AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 000:000–000 (2011)

Lifetime Reproductive Success of Female Mountain Gorillas

Andrew M. Robbins,[1] Tara Stoinski,[2] Katie Fawcett,[2] and Martha M. Robbins[1]*

[1]*Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*
[2]*Dian Fossey Gorilla Fund International, 800 Cherokee Ave SE, Atlanta, GA 30315-1440*

KEY WORDS fitness; longevity; fertility; offspring survival; dominance; life history

ABSTRACT Studies of lifetime reproductive success (LRS) are important for understanding population dynamics and life history strategies, yet relatively little information is available for long-lived species. This study provides a preliminary assessment of LRS among female mountain gorillas in the Virunga volcanoes region. Adult females produced an average of 3.6 ± 2.1 surviving offspring during their lifetime, which indicates a growing population that contrasts with most other great apes. The standardized variance in LRS (variance/mean^2 = 0.34) was lower than many other mammals and birds. When we excluded the most apparent source of environmental variability (poaching), the average LRS increased to 4.3 ± 1.8 and the standardized variance dropped in half. Adult lifespan was a greater source of variance in LRS than fertility or offspring survival. Females with higher LRS had significantly longer adult lifespans and higher dominance ranks. Results for LRS were similar to another standard fitness measurement, the individually estimated finite rate of increase (λ_{ind}), but λ_{ind} showed diminishing benefits for greater longevity. Am J Phys Anthropol 000:000–000, 2011. © 2011 Wiley-Liss, Inc.

Assessments of individual fitness are important for understanding population dynamics and evolutionary biology (Stearns, 1992; Metcalf and Pavard, 2007). Fitness data for individuals can be combined to provide estimates of population growth, population viability, and the effective population size (Soule, 1987; Caswell, 2001). Variance in fitness among individuals leads to natural selection when it is linked to differences in phenotypes that are heritable (Darwin, 1859; Price, 1996; Avise and Ayala, 2009). The standardized variance (variance/mean^2) in fitness has been defined as the "opportunity for selection," which reflects an upper limit on the rate of evolution (Crow, 1958; Shuster and Wade, 2003). Variance in fitness can also arise from environmental fluctuations or by chance (Sutherland, 1985, 1987; Coltman et al., 1999; Forcada et al., 2008).

Lifetime reproductive success (LRS) is a commonly used measure of individual fitness (Barrowclough and Rockwell, 1993; van Noordwijk and van Schaik, 1999; Rhine et al., 2000; Wasser et al., 2004). The LRS of a female equals the total number of surviving offspring that she produces in her lifetime. LRS can be expressed as the product of three components: adult lifespan (L), average fecundity per year (F), and offspring survival (S). All three components are expected to have positive correlations with their product (LRS) unless they have negative covariance amongst each other. For example, a negative correlation between fertility and adult lifespan could arise from life history trade-offs between reproduction versus somatic maintenance (Kirkwood, 1977; Kirkwood and Holliday, 1979; Hurt et al., 2006; Ricklefs and Cadena, 2007), and between genes that enhance survival or reproduction early in life at the expense of harmful effects later in life (Williams, 1957; Blomquist, 2009b). Conversely, positive covariance among all three components could arise if females in favorable environments have better physical condition that enhances many aspects of fitness ("silver spoon effect," Grafen, 1988). Body mass and social ranking have been considered indicators of female quality that could influence reproductive success (Ribble, 1992; Berube et al., 1999; White, 2005; Jones et al., 2010). Thus, a combination of factors can determine how each component contributes to variance in fitness (Brown, 1988).

Another commonly used measure of individual fitness is the individually estimated finite rate of increase, also known as the per-projection-interval multiplicative rate of increase (McGraw and Caswell, 1996; Kaar and Jokela, 1998; Weladji et al., 2006). The individually estimated finite rate of increase (λ_{ind}) is analogous to population-wide values of λ from Leslie matrix calculations, whose natural log is equal to the population growth rate "r," also known as the instantaneous rate of increase (Caswell, 2001). The value of λ is greater than one when a population is growing and less than one when a population is declining. The population growth rate would equal the natural log of a female's value for λ_{ind} if all other adult females gave birth to the same number of surviving offspring at the same ages.

Unlike LRS, values for λ_{ind} depend upon the ages at which a female reproduces because of the discounting inherent in age-structured population models (Caswell, 2001). Among females with the same LRS, earlier reproduction increases λ_{ind} when it is above one, and delayed reproduction increases λ_{ind} when it is below one. Thus, early breeding is generally considered favorable (i.e., it

---

*Correspondence to: Martha M. Robbins, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. E-mail: robbins@eva.mpg.de

Received 31 August 2010; accepted 28 July 2011

DOI 10.1002/ajpa.21605

leads to a greater number of descendants over multiple generations) when a population is increasing, and delayed breeding is considered favorable when a population is declining (Stearns, 1992; McGraw and Caswell, 1996; Brommer et al., 2002; but see Dugdale et al., 2010). When λ_{ind} is above one, the driving force for longer adult lifespans can become minimal, allowing deleterious mutations to accumulate, and senescence can evolve through "decelerating selection" (Medawar, 1946; Hamilton, 1966; Laird and Sherratt, 2009).

Species with longer adult lifespans typically have lower fertility, a combination known as "slow" life history (e.g., Charnov and Berrigan, 1993; Leigh and Blomquist, 2007). The life histories of great apes are among the slowest of all primates, a correlation which is consistent with their large body sizes (Purvis et al., 2003; Deaner et al., 2003). Studies of life history theory often involve inter-specific comparisons of demographic parameters, so data on great apes are relevant for understanding primate life history evolution generally and that of humans in particular (Leigh and Shea, 1996; Dunbar, 2003; Hawkes, 2003).

Despite the importance of LRS and λ_{ind} for studies of evolutionary biology and population dynamics, relatively few direct measurements are available for long-lived species, especially nonhuman primates (Rhine et al., 2000; Wasser et al., 2004). The lack of data reflects the challenges of tracking individuals in long-term studies, especially when those individuals disperse (e.g., Alberts and Altmann, 1995). In the absence of data that spans the entire lifetime of all individuals in a cohort, LRS and its variance are often estimated from measurements of short-term reproductive success (Rhine, 1992; Barrowclough and Rockwell, 1993; Storz et al., 2002; Cheney et al., 2004; Setchell et al., 2005; Robbins, 2010).

This paper provides a preliminary assessment of LRS and its variance among female mountain gorillas in the Virunga volcanoes region, including comparisons with λ_{ind}, partitioning into components (L, F, and S), and the use of dominance rank as a potential indicator of individual quality. The population of those groups has grown by 3–5% per year throughout this study, so we expect that λ_{ind} will typically be above one, and it will place diminishing value on reproduction later in life (Miller et al., 1998; Robbins and Robbins, 2004; Robbins, 2010). However adult females are almost always nursing or pregnant, so we see relatively little variation in how the timing of their reproduction is distributed throughout adulthood (Robbins et al., 2006; Robbins et al., 2011), and therefore we expect a close correlation between LRS and λ_{ind}.

Female mountain gorillas feed on abundant and evenly distributed vegetation, so variability in food density (from 4 to 66 g/m^2) and group size (from 2 to 65 individuals) have shown no significant influence on female reproductive success (Robbins et al., 2011). There was no evidence of leopard predation on gorillas during this study and we are unaware of any sightings of those predators since the 1960s (Schaller, 1963). Human disturbance, while considerable, has not substantially influenced fertility or offspring survival (Robbins et al., 2011), and our analysis controls for the effects of poaching. Mountain gorillas and other primates have relatively low variance in their annual rates of fertility and mortality, which may reflect low environmental stochasticity and/or enhanced buffering against such stochasticity (Morris et al., 2011). Therefore, we predict that female mountain gorillas have low standardized variance (variance/mean^2) in LRS, especially when poaching deaths are excluded from the calculations.

TABLE 1. Summary of the study groups

Group	Year 1	Year 2	Grp-years	Size	AF	Births
Amok's Grp	1969	1971	2.3	1.1	0.1	0
Beetsme's Grp	1985	2008	23.5	19.3	6.1	33
Bwenge	2006	2008	2.1	8.4	5.2	7
Group 4	1967	1979	11.3	11.0	4.0	12
Group 5	1967	1993	25.7	17.6	6.6	44
Group 8	1967	1974	6.7	4.2	0.7	1
Gwiza	2004	2008	4.8	1.1	0.1	0
Inshuti	2004	2008	5.1	1.7	0.6	1
Isabukuru	2007	2008	1.6	6.2	3.0	2
Kuryama	2007	2008	1.5	12.6	4.9	3
Nunkie's Grp	1972	1985	12.6	9.5	4.3	15
Pablo's Grp	1993	2008	15.7	42.2	15.5	67
PbSubgrp	2007	2007	0.1	14.0	3.0	0
Samson's Grp	1971	1976	4.6	1.6	0.6	1
Shinda's Grp	1993	2008	15.7	22.3	6.6	26
Susa Grp	1978	2008	30.4	27.7	9.5	75
Tiger's Grp	1981	1987	6.1	1.5	0.3	1
Umushikirano	2006	2008	2.3	1.2	0.2	0

First and last years of observation (year 1 and year 2), as well as the number of gorilla-years observed (grp-years). Average number of total gorillas (size) and adult females (AF) throughout the study. Number of births in each group.

