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Variance in the male reproductive success of western gorillas: acquiring females is just the beginning

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Abstract Variance in male reproductive success is expected to be high in sexually dimorphic mammals, even when it is modulated by the costs and benefits of group living. Here, we investigate the variance in reproductive success of male western gorillas (*Gorilla gorilla*), a highly dimorphic primate with long-term male–female associations, using 12.5 years of data collected at Mbeli Bai in northern Congo. Access to mates and offspring survival were both major sources of variance in male reproductive success. Males with larger harems had lower offspring mortality with no apparent reduction in female fertility or observed tenure length, so the size of harems did not seem to be limited by female feeding competition or by the risk of takeovers and infanticide by outsider males. The lower mortality in larger harems may reflect improved vigilance against predators, and females may cluster around males that enhance offspring survival. Thus, this study illustrates how a detailed analysis of the components of male reproductive success can shed light on the interrelated social and ecological aspects that affect it.

Keywords Harem size · Intrasexual competition · Mating success · Offspring survival · Variance in reproductive success

Introduction

High variance in male reproductive success is assumed to provide a potential for sexual selection that can lead to sexual dimorphism (Darwin 1871; Andersson 1994). Sexual selection has been broadly defined as the portion of natural selection that arises from reproductive competition with members of the same sex, or more narrowly defined as the selection that arises from variance in the number of mates per male (Darwin 1871; Wade 1987; Clutton-Brock 2004). Sexual selection can involve competition to kill, suppress, or exclude rivals (intrasexual selection: Clutton-Brock et al. 1982; Kappeler 1997) as well as competition to attract mates (intersexual selection: Clutton-Brock and McAuliffe 2009; Jones and Ratterman 2009), and other mechanisms such as coercion (Andersson and Iwasa 1996; Pradhan and Van Schaik 2009).

Male reproductive success can be decomposed into different components such as the number of mates, the fertility of those mates, offspring survival, and longevity (Brown 1988). The most apparent manifestation of reproductive competition is often the variance in the number of mates per male, including variance between mating versus non-mating males (Wade and Shuster 2004). The other three components are not typically associated with sexual

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selection on males, but they can be influenced by reproductive competition in some species. Variance in female fertility could arise if more competitive males have preferential access to better resources or higher quality mates (Kelly 2008; Lee et al. 2008). Variance in offspring survival may arise if more competitive males provide better protection against infanticide by their rivals (Packer et al. 1988; Borries et al. 1999). Variance in longevity and the length of reproductive careers (tenure length) could arise if males are killed during mating competition, or if mortality increases due to costly dimorphic traits (Dunbar 1984; Clutton-Brock and Isvaran 2007). Components of reproductive success can also vary due to factors that are not directly related to reproductive competition, including environmental fluctuations or chance (Sutherland 1985; Coltman et al. 1999).

Components of male reproductive success can be related to each other, particularly among group-living polygynous species. Socio-ecological models predict that female fertility may decrease with group size due to greater feeding competition within groups, or it may increase due to improved competitiveness against other groups (e.g., Sterck et al. 1997). Offspring survivorship may increase with group size due to improved vigilance against predators, or it may decrease due to greater threats from infanticidal outsider males (Dunbar 1984; van Schaik 1989; Crockett and Janson 2000; Steenbeek and van Schaik 2001). Male longevity may be reduced in larger groups if increased mating competition increases the risk of mortality, leading to a potential tradeoff between having a few mates for a long time versus many mates for a short time (Dunbar 1984; Robinson et al. 2006). Alternatively, female fertility, offspring survival, and male longevity may all be greater in larger groups; if those groups tend to have higher quality males or occupy better habitats (McElligott et al. 2002; West and Packer 2002; Bro-Jorgensen and Durant 2003). Thus, it becomes important to understand how variance in male reproductive success in group-living animals depends upon the complex interplay of ecological, demographic, social, and life history factors (Pereira et al. 2000).

