	1.4
Petunia	5.4	1.2
Ramona	4.2	na
Simone	5.0	na
<i>Tina Turner</i>	8.1	2.3

Individuals in italics were not used in the calculation of IBI given that the time between last observed suckling and the next birth was greater than two gestation periods.

RESULTS

Interbirth interval

Captive western lowland gorillas. Data were available for 64 IBIs from 36 mothers. Including each birth as an individual data point produced an overall mean IBI of 4.2 ± 1.3 years (median 4.0 years; range, 2.0–8.2 years). Because previous studies have found considerable individual heterogeneity in IBIs (Jones et al., 2010), we also calculated these variables using a single value for each female (mean values used for females with multiple births; Brewer Marsden et al., 2006), which produced an overall mean IBI of 4.3 ± 1.1 years; median 4.1 years; range 2.4–7.0 years.

Wild western lowland gorillas. Data were available for 20 interbirth intervals representing 20 females (Table 2). Using this entire dataset, the overall mean interbirth interval was 5.9 ± 1.5 years (median = 5.3 years; range = 4.3–9.0 years). When we excluded six IBIs for which the length of time between the last observed nursing bout of the previous infant and the birth date of the next infant was greater than two gestation periods, the mean IBI dropped to 5.2 ± 0.8 years (median: 5.0; range: 4.3–6.1, $n = 14$). This dataset included eight IBIs for which no data were available on the date of last suckling for the first infant. Thus, we also calculated IBI using only the six IBIs for which we knew that the length of time between the last observed nursing bout of the first infant and birth date of the second infant was two gestation periods or less and found essentially the same results: mean = 5.2 ± 0.5 years; median: 5.0 years; range: 4.7–6.1 years.

Weaning age

Captive western lowland gorillas. For all calculations of weaning age, each female contributed a single

data point. Including data for all 13 fully weaned individuals, the mean and median weaning ages were 4.1 years (range: 3.4–5.7 years; Table 1). However, when we only include females who were able to become pregnant again around the time of weaning, the mean age dropped to 3.8 ± 0.5 years (median: 3.6 years; range: 3.4–4.6 years). Alternatively, the average weaning age for infants whose mothers could not get pregnant was 4.6 ± 0.7 years (median 4.2; range: 4.0–5.7 years; includes infant that was not fully weaned as its age at the end of the study was 5.2 years and thus already greater than the mean). As predicted, the weaning age of this latter group was significantly older (Mann-Whitney U test $n_1=6$; $n_2=5$; $U = 23$; $P = 0.03$). To most closely represent the situation for surviving IBIs in the wild, we consider the weaning age of 3.8 years to be appropriate for comparison with wild gorilla populations.

Population comparisons

We compared IBI length and weaning age across all three populations. Weaning data for wild western lowland gorillas ($n = 30$) was from Breuer et al. (2009) and Breuer (unpublished). Weaning data for wild mountain gorillas ($n = 11$) was from Stewart (1981) and Fletcher (1994, 2001). Interbirth interval data from wild mountain gorillas ($n = 39$ females representing 91 IBIs) were extracted from the Dian Fossey Gorilla Fund's Karisoke Research Center based on Robbins, Steklis et al. (2007). Kruskal-Wallis tests revealed significant differences between groups (IBI: $H = 16.5$; $df = 2$; $P < 0.001$; weaning $H = 15.9$; $df = 2$; $P < 0.001$) with post hoc analyses revealing greater weaning ages and IBIs in wild western lowland gorillas as compared to both mountain and captive western lowland gorillas (Mann-Whitney U tests; $P < 0.005$ for all comparisons) but no differences between the latter two groups (Mann-Whitney U tests; $P > 0.05$).

DISCUSSION

We hypothesized that gorillas living in environments where food is predictable in space, time, and quality would show faster life histories than those living in environments with greater energetic risks. The comparisons in Table 3 support this hypothesis, showing earlier weaning and faster resumption of reproduction in mountain gorillas and captive western gorillas as compared to wild western lowland gorillas. One of the benefits of our comparison groups is that they largely control for other factors that can influence the timing of life history, such as body and relative brain size and arboreality. As mentioned earlier, the populations do likely differ in energetic costs with both wild populations experiencing significantly higher costs than captive gorillas given their increased time spent locomoting, thermoregulating, and even digesting a more fibrous diet. Thus, our finding of similar life history trajectories across populations that differ considerably in energetic costs but not risk further emphasizes the role that risk likely plays in gorilla life history schedules.