Female mountain gorillas form weak individualistic dominance hierarchies and competition for resources is generally ineffective (Stewart and Harcourt, 1987; Watts, 2001; Robbins et al., 2005). Female mountain gorillas had shorter interbirth intervals when high ranking, but rank was not significantly correlated with offspring survival or the annual rate of giving birth to surviving offspring (i.e., the product of fecundity times offspring survival, Robbins et al., 2007a,b). Those mixed results suggest that dominance rank may represent an approximate indication of differences in physical condition among females. This study builds upon those results by examining the relationships between rank versus adult lifespan, LRS, and λ_{ind}; and by looking for positive covariance among all reproductive parameters as additional evidence of differences in female quality.

Studies of individual fitness should ideally last several times longer than the lifespan of typical adults, which would take hundreds of years for long-lived species such as mountain gorillas. Even though this 40-year study is one of the larger ones for nonhuman primates, sample sizes are still small, so conclusions from this preliminary assessment should be considered tentative. It is also important to consider how the modern environment of mountain gorillas has been influenced by human activity (including the near-extirpation of nonhuman predators), although a full discussion of such influences is beyond the scope of this publication.

METHODS

Study population

The study population consists of mountain gorillas in the Virunga Volcano region of Rwanda, Uganda, and Democratic Republic of Congo. The data are taken from the long-term records of the Dian Fossey Gorilla Fund International (DFGFI) Karisoke Research Center from 1967 to 2008, along with one group (Susa) from the records of the Rwanda Development Board (Table 1). More groups have been followed per day later in the study than earlier. Female gorillas are considered

TABLE 2. Summary of lifetime reproductive success (LRS) and λ_{ind} for each female, and the components of LRS: adult lifespan in years (L), average fecundity per year (F), offspring survival (S), and their products (LF, LS, and FS)

Gorilla	IBIS	F	S	L	LF	LS	FS	LRS	λ_{ind}
CLO	43.4	0.308	71%	22.8	7.0	16.3	0.220	5.0	1.057
FUD	56.8	0.226	83%	26.6	6.0	22.2	0.188	5.0	1.049
GIT	–	0.273	33%	11.0	3.0	3.7	0.091	1.0	0.950
IMP	–	0.364	0%	2.8	1.0	0.0	0.000	0.0	–
JEN	49.6	0.225	100%	13.3	3.0	13.3	0.225	3.0	1.032
MAC	–	0.226	50%	8.8	2.0	4.4	0.113	1.0	0.950
MUR	46.0	0.239	75%	16.8	4.0	12.6	0.179	3.0	1.025
PAN	47.8	0.224	83%	26.8	6.0	22.4	0.186	5.0	1.043
PTY	50.8	0.282	71%	24.8	7.0	17.7	0.201	5.0	1.051
PAP	43.9	0.253	78%	35.6	9.0	27.7	0.197	7.0	1.054
PIC	47.6	0.179	100%	16.8	3.0	16.8	0.179	3.0	1.027
PUC	51.1	0.231	86%	30.3	7.0	26.0	0.198	6.0	1.054
SIM	50.2	0.382	33%	23.6	9.0	7.9	0.127	3.0	1.022
Main dataset									
Mean	48.7	0.262	67%	20.0	5.2	14.7	0.162	3.6	1.026
Std	3.9	0.059	29%	9.4	2.6	8.8	0.063	2.1	0.038
G'	–	14%	53%	60%	70%	120%	36%		–
R^2	1%	8%	44%	93%	68%	92%	63%		79%
No poaching									
Mean	49.0	0.258	74%	23.2	6.0	17.4	0.181	4.3	1.034
Std	4.1	0.057	24%	7.6	2.3	7.6	0.041	1.8	0.032
G'	–	30%	64%	67%	93%	124%	30%		–
R^2	4%	2%	18%	86%	46%	86%	43%		74%

The age of death is 8 years more than the adult lifespan. IBIS is the average length of inter-birth intervals (months) with offspring that survive to reach age 3, *LF* equals the total number of offspring per female, *FS* equals annual rate of giving birth to offspring that survive to reach age 3, and LRS equals the number of offspring that survived to reach age 3. The G' and R^2 values indicate how each component contributes to variance in LRS (see Methods).

infants until they reach the age of 3 years, then juveniles until age 6, then subadults until age 8, and then adults thereafter.

The "main dataset" in this study consists of 13 breeding females that were monitored for essentially their entire adult lifespan (Table 2). Eleven of those females definitely or probably died, and results were similar whether we included or excluded the other two females (Clo and Jen) whose disappearances were unexplained (not shown). We always excluded two additional adult females who disappeared for unknown reasons while nulliparous. These disappearances were most likely due to dispersal, given that 31 known or probable transfers by nulliparous adult or subadult females occurred through 2005 (including transfers among the study groups, Robbins et al., 2009a) and only one known death. One female (Pan) was estimated to be 10 years old when first observed, so she could have already had an infant that died before weaning, but results were similar when we added another deceased offspring to her records (not shown).

Lifetime reproductive success

The LRS of each female in the main dataset ($N = 13$) was defined as her total number of offspring that survived to reach the age of 3 years, the typical age of weaning in this population (Watts, 1991). Values of LRS do not include any offspring that died during infancy (i.e., before age 3), regardless of their cause of death. LRS values include all offspring that survived through infancy, regardless of their subsequent fate as juveniles and beyond.

We report the mean, standard deviation, and standardized variance (variance/mean^2) in LRS for the main dataset, which includes three adult females that died from poaching (Imp, Mac, Mur). It is unclear whether poaching deaths are typical of the evolutionary history of this population (Harcourt and Stewart, 2007), so we performed a separate set of LRS calculations without those females. The remaining 10 females did not have any offspring that died from poaching during infancy. We performed an ANOVA to quantify how the poaching deaths of adult females contributed to variance in LRS in the main dataset. In that analysis, the dependent variable was the LRS of each female in the main dataset. The category variable was whether the female died from poaching ("yes" or "no"). The coefficient of interclass correlation (r_i or R^2) from that ANOVA indicated how much variance in the dependent variable (LRS) could be explained by the category variable (e.g., Sokal and Rohlf, 1995).

Other measures of lifetime fitness

Studies of LRS often consider offspring survival until adulthood (Brown, 1988; Strassmann and Gillespie, 2003), so for comparison purposes, we estimated the average value for the females in the main dataset. We multiplied the average LRS of those females by the overall survivorship from ages 3 to 8 of all habituated gorillas in the Virungas (Robbins et al., 2011). We performed a similar calculation using the LRS of the 10 adult females who did not die from poaching, and a survivorship value for ages 3–8 that excluded poaching deaths at those ages (Robbins et al., 2011).

Studies of female LRS occasionally focus on the number of daughters that survive to reach adulthood, which reflects the capacity for one generation of females to replace itself with another generation of females (Kaar and Jokela, 1998; Brommer et al., 2004). The birth sex ratio of this population has not been significantly different from 50:50 (Robbins et al., 2007a), and the probability of dying at each age until adulthood has not been significantly different for male versus females (Robbins et al., 2011). Therefore, to avoid any bias from stochasticity in our relatively small dataset, we assumed that the average number of "replacements" per adult female was equal to 50% of the average number of total offspring that survived to reach adulthood.

We calculated the individually estimated finite rate of increase (λ_{ind}) for each female, using an individual-based discrete-time renewal equation:

$$1 = 0.5 * \sum_{x=1}^{\Omega} f_x * s_x * (\lambda_{\text{ind}}{}^{\wedge -x}) \tag{1}$$

in which "f_x" is the number of offspring that the female produced at each age "x" until the last observed age "Ω," and s_x is the proportion of those offspring that survived to reach the age of 3 years. Calculations of λ_{ind} often do not account for variability among females in the sex ratio of their offspring (McGraw and Caswell, 1996; Brommer et al., 2004), so the coefficient of "0.5" reflects the assumption of a 50:50 male: female ratio throughout the population (Robbins et al., 2007a). For each female, we used iterative calculations with the bisection method to find the value of λ_{ind} that corresponds to a value of "one" for the right-hand side of Eq. (1) (Byrne, 2008).

