Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*):

Influential factors

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Abstract

Weaning marks an important milestone during life history in mammals indicating

nutritional independence from the mother. Age at weaning is a key measure of maternal

investment and care, affecting female reproductive rates, offspring survival and

ultimately the viability of a population. Factors explaining weaned age variation in the

endangered mountain gorilla are not yet well understood. This study investigated the

impact of group size, group type (one-male versus multi-male), offspring sex, as well as

maternal age, rank, and parity on weaned age variation in the Virunga mountain gorilla

population. The status of nutritional independence was established in 69 offspring using

long-term suckling observations. A Cox-regression with mixed effects was applied to

model weaned age and its relationship with covariates. Findings indicate that offspring

in one-male groups are more likely to be weaned earlier than offspring in multi-male

groups, which may reflect a female reproductive strategy to reduce higher risk of

infanticide in one-male groups. Inferior milk production capacity and conflicting

resource allocation between their own and offspring growth may explain later weaning

in primiparous mothers compared to multiparous mothers. Sex-biased weaned age

related to maternal condition defined by parity, rank, and maternal age will be discussed

in the light of the Trivers-Willard hypothesis. Long-term demographic records revealed no disadvantage of early weaning for mother or offspring. Population growth and two peaks in weaned age within the Virunga population encourage future studies on the potential impact of bamboo shoots as a weaning food and other environmental factors on weaning.

Keywords: weaning, mountain gorilla, group, parity, dominance rank, offspring sex.

Significance Statement

Female reproductive rates are key in determining the viability of endangered populations. Using suckling observations from the Virunga mountain gorilla population spanning nearly forty years, we investigated factors affecting variation in age at weaning, a principal determinant of reproductive rate. Our findings provide evidence that females in one-male groups that have higher risk of infanticide wean offspring earlier than those in multi-male groups, that there is differential investment in males depending on age and reproductive experience of the mother, and that we should focus more on the availability of easily digestible foods (here bamboo) in relation to age at weaning. Improved understanding of such influencing factors enables us to more readily predict future population dynamics of these great apes as they grow towards their carrying capacity with continued change in their environment.

Introduction

Lactation is a distinct feature of mammals and has been subject to highly diverse and complex selection pressures (Hayssen 1993; van Noordwijk et al. 2013). Offspring age at the termination of direct nutritional support by the mother, here referred to as 'weaned age', is a measure of a mother's investment and care (Clutton-Brock 1991; Lee

1996; Quinn 2013) as it can determine both female future reproductive rates and offspring fitness in mammals (Trivers 1972; Hayssen 1993; Lee 1996; Kennedy 2005). Suckling stimuli induce postpartum anovulation (see McNeilly 1979; Lee et al. 1991; McNeilly et al. 1994). Cessation of lactation has been linked to the resumption of cycling and re-conception in primates (Pharye's leaf monkeys [*Trachypithecus phayrei crepusculus*]: Borries et al. 2014) and may be triggered by a steady energy gain (Toba women: Ellison and Valeggia, 2003; Valeggia and Ellison, 2004; chimpanzees [*Pan troglodytes*]: Thompson et al. 2012). A mother needs to balance costs and benefits of the timing of weaning to maximise her lifetime reproductive success, measured by the survival and fecundity of current dependent offspring, and the mother's capacity to produce future offspring (Williams 1966; Trivers 1972, 1974; Fairbanks and McGuire 1995; Lee 1996). Premature weaning can reduce the offspring's chance of survival and future reproductive success, due to potentially higher morbidity risks and restricted growth and development respectively, while delayed weaning can reduce mother's future reproductive success through a prolonged anovulation period and increasing energetic costs, leading to the depletion of nutritional reserves (Trivers 1972; Lee 1996; Kennedy 2005).

Factors influencing variation in weaned age

Weaned age varies greatly within and among mammalian species, including humans, and has been attributed to various, often interrelated, factors encompassing ecological and social conditions, mother's ability to cope with the offspring's nutritional demands, and offspring characteristics. Ecological determinants of weaned age include food availability, predation risk, climate, and the degree of environmental uncertainty (nonhuman primates: Lee 1984, 1996; Boinski 1987; Lee et al. 1991; Lycett et al. 1998; Nowell 2005; other mammals: Low 1978; Arnold et al. 1979; Kleiman 1981; Carlisle

1982; Blumstein and Foggin 1997; Fisher et al. 2002). For example, dichotomous adaptation in anti-predator strategies can explain weaned age differences in ungulates, with fawn of 'hiders' being weaned earlier than fawn of 'followers', as the latter may have to allocate more of the energy gained from milk to locomotion activities, resulting in slower growth rates (Fisher et al. 2002). When food is scarce and unpredictable, early weaning can increase the offspring's mortality risk but also improve the mother's chance of survival (Low 1978; Carlisle 1982). In many field and experimental studies, extremely poor, stressful, and uncertain environmental conditions have been associated with early weaning, suggesting that parents increase their own chance of survival by reducing survival of offspring which are of lower reproductive value (Tait 1980; Carlisle 1982; Lee 1984; Laurien-Kehnen and Trillmich 2004). In addition, a comparative study of placental mammals and marsupials suggests that high environmental uncertainty, e.g. irregular drought, that is associated with a high infant mortality but which is out of the control of parental effort, has exerted a strong selection pressure on parental investment strategies of Australian marsupials, favouring early weaning (Low 1978). In contrast, a comparative study on wild baboon populations (*Papio cynocephalus ursinus*) ranging between high- and low-quality habitat found delayed weaned age was linked to poor habitat quality (Lycett et al. 1998). The authors explained this through different levels of predation risk between habitats, largely independent of maternal effort, and driving weaning strategies in *P. cynocephalus ursinus*. In Galapagos fur seals (*Arctocephalus galapagoensis*), temporal adjustments in weaning strategies towards early termination have been observed during years with high food availability (Trillmich 1986). All of these studies demonstrate the importance of taking into account the mother's ability, or lack of it, to influence offspring mortality, when investigating evolution and variation in maternal investment strategies as well as

the fact that future reproductive value may be altered by certain ecological factors (see Pennington and Harpending 1988).