One element that our study did not address is predation risk, which the ecological risk aversion hypothesis also posits should affect life history through increased juvenile growth rates in species experiencing higher predation (Janson and van Schaik, 1993). Given their large size, predation risk is low for gorillas as compared to other primate species. Rare predation on gorillas by

TABLE 3. Comparison of weaning and interbirth intervals across three gorilla populations

	Mountain Gorilla ^a (<i>Gorilla beringei beringei</i>)	Western Lowland ^b (<i>Gorilla gorilla gorilla</i>)	Western Lowland ^c (<i>Gorilla gorilla gorilla</i>)
Location	Wild Karisoke, Rwanda	Captivity	Wild Mbeli Bai, Rep of Congo
Interbirth interval: avg; median (range)	4.1 yrs; 4.1 yrs (3.2 yrs to 6.1 yrs) (<i>n</i> = 39)	4.3 yrs; 4.1 yrs (2.4 yrs to 7.0 yrs) (<i>n</i> = 36)	5.2 yrs; 5.0 yrs (4.3 yrs to 6.1 yrs) (<i>n</i> = 14)
Weaning ^d : avg; median (range)	3.4 yrs ^e ; 3.7 yrs (1.8 yrs to 5.2 yrs) (<i>n</i> = 11)	3.8 yrs; 3.6 yrs (3.4 yrs to 4.6 yrs) (<i>n</i> = 5)	4.7 yrs; 4.7 yrs; (3.0 yrs to 6.1 yrs) (<i>n</i> = 30)

For all datasets, *n* = number of females as a single average value is used for females with multiple data points.

^a Weaning data: Stewart (1981); Fletcher (1994, 2001); IBI data: adapted from Robbins, Steklis et al. (2007) using the Karisoke long-term database.

^b Current study.

^c Weaning data: Nowell and Fletcher (2007); Breuer et al. (2009) and Breuer (unpublished). IBI data: current study.

^d Defined as age last observed suckling.

^e For four infants reported by Fletcher (1994, 2001), weaning occurred between 40 and 44 months. To be conservative, the upper limit of 44 months was used for these three individuals to generate the average.

leopards has been reported for both western and mountain gorilla populations (Schaller, 1963; Robbins et al., 2004), although leopards are thought to have been extirpated from the Virungas sometime in the last few decades. Infanticide represents another predation risk; it has been observed in rare cases in captive western lowland gorillas and is strongly suspected but has yet to be observed in wild western gorillas (Robbins et al., 2004; Breuer et al., 2009). Although infanticide was a significant cause of infant mortality for mountain gorillas in the 1970s and 1980s (Watts, 1989), its frequency during this period may have been elevated by social instability resulting from high levels of poaching, which has also been suggested for Grauer's gorillas (Yamagiwa et al., 2012b). This hypothesis is underscored by the absence of infanticide observed in the Karisoke population during an extended period (10+ years) of group stability (Karisoke long-term records).

Re-evaluating comparative ape life histories

The dataset now available on gorillas enables hypotheses of gorilla life history as compared with other apes to be readdressed. Based on the limited data previously available, gorillas are repeatedly described in comparative analyses as having faster life histories than chimpanzees and orangutans (Kelley and Schwartz, 2010; Robson and Wood, 2008). What the data now clearly demonstrate is that mountain gorillas may indeed have faster life histories but that this is not true for the genus as a whole. The wild western gorilla data presented here, which are consistent with preliminary data from two other western gorilla sites (Doran-Sheehy et al., 2012; Yamagiwa et al., 2012a), suggest that developmental life history patterns of western gorillas are potentially quite similar to those of chimpanzees (Boesch and Boesch-Achermann, 2000; Emery Thompson et al., 2007; Breuer et al., 2009; Jones et al., 2010). This finding is critically important to our understanding of the evolution of hominid life history, particularly as many previous analyses specifically highlight the "faster" life histories of gorillas to explain how social and environmental factors may influence life history schedules (see below).