We performed an ANOVA to quantify the proportion of variance in λ_{ind} among females that could be explained by differences in their LRS, versus the proportion that arose from differences in the timing of reproduction among females that had the same LRS. In that analysis, the dependent variable was the λ_{ind} of each female and the category variable was her LRS. The analysis used the main dataset that includes females who died from poaching, because we are mainly comparing mathematical relationships that are not expected to depend upon the cause of death.

Our results for λ_{ind} do not include the one adult female (Imp) that was killed before weaning any offspring, because when $\lambda_{\text{ind}} = 0$, it was many ($\sim$25) standard deviations away from the mean of the remaining data (for a similar approach see Kaar and Jokela, 1998). If that data point was included, it would further increase the proportion of variance in λ_{ind} that arose from differences in LRS, and further decrease the linearity of the relationship between adult lifespan and λ_{ind}.

Contributions to variance in LRS

The LRS of each female equals the product of three components: her adult lifespan (L), her average fecundity per year (F), and the proportion of her offspring that survived to reach the age of 3 years (S). Adult lifespan equals the age of death minus the age when females become adults (8 years). The average fecundity of each female equals her total number of offspring (all offspring, not just those that survived to reach the age of 3 years) divided by her adult lifespan. Offspring survival for each female equals her number of offspring that survived to reach the age of 3 years, divided by her total number of offspring (all offspring). Female mountain gorillas have shorter interbirth intervals after an infant dies (Gerald, 1995; Robbins et al., 2006), so we use the average length of interbirth intervals with surviving offspring (IBIS) as an additional measure of female fertility, as well as the rate of giving birth to offspring that survive to reach the age of 3 years ($F{*}S$).

To quantify how L, F, and S (and their products) contribute to variance in LRS among breeders, we report the G' values from upward partitioning as presented in Table 27.1 of Brown (1988). G' is an indicator of how the variance in a parameter contributes to the variance in its product with other parameters (cf. references in Breuer et al., 2010, for additional literature about this approach and others). The first step in our calculations was to normalize the data for each component, by dividing the value for each female by the mean of the component among all females. For example, if Y_{L} is the array of values for adult lifespan (one value for each female), and X_{L} is the array of normalized values, then $X_{\text{L}} = Y_{\text{L}}/\text{mean}(Y_{\text{L}})$. Next we calculated the product of all three normalized components for each female (i.e., $X_{\text{L}}{*}X_{\text{F}}{*}X_{\text{S}}$, in which X_{S} and X_{S} are the arrays of normalized values for fecundity and offspring survival). Then, we calculated the variance for each of the normalized components and their product. For example,

$$G_{\text{L}} = \text{Var}(X_{\text{L}}) \tag{2}$$

$$G_{\text{LFS}} = \text{Var}(X_{\text{L}} * X_{\text{F}} * X_{\text{S}}) \tag{3}$$

in which "Var" signifies the variance among females for the value in parentheses. G_{F} and G_{S} were calculated with an analogous form of Eq. (2); G_{LF}, G_{LS}, and G_{FS} were calculated with an analogous form of Eq. (3). Finally, we multiplied each of the G values by ($100/G_{\text{LFS}}$) to produce the G' values.

In addition to the G' values, we also used linear regressions to quantify how each component and their products contributed to the variance in LRS among breeders. In each regression, the dependent variable was the LRS of each female, and the independent variable was one of the components of LRS (L, F, S) or their products. The coefficient of determination (R^2) from those regressions indicated how much variance in the dependent variable (LRS) could be explained by the independent variable (e.g., Sokal and Rohlf, 1995). For example, when the LRS of each female was the dependent variable and the adult lifespan of each female was the independent variable, the R^2 value from a linear regression equaled 0.93, which indicated that adult lifespan could explain 93% of the variance in LRS (as shown for the "main dataset" in Table 2).

Neither the G' nor R^2 values for the three components will typically add up to 100%, due to covariance among the components. The G' value for each component shows how the variance in LRS would change, if that component varied over its observed range while the other components were held constant at their average values. The R^2 values show how variance in each component affects LRS while the other components also vary over their observed range. Thus, any effect of covariance between two components is not included in the G' value for either component, but it is included in the R^2 values for both components.

We examined covariance among the components when needed to interpret their G' and R^2 values. Although we used linear regressions to describe variance contributions, we used nonparametric Spearman rank correlations for testing the statistical significance of the relationships among variables (due to small sample sizes). P-values for the Spearman rank correlations were determined by using bootstrap calculations with 10,000 permutations (Mundry and Fischer, 1998).

No infertile females have been observed in this population, so we did not use the Brown (1988) equation for estimating the variance in LRS that arises between breeders versus nonbreeders. Only one "nonbreeding adult" has been observed, a female that died from disease 3 months after reaching the age of 8 years (Qin, see Fossey, 1983). Thus her contribution to variance in LRS essentially arises from her very short adult lifespan, which is considered in the "broader" and "broadest" datasets that are described next.

Bias estimation for adult lifespan

This study did not follow a prespecified cohort of females through their adulthood, so we expected results to be biased toward females that died relatively young (e.g., Nishida et al., 2003). To estimate the bias, we compared the survivorship curve derived from the main dataset ($N = 13$) with more complete survivorship curves that included censoring of females that were still alive when the study ended. A "broader" dataset added 63 other adult females that were observed since reaching the age of 8 years but did not die during this study. The "broadest" dataset added another 20 females whose adult lifespan had already begun when first observed, including some that died during the study. Age estimates are considered accurate to within ± 2 years for females in the broader dataset and up to 4–10 years for females in the broadest dataset. The comparisons excluded the unexplained disappearances of nulliparous females because they most likely dispersed, as well as poaching deaths, so those females were also censored at the age when they were last observed.

For each survivorship curve, the period mortality probability (q_x) at each age (x) was calculated as the number of deaths (d_x) divided by the number of adult females that reached that age (Stearns, 1992). The period survival probability (p_x) equaled $1 - q_x$. Survivorship (l_x) to reach age x was calculated as the product of p_x from all preceding ages. The mean and variance in adult lifespan was estimated for each survivorship curve by assuming that the proportion of adult females that die at each age (T_x) is equal to $l_x - l_{x+1}$. The mean total lifespan (M_{TL}) was calculated as ($\sum T_x * x$), which was converted into mean adult lifespan (M_{AL}) by subtracting the age when females are first considered adults (8). The variance in both measures of lifespan (V_{L}) was calculated as $\sum T_x * (M_{\mathrm{TL}} - x)^2$.

Dominance rank

Dominance data came from fifteen hierarchies measured from 1971–2001 involving all of the major groups except the tourist group (Robbins et al., 2005). Ordinal rankings were developed from a combination of focal and ad libitum observations of approach-retreat interactions (e.g. Watts, 1994) using the I & SI method (de Vries, 1998). We standardized the rankings using Eq. (4):

$$\text{Standardized rank} = (N_{\mathrm{F}} - R_{\mathrm{F}})/(N_{\mathrm{F}} - 1) \qquad (4)$$

In that equation, R_{F} is the ordinal rank to be standardized, and N_{F} is the number of females in the matrix. The standardized rank of each female equals the proportion of other females that are below her in the matrix, so the lowest female in each matrix has a standardized rank of "0," and most dominant female has a standardized rank of "1" (for similar approaches see Rhine et al., 1989; Cote, 2000). The overall standardized rank for each female was calculated as the average of all measured values throughout her adulthood. On average, the overall standardized ranks are based on 50% of the years that a female was an adult ("% years ranked," range = 25–93%). The overall standardized ranks may be less reliable when based upon a relatively small proportion of a female's adulthood, but when we used the "% years ranked" as a weighting factor to make the analyses less sensitive to those females, results were similar and are not shown (for a description of weighting factors, see Chatterjee and Price, 1991).

RESULTS

Lifetime reproductive success

Among the 13 breeding female mountain gorillas that were observed for essentially their entire adulthood (the "main dataset"), LRS averaged 3.6 ± 2.1 SD offspring that survived to reach age three (range = 0–7, median = 3). The standardized variance equaled 0.34. When we excluded the three females that died from poaching, LRS averaged 4.3 ± 1.8 surviving offspring, which equals a standardized variance of 0.17. Thus poaching decreased the mean LRS by 19% and doubled the standardized variance. According to the R^2 value from an ANOVA, poaching accounted for 38% of the variance in LRS among breeders ($F_{11,1} = 6.8$, $P = 0.024$).