This paper examines the variance in reproductive success of male western gorillas using 12.5 years of data from Mbeli Bai, a large swampy forest clearing in the Nouabalé-Ndoki National Park of the Republic of Congo. Gorillas are the largest primates and among the most sexually dimorphic, with adult males (silverbacks) weighing twice as much as females (Leigh and Shea 1995; Smith and Jungers 1997). The extreme sexual dimorphism of gorillas is expected to coincide with high variance in male reproductive success (Darwin 1871; Leigh and Shea 1995), but the relative contributions from each component of male reproductive success are not well understood.

Western gorillas have a one-male mating system in which subordinate males typically emigrate to become solitary before reaching full maturity (Parnell 2002b; Robbins et al. 2004). In that regard, western gorillas differ from mountain gorillas where roughly half of maturing males remain in their natal group, and up to 40% of groups are multi-male (Kalpers et al. 2003; Stoinski et al. 2009). Up to 45% of silverbacks live alone or in non-breeding groups with other males, but it is unknown how many eventually acquire females (Parnell 2002b; Gatti et al. 2004). Harems of western gorillas form when females join a solitary male or non-breeding group, and they disintegrate when all females leave a harem holder or he disappears (ibid).

Unlike silverbacks, female gorillas transfer directly from one group to another during inter-group encounters, so they do not become solitary (Harcourt et al. 1976; Stokes et al. 2003). Females are believed to rely on males for protection against predators (leopards and humans) and infanticide (Stokes et al. 2003; Harcourt and Stewart 2007). Females do not transfer while lactating or pregnant, presumably due to the risk of infanticide if they joined a male who had not sired their offspring (Robbins et al. 2009a). Female western gorillas have not been reported to mate with subordinate or extra-group males (Mbeli Bai: Breuer, personal observation; Bai Hokou: Todd, personal communication; Mondika: Doran-Sheehy, personal communication), which is consistent with genetic analyses that assigned no paternity to those males (Mondika: Bradley et al. 2004).

The potential for sexual selection in gorillas reflects a combination of intrasexual selection, intersexual selection, and other mechanisms. As expected under intrasexual selection, male–male competition during inter-group encounters can involve intense physical fights that are occasionally fatal (Watts 1989; Robbins 2003; Jeffery et al. 2007). However, there is no clear winner during many encounters between males, so female transfers during those encounters could be considered mate choices that lead to intersexual selection. Dominant males may limit the emigration of their females through coercion and herding (Sicotte 1993; Levréro 2005; Robbins 2009).

Essentially all adult females reproduce in this population, so we predict that much of the variance in male reproductive success will arise from differences in the ability to acquire and retain those females. We predict that differences in female fertility will be a relatively minor source of variance in male reproductive success because competition for resources is considered to be low (Stokes et al. 2003). We predict that predation and infanticide will create variance in offspring survival that reflects the ability of males to protect their infants. We are unable to confirm the cause of offspring mortality, but we propose that infanticide can occur throughout all ages of infancy, whereas predation by leopards may become more likely as offspring approach weaning age and become more independent from their mothers. This study was not long enough to assess the longevity of western gorillas, but we used the observed tenure length to begin examining the potential tradeoff between having a few mates for a long time versus many mates for a short time. We examine the potential influences upon each component of reproductive success and discuss the implications for selection within this population and others.

Methods

Study population

We studied western gorillas at Mbeli Bai, a large (12.9 ha) swampy forest clearing in the southwest of the Nouabalé-Ndoki National Park, Republic of Congo, that is characterized by superabundant aquatic herbs (for details about the study site, see Parnell 2002a, b; Stokes et al. 2003; Breuer 2008). Four principal investigators (C.O.: 1995–1997; R.J. P.: 1997–1999; E.J.S.: 1999–2002; T.B.: 2002–2007) and assistants monitored the gorillas visiting the clearing between February 1995 and July 2007 (3,957 days, average of 9.1 h/day) with an absence from the clearing for 2 months in 1997 due to civil unrest in the country. Gorillas were observed with help of telescopes and binoculars from an observation platform that provides almost 100% visibility from the edge of the clearing. Due to the unrestricted visibility in the forest clearing, solitary males could be observed just as easily as breeding groups, so our study should provide an unbiased estimate of non-mating males (Parnell 2002b; Gatti et al. 2004). Identification of gorillas was based upon features such as shape of brow-ridges, ears, nose-prints, and pelage (Parnell 2002a). We did not use group membership as criterion for identification of individuals. After a period of approximately 3 months training with the previous investigator, it was generally possible to identify all gorillas with the help of photos, videos, and “identity cards” that highlighted the distinguishing features of each individual. We tried to have at least two observers on the platform at any time, who discussed the identity of gorillas to further reduce any risk of inter-observer variability. In addition, TB reviewed more than 200 h of video footage and confirmed the identifications of prior investigators (Breuer et al. 2009).