Second, earlier studies comparing captive western lowland and wild mountain gorilla IBIs had suggested that gorillas differ from other apes in that they reproduce at

the species "genetic potential" (Tutin, 1994) or near "maximum rates" in the wild (de Lathouwers and van Elsacker, 2005). Our results clearly show that this is not true, at least for wild western lowland gorillas. What is interesting, particularly as relates to the role of ecological risk in the timing of life history, is that mountain gorillas appear to be the only ape where an unprovisioned wild population shows developmental life history patterns that are similar to captive animals. In western gorillas, chimpanzees, and orangutans (data are unavailable for bonobos; although Knott (2001) reports IBI data for unprovisioned bonobos, these data were indirectly estimated from birth rates rather than by direct observation of sequential births (Fruth, personal communication) and are thus not comparable to available data on the other apes), captive populations consistently show shorter IBIs than unprovisioned wild ones (Fig. 4). From a comparative perspective, mountain gorillas likely have the highest quality and most abundantly available diet of all the apes, and thus we would argue that this further emphasizes the role that ecological risk plays in ape life history schedules.

Finally, it has been argued that gorillas have a decreased plasticity in life history as compared to chimpanzees and orangutans (Anderson et al., 2008). The three comparison groups presented in the current study show that there is actually considerable phenotypic plasticity in life history schedules within the genus *Gorilla*. For example, the gorilla weaning ages and IBIs presented here vary by roughly 25%, which is similar to variability seen across populations and locations in other apes (see, for example, Anderson et al. 2008). Bonobos have also been hypothesized to have decreased life history plasticity based on a lack of difference between provisioned wild and captive populations (de Lathouwers and van Elsacker, 2005; Anderson et al., 2008), but data from unprovisioned wild bonobos are needed before the extent of variability in bonobo life history can be assessed. Bonobos will be a very interesting species on which to have additional data because of their potential increased reliance on terrestrial herbaceous vegetation as compared to chimpanzees (Malenky and Wrangham, 1994; Wrangham et al., 1996).

In addition to diet, it has been hypothesized that gorillas have relatively faster life histories as a result of their social organization. For example, Tutin (1994) suggested

that the more cohesive nature of gorilla groups as compared to chimpanzees might enable earlier weaning in gorillas through continued protection and socialization opportunities outside the mother. Similarly, it has been hypothesized that gregariousness enables earlier weaning in that individuals do not need to have full ecological competence to be weaned, with the inverse relationship for orangutans, chimpanzees and gorillas between gregariousness level and weaning age cited for support (van Noordwijk and van Schaik, 2005; Robson et al., 2006; Robson and Wood, 2008). As with previous studies, these hypotheses were based on mountain gorilla and/or captive western lowland gorilla data. With the data now available for wild western lowland gorillas, the suggested relationships between ape social organization and the speed of life history are less clear. Comparisons between chimpanzees and western lowland gorillas—species that inhabit more similar ecological niches than do chimpanzees and mountain gorillas—show similarities in both weaning age and IBI despite differences in social organization (Breuer et al., 2009; Boesch and Boesch-Achermann 2000; Emery Thompson et al., 2007; Jones et al., 2010; Pusey 1983). We do know that western gorilla groups show lower levels of social cohesion than mountain gorilla (summarized in Doran and McNeilage, 2001), although they are not considered to have the fission-fusion social structure of chimpanzees. Still, it would be useful to examine what role social organization and cohesion may play in developmental life history schedules at a level of detail finer than the overarching categories (e.g., cohesive groups versus fission-fusion communities versus semi-solitary) that are generally applied to the ape species. This could be particularly relevant for shedding light on the evolution of developmental life history patterns in humans: despite having the slowest life history among the apes, humans have the shortest IBIs and earliest weaning ages, which is often attributed to social factors (Robson et al., 2006). In addition, more comparisons like those of van Noordwijk et al. (2010), which looked at the timing of other measures of infant development, such as independent locomotion, foraging, and technological development, and the relationship to sociality would be useful.