Other measures of lifetime fitness

When poaching deaths that occurred from ages 3 to 8 are included, survivorship from ages 3 to 8 has been 91% among all habituated gorillas in the Virungas (Robbins et al., 2011). Therefore, for the thirteen females in the main dataset, the average LRS of 3.6 corresponds to an average of $3.6 \times 0.91 = 3.3$ offspring that survive to reach adulthood. If 50% of surviving offspring are daughters, then the average adult female has been producing $3.3 \times 0.5 = 1.64$ adult female offspring ("replacements"). When poaching deaths that occurred from ages 3 to 8 are excluded, survivorship from ages 3 to 8 has been 93% (Robbins et al., 2011). Therefore, if poaching did not occur, then the average adult female would produce $4.3 \times 0.93 = 4.0$ offspring that survive to reach adulthood and 2.0 replacements.

Among the 12 adult females in the main dataset with at least one surviving offspring, the average value for λ_{ind} was 1.026 ± 0.038 (range = $0.95 - 1.057$, median = 1.037). The R^2 values from an ANOVA indicated that differences in LRS could account for up to 99% of the variance in λ_{ind} among females (Fig. 1), with only 1% of the variance arising from differences in the timing of reproduction among females that had the same LRS (e.g., while including all thirteen females in the main dataset, $F_{7,4} = 174.1$, $P < 0.001$).

Components of LRS

Adult lifespan was the greatest source of variance in LRS in the main dataset and when we excluded the three females that died from poaching (Table 2). Females with longer adult lifespans had significantly higher values of LRS (Tests 3.1a and 3.1b in Table 3). The positive

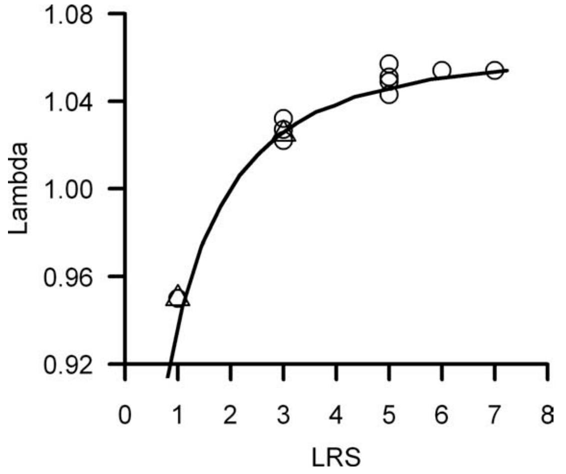

Fig. 1. LRS versus λ_{ind} (Lambda) for females with at least one surviving offspring. Not shown is one female (Imp) with no surviving offspring (LRS = λ_{ind} = 0), who was killed shortly after reaching adulthood.

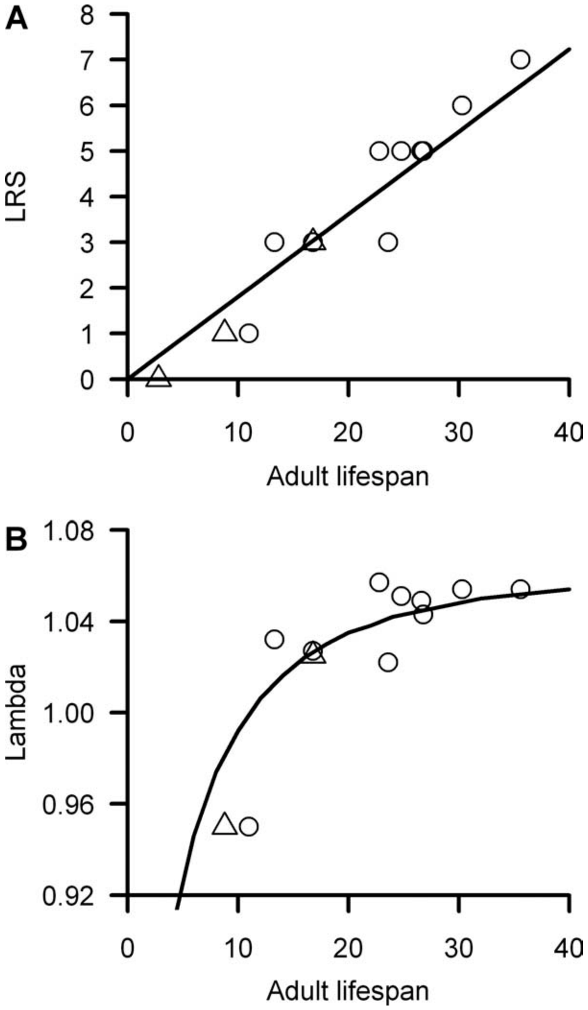

Fig. 2. Correlations between adult lifespan versus lifetime reproductive success (LRS) and the per-projection-interval multiplicative rate of increase (λ_{ind}) for females who died from natural causes (circles) and from poaching (triangles). Figure 2b does not show one female (Imp) with no surviving offspring (LRS = λ_{ind} = 0), who was killed shortly after reaching adulthood. Solid lines show hypothetical results in which the product of the other two components of LRS was held constant at the average rate of 0.162 surviving offspring per year ($F{*}S$).

TABLE 3. Spearman correlations between lifetime reproductive success (LRS) and λ_{ind}.versus adult lifespan (L), offspring survival (S), fecundity (F), the average dominance rank (rank), and the average length of interbirth intervals with surviving infants (IBIS)

Test	Var1	Var2	Include poaching	N	rho	P	
3.1a	L	LRS	Yes	13	0.95	0.0001	
3.1b	L	LRS	No	10	0.91	0.0003	
3.1c	L	λ_{ind}	Yes	12	0.73	0.0079	
3.1d	L	λ_{ind}	No	10	0.61	0.0695	
3.2a	S	F	No	10	–0.87	0.0020	
3.2b	S	F	Yes	13	–0.82	0.0012	
3.2c	S	L	Yes	13	0.44	0.1270	
3.3a	Rank	L	No	9	0.83	0.0081	(0.0718)
3.3b	Rank	LRS	No	9	0.86	0.0045	(0.0390)
3.3c	Rank	λ_{ind}	No	9	0.85	0.0053	(0.0270)
3.4a	L	$F{*}S$	No	10	0.22	0.5416	
3.4b	L	IBIS	No	9	0.20	0.6246	

Statistical results include the sample size (N), the correlation coefficient (rho), and the P-value. Values in parentheses are the P-values when dominance rank was based on measurements before age 20.

correlation between λ_{ind} versus adult lifespan was significant when we included females that died from poaching (Test 3.1c in Table 3), but not when those females were excluded (Test 3.1d in Table 3). Visual inspection showed that λ_{ind} started to level off at longer adult lifespans (Fig. 2), as expected when λ_{ind} is greater than one.

We compared the main dataset with two other survivorship curves to assess the potential bias toward females that died at relatively young ages (Fig. 3). Adult lifespan averaged 23.1 ± 7.2 years in the main dataset, 25.9 ± 6.7 years in the "broader" dataset of females that were observed since they reached the age of 8 years (including censored data for those that have not died), and 25.2 ± 7.9 years in the "broadest" dataset that also includes females that had already reached adulthood when first observed. Thus the main dataset may underestimate the mean adult lifespan (and LRS) by about 10% and the precision of its variance is approximately ±15%.

When we excluded the females that died from poaching, the G' value for offspring survival was 64% versus only 18% for the R^2 value (Table 2). This difference arose because R^2 values include the effects of covariance among components and G' values do not. Offspring survival had a strong negative correlation with fecundity (Test 3.2a in Table 3), as expected because females give birth sooner after their infants die. Thus the G' value illustrates how offspring survival would affect variance in LRS if females did not give birth sooner after an infant dies, and the R^2 value is more representative of the actual biological relationships.

