



Phenotypic Plasticity Rather Than Ecological Risk Aversion or Folivory Can Explain Variation in Gorilla Life History

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INTRODUCTION

At its core, life history reflects the outcome of energy allocation toward maintenance, growth, and reproduction over an individual's lifetime (van Noordwijk and de Jong, 1986; Stearns, 1992). This allocation of energy can be estimated via life history traits, such as the age at weaning or first reproduction and the rate of reproduction (Lande, 1982). In primates and other mammals, life history traits are negatively allometrically related to adult female body mass (Harvey et al., 1987; Martin et al., 2005). However, gorillas seem to defy this principle as previous estimates suggested the mountain gorilla (*Gorilla beringei*) to be heavier and to have a faster life history (Table 1) than the lighter western gorilla (*Gorilla gorilla*) (Stoinski et al., 2013). We will argue in the following that some of the body mass data used in the past were flawed. Recent data (see below) confirm that females in both species are of similar mass and consequently their life histories should be similar, all else being equal.

Apart from the question of body mass, variation in gorilla life history has mainly been interpreted in light of two ecological hypotheses, namely “ecological risk aversion” and the importance of “folivory” (Janson and van Schaik, 1993; Leigh, 1994). Both hypotheses predict slower life histories in more frugivorous primates. This is relevant because the diet of western gorillas—with the slower life history (Stoinski et al., 2013)—contains much more fruits compared to that of mountain gorillas (e.g., Lodwick and Salmi, 2019). On the one hand, more frugivorous primates are assumed to face higher food uncertainty given the seasonally restricted availability of fruits, in combination with extended periods of low fruit availability (Knott and Harwell, 2020). Frugivores should thus have a generally slower life history (late weaning, late onset of reproduction, and a slow reproductive rate) to avoid starvation (ecological risk aversion, Janson and van Schaik, 1993). On the other hand, the mainly folivorous diet of the faster mountain gorilla, is much less seasonal (Wright et al., 2015). The year-round consumption of protein contained in high-quality leaves is assumed to promote growth and thus to accelerate their life history (Janson and van Schaik, 1993; Leigh, 1994).

The above concept of ecological risk aversion implies that the life histories of gorillas living in different environments are the consequence of adaptation to the respective food availability. However, we will argue here that it is more likely that the variation in gorilla growth and reproductive rates (i.e., life history) is simply a direct and flexible phenotypic response to the actual nutrient availability (phenotypic plasticity below). In addition, we challenge, based on earlier and

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TABLE 1 | Examples of phenotypic plasticity in primate life history (mean values in months, except when noted).

Species	Study site/ Gorilla species	Condition	Infant development	Female age at first parturition	Interbirth interval [†]
<i>Papio cynocephalus</i>	Amboseli	Food enhanced	9 [‡]	44.6 [§]	15.4
		Wild feeding improved habitat ^{‡‡}	5 [‡]	51.7 [§]	19.4
		Wild feeding poor habitat ^{‡‡}		56.3 [§]	21.7
<i>Macaca fuscata</i>	Mt. Ryozen	Food enhanced ^{‡‡}		62.5	20.2 [†]
		Wild feeding ^{‡‡}		80.9	35.7 [†]
<i>Semnopithecus entellus</i>	Jodhpur	Food enhanced	12.8 ^{††}	42.5	16.7
<i>Semnopithecus schistaceus</i>	Ramnagar	Wild feeding	24.9 ^{††}	80.4	32.4
<i>Pan troglodytes</i> ^{§§}	Ngogo	Wild feeding high fruit abundance			62.9
	Kanyawara	Wild feeding low fruit abundance			81.8
<i>Gorilla beringei</i>	Mountain gorilla	Wild feeding	40.8 ^{††}	118.8	48.0
<i>Gorilla gorilla</i>	Western gorilla	Captive	46.8 ^{††}	98.4	50.4
		Wild feeding	56.4 ^{††}	136.8	67.2

Values for gorillas at the bottom (for study sites, basic ecological data, and references for gorillas please see **Supplementary Table S1**). References are given in-text; food enhanced identifies access to human-made food collected from a dumpster or provided by people; [†]interbirth interval after surviving infants; [‡]body mass gain in grams/day; because of small sample sizes only one value for wild feeding independent of habitat quality; [§]age at menarche; ^{††}converted from birth rates; ^{‡‡}age at last nipple contact; ^{‡‡}same group under different nutritional conditions; ^{§§}data for chimpanzees inhabiting the same forest (Kibale) for which fruit abundance was determined with identical methods. Data for infant development and female age at first reproduction have not yet been published for Ngogo.

recent data, the assumed importance of protein intake for growth and reproduction (advantages of folivory below).