Disentangling energetic and predation risk

The general pattern across apes argues for a strong role of energetic risk in shaping ape developmental life history schedules with the more frugivorous species (chimpanzees, western gorillas, and orangutans) maturing more slowly than the primarily folivorous mountain gorilla (Table 4). However, more intraspecific comparative data from wild populations are needed to disentangle the relative roles of energetic versus predation risk. For example, orangutans nicely fit the ecological risk aversion model when comparing across apes: orangutans are weaned at later ages than the African apes (Knott, 2001; van Noordwijk and van Schaik, 2005), and ecology likely plays a significant role as southeast Asian rainforests have low mean productivity and considerably greater intra- and inter-annual variation in productivity as compared to African rainforests (Terborgh and van Schaik, 1987; Knott and Kahlenberg, 2007). However, recent interspecific comparison of wild orangutan populations show the opposite pattern as relates to energetic risk: interbirth interval lengths are longer in Sumatran than Bornean orangutans, despite the latter living in

TABLE 4. Comparison of surviving IBIs in hominids

	Wild	Captive	Hunter-gather
Chimpanzee (sp)	5.8 (5.4–6.1)	4.4	x
<i>verus</i> subsp	5.6 (5.4–5.8)		x
<i>troglodytes</i> subsp	5.8 (5.6–6.1)		x
Western gorilla (sp)			
<i>gorilla</i> subsp	5.2	4.3	x
Eastern gorilla (sp)	4.3 (4.0–4.6)		x
<i>beringei</i> subsp	4.1		x
<i>graueri</i> subsp	4.6		x
Bonobo	na*	4.9	x
Sumatran orangutan	8.8 (8.2–9.3)	5.2	x
Bornean orangutan (sp)	6.8 (6.1–7.7)	5.0	x
<i>wurmbii</i> subsp	7.4 (7.1–7.7)		x
<i>morio</i> subsp	6.3 (6.1–6.5)		x
Humans	x	x	3.7 (3.1–4.1)

Values represent average IBI length in years where previous infant lived until birth of subsequent infant; where data for multiple populations were available, average values and ranges for the species or subspecies are presented.

Chimpanzee: wild: Emery Thompson, personal communication based on Emery Thompson et al., 2007; Boesch and Boesch-Achermann, 2000. Captive: de Lathouwers and van Elsacker, 2005.

Western gorilla: wild: current paper; captive: current paper and Sievert et al., 1991.

Eastern gorillas: current paper based on Robbins et al., 2007 sample; Yamagiwa and Kahekwa, 2001.

Bonobo: only comparable data are from a wild, provisioned population, which showed an IBI of 4.8 years: Furuichi et al., 1998; Furuichi and Hashimoto, 2002; captive: de Lathouwers and van Elsacker, 2005.

Sumatran orangutan: wild: Wich et al., 2010; captive: data collected for this paper using same methodology applied to gorilla IBI data ($n = 2$ females and IBIs) but similar to median values reported by Wich et al., 2010.

Bornean orangutan: wild: Wich et al., 2010; captive: data collected for this paper using same methodology applied to gorilla IBI data ($n = 3$ females, 4 IBIs) but similar to median values reported by Wich et al., 2010.

Humans: Kaplan et al., 2000; Robson et al., 2006; Robson and Wood, 2008.

less productive habitats (Wich et al., 2010). Captive orangutans show little variation between the species, suggesting the difference is not genetic (Anderson et al., 2008; Table 4). van Noordwijk et al. (2010) proposed that different sources of mortality between the two species, specifically increased predation risk in Sumatran orangutans, could drive the observed differences in early life history. Others have suggested that there is no evidence for species differences in infant mortality (Anderson et al., 2008). This hypothesis remains an important one to be tested both in orangutans and other apes by comparing life history strategies from sites with similar ecologies but varying degrees of predation pressure.