Monitoring demographic changes (transfer, birth, and mortality dates)

Mbeli Bai has an open population of gorillas. Since each gorilla does not visit the clearing every day, there are gaps of observation, and we had to estimate the dates of birth, death, and dispersal. Some gorillas have been observed within 1–2 days after their birth, as confirmed because their group had just been seen without them. When gorillas were first observed beyond that age, their birthdates were estimated by comparing their morphological and behavioral characteristics with other gorillas whose age was already determined (Parnell 2002a; Nowell 2005; Breuer et al. 2009). We believe the precision of those birthdates is within a few weeks for most gorillas who were first observed as infants, and within 1–2 years for gorillas who were first observed as they approached adulthood. Adulthood was defined to begin at age ten for females and 18 for males, which is when they begin to reproduce (Breuer et al. 2009).

Dispersal dates were typically determined as the midpoint between visits of the group of origin and the group of destination (Stokes et al. 2003). When a gorilla stopped visiting the Bai, we were generally unable to confirm whether it had died or dispersed. If the missing gorilla had been a harem holder, we assumed that he died. This was a plausible assumption because in nine out of 15 cases, the silverback had signs of serious injuries or was extremely thin in previous visits before disappearance. After disappearing from their group, harem holders were almost never seen again, whereas most maturing subordinate males were still seen following their emigration to become solitary. Dates of disappearance were typically determined as the midpoint between the last time an individual was observed and the first time that the group was seen without him.

It is unlikely that unweaned infants (<4 years) could survive without their mothers (Nowell and Fletcher 2007; Breuer et al. 2009), so if they disappeared before that age, we assumed that they had died. Due to the nature of the study and intermittent observations, we might have missed a few infants who were born and died before we saw them, which would lead to an underestimation of female fertility and offspring mortality. As evidence of such missed infants, the apparent mortality rate was lower than in mountain gorillas during the first 6 months of infancy, despite higher mortality throughout the rest of infancy (Fig. 1). Nonetheless, the results of this study did not change appreciably when we limited the analyses to groups that made at least 12 visits per year, with no observation gaps longer than 3 months. Therefore, we present the results that do not exclude groups which were observed less frequently.

Measures of male reproductive success

Our first two measures of male reproductive success involve a subtle distinction between harem size (H) and the number of mates per male (N_{MATE}). Both parameters are based upon the number of adult females that were with a male, but whereas our calculations of harem size exclude

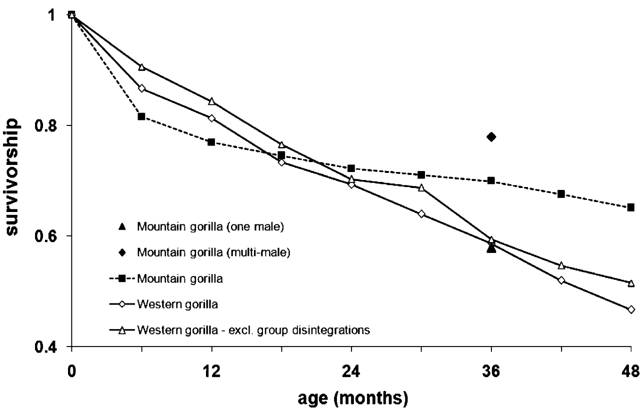

Fig. 1 Comparison of infant survivorship to age four between mountain gorillas (Gerald 1995; Robbins et al. 2007) and western gorillas with and without cases of mortality that happened after group disintegrations

males when they have no harem, those males are assigned a value of zero in calculations of N_{MATE} (e.g., Wade and Shuster 2004). For example, if we observed one harem with two females, another harem with four females, and one solitary male, then the mean harem size (M_{HAREM}) would be $(2+4)/2=3$, and the mean number of mates per male (M_{MATE}) would be $(2+4+0)/3=2$.