Quality of social environment can affect the age at weaning (Lee 1996; brown bear [*Urus artus*]: Dahle and Swenson 2003; Phayre's leaf monkeys, [*Trachypithecus phayrei*]: Borries et al. 2014; human: Kaufman and Hall 1989). For instance, offspring in large groups of Phayre's leaf monkey reach nutritional independence later than those in small groups, which may reflect slower infant development when foraging costs rise with growing group size (Borries et al. 2014). In house mice, offspring of small litters are weaned earlier than those of large litters as they grow faster and reach the threshold body weight for weaning earlier (Koenig and Markl 1987; Lee 1996). Extremely late weaned age occurs in semi-solitary living orangutans (*Pongo pygmaeus abelii*) (solitary lifestyle hypothesis: van Noordwijk and van Schaik 2005) compared to other more gregarious great apes (Stewart 1981; Watts and Pusey 1993; Pusey et al. 1997; Nowell and Fletcher 2007). Orangutan females wean their offspring when those offspring have acquired sufficient ecological knowledge skills to survive in habitats where food is unpredictable and often scarce.

Variations in weaned age have also been linked to maternal condition, i.e. a measure of the mother's ability to cope with offspring's nutritional demands, involving parity, maternal age and dominance rank. In several species, milk secretion capability (quantity and quality) increases with parity (humans: Amatayakul et al. 1999; macaques: Tanaka 1997; Hinde 2009; Hinde et al. 2009; seals: Lang et al. 2012; cows: Miller et al. 2006; sheep: Sevi et al. 2000; rabbits: Xiccato et al. 2004) which can translate into delayed weaning for primiparous mothers (rabbits: Xiccato et al. 2004; humans: Akter and Rahman 2010). Maternal age is a determinant of reproductive rates in female mammals (Lee 1996) and in young women has been associated with early

weaning (Baxter et al. 2009; Wijndaele et al. 2009). In primates, female dominance rank is probably the most commonly used proxy of maternal condition (Brown 2001; Grant 2003). Rank can reflect the nutritional status of females and relates to their level of testosterone, and both these can affect reproductive processes such as increased fertility and birth sex ratio, respectively (see review by Harcourt 1987; Grant 2003). However, studies that have used rank as a proxy for maternal condition have produced conflicting results. For example, high-ranking female vervet monkeys (*Cercopithecus aethiops*) with priority of food access wean their offspring at an earlier age than low-ranking females (Whitten 1983), whereas rank-related effects on weaned age were absent in olive baboons (*Papio anubis*) (Smuts and Nicolson 1989).

When sex differences in reproductive success occur, maternal investment is expected in favour of the sex which provides more grand-offspring (Hamilton 1967; Trivers and Willard 1973). Across mammal species though, there is limited evidence for sex-bias in weaned age. The most consistent findings have emerged from studies of pinnipeds that have polygynous mating systems and show a high sexual dimorphism in body size. Male seal pups, who will attain a much larger adult size than females, are weaned later than female pups (Northern elephant seal [*Mirounga angustirostris*]: Reiter et al. 1978; Galapagos fur seal [*Arctocephalus galapagoensis*]: Trillmich 1986; Antarctic fur seal [*Arctocephalus gazella*]: Lunn and Arnould 1997). A sex-bias in weaned age in favor of sons also emerged in wild spider monkeys (Symington 1987), although in primates generally there is a lack of sex differences in weaned age (Brown 2001). In contrast, daughters which inherit the dominance status of their mothers are weaned later than sons in pronghorn antelopes (*Antilocapra americana*) (Hewison and Gaillard 1999).

Several models have been used to predict the crucial mechanism(s) affecting adjustment of sex-biased maternal investment. The Trivers-Willard hypothesis (Trivers and Willard 1973) postulates that natural selection should favour mothers who are able to adjust their investment with respect to maternal condition, with those in good condition investing more in the sex of offspring with the greatest potential fitness return. Underlying model assumptions are that mothers in good condition produce offspring in good condition by the end of maternal investment, an advantage that is maintained into adulthood and that male and female offspring benefit differently, in terms of their future reproductive success, from additional resources received from mothers in good condition. The 'local resource competition' model predicts sex-biased maternal investment toward the dispersing sex, thus decreasing local competition between parent and their philopatric offspring (Clark 1978; Johnson 1988). Later, this model was modified by adding dominance rank 'inheritance' as key factor (Simpson and Simpson 1982), known as 'advantage-daughter' model (Altmann 1980) and 'local resource enhancement' model (Gowaty and Lennartz 1985), stating that in female philopatric societies raising daughters is more costly than raising sons because additional females in the group cause an increase in competition for limited resources.