When we included females that died from poaching, offspring survival still had a strong negative correlation with fecundity (Test 3.2b in Table 3), but its R^2 value was boosted by a nonsignificant positive correlation with adult lifespan (Test 3.2c in Table 3). Because of those offsetting covariances, the G' and R^2 values for offspring survival were both relatively high when we included

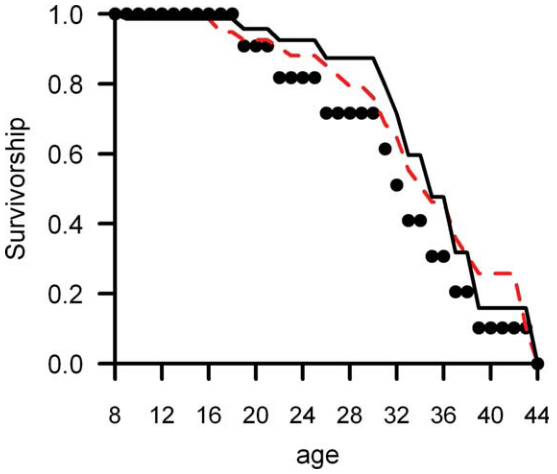

Fig. 3. Survivorship curves for adult females in the analyses of LRS (circles), versus a "broader" dataset of adult females who were observed before their first parturition (including those who are still alive, solid line), and versus the "broadest" dataset which also includes adult females who were already reproducing when first observed (dashed line). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

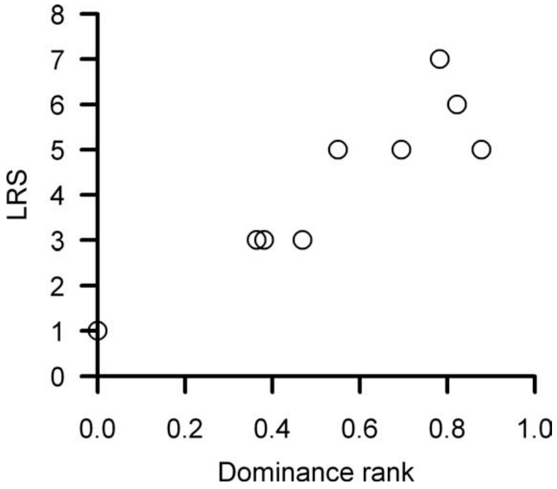

Fig. 4. LRS versus the average dominance ranking of each female. A dominance ranking of 1.0 would represent a female who had the top rank throughout her lifetime, and value of 0.0 would represent a female who had the lowest ranking throughout her lifetime.

poaching deaths (53 and 44%). The nonsignificant positive correlation between S and L arose because two young females (Imp and Mac) killed by poachers had infants that subsequently died and were large proportions of their total reproductive outputs. In contrast, there have been relatively few cases of offspring mortality when adult females die from natural causes (Robbins et al., 2006), and such offspring mortality would have a smaller impact on the overall offspring survival of older mothers. Among the 10 adult females in the main dataset that died of natural causes, only one lost an infant as a result of her death (Clo). Another mother had already lost her last offspring two months before she died (Sim), and the last offspring of the other eight adult females had already reached the age of 3 years when their mothers died of natural causes, and they continued to survive afterwards.

When we excluded females that died from poaching, only 1% of the variance in LRS was explained by the average length of interbirth intervals with surviving offspring (R^2 value for IBIS in Table 2). Thus fertility was the smallest source of variance in LRS. Adult lifespans were not significantly correlated with IBIS or the rate of giving birth to offspring that survive to reach age three (Tests 3.4a and 3.4b in Table 3).

Dominance rank

When we excluded females that died from poaching, females with higher dominance ranks had significantly longer adult lifespans as well as higher values of both λ_{ind} and LRS (Test 3.3 in Table 3, Fig. 4). Dominance rank typically increases with age in this population (Robbins et al., 2005), so hypothetically our results could mean that females with longer lifespans (and higher fitness) simply had more time to achieve higher ranks. When we limited the analyses to dominance data before each female reached the age of 20 years, which enabled us to compare all females over essentially the same age range, the P-values increased and the correlation with adult lifespan was no longer significant (values in parentheses for Test 3.3 in Table 3). Thus, although we consistently found significant evidence that female dominance rankings may reflect differences in physical condition that affect their LRS, the potential relationship with adult lifespan is still tentative.

DISCUSSION

Lifetime fitness and its variance

This study has provided the first assessment of variance in LRS among female mountain gorillas, and one of the few such assessments for any nonhuman primate (but see Fedigan et al., 1986; Wasser et al., 2004, and references in Table 4). Despite poaching deaths, adult females produced an average of 1.6 adult female offspring during their lifetime, which indicates a growing population that contrasts with most other great apes (e.g., Sugiyama, 1994; Hill et al., 2001). Despite such recent growth within the study groups, however, the Virungas still contain only a few hundred mountain gorillas (Gray et al., 2009). The nearby Bwindi Impenetrable National Park contains a similar number of mountain gorillas at a similar density, but the two populations collectively remain a critically endangered subspecies (IUCN, 2008; Guschanski et al., 2009).

Adult female mountain gorillas produced an average of 3.6 ± 2.1 SD offspring that survived to reach the age of 3 years, which represents a standardized variance in LRS of 0.34. When we removed a major source of environmental variability from this study (poaching), the standardized variance in LRS dropped in half to 0.17. Comparable values are not available for most other populations of great apes, but the standardized variances from this study are lower than many other mammals and birds (Table 4). Thus this study illustrates that the standardized variance in LRS can become quite low in a population where major sources of environmental variability are naturally missing (no severe climate), or have disappeared (no more predators), or can be excluded from the calculations (our results without poaching). The

TABLE 4. Standardized variance (variance/mean^2) in lifetime reproductive success (LRS) for female mountain gorillas versus females of other species

Common name	Genus/species	Reference	*N*	LRS	OFS
Mountain gorilla	*Gorilla beringei beringei*	(This study, without poaching)	10	4.3	0.17
Ache	*Homo sapiens*	(Hill and Hurtado, 1996)	n.r.	4.2	0.20
Mountain gorilla	*Gorilla beringei beringei*	(This study, with poaching)	13	3.6	0.34
California mouse	*Peromyscus californicus*	(Ribble, 1992)	16	4.7	0.35
Collared flycatcher	*Ficedula albicollis,*	(Merila and Sheldon, 2000)	719	2.2	0.40
African lion	*Panthera leo*	(Packer et al., 1988)	47	3.8	0.41
Red deer	*Cervus elaphus*	(Kruuk et al., 2000)	202	5.2	0.41
Chacma baboon	*Papio ursinus griseipes*	(Cheney et al., 2004)	42	2.8	0.46
Rhesus macaque	*Macaca mulatta*	(Blomquist, 2009b)	208	5.9	0.47
Tawny owl	*Strix aluco*	(Millon et al., 2010)	64	6.4	0.50
Roe deer	*Capreolus capreolus*	(Vanpe et al., 2008)	28	n.r.	0.53
Bengal tiger	*Panthera tigris tigris*	(Smith and McDougal, 1991)	13	4.5	0.56
Eastern Kingbird	*Tyrannus tyrannus*	(Murphy, 2007)	159	4.4	0.65
Vervet monkey	*Cercopithecus aethiops*	(Cheney et al., 1988)	31	1.7	0.76
Chimpanzee	*Pan troglodytes*	(Nishida et al., 2003)	26	1.4	0.83
Common buzzard	*Buteo buteo*	(Kruger and Lindstrom, 2001)	106	3.5	1.14
Subantarctic fur seal	*Arctocephalus tropicalis*	(Beauplet and Guinet, 2007)	126	2.0	1.17
Cheetah	*Acinonyx jubatus*	(Kelly et al., 1998)	108	1.7	1.87
Great tit	*Parus major*	(McCleery et al., 2004)	1795	1.1	1.90
European rabbit	*Oryctolagus cuniculus*	(von Holst et al., 2002)	197	1.4	2.02
European badger	*Meles meles*	(Dugdale et al., 2010)	124	1.5	2.18
Northern elephant seal	*Mirounga angustrostris*	(Le Boeuf and Reiter, 1988)	204	0.8	5.23

OFS, opportunity for selection (standardized variance); *N*, sample sizes; n.r., not reported. Comparisons are tentative because of differences in assumptions as summarized in (Kelly et al., 1998).

low standardized variance in LRS could be a direct result of the low environmental variability, or it could indicate that the mountain gorillas have low genetic diversity, or it could have arisen by chance (cf. Downhower et al., 1987; Grafen, 1988; Ferguson and Fairbairn, 2001; Shuster and Wade, 2003).

LRS was highly correlated with λ_{ind} as expected because reproduction is distributed fairly evenly throughout adulthood for most females. This mathematical relationship is unlikely to depend upon poaching deaths or other human influences upon the population. The results for λ_{ind} became increasingly insensitive to higher values of LRS, because those higher values mainly arose from greater adult lifespan (Figs. 1 and 2). Similarly, more than 90% of the variance in λ_{ind} among premodern humans arose from differences in LRS, despite diminishing increases in λ_{ind} at higher values of LRS (Kaar and Jokela, 1998). Conversely, the two fitness measures have led to differing conclusions about the optimal age of first reproduction in several species of birds (Brommer et al., 2002). Theoretical studies of lifetime fitness typically focus on λ_{ind}, but empirical studies have often used LRS (Brommer et al., 2004).

Components of LRS

Adult lifespan was the greatest source of variance among the components of LRS, even after adjusting for poaching deaths. In contrast, earlier studies of LRS in mammals and birds had indicated that offspring survival was the most important component, although complete data was not yet available for most long-lived species (Clutton-Brock, 1988). More recent data on large mammals show that longevity has major importance because of its influence on the number of breeding attempts (Berube et al., 1999; Weladji et al., 2006; Pettorelli and Durant, 2007). Among primates, adult lifespan has accounted for 50–70% of the variation in LRS for yellow baboons (Rhine et al., 2000), and 66% of the variation in LRS for female rhesus macaques (Bercovitch and Berard, 1993).