In addition to the mean for both measures of male reproductive success, we also calculated the variance and the standardized variance (variance/mean^2). The standardized variance in reproductive success has been defined as the "opportunity for selection", which reflects an upper limit to the strength of natural selection including sexual selection (Crow 1958; Trail 1985; Downhower et al. 1987; Shuster and Wade 2003; Mills et al. 2007). The standardized variance in the number of mates per male (I_{MATE}) has been defined as the "opportunity for sexual selection" (Wade 1979; Wade and Arnold 1980; Jones 2009). The variance in the number of mates per male (V_{MATE}) includes variance among harem-holding males as well as variance between harem-holding versus non-harem-holding males. The proportion of variance that arose between harem-holding males versus non-harem-holding males is indicated by the R^2 value from an analysis of variance, in which the dependent variable was the value of N_{MATE} for each male, and the category variable indicated whether he was a harem holder.

We examined both H and N_{MATE} from two perspectives: "snapshots" of the population on a particular day, as well as longitudinal analyses throughout the adulthood of each male. The snapshot calculations used the actual number of adult females that were with each male on the day of the snapshot. For example, on January 1st 1996, the study population contained harems with 5, 5, 7, 7, 8, 8, 8, 9, 9, 11, and 12 females, for a average harem size of 3.1 females. We performed a separate snapshot calculation for the first day of each year in the study. There is a continuous male–female association in harems of western gorillas; hence, there is no reason to expect different results on other days of the year.

The longitudinal analyses used overall values from throughout the observations of each male. For example, if one male had an average harem size of 2.1 females throughout our observations of his adulthood and another male had an average harem size of 3.3 females throughout our observations of his adulthood, then the average harem size among those two males would be $(2.1+3.3)/2=2.7$ females per male. For all other measures of reproductive success (below), we performed only the longitudinal analyses based on the overall observations of each male.

Our next two measures of reproductive success for each male were the average birth rate of his females (*BR*) and the proportion of his offspring that survived to a specified age (*SV*). The average birth rate of his females equaled the number of births that occurred in his group during the study, divided by the number of female-years observed in that group (e.g., see Robbins et al. 2007). We used three criteria for offspring survival: ages one, three, and four. Age four was chosen because it is the typical weaning age in the Mbeli Bai population (Nowell and Fletcher 2007; Breuer et al. 2009). Studies of reproductive success often consider offspring survival until their age of first reproduction (Brown 1988; Strassmann and Gillespie 2003), but the weaning age should be a reasonable approximation for this study because subsequent mortality until the age of first reproduction is minimal for mountain gorillas (Gerald 1995). Mountain gorillas are typically weaned at a younger age than western gorillas (Watts 1991), so age three is often used as the criterion for offspring survival in that population (Bradley et al. 2005), and we present such results for comparative purposes. All analyses involving infant survival were limited to dates in which it could be fully evaluated, which led to differences in sample sizes among some analyses (e.g., for survival to age four, we excluded infants born during the last 4 years of the study). Therefore, we also performed analyses based on survival to age one because it enabled us to use a greater proportion of the dataset.

The siring rate of each male (*SR*) was calculated as the number of offspring born in his group that survived to a specified age, divided by the number of years that he was observed as an adult. Again, we used three criteria for offspring survival: ages one, three, and four; and the analyses were limited to dates in which it could be fully evaluated. For example, if a male was observed for 5 years before July 2003 (thus excluding the last 4 years of the study) and three of the offspring that were born in his group during those years survived to reach age four, his rate of siring offspring that survived to reach age four would be 3/5=0.60 surviving offspring per male-year. For the siring rate at each age criterion, we report the mean, standard deviation, and the standardized variance.