In Virunga mountain gorillas, dispersal from the natal group is common for both sexes (Watts 1980; Robbins 1995) and mating occurs all year round (Stewart 1988; Gerald 1995). They also lack natural predators (Schaller 1963) and predominantly feed on abundant foliage, which is relatively evenly distributed in time and space (Fossey and Harcourt 1977; Vedder 1984; Watts 1984; McNeilage 1995), with the only exception being bamboo shoots (*Yushania alpine*), a bi-annual food resource (Fossey and Harcourt 1977; Vedder 1984; Watts 1998). Thus, the 'local resource competition' model and 'local resource enhancement model' are unlikely to determine maternal

investment. However, the Trivers-Willard hypothesis could apply to the mountain gorilla, given their high sexual dimorphism in body size (Taylor 1997) and polygynous mating system (Harcourt and Stewart 2007), resulting in a greater variance in reproductive success in males than female gorillas (Bradley et al. 2005).

Long-term demographic records of Virunga mountain gorillas from 1967-2012 revealed effects related to proxies of maternal condition. Inter-birth intervals (IBIs), commonly used as proxy of maternal investment, were 20% longer for primiparous females than for multiparous females and infant mortality was 50% higher for primiparous mothers (Robbins et al. 2006) which would be expected if young females start to reproduce before completing their own growth and thus face a tradeoff between investing in their growth and investing in reproduction (Bercovitch et al. 2000; Künkele and Kenagy 2013). Age-specific female reproductive success followed a quadratic relationship, with relatively low success for the youngest and oldest females (Robbins et al. 2006). Mountain gorilla females also develop detectable dominance relationships which are not inherited (Harcourt and Stewart 1987; Watts 1994; Robbins et al. 2005) and IBIs could be partly explained by female's rank, with shorter IBIs in high-ranking females than in low-ranking females (Robbins et al. 2007a). Additionally, high-ranking females had longer IBIs after giving birth to sons than to daughters, whereas low-ranking females had shorter IBIs after daughters. Given that such effects could result partly from variation in maternal condition and IBIs should depend partly on age at weaning (Borries et al. 2014), we might expect similar condition-related effects on weaned age and a similar quadratic relationship between maternal age and weaned age.

The folivorous diet may be responsible for relatively early weaning in mountain gorillas compared to other nonhuman great apes (Lee and Kappeler 2003; Nowell and Fletcher 2007) which are more reliant on less predictable, unevenly distributed fruit

resources (Tutin and Fernandez 1993; van Noordwijk and van Schaik 2005). In addition, there is a higher risk of infanticide risk in this species (see Parker 1999; Nowell 2005); mothers with dependent offspring are most vulnerable to infanticide attacks from extra-group males (Watts 1989) and such males may kill dependent offspring resulting in earlier re-conception (Hrydy 1974).

Most studies of wild mammalian populations have focused on variation in indirect measures of maternal care and investment, such as IBI patterns and offspring survival. However, relying only on indirect measures can mask true effects. For example, varying length of lactation into subsequent pregnancy (Eckardt 2010; Borries et al. 2014), miscarriages, and unsuccessful conception may all cause discrepancies between IBIs and the actual weaned age. Comparatively few studies provide information on weaned age as either a direct measure of the length of lactation or close approximation of age at independence (Borries et al. 2014). This omission stems from challenges in establishing weaning status, especially in wild settings, where regular observations of suckling behavior are necessary, often over several years, both day and night, and where distinguishing real milk intake from comfort suckling (see Cameron, 1998; Reitsema, 2012) is important.

In this study, we used data on diurnal suckling by wild mountain gorilla offspring, collected over five study periods, to investigate variation in weaned age in relation to variation in group size, group type (one-male versus multi-male group), offspring sex, and maternal parity, dominance rank, and age. We further tested the suitability of using IBIs as indicator of weaned age. We used demographic data to explore potential consequences of weaned age variation for offspring and mother, including offspring age at first parturition and death, survival of mother's subsequent

offspring beyond year one, and the timing of re-conception relative to completed weaning.

Methods

Study site and subjects

The study focused on habituated wild Virunga mountain gorillas in the Parc National des Volcans, Rwanda. All study individuals, observed over five different field periods (Table 1), were members of research groups that have been monitored by the Karisoke Research Center since 1967, including Group 4, Group 5, and Groups: Nunki, Beetsme, Pablo, Shinda, Kuryama, Titus, Ugenda, Ntambara, Urugamba, Isabukuru, Inshuti, and Bwenge (Table 2). Only mothers and their current offspring at time of observation were included in the study.

Data collection

Different measures are commonly applied to assess weaning (see review by Borries et al. 2014). Age at last nipple contact is proposed to best reflect offspring independence and capability to survive (Borries et al. 2014). In this study, weaning status was derived from diurnal suckling observations. Recording and sampling rules differed between study periods. None of the study periods used blinded recording methods because our study involved focal animals in the field. In 1973 and 1977, behaviour sampling on all mothers and offspring in view was conducted at 1-min intervals (Stewart 1988). In 1981-1983, focal sampling sessions (Altmann 1974) lasting 30 minutes (Stewart 1988) to five hours (Fletcher 1994; Eckardt 2010) were conducted on mothers and offspring at least once per month, where possible. During focal sessions, suckling was recorded in 30-sec intervals (Stewart 1988) or continuously

(Fletcher 1994; Eckardt 2010). Suckling behavior was also recorded *ad libitum* on non-focal subjects throughout each group visit by research assistants in 1981-1983. Weaned age was defined as being between the last observed suckling event and the following month. For example, if an offspring was last suckling at the age of 36 months, weaned age was estimated at 36.5 months. Seven offspring were weaned during a period of two or more months without data collection due to logistical difficulties in the field, leading to less accurate weaned ages. In such cases, the termination of weaning was assumed to have taken place between the date of the last suckling observation and the date of the subsequent observation without suckling events. The accuracy of the weaned age thus ranged from one day (weaning through emigration of mother) up to five months (median / mean accuracy = 1 / 1.5 months).