When we excluded females that died from poaching, offspring survival had relatively little net influence on the variance in LRS, mainly due to the negative covariance with fecundity that arose because females give birth sooner after an infant dies. However, offspring survival could cause more variance in LRS if this population approaches its carrying capacity, even if such variance does not contribute to natural selection. As a population of large mammals approaches its carrying capacity, a decrease in offspring survival typically begins to reduce the growth rate (Eberhardt, 1977; but see Robbins et al., 2009b). Demographic stochasticity can increase the standardized variance in dichotomous variables as their mean decreases (e.g., Fig. 1 of Morris and Doak, 2004), so lower offspring survival could lead to more variance in LRS. Demographic stochasticity can also increase when sample sizes are small (Cabana and Kramer, 1991), so offspring survival may cause more variance in LRS when populations are not growing and/or nonbreeders are rare, because the number of surviving offspring per breeder will be low (Shuster and Wade, 2003; Wade and Shuster, 2004).

Fertility made the smallest contribution to variance in LRS among female mountain gorillas, especially when the analyses were based on interbirth intervals with surviving offspring (IBIS). These results did not include females who died from poaching. Adult lifespans were not significantly correlated with IBIS or the rate of giving birth to offspring that reach weaning age ($F{*}S$), so we did not find evidence of a trade-off between reproduction and longevity. Similarly, Ricklefs and Cadena (2007) found no evidence that more frequent reproduction reduced the lifespan of 30 species of captive mammals and birds. Mixed results have emerged from analyses of total births versus postreproductive longevity in humans, perhaps due to lower fertility for unhealthy women, differences in birth spacing, and variability in the socioeconomic benefits of having large families (Pettay et al., 2005; Hurt et al., 2006; Le Bourg, 2007; Gagnon et al., 2009).

Another potential life history trade-off involves the optimal age for females to begin diverting resources away from their own growth and into reproduction (e.g., Festa-Bianchet et al., 1995; Hill and Hurtado, 1996; Allal et al., 2004; Helle, 2008; Stearns et al., 2010). Females who begin reproducing earlier should typically have more time for subsequent reproduction, unless the early start comes at the expense of harmful effects later in life (Ransome, 1995; Blomquist, 2009b). Studies generally have not discussed how human disturbances would influence this trade-off in other species, but assessments may be complicated by long-term environmental and demographic stochasticity and by differences in female quality (Bercovitch and Berard, 1993; Berube et al., 1999; Neuhaus et al., 2004; Descamps et al., 2006). Larger sample sizes are needed to evaluate this life history trade-off in mountain gorillas.

Dominance rank

Female mountain gorillas with higher dominance rank had significantly longer adult lifespans and greater fitness. Those results excluded females who died from poaching, but the correlations weakened after adjusting for the relationship between rank versus age. In comparison with nepotistic species such as baboons and macaques, the individualistic dominance hierarchies of female mountain gorillas are considered weak, and correlations between rank and different measures of reproductive success have been correspondingly inconsistent (Robbins et al., 2007a,b). Nonetheless, relationships between rank and reproductive success also have been reported for other species with individualistic dominance hierarchies, such Hanuman langurs (Borries et al., 1991). In nepotistic species and some individualistic species, correlations between rank and reproductive success can mainly reflect social influences such as reproductive suppression and competition for resources (von Holst et al., 2002; Blomquist, 2009a). Those social influences are minimal for female mountain gorillas, as are the other typical sources of environmental variability, so any correlations between their rank and reproductive success are more likely to arise from genetic influences upon differences in physical condition (Robbins et al., 2007b).

Evolution of mountain gorilla life history

The genetic lineage for eastern gorillas diverged from western gorillas approximately 0.9–1.6 million years ago, with gene flow continuing until about 80,000–200,000 years ago (Thalmann et al., 2007). The Virunga mountain gorillas live only 25 km away from the Bwindi mountain gorillas, and 200 km away from eastern lowland gorillas, so it seems likely that gene flow continued among those eastern gorilla populations until barriers to dispersal were created by human agricultural expansion within the past few centuries or millennia (Yamagiwa and Kahekwa, 2001; Robbins et al., 2009b). The adaptive landscape could have shifted repeatedly during the evolution of the modern mountain gorilla, particularly through interglacial oscillations in the climate and the distribution of rain forests (Dupont et al., 2000, 2001; Arnold et al., 2001; Kingsolver and Pfennig, 2007). Overall, however, it seems likely that mountain gorilla life history evolved in an environment that had fewer humans but more nonhuman predators than this during study, and their habitat encompassed lower elevations that supported a more frugivorous diet (Robbins et al., 2004; Harcourt and Stewart, 2007; Thalmann et al., 2007).

A higher risk of predation has been predicted to favor faster life histories (Promislow and Harvey, 1990; Charnov and Berrigan, 1993; Purvis et al., 2003). Predation by leopards is reported for western lowland gorillas, but the impact on their demography is not well understood (Fay et al., 1995; Robbins et al., 2004). Predation by humans (poaching) reduced the average growth rate of habituated groups in the Virungas from 4.5 to 4.1% during this study, and is probably a major reason why the overall population has grown by only 1% per year (Robbins et al., 2011). Although poaching may have severely reduced the Virunga population prior to this study, the level of poaching during the study could be more comparable to predation pressures throughout the evolutionary history of gorillas.

A more frugivorous diet has been predicted to favor slower life histories, as observed in comparisons among great apes and other primates (Janson and van Schaik, 1993; Wich et al., 2004, 2007). Preliminary evidence suggests a similar correlation among current gorilla populations, notwithstanding any phylogenetic inertia and/or differences in predation pressures (Nowell and Fletcher, 2007; Breuer et al., 2009; Robbins et al., 2009b). It remains unknown, however, whether demographic differences among gorilla populations reflect long term selection pressures on their life history evolution, or if they mainly arise from phenotypic plasticity in response to current ecological conditions including human disturbances (Knott, 2001; Harcourt and Stewart, 2007; Robbins et al., 2009b).

ACKNOWLEDGMENTS

The Karisoke Research Center is a project of the Dian Fossey Gorilla Fund International (DFGFI). We thank the Rwandan government and national park authorities for their long-term commitment to gorilla conservation and their support of the Karisoke Research Center. We are greatly indebted to the many Karisoke field assistants and researchers for their work in collecting demographic data over the past 40 years and to Netzin Gerald Steklis for developing the demographic database and maintaining it for over a decade. We also thank the public and private agencies, foundations, and individuals that have provided support for the Karisoke Research Center over the last 4 decades. We thank Maryke Gray, the International Gorilla Conservation Program, and the Ranger Based Monitoring program for the use of the demographic data from the Susa Group. Max Planck Society provided support for data analysis and write up of the project. We are grateful to Christopher Ruff and three anonymous reviewers for their helpful comments about earlier versions of this manuscript.

LITERATURE CITED

Alberts SC, Altmann J. 1995. Balancing costs and opportunities—dispersal in male baboons. Am Nat 145:279–306.

Allal N, Sear R, Prentice AM, Mace R. 2004. An evolutionary model of stature, age at first birth and reproductive success in Gambian women. Proc R Soc Lond B Biol Sci 271:465–470.

Arnold SJ, Pfrender ME, Jones AG. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetica 112:9–32.

Avise JC, Ayala FJ. 2009. In the light of evolution III: two centuries of Darwin. Proc Natl Acad Sci USA 106:9933–9938.

Barrowclough GF, Rockwell RF. 1993. Variance of lifetime reproductive success—estimation based on demographic data. Am Nat 141:281–295.

Beauplet G, Guinet C. 2007. Phenotypic determinants of individual fitness in female fur seals: larger is better. Proc R Soc B Biol Sci 274:1877–1883.

Bercovitch FB, Berard JD. 1993. Life-history costs and consequences of rapid reproductive maturation in female rhesus macaques. Behav Ecol Sociobiol 32:103–109.

Berube CH, Festa-Bianchet M, Jorgenson JT. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology 80:2555–2565.

Blomquist GE. 2009a. Environmental and genetic causes of maturational differences among rhesus macaque matrilines. Behav Ecol Sociobiol 63:1345–1352.

Blomquist GE. 2009b. Fitness-related patterns of genetic variation in rhesus macaques. Genetica 135:209–219.

Blomquist GE. 2009c. Trade-off between age of first reproduction and survival in a female primate. Biol Lett 5:339–342.