The siring rate for each male equals the product of three components: his longitudinal values for N_{MATE}, *BR*, and *SV*. We used the calculations from Brown (1988) to determine how each component contributes to the variance among breeders (see Arnold and Wade 1984a, b; Spong et al. 2008 for alternative approaches). Specifically, we report the G′ values from upward partitioning as presented in Table 27.1 of Brown (1988), although that example uses the method with a different set of components (see Clutton-Brock 1988; Brown and Alexander 1991; Coltman et al. 1999; Setchell et al. 2005; Hodge et al. 2008 for additional descriptions of the approach). The first step in our calculations was to normalize the data for each component, by dividing the value for each male by the mean of the component among all males. For example, if Y_{n} is the array of values for N_{MATE} (one value for each male) and X_{n} is the array of normalized values, then $X_{\mathrm{n}}=Y_{\mathrm{n}}/\mathrm{mean}\ (Y_{\mathrm{n}})$. Next, we calculated the product of all three normalized components for each male (i.e., $X_{\mathrm{n}}\times X_{\mathrm{b}}\times X_{\mathrm{s}}$, in which X_{b} and X_{s} are the arrays of normalized values for *BR* and *SV*). Then, we calculated the variance for each of the normalized components and their product. For example,

$$G_{\mathrm{n}} = \mathrm{Var}(X_{\mathrm{n}}) \tag{1}$$

$$G_{\mathrm{nbs}} = \mathrm{Var}(X_{\mathrm{n}} \times X_{\mathrm{b}} \times X_{\mathrm{s}}) \tag{2}$$

in which “Var” signifies the variance among males for the value in parentheses. G_{b} and G_{s} were calculated with an analogous form of Eq. 1. Finally, we multiplied each of the G values by $(100/G_{\mathrm{nbs}})$ to produce the G′ values. The G′ value for each component indicates how much of the variance in the siring rate arose from the variance of the component by itself, as if each male had the mean value for the other components. We used the bootstrap procedure from Brown (1988) to estimate the 95% confidence intervals of the G′ values.

In addition to examining the variance in the siring rate among breeders, we also calculated the variance among all males:

$$\mathrm{Var}(SR_{\mathrm{a}}) = [p \times \mathrm{Var}(SR_{\mathrm{b}})] + \left[p \times (1-p) \times \mathrm{Mean}(SR_{\mathrm{b}})^2\right] \tag{3}$$

in which “SR_{a}” is the array of siring rates for all males, “SR_{b}” is the siring rates for all breeders, and “p” is the proportion of males that were breeders (Brown 1988). The term in the first brackets is the contribution due to variance among breeders. The term in the second brackets is the contribution due to the difference between breeders versus non-breeders. We report the proportion of the total variance that was due to the difference between breeders versus non-breeders (ibid).

The lifetime reproductive success of each male will equal his siring rate multiplied by his longevity. This study was not long enough to measure the longevity of western gorillas, but we made some preliminary assessments using the observed tenure length as a proxy (e.g., see Lawler 2007). The observed tenure length was calculated as the interval between the first and last date that a silverback was observed as a harem holder. This data includes tenures that were ongoing at the beginning or the end of the study, and the observed tenure is the portion of those tenures that was observed. We limited the analysis to harem holders that could have sired offspring surviving to weaning age to reduce the bias towards males that were only briefly monitored. Three silverbacks temporarily lost all of their females, but we still included time in the non-breeding group as part of their observed tenure because such intervals can be important for infant survivorship if the group still contains offspring of the silverback.

The calculations for harem size and the number of mates per male were performed using Systat 11 (2004, SYSTAT Software Inc., Richmond, CA, USA). The Brown (1988) partitioning calculations were performed in an Excel spreadsheet. Spearman rank correlations were calculated to examine relationships among the three components with an Excel macro and are either exact (when $n\leq 9$) or based on 10,000 permutations (Mundry and Fischer 1998). We used the same macro to separately investigate the correlation of tenure length with male reproductive success. Unless otherwise stated, values are given as mean ± standard deviation.