Data analysis

A Cox proportional-hazards regression for survival data (Cox 1972) with mixed effects (Therneau 2015) was used to model offspring weaned age and to examine its relationship to other predictor variables. The dataset included right-censored observations, due to offspring who were not fully weaned at the end of the observation period or who died during the observation period (Table 1). When weaning was induced through maternal death, those data were not considered in the data analysis. Only offspring who were at least 21 months old at the end of the observation period were involved in the analysis, since weaning by the mother has never been observed earlier than this in mountain gorillas. The youngest known age at which an offspring was observed to be naturally weaned (excluding weaning by death of the mother or separation from the mother) was 22 months (Stewart 1981). The weaning stage of offspring (0 = not weaned, 1 = weaned) was defined as the status variable and weaned age, measured in months, was set as the time variable. The model returns hazard ratios

(*HR*). A *HR* above "1" indicates that this group of interest is more likely to be weaned, whereas a *HR* less than "1" indicates that the group of interest is less likely to be weaned. If *HR* equals "1", there was no difference between groups of interest. Cox models were carried out in R version 2.13.0 using 'coxme' package version 2.2.-5 (Therneau 2015).

Predictor variables

The offspring sex, mean monthly group size from birth to completed weaning, including all age-sex classes, group type (one-male and multi-male), mother's parity (primiparous and multiparous), mother's age and dominance rank (high-ranking and low-ranking) were entered in the survival analysis as predictor variables. Two offspring (field period 1973-1977) were born into a one-male group which turned into a multi-male group, following the maturation of a young male before weaning. The offspring group type was categorized as multi-male since blackbacks help silverbacks to defend the group (Yamagiwa 1987). Reproductive performance is reduced for young and old female mountain gorillas (Robbins et al. 2006). Thus, the squared term of maternal age was also included as a predictor variable. Females in each group were divided into high (top 50%) and low rank (bottom 50%) without adjusting for the number of females in each group following previous maternal investment studies (Robbins et al. 2007a, b). The rank of mothers during the first three field periods was extracted from published dominance matrices (Robbins et al. 2005). For the two most recent field periods, mothers' ranks were calculated using established methods (Robbins et al. 2005). From all field periods, we excluded females below the age of eight years from dominance matrices since these were below the age considered to represent adult females (Harcourt et al. 1980). For nine mother-offspring pairs the female's rank could not be clearly categorized. To test whether weaned age pattern provides support for the Trivers-

Willard hypothesis, we considered interactions between offspring sex and commonly used proxies of maternal condition defined by parity, rank and mean age. As a female's rank may play a more important role with growing group size (Robbins et al. 2007b), the interaction between mother's rank and group size was also entered as a covariate in the model.

Random effects

Seventeen out of 46 study mothers were represented twice in the longitudinal dataset with subsequent offspring and three mothers were presented three times. To account for repeated measures, we included mother's identity as a random effect nested in their social group. As weaned age data were collected during distinct field periods, field period was also treated as a random effect to control for clustered data design.

Inter-birth interval as indicator of weaned age

To examine whether inter-birth interval is a suitable indicator of weaned age, we correlated weaned age data with an accuracy of one month and better with the corresponding inter-birth interval (N = 20) using the Spearman's rank correlation test.

Consequences of weaned age variation

Long-term demographic records collected from the study groups by the Karisoke Research Center were used to explore potential consequences of weaned age variation for offspring and mother including the age at first parturition in female offspring ($N = 8$), age at death of weaned offspring ($N = 4$), survival of subsequent offspring beyond the first year ($N = 18$) and the timing of re-conception relative to completed weaning ($N = 16$). For these analyses, we also considered only weaned age data with an accuracy of at least one month. Spearman's rank correlation tests were conducted to examine the relationship between weaned age and age at first parturition, age at death and the timing of re-conception relative to the completed weaning. The re-

conception date was approximated by subtracting the median gestation length of 255 days in the population (Harcourt et al. 1980) from the date of the mother's subsequent parturition. We then calculated the relative time gap between re-conception and completed weaning. Negative values represented re-conception after weaning, while positive values indicated re-conception before weaning was completed. The Mann-Whitney U test for two-independent samples was used to compare weaned ages of two sets of offspring, those with subsequent siblings surviving the first year of life and those with subsequent sibling who died before reaching one year.

Results

When considering only offspring with a weaned age accuracy of one month or better ($N = 27$), the mean weaned age was 39.9 months (median = 40). Including all weaned offspring (n = 34) increased the mean to 40.8 months (median = 40.5). The distribution of weaned ages was bimodal, with peaks at relatively early age (35-40 months) and a relatively late age (45-50 months) (Fig. 1); thus the mean may not be biologically meaningful.

Cox proportional-hazards regression model output

Group characteristics

Group type had the strongest effect on weaned age, with offspring growing up in one-male groups ($N = 17$) being on average ~13 times more likely to be weaned earlier than offspring growing up in multi-male groups (N = 52) (Fig. 2; $HR = 13.18$, $z = 3.38$, $p < 0.001$). Two females had offspring with known weaned age in one-male and multi-male groups. Although no statistical test could be performed, the early weaned ages of their offspring born into one-male groups (37 and 29 months) compared to weaned ages

of their offspring born into multi-male groups (45.5 and 45 months respectively) were in line with the statistical group type effect on weaned age.