NO DIFFERENCE IN ADULT FEMALE BODY MASS BETWEEN GORILLA SPECIES

Although rarely emphasized in the literature, the negative allometric relationship between adult female body mass and life history did not seem to apply to species within the genus *Gorilla*, as previous estimates suggested wild mountain gorillas to be heavier [97.5 kg (Smith and Jungers, 1997)] and to have a faster life history (e.g., Stoinski et al., 2013) than the lighter wild western gorillas [71.5 kg, (Smith and Jungers, 1997)]. This may relate to the fact that the mass value for mountain gorillas was based on a single female specimen of undisclosed origin. Recently, new body mass data for mountain gorillas reversed this relationship. Rather than being much heavier, adult female mountain gorillas at Karisoke turned out to be slightly lighter [66.3 kg (Burgess et al., 2018)] than western gorillas. This much smaller difference (−5.2 kg vs. formerly +26.0 kg) should only marginally affect life history, if at all.

In addition, genetic data suggest a late split between western and mountain gorillas with gene flow occurring up until about 80–500 kya (Thalmann et al., 2007; Scally et al., 2012). This recent divergence is consistent with their similar body mass and with craniometric data demonstrating a much higher phenotypic variation within (80%) rather than between species (20%) (Leigh et al., 2003). Similarly, gestation length, the only

life history trait that is tightly linked to phylogeny (Martin and MacLarnon, 1985; Lee, 2012), is identical in the different gorilla species (Smith et al., 1999; Doran-Sheehy et al., 2009; Habumuremyi et al., 2016). This all adds to the notion of small genetic distance such that strong similarities in life history are to be expected for all gorillas although genetic differences in gorilla life history cannot be ruled out.

ADVANTAGES OF FOLIVORY—HAS PROTEIN INTAKE BEEN MISINTERPRETED?

The different gorilla populations vary greatly in the proportion of leaves and herbs in their diet (Rogers et al., 2004; Rothman et al., 2007). Consequently, the higher protein intake in the more folivorous mountain gorillas (Plumptre, 1995) was thought to contribute to their faster growth and reproduction (Janson and van Schaik, 1993).

However, the effect of protein on the body is dependent on intake, as was for example shown in deprivation experiments on capuchins (*Cebus* spp.), where signs of protein deficiency emerged only in animals with <3% protein intake but not in those with 6.7% intake (Fleagle et al., 1975; Elias and Samonds, 1977). An intake of 6.4–8.0% protein has been established as sufficient for several primate species (National Research Council US, 2003). In comparison, for the three gorilla populations for which protein intake has been estimated, it averaged at least 12% [i.e., mountain gorillas: 18% at Karisoke, 17% at

Bwindi, (Rothman et al., 2007); western gorillas: 12% at Mondika (Lodwick and Salmi, 2019, with 8.4% as the lowest monthly protein intake)]. From a growth perspective, the protein intake is, thus, always sufficient across sites. Furthermore, studies of nutrient intake (Rothman et al., 2011) suggested that folivorous primates usually did not select for protein [this generally only happened in primates when protein availability is very low (Ganzhorn et al., 2017)] but instead prioritized non-protein energy (Rothman et al., 2011). Especially in tropical forests, nitrogen, the building block of proteins, is not a limiting factor for folivores, and thus differences in protein intake are unlikely to explain the variation in gorilla life history. If more protein is consumed than can be assimilated, it is metabolized and may render the energy balance more positive (see also below), but it cannot be stored as protein or nitrogen (Pesta and Samuel, 2014). Thus, a protein heavy diet *per se* will not accelerate growth.

PHENOTYPIC PLASTICITY—A RESPONSE TO THE PRESENT ECOLOGICAL CONDITIONS

As has been demonstrated in several species, individuals respond to local ecological conditions (Ricklefs and Wikelski, 2002; Lee and Kappeler, 2003; Wells and Stock, 2011), a phenomenon known as phenotypic plasticity (Scheiner, 1993). Within the inherited limits, the same genotype can produce different phenotypes in different environments or changing environments, leading to changes in phenotype over time (Fusco and Minelli, 2010). While the range of possible reactions to environmental influences is genetically determined, gene expression and cellular processes are regulated by hormones, thus implementing flexible responses to the current environmental conditions (Emery Thompson, 2017).

One of the strongest phenotypic effects on life history traits likely results from differences in energy balance. Energy balance is the net amount of energy available to the body for maintenance, growth, and reproduction (Emery Thompson, 2017). If food is superabundant and of high quality, energy intake of the individuals can exceed their energy expenditure, thus rendering energy balance positive (Ellison, 2017). This surplus energy can be stored as fat, which is, however, rare in wild primates (Altmann et al., 1993). Extra energy is mainly allocated for growth and reproduction leading to faster growth, younger maturation ages, and higher reproductive rates (Emery Thompson, 2013).