Results

Harem size and the number of mates per male (N_{MATE})

Harem size is often reported from census data, so for comparative purposes, we examined “snapshots” of our study population on the first day of each year (Table 1). From 1996 to 2007, the mean harem ranged from 2.9 to 4.3 adult females per harem-holding male. The standardized variance in harem size ranged from 0.28 to 0.47, which is higher than only 33–55% of the comparable values in a wide-ranging survey of crustaceans, insects, amphibians, reptiles, birds, and mammals (Wade and Shuster 2004). From that perspective, the standardized variance in harem size for western gorillas does not seem exceptionally large in comparison with other species.

Table 1 Analyses of harem size and the number of mates per male

Year	N_{M}	NHH(%)	M_{HAREM}	M_{MATE}	V_{HAREM}	V_{MATE}	Between(%)	I_{MATE}
1996	17	35	3.1	2.0	2.7	4.0	58	1.0
1997	18	28	3.2	2.3	4.4	5.3	42	1.0
1998	18	28	3.5	2.6	4.8	6.0	44	0.9
1999	17	24	3.7	2.8	6.4	7.4	35	0.9
2000	16	31	3.8	2.6	5.8	7.2	47	1.0
2001	20	35	4.3	2.8	6.4	8.5	52	1.1
2002	19	32	3.6	2.5	4.6	6.0	49	1.0
2003	18	39	3.6	2.2	5.3	6.4	52	1.3
2004	18	33	3.4	2.3	4.8	5.9	47	1.1
2005	23	35	2.9	1.9	3.8	4.4	46	1.2
2006	22	41	3.4	2.0	4.1	5.2	55	1.3
2007	21	43	3.3	1.9	4.8	5.5	52	1.5
Mean	19	34	3.5	2.3	4.8	6.0	48	1.1
Stdev	2	6	0.4	0.3	1.1	1.3	6	0.2
Median	18	34	3.5	2.3	4.8	5.9	48	1.1
Min	16	24	2.9	1.9	2.7	4.0	35	0.9
Max	23	43	4.3	2.8	6.4	8.5	58	1.5
Longitudinal	41	29	3.0	1.8	3.2	4.0	36	1.2

The number of adult males (N_{M}) in the study population, the proportion of those males that were harem holders (%NHH), the average harem size (M_{HAREM}), the average number of mates per male (M_{MATE}), the variance in harem size (V_{HAREM}), the variance in the number of mates per male (V_{MATE}), the proportion of V_{MATE} that was due to differences between harem and non-harem holders (%between), and the standardized variance in the number of mates per male (I_{MATE}). The values are presented for the first day of each calendar year and from longitudinal analysis of all observations for each male

Under strong sexual selection, a large portion of the variance in access to mates is predicted to arise from the difference between harem holders versus non-harem holders, but the latter category of males is often difficult to quantify accurately (Wade and Shuster 2004). At Mbeli Bai, solitary males can be detected just as easily as groups, so we examined their contribution to the overall variance among all males. On the first day of each year from 1996 to 2007, the average number of mates per male (M_{MATE}) ranged between 1.9 and 2.8 adult females. (M_{MATE} differs from the mean harem size because it includes males when they had no mates). Those snapshot values of M_{MATE} are equivalent to the adult sex ratio, and they partly reflect the difference in the ages at which each sex is considered an adult (age ten for females versus 18 for males). The standardized variance in N_{MATE} equaled 1.1±0.2 (see the rows for mean and standard deviation of I_{MATE} in Table 1). On average, 34% of adult males were non-harem holders, and 48% of the variance in N_{MATE} arose between harem holders versus non-harem holders. Thus, our calculations support theoretical predictions that non-harem holders can account for much of the variance in access to mates.