One-male groups were significantly smaller ($N = 17$, mean $\pm$ SD = 10.3 $\pm$ 3.2) than multi-male groups ($N = 52$, mean $\pm$ SD = 27.2 $\pm$ 16.7) (Mann-Whitney U test: $N = 69$, $W = 789$, $p < 0.001$). To disentangle the effect of group type from the effect of group size, we re-ran the model for one-male and multi-male groups separately. If the group type effect is simply reflecting a group size effect, weaned age should increase with group size. However, there was no effect of group size in one-male groups ($HR = 0.63$, $z = -1.18$, $p = 0.240$), whereas offspring in multi-male groups were weaned earlier with increasing group size ($HR = 1.05$, $z = 1.99$, $p = 0.047$), suggesting that the group type effect was independent of group size.

The effect of group size on weaned age depended on the mother's rank. The larger the group, the earlier low-ranking females weaned offspring ($HR = 1.10$, $z = 3.44$, $p = 0.012$), but this wasn't the case for high-ranking females ($HR = 1.01$, $z = 0.33$, $p = 0.740$).

Characteristics of mother and offspring

Overall, weaned age of daughters varied more than weaned age of sons (Fig. 3, coefficient of variation [CV]: $CV_{daughters} = 25.1$, $CV_{sons} = 13.7$). The three earliest weaned ages (22, 28, 29 months) were recorded for daughters of mid-aged multiparous mothers with unclassified or high rank, while the latest weaned individual (57 months) was observed in the daughter of a young, primiparous mother with low rank.

Furthermore, the likelihood of being weaned early reduced with increasing age of the mother ($HR = 0.56$, $z = 2.03$, $p = 0.042$). Although the squared term of maternal age did not reach statistical significance, its positive z-value ($HR = 1.01$, $z = 1.58$, $p = $

0.120) indicates a slightly convex weaned age curve for maternal age, with higher weaned age in young and older mothers compared to mid-aged mothers (Fig. 4). The group type effect was not caused by different age patterns of females in one-male and multi-male groups (Mann-Whitney U test: N_{multi} = 52, N_{one} = 17, W = 400, p = 0.563).

Primiparious mothers weaned their offspring later (N = 13, mean weaned age $\pm$ SD = 43.7 $\pm$ 7.9 months) than multiparous mothers (N = 21, mean weaned age $\pm$ SD = 39 $\pm$ 7.8 months) (HR = 0.08, z = -2.14, p = 0.032). Considering that weaned age increased with maternal age and primiparous mothers were younger (N = 24, mean age $\pm$ SD = 12.4 $\pm$ 4) than multipares (N = 45, mean age $\pm$ SD = 24 $\pm$ 6.2 years) (Fig. 4, Mann-Whitney U test: W = 1034, p < 0.001), we would expect opposite parity patterns. This contradiction might be caused by late weaned ages in the oldest multipares (Fig. 4).

There was no difference in weaned age between sexes (HR = 6.25, z = 1.74, p = 0.082) and between high- and low-ranking females (HR = 1.29, z = 0.60, p = 0.550). However, weaned age tended to depend on female rank (HR = 6.25, z = 1.47, p = 0.082). High-ranking mothers weaned sons significantly later than daughters (HR = 0.18, z = -2.36, p = 0.018). A reversed sex-bias in weaned age was not found within low-ranking mothers (HR = 1.10, z = 0.13, p = 0.900).

Low-ranking females were younger (N = 25, mean age $\pm$ SD = 16.2 $\pm$ 7.3) compared to high-ranking females (N = 35, mean age $\pm$ SD = 22.8 $\pm$ 7.3) (Mann-Whitney U test: W = 654, p = 0.001) and included a higher proportion of primiparous mothers (64%) than high-ranking females (14%) (N = 60, X^2 = 15.84, p < 0.001). As maternal condition might vary predictably with maternal age and parity, we re-ran two separate models entering offspring sex in interaction with either maternal age or parity. The effect of offspring sex depended on parity (HR = 10.34, z = 2.31, p = 0.021).

Multiparous mothers weaned daughters earlier than sons (HR = 0.14, z = -2.73, p = 0.006) while no sex difference occurred in primiparous mothers (HR = 1.46, z = 0.53, p = 0.600). The effect of maternal age also depended on offspring sex. Sons were weaned earlier by young and old mothers than by mid-aged mothers (maternal age x son: HR = 0.48, z = -2.10, p = 0.036; maternal age^2 x sex: HR = 1.01, z = 1.98, p = 0.048), whereas maternal age had no effect on weaned age of daughters (maternal age x daughters: HR = 1.00, z = -0.01, p = 0.990; maternal age^2 x sex: HR = 1.00, z = -0.37, p = 0.710). These findings suggest that mid-aged, high-ranking, multiparous females invest more in sons than in daughters in form of later weaning, and that only primiparous females provide milk longer to their daughters than sons.

A summary of tested variables and their effect on weaned age is provided in Table 3. To ensure that offspring with low accuracy of weaned age in the data set did not produce unreliable results, we re-ran the Cox-model but without offspring whose weaned age accuracy was less than one month (N = 61). Apart from the interaction effect of offspring sex with parity (p = 0.062) and maternal age (maternal age & sons: p $_{maternal\ age}$ = 0.180, p $_{maternal\ age}{}^2$ = 0.210), which did not reach statistical significance anymore, the importance of the remaining predictors in the model did not change.