Phenotypic plasticity is a well-established phenomenon that has been documented in various animal orders (Sadleir, 1969; Gilmore and Cook, 1981; Stearns and Koella, 1986), including primates (Table 1). At Amboseli, Kenya, one of the yellow baboon groups (*Papio cynocephalus*) frequently fed at a dumpster, which led to high energy intake and a particularly low energy expenditure. The individuals in this group grew, matured, and reproduced significantly faster than those in groups lacking access to energy-dense foods (Altmann and Alberts, 2003, 2005). We documented similar, significant effects in an intrageneric comparison of gray langurs (*Semnopithecus* spp.) from a

provisioned (India) and an unprovisioned (Nepal) population (Borries and Koenig, 2000; Borries et al., 2001). In these two comparisons, the surplus energy was provided by humans, but natural habitats can also differ markedly in quality, as in the Kibale forest, Uganda (Potts et al., 2015). Here, the chimpanzees (*Pan troglodytes*) inhabiting the area with high fruit availability at Ngogo, had a mean interbirth interval that was 19 months shorter compared to the neighboring community at Kanyawara (Emery Thompson et al., 2007; Watts, 2012).

Phenotypic plasticity becomes even more apparent when changes in energy balance occur within the course of an individuals' lifetime (Table 1). For example, one group of the Amboseli baboons eventually relocated to a more productive habitat, which shortened interbirth intervals (Altmann and Alberts, 2003). Similar changes, although in the opposite direction, occurred in free-ranging Japanese macaques (*Macaca fuscata*) from Mt. Ryozen, Japan, after regular provisioning was discontinued (Sugiyama and Ohsawa, 1982). The same individuals, with identical genetic makeup, exhibited different speeds of life history, contingent on energy availability. More broadly, all of the above examples illustrate that excess energy can lead to predictable and non-trivial accelerations of primate life history.

Currently, it remains difficult to apply this concept to gorillas because very few comparative data on energy intake and expenditure, and thus on energy balance, are available. However, mountain gorillas at the long-term site, Karisoke, have a very short daily path length and a high energy intake from mainly terrestrial herbaceous vegetation (Supplementary Table S1). A recent analysis of C-peptide concentrations in feces, a proxy for energy intake, suggests that there were no seasonal, energetic bottlenecks (Grueter et al., 2014). It seems therefore reasonable to assume that gorillas at Karisoke live year-round under nearly ideal energetic conditions similar to those experienced in captivity (Wright et al., 2015). This could be the reason why previous comparisons found gorilla life history to be unaffected by the improved nutritional conditions in captivity (Harcourt et al., 1980; Tutin, 1994). The conclusion was based on data for wild mountain gorillas from Karisoke and captive western gorillas. Only more recently has it become clear that wild western gorillas have a much slower life history compared to their captive counterparts (Breuer et al., 2009; Stoinski et al., 2013; Manguette et al., 2019; cf. Table 1). The latter do not experience seasonal, nutritional restrictions and have a low energy expenditure.

DISCUSSION

We hope to have shown that variation in gorilla life history is unlikely to be an adaptive strategy with a generally reduced speed of life history in habitats where negative energy balances are likely to occur regularly (ecological risk aversion, Janson and van Schaik, 1993). Rather, growth and reproduction could simply fluctuate locally in relation to how positive the current energy balance is and remains over time. Furthermore, we now know that the gorilla species are very similar in adult female body mass and that excess protein intake *per se* does not accelerate

life history. It seems therefore most parsimonious to predict that the overall availability of nutrients and seasonal fluctuations in energy balance should directly and flexibly affect the speed of gorilla life history.

Moving forward, quantifying individual female energy balance (intake and expenditure) over time in a standardized manner at different gorilla study sites is required to determine whether phenotypic plasticity is indeed the main explanation for variation in gorilla life history. Such a study will need to also account for differences e.g., in the digestibility of leaves and in the amount of energy invested in thermoregulation (Wright et al., 2015), as well as in arboreal locomotion. Non-energetic factors, such as the density of large food competitors (impacting food availability) and genetic differences between gorilla populations, resulting in different metabolic or other physiological adaptations should also be examined.

AUTHOR CONTRIBUTIONS

CB collated the core arguments and wrote the first draft. The ideas were refined and tailored to gorillas by all authors who

also commented on and edited all versions of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.873557/full#supplementary-material>

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