Borries C, Sommer V, Srivastava A. 1991. Dominance, age, and reproductive success in free ranging female hanuman langurs (*Presbytis entellus*). Int J Primatol 12:231–257.

Breuer T, Hockemba MBN, 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.

Breuer T, Robbins AM, Olejniczak C, Parnell RJ, Stokes EJ, Robbins MM. 2010. Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. Behav Ecol Sociobiol 64:515–528.

Brommer JE, Gustafsson L, Pietiainen H, Merila J. 2004. Single-generation estimates of individual fitness as proxies for long-term genetic contribution. Am Nat 163:505–517.

Brommer JE, Merila J, Kokko H. 2002. Reproductive timing and individual fitness. Ecol Lett 5:802–810.

Brown D. 1988. Components of lifetime reproductive success. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 439–453.

Byrne CL. 2008. Applied iterative methods. Wellesley, MA: A K Peters, Ltd.

Cabana G, Kramer DL. 1991. Random offspring mortality and variation in parental fitness. Evolution 45:228–234.

Caswell H. 2001. Matrix population models. Sunderland, MA: Sinauer Associates.

Charnov EL, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? or Life in the slow lane. Evol Anthropol 1:191–194.

Chatterjee S, Price P. 1991. Regression analysis by example. New York: Wiley-Interscience.

Cheney DL, Seyfarth RM, Andelman SJ, Lee PC. 1988. Reproductive success in vervet monkeys. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 384–402.

Cheney DL, Seyfarth RM, Fischer J, Beehner J, Bergman T, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB. 2004. Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. Int J Primatol 25:401–428.

Clutton-Brock T. 1988. Reproductive success. Chicago: University of Chicago Press.

Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl ADC, Clutton-Brock TH, Pemberton JM. 1999. Density-dependent variation in lifetime breeding success and natural and sexual selection in Soay rams. Am Nat 154:730–746.

Cote SD. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. Behaviour 137:1541–1566.

Crow JF. 1958. Some possibilities for measuring selection intensities in man. Hum Biol 30:1–13.

Darwin C. 1859. The origin of species. London: Murray.

de Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim Behav 55:827–843.

Deaner RO, Barton RA, van Schaik C. 2003. Primate brains and life histories: renewing the connection. In: Kappeler PM, editor. Primate life histories and socioecology. Cambridge: Cambridge University Press. p 233–265.

Descamps S, Boutin S, Berteaux D, Gaillard JM. 2006. Best squirrels trade a long life for an early reproduction. Proc R Soc B Biol Sci 273:2369–2374.

Downhower JF, Blumer LS, Brown L. 1987. Opportunity for selection—an appropriate measure for evaluating variation in the potential for selection? Evolution 41:1395–1400.

Dugdale HL, Nouvellet P, Pope LC, Burke T, MacDonald DW. 2010. Fitness measures in selection analyses: sensitivity to the overall number of offspring produced in a lifetime. J Evol Biol 23:282–292.

Dunbar R. 2003. Why are apes so smart. In: Kappeler PM, editor. Primate life histories and socioecology. Cambridge: Cambridge University Press. p 285–300.

Dupont LM, Bonner B, Schneider R, Wefer G. 2001. Mid-Pleistocene environmental change in tropical Africa began as early as 1.05 Ma. Geology 29:195–198.

Dupont LM, Jahns S, Marret F, Ning S. 2000. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. Palaeogeogr Palaeoclimatol Palaeoecol 155:95–122.

Eberhardt LL. 1977. Optimal policies for conservation of large mammals, with special references to marine ecosystems. Environ Conserv 4:205–212.

Fay JM, Carroll R, Peterhans JCK, Harris D. 1995. Leopard attack on and consumption of gorillas in the Central-African-Republic. J Hum Evol 29:93–99.

Fedigan LM, Fedigan L, Gouzoules S, Gouzoules H, Koyama N. 1986. Lifetime reproductive success in female Japanese macaques. Folia Primatol (Basel) 47:143–157.

Ferguson IM, Fairbairn DJ. 2001. Is selection ready when opportunity knocks? Evol Ecol Res 3:199–207.

Festa-Bianchet M, Jorgenson JT, Lucherini M, Wishart WD. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871–881.

Forcada J, Trathan PN, Murphy EJ. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. Global Change Biol 14:2473–2488.

Fossey D. 1983. Gorillas in the mist. New York: Houghton Mifflin.

Gagnon A, Smith KR, Tremblay M, Vezina H, Pare PP, Desjardins B. 2009. Is there a trade-off between fertility and longevity? A comparative study of women from three large historical databases accounting for mortality selection. Am J Hum Biol 21:533–540.

Gerald CN. 1995. Demography of the Virunga mountain gorilla (*Gorilla gorilla beringei*). MSc thesis, Princeton University, Princeton. 81p.

Grafen A. 1988. On the uses of data on lifetime reproductive success. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 454–471.

Gray M, McNeilage A, Fawcett KT, Robbins MM, Ssebide JB, Mbula D, Uwingeli P. 2009. Census of the Virunga mountain gorillas: complete sweep method versus monitoring. J Afr Ecol 48:588–599.

Guschanski K, Vigilant L, McNeilage A, Gray M, Kagoda E, Robbins MM. 2009. Counting elusive animals: comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. Biol Conserv 142:290–300.

Hamilton WD. 1966. Moulding of senescence by natural selection. J Theor Biol 12:12–45.

Harcourt AH, Stewart KJ. 2007. Gorilla society: conflict, compromise, and cooperation between the sexes. Chicago: University of Chicago Press.

Hawkes K. 2003. Grandmothers and the evolution of human longevity. Am J Hum Biol 15:380–400.

Helle S. 2008. A tradeoff between reproduction and growth in contemporary Finnish women. Evol Hum Behav 29:189–195.

Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. J Hum Evol 40:437–450.

Hill K, Hurtado AM. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine de Gruyter.

Hurt LS, Ronsmans C, Thomas SL. 2006. The effect of number of births on women's mortality: systematic review of the evidence for women who have completed their childbearing. Pop Stud 60:55–71.

IUCN. 2008. Red list of threatened species. Gland, Switzerland: IUCN-The World Conservation Union.

Janson CH, van Schaik C. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. Juvenile Primates: life history, development, and behavior. New York: 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.

Kaar P, Jokela J. 1998. Natural selection on age-specific fertilities in human females: comparison of individual-level fitness measures. Proc R Soci Lond B Biol Sci 265:2415–2420.

Kelly MJ, Laurenson MK, FitzGibbon CD, Collins DA, Durant SM, Frame GW, Bertram BCR, Caro TM. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. J Zool 244:473–488.

Kingsolver JG, Pfennig DW. 2007. Patterns and power of phenotypic selection in nature. Bioscience 57:561–572.

Kirkwood TBL. 1977. Evolution of aging. Nature 270:301–304.

Kirkwood TBL, Holliday R. 1979. Evolution of aging and longevity. Proc R Soc Lond B Biol Sci 205:531–546.

Knott C. 2001. Female reproductive ecology of the apes. In: Ellison PT, editor. Reproductive ecology and human evolution. New York: Aldine de Gruyter. p 429–464.

Kruger O, Lindstrom J. 2001. Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. Oikos 93:260–273.

Kruuk LEB, Clutton-Brock TH, Slate J, Pemberton JM, Brotherstone S, Guinness FE. 2000. Heritability of fitness in a wild mammal population. Proc Natl Acad Sci USA 97:698–703.

Laird RA, Sherratt TN. 2009. The evolution of senescence through decelerating selection for system reliability. J Evol Biol 22:974–982.

Le Boeuf BJ, Reiter J. 1988. Lifetime reproductive success in northern elephant seals. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 344–362.

Le Bourg E. 2007. Does reproduction decrease longevity in human beings? Ageing Res Rev 6:141–149.

Leigh SR, Blomquist GE. 2007. Life history. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. Oxford: Oxford University Press. p 396–407.

Leigh SR, Shea BT. 1996. Ontogeny of body size variation in African apes. Am J Phys Anthropol 99:43–65.

McCleery RH, Pettifor RA, Armbruster P, Meyer K, Sheldon BC, Perrins CM. 2004. Components of variance underlying fitness in a natural population of the great tit *Parus major*. Am Nat 164:E62–E72.

McGraw JB, Caswell H. 1996. Estimation of individual fitness from life-history data. Am Nat 147:47–64.

Medawar PB. 1946. Old age and natural death. Mod Quarterly 1:30–56.

Merila J, Sheldon BC. 2000. Lifetime reproductive success and heritability in nature. Am Nat 155:301–310.

Metcalf CJE, Pavard S. 2007. Why evolutionary biologists should be demographers. Trends Ecol Evol 22:205–212.