Inter-birth interval as indicator of weaned age

Weaned age with an accuracy of one month or better showed a strong positive correlation with length of subsequent inter-birth intervals (IBIs) (N = 20, r_S = 0.678, p = 0.001, Fig. 5). The discrepancy between weaned age and IBIs ranged from 0 to 20.5 months (mean ± SD = 9.5 ± 4.9 months).

Consequences of weaned age

Historical demographic records to investigate consequences of weaned age variation on offspring survival and fitness are still few. Preliminary findings suggest that weaned age is unrelated to age at first parturition (mean ± SD = 11.2 ± 1.5 years, N = 8, r_S = -0.357, p = 0.389). Timing of re-conception by a mother relative to completed weaning was also unrelated to weaned age (mean ± SD = 4 ± 132 days, N = 16, r_S = 0.165, p = 0.541, Fig. 6).

Age at death and completed weaning were available for four out of 34 gorillas showing no relationship (N = 4, r_s = 0.2, p = 0.917). Twenty two weaned offspring were still alive at the end of 2012 (age range: 3.8 – 25.2 years, weaned age range: 28 – 57 months) suggesting that there is no strong impact of weaned age on offspring survival. The life history of seven weaned offspring remains unknown due to emigration events. One offspring died due to anthropogenic influences.

Mothers' subsequent offspring who survived the first year were linked to an earlier weaned age of the previous offspring compared to mothers' subsequent offspring who died before the age of one (Mann-Whitney U test: $N_{survived}$ = 13, N_{died} = 5, W = 57, p = 0.014, Fig. 7). This difference was not caused by different age distribution in both groups of mothers (Mann-Whitney U test: W = 34, p = 0.920).

Discussion

The primary goal of this study was to investigate factors that may explain weaned age variation in the endangered Virunga mountain gorillas, combining data from five different study periods. Weaned age was strongly associated with group type, being higher in multi-male groups than single male groups but was not associated with group size. In mountain gorillas, multi-male groups face lower infanticide risks and have higher offspring survival than one-male groups (Watts 2000; Robbins et al. 2007b;

Robbins et al. 2013), this may explain later weaning in these groups. Mothers with dependent offspring are vulnerable to infanticidal attacks by external silverbacks during inter-unit interactions or after the death of the group leader (Watts 1989; Robbins et al. 2007b). Therefore, females in one-male groups can benefit by weaning offspring early because of resumption of ovulation and infanticide risk. Exposure to high infanticide risk can cause stress (baboons [*Papio hamadryas* spp.]: Engh et al. 2006), reflected in increased cortisol levels (Romero 2004). In turn, high levels of cortisol in mother's milk can trigger faster infant weight gain by altering offspring behavioral phenotype and metabolism (rhesus macaques [*Macaca mulatta*]: Hinde et al. 2015). As age at weaning is linked to a threshold weight of roughly four times the neonatal birth weight in many mammals including primates (Clutton-Brock 1991; Lee et al. 1991; Lee 1996), maternal cortisol transferred to offspring through milk might contribute to regulation of an infant's development trajectory and thus weaned age (Love et al. 2013; Hinde et al. 2015).

In some cases, cortisol levels are positively associated with group size (e.g., male spotted hyenas [*Crocuta crocuta*]: Goymann et al. 2003) and/or negatively associated with rank (e.g., review: Creel et al. 2013; female spotted hyena [*Crocuta crocuta*]: Goymann et al. 2001). Cortisol might contribute to variation in weaned age in mountain gorillas, if levels are also inversely related to rank among females. However, cortisol and rank in nonhuman primates show complex relationships (olive baboons, Sapolsky 1982; Japanese macaques, *Macaca fuscata,* Barrett et al. 2002; review by Goymann and Wingfield 2004; baboons, *Papio cynocephalus*, Gesquiere et al. 2011; review by Creel et al. 2013; chimpanzees, *Pan troglodytes schweinfurthii*, Markham et al. 2013). To better understand the effect of group size on weaned age, especially when

multi-male groups grow beyond the size of the largest one-male group composed of 15 gorillas in this dataset, more data are required.

Group type (one- or multi-male) had no effect on inter-birth intervals (IBIs) of mountain gorillas (Robbins et al. 2007b, 2013). Different relationships of IBI and weaned age with group type despite the strong relationship between IBI and weaned age suggest that direct behavioural measures of maternal investment and care need to be integrated into studies of female reproductive strategies. However, discrepancy between measures may be caused by small sample size and the use of nipple contact rather than actual milk intake to assess weaned age in this study (see Cameron 1998). Recent non-invasive techniques enable assessment of stable carbon and nitrogen isotope ratios from fecal samples, indicating plant versus animal (including milk) food intake, and could be used in future to assess weaning status more reliably (Reitsema 2012).

Offspring sex and maternal condition

Greater variation in weaned age in daughters compared to in sons may indicate limited capacity to influence early maternal investment in sons due to neonatal sexual dimorphism, reflected in higher birth body mass in gorilla males than in females (Meder 1990; Leigh and Shea 1996), and higher metabolic requirements in male infants (Clutton-Brock et al. 1985). Thus, raising sons may mean greater lactational demands on mountain gorilla mothers and less ability to adjust weaned age. Galápagos sea lion offspring (*Zalophus wollebaeki*) show neonatal sexual dimorphism and have varying lactational demands associated with the level of independent feeding, indicating an offspring's contribution to its own survival and growth (Piedrahita et al. 2014). Thus, the mother's supply of resources and offspring's food intake through independent feeding should to be studied concurrently to understand sex-biased investment and underlying behavioral mechanism in mammals (see Royle et al. 2004).