CONCLUSIONS

We found earlier weaning ages and shorter IBIs in populations of gorillas that experience lower levels of energetic risk. This is consistent with the ecological risk aversion hypothesis (Janson and van Schaik, 1993), which posits that decreased ecological risk should be associated with faster life histories. These results, as well as comparative analyses across the apes, suggest a considerable influence of ecology, and in particular the ecological risks associated with seasonal variation in food abundance and

or quality associated with frugivory, on the timing of ape life history. What role social organization may play in determining ape life history remains to be determined, although the similarities between western lowland gorillas and chimpanzees suggest it is not as large as previously hypothesized. Contrary to previous assertions, gorillas clearly show plasticity in life history schedules and, at least for western gorillas, do not have considerably faster life histories than chimpanzees. The current findings highlight the importance of comparative data for understanding ape life histories and, in particular, the need for more data from different populations living under variable ecological—both with respect to energetics and predation—and social conditions.

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LITERATURE CITED

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Anderson HB, Emery Thompson M, Knott CD, Perkins L. 2008. Fertility and mortality patterns of Bornean and Sumatran orangutans: is there a species difference in life history? *J Hum Evol* 54:34–42.
- Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CDL, Purvis A. 2007. The slow fast continuum in mammalian life history: an empirical evaluation. *Am Nat* 169: 748–757.
- Boesch C, Boesch-Achermann H. 2000. *The chimpanzees of the Tai Forest: behavioral ecology and evolution*. Oxford: Oxford University Press.
- 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. *Am J Phys Anthropol* 144: 286–299.
- Breuer T, Breuer-Ndoundou Hockemba M, Olejniczak C, Parnell RJ, Stokes EJ. 2009. Physical maturation, life-history classes and age estimates of free-ranging western gorillas—insights from Mbeli Bai, Republic of Congo. *Am J Primatol* 71:106–119.
- Brewer Marsden S, Marsden D, Emery Thompson M. 2006. Demographic and female life history patterns of free-ranging chimpanzees at the Chimpanzee Rehabilitation Project, River Gambia National Park. *Int J Primatol* 27: 391–410.
- Chapman CA, Rothman JM. 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates* 50:12–22.
- Charnov EL. 1991. Evolution of life history variation among female mammals. *Proc Natl Acad Sci USA* 88:1134–1137.
- de Lathouwers M, van Elsacker L. 2005. Reproductive parameters of female *Pan paniscus* and *P. troglodytes*: quality versus quantity. *Int J Primatol* 26:55–71.
- Doran DM, McNeilage A, Greer D, Bocian C, Mehlman PT, Shah N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *Am J Primatol* 58:91–116.
- Doran DM, McNeilage A. 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Robbins MM, Sicotte P, Stewart KJ, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press. p 123–149.
- Doran-Sheehy D, Mongo P, Lodwick JL, Salmi R, Borries C. 2012. Life history of wild western gorillas (*Gorilla gorilla*): new data and cross site comparisons indicate gorillas do not grow and reproduce as fast as you think. *Am J Phys Anthropol* 147, Suppl 54:133.
- Emery Thompson M, Jones JH, Pusey AE, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T, Nishida T, Reynolds V, Sugiyama Y, and Wrangham RW. 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Curr Biol* 17: 1–7.
- Fletcher AW. 1994. *Social development of immature mountain gorillas (Gorilla gorilla beringei)*. Dissertation, University of Bristol.
- Fletcher AW. 2001. Development of infant independence from the mother in wild mountain gorillas. In: Robbins MM, Sicotte P, Stewart, KJ, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press. p 153–182.
- Furuichi T, Idani G, Ihobe H, Kuroda S, Kitamura K, Mori A, Enomoto T, Okayasu N, Hashimoto C, and Kano T. 1998. Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *Int J Primatol* 19: 1029–1043.
- Furuichi T, Hashimoto C. 2002. Why do female bonobos have a lower copulation rate during estrus than chimpanzees? In: Boesch C, Hohmann G, and Marchant LF, editors. *Behavioral diversity in chimpanzees and bonobos*. New York: Cambridge University Press. p 156–167.
- Garber PA, Leigh SR. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol* 68:1–22.
- Godfrey LR, Samonds KE, Jungers WL, Sutherland MR, Irwin MT. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *Am J Phys Anthropol* 123:250–276.
- Harcourt AH, Stewart KJ. 2007. *Gorilla society: conflict, compromise, and cooperation between the sexes*. Chicago: University of Chicago Press.
- Harvey PH, Clutton-Brock TH. 1985. Life history variation in primates. *Evolution* 39:559–581.
- Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 181–196.
- Hoff MP, Nadler R, Hoff KT, Maple TL. 1994. Separation and depression in infant gorillas. *Dev Psychobiol* 27:439–452.
- Janson CH, van Schaik CP. 1993. Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. *Juvenile primates: life history, development, and behavior*. Oxford: Oxford University Press. p 57–74.
- Jones JH, Wilson ML, Murray C, Pusey A. 2010. Phenotypic quality influences fertility in Gombe chimpanzees. *J Anim Ecol* 79:1262–1269.
- Kaplan H, Hill, K, Lancaster J, Hurtado AM. 2000. Theory of human life history evolution: diet, intelligence, and longevity. *Evol Anthropol* 9:167–185.
- Kappeler PM, Pereira ME, van Schaik CP. 2003. Primate life histories and socioecology I. In: Kappeler PM, Pereira ME, editors. *Primate life history and socioecology*. Chicago: University of Chicago Press. p 3–20.
- Kelley J, Schwartz GT. 2010. Dental development and life history in living African and Asian apes. *Proc Natl Acad Sci USA* 107:1035–1040.
- Knott CD. 2001. Ape models of female reproductive ecology. In: Ellison PT, editor. *Reproductive ecology and human evolution*. Chicago: Aldine. p 429–463.