Miller P, Babaasa D, Gerald-Steklis N, Robbins MM, Ryder OA, Steklis D. 1998. Can the mountain gorilla survive? Population and habitat viability assessment for *Gorilla gorilla beringei*. In: Werikhe S, Macfie L, Rosen N, Miller P, editors. Population biology and simulation modeling working group report. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group. p 71–105.

Millon A, Petty SJ, Lambin X. 2010. Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. J Anim Ecol 79:426–435.

Morris WF, Altmann J, Brockman DK, Cords M, Fedigan L, Pusey A, Stoinski TS, Bronikowski AM, Alberts SC, Strier K. 2011. Low demographic variability in wild primate populations: fitness impacts of variation, covariation, and serial correlation in vital rates. Am Nat 177:E14–E28.

Morris WF, Doak DF. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. Am Nat 163:579–590.

Mundry R, Fischer J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect P values: examples from animal behaviour. Anim Behav 56:256–259.

Murphy MT. 2007. Lifetime reproductive success of female Eastern Kingbirds (*Tyrannus tyrannus*): influence of lifespan, nest predation, and body size. Auk 124:1010–1022.

Neuhaus P, Broussard DR, Murie JO, Dobson FS. 2004. Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. J Anim Ecol 73:36–43.

Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K. 2003. Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121.

Nowell AA, Fletcher AW. 2007. Development of independence from the mother in *Gorilla gorilla gorilla*. Int J Primatol 28:441–455.

Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ, Borgerfoff-Muller M. 1988. Reproductive success in lions. In: Clutton-Brock T, editor. Reproductive success. Chicago: University of Chicago Press. p 363–383.

Pettay JE, Kruuk LEB, Jokela J, Lummaa V. 2005. Heritability and genetic constraints of life-history trait evolution in preindustrial humans. Proc Natl Acad Sci USA 102:2838–2843.

Pettorelli N, Durant SM. 2007. Longevity in cheetahs: the key to success? Oikos 116:1879–1886.

Price PW. 1996. Biological evolution. Orlando: Saunders College Publishing.

Promislow DEL, Harvey PH. 1990. Living fast and dying young—a comparative-analysis of life-history variation among mammals. J Zool 220:417–437.

Purvis A, Webster AJ, Agapow PM, Jones KE, Isaac NJB. 2003. Primate life histories and phylogeny. In: Kappeler PM, editor. Primate life histories and socioecology. Cambridge: Cambridge University Press. p 25–40.

Ransome RD. 1995. Earlier breeding shortens life in female greater horseshoe bats. Philos Trans R Soc Lond B Biol Sci 350:153–161.

Rhine RJ. 1992. Estimating reproductive success of primates and other animals with long and incompletely known reproductive life spans. Am J Primatol 27:245–259.

Rhine RJ, Cox RL, Costello MB. 1989. A 20-year study of long-term and temporary dominance relations among stumptailed macaques (*Macaca arctoides*). Am J Primatol 19:69–82.

Rhine RJ, Norton GW, Wasser SK. 2000. Lifetime reproductive success, longevity, and reproductive life history of female yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Am J Primatol 51:229–241.

Ribble DO. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. J Anim Ecol 61:457–468.

Ricklefs RE, Cadena D. 2007. Lifespan is unrelated to investment in reproduction in populations of mammals and birds in captivity. Ecol Lett 10:867–875.

Robbins MM. 2010. Gorillas: diversity in ecology and behavior. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. Primates in perspective, 2nd ed. Oxford: Oxford University Press. p 326–339.

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 MM, Gray M, Fawcett KA, Nutter F, Uwingeli P, Mburanumwe I, Kagoda E, Basabose A, Stoinski TS, Cranfield MR, Byamukama J, Spelman LH, Robbins AM. 2011. Extreme conservation leads to recovery of Virunga mountain gorillas. PLoS One 6:e19788.

Robbins MM, Gray M, Kagoda E, Robbins AM. 2009b. Population dynamics of the Bwindi mountain gorillas. Biol Conserv 142:2886–2895.

Robbins MM, Robbins AM. 2004. Simulation of the population dynamics and social structure of the Virunga mountain gorillas. Am J Primatol 63:201–223.

Robbins AM, Robbins MM, Fawcett K. 2007a. Maternal investment of the Virunga mountain gorillas. Ethology 113:235–245.

Robbins MM, Robbins AM, Gerald-Steklis N, Steklis HD. 2005. Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. Behaviour 142:779–809.

Robbins AM, Robbins MM, Gerald-Steklis N, Steklis HD. 2006. Age-related patterns of reproductive success among female mountain gorillas. Am J Phys Anthropol 131:511–521.

Robbins MM, Robbins AM, Gerald-Steklis N, Steklis HD. 2007b. Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*). Behav Ecol Sociobiol 61:919–931.

Robbins AM, Stoinski T, Fawcett K, Robbins MM. 2009a. Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Anim Behav 77:831–838.

Schaller GB. 1963. The mountain gorilla: ecology and behavior. Chicago: University of Chicago Press.

Setchell JM, Charpentier M, Wickings EJ. 2005. Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). Behav Ecol Sociobiol 58:474–485.

Shuster SM, Wade MJ. 2003. Mating systems and strategies. Princeton, NJ: Princeton University Press.

Smith JLD, McDougal C. 1991. The contribution of variance in lifetime reproduction to effective population size in tigers. Conserv Biol 5:484–490.

Sokal R, Rohlf F. 1995. Biometry. New York: W. H. Freeman and Company.

Soule ME, editor. 1987. Viable populations for conservation. Cambridge: Cambridge University Press.

Stearns SC. 1992. The evolution of life histories. Oxford: Oxford University Press.

Stearns SC, Byars SG, Govindaraju DR, Ewbank D. 2010. Measuring selection in contemporary human populations. Nat Rev Genet 11:611–622.

Stewart K, Harcourt A. 1987. Gorillas: variation in female relationships. In: Smuts B, Cheney D, Seyfarth R, Wrangham W, Struhsaker T, editors. Primate societies. Chicago: University of Chicago Press. p 155–164.

Storz JF, Ramakrishnan U, Alberts SC. 2002. Genetic effective size of a wild primate population: influence of current and historical demography. Evolution 56:817–829.

Strassmann BI, Gillespie B. 2003. How to measure reproductive success. Am J Hum Biol 15:361–369.

Sugiyama Y. 1994. Age-specific birth-rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. Am J Primatol 32:311–318.

Sutherland WJ. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. Anim Behav 33:1349–1352.

Sutherland WJ. 1987. Random and deterministic components of variance in mating success. In: Bradbury JW, Andersson MB, editors. Sexual selection: testing the alternatives. Chichester: Wiley. p 209–219.

Thalmann OH, Fischer AH, Lankester FH, Paabo SH, Vigilant LH. 2007. The complex evolutionary history of gorillas: insights from genomic data. Mol Biol Evol 24:146–158.

van Noordwijk MA, van Schaik CP. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. Primates 40:105–130.

Vanpe C, Kjellander P, Galan M, Cosson JF, Aulagnier S, Liberg O, Hewison AJM. 2008. Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. Behav Ecol 19:309–316.

von Holst D, Hutzelmeyer H, Kaetzke P, Khaschei M, Rodel HG, Schrutka H. 2002. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). Behav Ecol Sociobiol 51:245–254.

Wade MJ, Shuster SM. 2004. Sexual selection: harem size and the variance in male reproductive success. Am Nat 164:E83–E89.

Wasser SK, Norton GW, Kleindorfer S, Rhine RJ. 2004. Population trend alters the effects of maternal dominance rank on lifetime reproductive success in yellow baboons (*Papio cynocephalus*). Behav Ecol Sociobiol 56:338–345.

Watts DP. 1991. Mountain gorilla reproduction and sexual behavior. Am J Primatol 24:211–225.

Watts DP. 1994. Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). Behav Ecol Sociobiol 34:347–358.

Watts DP. 2001. Social relationships of female mountain gorillas. In: Robbins M, Sicotte P, Stewart K, editors. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 215–240.

Weladji RB, Gaillard JM, Yoccoz NG, Holand O, Mysterud A, Loison A, Nieminen M, Stenseth NC. 2006. Good reindeer mothers live longer and become better in raising offspring. Proc R Soc B Biol Sci 273:1239–1244.

White PA. 2005. Maternal rank is not correlated with cub survival in the spotted hyena, *Crocuta crocuta*. Behav Ecol 16:606–613.

Wich SA, Steenbeek R, Sterck EHM, Korstjens AH, Willems EP, Van Schaik CP. 2007. Demography and life history of Thomas Langurs (*Presbytis thomasi*). Am J Primatol 69:641–651.

Wich SA, Utami-Atmoko SS, Setia TM, Rijksen HD, Schurmann C, van Schaik C. 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). J Hum Evol 47:385–398.

Williams GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411.

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.