Primiparous mothers weaned their offspring at later ages than their multiparous counterparts consistent with findings on IBIs (Robbins et al. 2007a), whereas weaned age was not affected by female rank which contrasts with findings on IBIs. This suggests that parity might be a better proxy of maternal reproductive condition in mountain gorillas than female rank. Primipares compared to multipares may have impaired reproductive success (see review by Anderson 1986; Bercovitch et al. 1998; Robbins et al. 2006), lack maternal experience and skills leading to lower efficiency of maternal investment and may face a conflict between allocating energy resources to the offspring while still investing in their own growth (Bercovitch et al. 2000; Künkele and Kenagy 2013). It should be also considered that accounting for the number of adult females in a group when allocating ranks to females may be important as consequences of being high- or low-ranking is likely to be affected by the presence of competitors.

Similar to findings on IBIs (Robbins et al. 2007a) and suckling frequency (Eckardt 2010), sex-differences in weaned age depend on proxies of maternal condition, defined by rank, parity, and age. High-ranking and multiparous females weaned sons later than daughters. However, reversed sex-bias patterns in weaned age consistent with Trivers-Willard hypothesis (1973) did not occur for rank, parity, and age. Later weaning in primiparous mothers and in sons of the oldest females, supports previous findings in mountain gorillas and other primate species suggesting an inverted U-shaped curve with relatively low reproductive performance in the young primipares and in the oldest females (Caro et al. 1995; Robbins et al. 2006). Despite a lack of extended post-reproductive lifespan in female mountain gorillas, five out of seven miscarriages were observed in multiparous mothers above the age of 27 which may reflect a reduced physiological capacity to reproduce in older females (Robbins et al. 2006); uterine and ovarian aging has been associated with declining fertility in aging women (Frank et al.

1994), rodents (Kong et al. 2012), red deer (*Cervus elaphus*) (Fisher et al. 2000) and

Japanese macaques (Nozaki et al. 1995). Thus, our findings also lend some support for

the terminal investment hypothesis which predicts that aging females invest more in

their current offspring as their reproductive value declines (see review by Caro et al.

1995).

Support for the Trivers-Willard hypothesis (1973) from different measures of

maternal investment in mountain gorillas (i.e. IBIs and weaned age) is limited, and it

remains questionable if this hypothesis can ever be proven or disproved in mammals,

especially in those with slow reproduction rates and relatively long life span. Our study

tested a population of females over limited periods (Carranza 2002) rather than

individual mothers over different reproductive efforts as proposed by Cameron and

Linklater (2002). Long-term effects of variation in weaned age will be more conclusive

as combined data on weaned age and reproductive success of offspring accumulate.

Furthermore, we currently lack evidence for two assumptions of the Trivers-Willard

hypothesis; namely, that females in good condition produce offspring in good condition

by the end of the maternal investment period, and that the advantage gained through

being in good condition maintains into adulthood. Assessing energy balance of mother

and offspring using urinary C-peptide measures (see Grueter et al. 2014) would allow

monitoring how mother's energetic budget translates into offspring energetic budget

and growth trajectory throughout the period of maternal investment and beyond.

Growth rates in wild animals can be assessed reliably through photogrammetry (Breuer

et al. 2007; Caillaud et al. 2008; Abavandimwe et al. 2015). Preliminary results provide

no support that early weaning is disadvantageous for mother and offspring. Subsequent

offspring of mothers who weaned offspring early also had a higher survival chance

indicating that mothers who wean early can also still succeed: "Do what you can, with what you have, where you are" (Roosevelt 1913, ch. 9).

Two weaning peaks – evidence of seasonality in weaning?

Mountain gorillas in the Virungas face only limited temporal variation in food abundance (Fossey and Harcourt 1977; Vedder 1984; Watts 1984); thus it is unsurprising that they are not seasonal breeders (Stewart 1988). However, in 2007, five offspring were weaned during a rich bamboo-shoot season. Bamboo shoot (*Yushania alpine*) is a highly preferred and only biannually available food item of mountain gorillas (Fossey and Harcourt 1977; Vedder 1984). A recent unpublished study on mechanical characteristics of food plants that make up 90% of the Virunga mountain gorilla diet revealed that bamboo shoots after removal of epithelium (as gorillas do before ingestion) has the lowest average toughness (~250 joules/metre squared) (Glowacka H pers. communication, 25th June and 18th August 2013). Low toughness of food facilitates mastication for gorilla weanlings which are commonly equipped with only deciduous dentition and lack most of their molars (Godfrey et al. 2003) that are needed for processing mature foliage and seeds efficiently (Kay 1978). Bamboo shoots are thus a suitable food for gorilla weanlings in the Virunga mountains where large, soft fruit sources are absent (Harcourt and Stewart 2007), in contrast with Western lowland gorilla (*Gorilla gorilla gorilla*) habitat where fruits are the preferred weaning food in young gorillas (Nowell and Fletcher 2008). In addition, bamboo shoots are high in energy and protein compared to other gorilla food items (Grueter et al. 2014), which makes them a suitable replacement for milk. Higher concentrations of urinary C-peptide in female Virunga mountain gorillas during the bamboo shoot season compared to other seasons support higher energetic intakes when bamboo shoots are available (Grueter et al. 2014). The two peaks in weaned age were about six months apart; this corresponds

with the typical six month interval between periods of bamboo shoot production (Fossey and Harcourt 1977; Vedder 1984), suggesting that seasonal access to supplementary weaning food may be more important for reproductive strategies in mountain gorillas than previously thought, and thus should be targeted in future investigations. As primates with seasonal mating patterns delay weaning to the subsequent mating season after missing a season (Lee and Kappeler 2003) gorilla mothers can wait to wean until the next bamboo shoot season with optimal weaning conditions. The alternative scenario allows mothers to wean earlier (see Lee 1996) despite impaired food processing competence of the weanling, due to supplementary weaning food provided by a rich bamboo shoot season. More weaned age data are required to confirm the bimodal distribution along data on bamboo phenology.