- Knott CD, Kahlenberg SM. 2007. Orangutans in perspective. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. New York: Oxford University Press. p 290–305.
- Koenig A, Borries C, Chalise MK, Winkler P. 1997. Ecology, nutrition and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *J Zool (Lond)* 243: 215–235.
- Lee PC, Kappeler PM. 2003. Socioecological correlates of phenotypic plasticity of primate life histories. In: Kappeler PM, Pereira ME, editors. *Primate life histories and socioecology*. Chicago: University of Chicago Press. p 41–65.
- Leigh SR. 1994. Ontogenetic correlates of diet in anthropoid primates. *Am J Phys Anthropol* 94:499–522.
- Leigh SR, Blomquist GE. 2011. Life history. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. *Primates in perspective*. New York: Oxford University Press. p 418–428.
- Malenky RK, Wrangham RW. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. *Am J Primatol* 32:1–12.
- Masi S, Cipolletta C, Robbins MM. 2009. Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns with response to frugivory. *Am J Primatol* 70:1–10.
- McFarlin S, Barks SK, Tocheri MW, Massey JS, Eriksen AB, Fawcett KA, Hof PR, Bromage TG, Mudakiwkwana A, Cranfield MR, Stoinski TS, Sherwood CC. 2012. Early brain growth cessation in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Am J Primatol* DOI: 10.1002/ajp.22100
- Nowell A, Fletcher A. 2007. Development of independence from the mother in *Gorilla gorilla gorilla*. *Int J Primatol* 28:441–455.
- Parnell RJ. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am J Primatol* 56:193–206.
- Purvis A, Webster AJ, Agapow P, Jones KE, Isaac NJB. 2003. Primate life histories and phylogeny. In: Kappeler PM, Pereira ME, editors. *Primate life history and socioecology*. Chicago: University of Chicago Press. p 25–30.
- Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *Am J Primatol* 43:87–109.
- Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E. 2004. Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 64: 145–159.
- Robbins A, Robbins MM, Steklis N, Steklis D. 2006. Age-related patterns of reproductive success among female mountain gorillas. *Am J Phys Anthropol* 131: 511–521.
- Robbins AM, Robbins MM, Fawcett K. 2007. Maternal investment of the Virunga mountain gorillas. *Ethology* 113:235–245.
- Robbins MM, Steklis D, Steklis N, Robbins AM. 2007. Sociological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*). *Behav Ecol Sociobiol* 61: 919–931.
- Robson SL, van Schaik CP, Hawkes K. 2006. The derived features of human life history. In: Hawkes K, Paine RP, editors. *The evolution of human life history*. Santa Fe: School of American Research Press. p 17–44.
- Robson SL, Wood B. 2008. Hominin life history: reconstruction and evolution. *J Anat* 212:294–425.
- Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG. 2004. Western gorilla diet: a synthesis from six sites. *Am J Primatol* 64: 173–192.
- Ross C, Jones KE. 1999. Socioecology and the evolution of primate reproductive rates. In: Lee PC, editor. *Comparative primate socioecology*. Cambridge: Cambridge University Press. p 73–110.
- Schaller GB. 1963. *The mountain gorilla: ecology and behavior*. Chicago: University of Chicago Press.
- Sievert J, Karesh WB, Sunde V. 1991. Reproductive intervals in captive female western lowland gorillas with a comparison to wild mountain gorillas. *Am J Primatol* 24: 227–234.
- Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Stewart KJ. 1981. *Social development in wild mountain gorillas*. PhD dissertation. Cambridge: University of Cambridge.
- Stoinski TS, Hoff MP, Maple TL. 2001. Habitat use and structural preferences of captive western lowland gorilla (*Gorilla gorilla gorilla*): effects of environmental and social variables. *Int J Primatol* 22: 431–447.
- Terborgh J, van Schaik CP. 1987. Convergence vs. nonconvergence in primate communities. In: Gee JHR, Giller PS, editors. *Organization of communities: past and present*. Symposium of the British Ecological Society. Boston: Blackwell Scientific Publications. p 205–226.
- Tutin CEG. 1994. Reproductive success story: variability among chimpanzees and comparisons with gorillas. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, Marquardt LA, editors. *Chimpanzee cultures*. Cambridge, MA: Harvard University Press. p 181–193.
- Tutin CEG. 1996. Ranging and social structure of lowland gorillas in the Lope Reserve, Gabon. In: McGrew WC, Marchant FL, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 58–70.
- van Noordwijk MA, van Schaik CP. 2005. Development of ecological competence in Sumatran orangutans. *Am J Phys Anthropol* 127:79–94.
- van Noordwijk MA, Sauren SEB, Nuzuar, Abluani A, Morrough-Bernard HC, Atmoko SSU, van Schaik CP. 2010. Development of independence: Sumatran and Bornean orangutans compared. In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP, editors. *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford; New York: Oxford University Press. p 189–203.
- Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *Am J Primatol* 7:323–356.
- Watts DP. 1988. Environmental influences on mountain gorilla time budgets. *Am J Primatol* 15:195–211.
- Watts DP. 1989. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81:1–18.
- Watts DP. 1996. Comparative socio-ecology of gorillas. In: McGrew WC, Marchant FL, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 16–28.
- Wich SA, de Vries H, Ancrenaz M, Perkins L, Shumaker RW, Suzuki A, van Schaik CP. 2010. Orangutan life history variation. In: Wich SA, Utami SS, Mitra Setia T, van Schaik CP, editors. *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford; New York: Oxford University Press. p 65–75.
- Wrangham RW, Chapman CA, Clark-Ardcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant FL, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 45–57.
- Yamagiwa J, Kahekwa J. 2001. Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins MM, Sicotte P, Stewart K editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press. p 89–122.
- Yamagiwa J, Ando C, Kahekwa J, Basabose AK. 2012a. Factors influencing the life history of eastern and western gorillas. Abstracts of the XXIVth Congress of the International Society of Primatologists. p 235.
- Yamagiwa J, Basabose AK, Kahekwa J, Bikaba D, Ando C, Matsubara M, Iwasaki N, Sprague DS. 2012b. Long-term research on Grauer's gorillas in Kahuzi-Biega National Park, DRC: life history, foraging strategies, and ecological differentiation from eastern chimpanzees. In: Kappeler PM, Watts D, editors. *Long term field studies of primates*. Berlin; Heidelberg: Springer-Verlag. p 385–412.