Findings in the light of current population changes

Through long-term and intensive conservation efforts in the Virungas, the mountain gorilla population is growing (Gray et al. 2013). This growth is resulting in higher group density and more solitary silverbacks in the population (Gray et al. 2013; Caillaud et al. 2014) leading to a sixfold increase in annual inter-unit interaction rates in the study groups (see Fig. 13 in Caillaud et al. 2014) and thus a potential increase in infanticide risk (Yamagiwa et al. 2009). Our findings suggest that continued population growth will exert an increasing selection pressure on maternal investment strategies in this population. Females, in particular those living in one-male groups with higher infanticide risk (Watts 2000), might "push" weaned age to the earliest possible developmental stage that allows successful weaning. To our knowledge the earliest age a mountain gorilla infant survived without milk provision by the mother was 22 months. However, a rare incident observed in November 2007 provided a unique perspective on

the ability of offspring to survive without any nutritional or physical support of the mother proposing that total independence may not be possible at such a young age (Eckardt et al. 2007). Two infants died after a sudden separation from their mothers due one group split during an interaction with a solitary silverback at the age of 23 and 29 months whereas another 30 months old infant survived 18-days without his mother before being reunited showing signs of malnutrition similar to kwashiorkor in humans (Tierney et al. 2010). This reinforces the fact that nutritional independence is likely to be only one facet of true independence from the mother but also that weaning before 29 months is only possible if the mother remains in the group.

If maternal cortisol affects infant development trajectory (Love et al. 2013; Hinde et al. 2015), a higher frequency of stressful inter-unit interaction (Eckardt et al. 2014) might contribute to earlier weaned age adjustments in the population. This study suggests that the gestation-lactation overlap varies substantially among female mountain gorillas. It might be expected that females would increase the overlap between the current lactation period and the subsequent gestation through pressures from extra group males, with multiparous, mid-age mothers likely to be in a better position to engage in such energetically demanding strategies.

Further focus on maternal strategies in a changing social environment is warranted. For this to be possible, adult females with offspring approaching weaning age (~2 years) should be regularly tested for pregnancy (optimally once to twice a month) to provide precise data on the length of gestation-lactation overlap, but also to detect miscarriages more reliably.

The availability and abundance of the five key gorilla food plants has also been changing alongside the growth of the Virunga mountain population, with two (*Galium* spp*., Laportea alatipes*) of the five decreasing in abundance (Grueter et al. 2013).

Continuing population growth may lead to increased food competition within groups which could be reflected in a stronger effect of mother's parity, rank, and maternal age on weaned age patterns. Such changing environmental factors demonstrate the importance of long-term research and monitoring of this key life history marker, weaned age, as well as of other associated measures of maternal investment, due to the importance of understanding their relationship with population dynamics of the Virunga mountain gorillas as they grow towards their carrying capacity.

Ethical Standards

This study was funded by University of Chester Gladstone fellowship. We declare that the study complies with the current laws of the country in which it was conducted. All applicable international, national, and/or institutional guidelines for the care of animals

were followed. This article does not contain any studies with human participants

performed by any of the authors.

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Table and Figure captions

Table 1 Distribution of study offspring (> 2 years) across the five field periods including offspring which were weaned by the end of a given field period and offspring which either died or were not yet weaned at the end of a given field period (unknown weaned age)

Table 2 Number of silverbacks, (sub)adult females and total number of group members of study groups for each field period

Table 3 Outcome summary of effects on weaned age including all offspring. *HR* presents hazard ratio and "*" indicate p-values equal or less than 0.05

Figure 1 Weaned age distribution in mountain gorillas

Figure 2 Cox regression plot showing the proportion of non-weaned offspring in one-male and multi-male groups until the age of 60 months (N = 69). Note that the survival curves include offspring who were not yet weaned in the end of the study period

Figure 3 Boxplot of offspring weaned age (in month) presented by **a** offspring sex (F female, M male) and **b** offspring sex and female rank (H high, L low) (N_{HF} = 6, N_{HM} = 7, N_{LF} = 6, N_{LM} = 11). Boxplots indicate the median, the inter-quartile range, the maximum and minimum value excluding outliers

Figure 4 Distribution of offspring weaned age by mother's mean age (black vertical lines separate young, mid-aged, old mothers) and parity (empty dots = primiparous, black dots = multiparous)

Figure 5 Relationship between weaned age (in months) and subsequent inter-birth interval (N = 20)

Figure 6 Timing of subsequent conception date (y = 0) in relation to completed weaning. Negative values indicate weaning after conception and positive values indicate weaning before conception

Figure 7 Boxplot of offspring weaned age (in months) presented by survival of subsequent offspring ($N_{survived}$ = 13, N_{died} = 5). Boxplots indicate the median, the inter-quartile range, the maximum and minimum value excluding outliers and outliers showing data points less or more than 1.5 times outside the lower or upper quartile respectively