The snapshot calculations from the first day of each year may either overestimate or underestimate the variance in the lifetime reproductive success among males, depending upon how N_{MATE} typically changes throughout adulthood (Wade and Shuster 2004). To assess such potential bias, we repeated the calculations by using the longitudinal average of N_{MATE} for each male, taken from all observations of the male rather than a snapshot value (Fig. 2). Whereas 34% of adult males were typically non-harem holders during the snapshot calculations of a single year, 12 of 41 males (29%) were never harem holders throughout our observations. Those on-going non-harem holders accounted for 36% of standardized variance in N_{MATE}, which equaled 1.2 in the dataset with all males. Next, we repeated the calculations with the 11 males who were observed for at least 10 years or their complete adulthood. In that data subset, the proportion of non-harem holders dropped to 18% (two males who were either solitary or living in non-breeding groups for at least 12 years of observations). The standardized variance in N_{MATE} was 1.0, with 40% of that variance coming from non-harem holders. So although the snapshot calculations may have overestimated the proportion of males who will never become harem holders, they seem to provide reasonable estimates for the long-term variance in N_{MATE}.

Female fertility and offspring survival

To assess whether harem sizes might be limited by feeding competition among females, we looked for lower female fertility in larger harems. Among the 29 harem holders, the

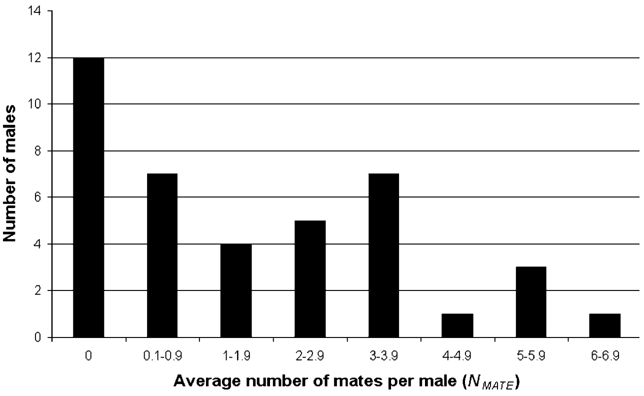

Fig. 2 Observed frequency distribution for the number of males with each value of N_{MATE}. For this longitudinal analysis, the number of mates for each male (N_{MATE}) was calculated as the average value from the first day of all months that he was observed as an adult. Whereas the average harem size would exclude months when a male had no harem, this calculation includes a value of zero for those months. The first bar shows 12 males who were never harem holders. The second bar shows seven males whose average number of mates was less than one, even though they were harem holders at some point during the study

average female fertility was 0.16±0.14 offspring per female-year. Males with larger harems had significantly higher female fertility, which is in the opposite direction of predictions for female feeding competition within groups (r_S=0.48, p=0.011). However, those values may be biased because female fertility was zero for nine males (31%) who were observed only briefly as harem holders (e.g., because all of the females in the group were already nursing when the study began, and then the male died before any of those females were ready to give birth again). After excluding those nine males, female fertility was 0.24±0.10 offspring per female-year, and it was not significantly correlated with harem size (r_S=−0.11, p=0.64). Thus, we did not find evidence that feeding competition among females has reduced their fertility in larger harems.

To examine whether the optimal harem size might be influenced by predation or infanticide, we looked for correlations between harem size and offspring survival at each age criterion. Predation is considered more likely to afflict smaller groups and older infants, whereas infanticide is more likely for larger groups and all infants (e.g., van Schaik 1983; Crockett and Janson 2000). As we increased the criteria for offspring survival from age one to four, the average offspring survival per male dropped from 82% to 39%. Males with larger harems had significantly higher offspring survival to age four, but the correlations were not significant for ages one and three (Table 2). Those results are more consistent with the predictions for predation than infanticide, and they give no indication that the optimal harem size might be limited by the risk of offspring mortality.

Siring rate

Having analyzed the variance in N_{MATE}, female fertility, and offspring survival, we next used the Brown (1988) partitions to examine the variance in their product: the rate that each male sired offspring who survived to each age criterion. As we increased the criteria for offspring survival from age one to age four, the mean siring rate among all males declined from 0.34 to 0.20 surviving offspring per male-year, and the standardized variance increased from 1.8 to 3.5 (Table 3). The proportion of non-breeders remained near 50%, but their contribution to the variance in siring rate dropped from 51% to 25%. Therefore, as offspring survival increased the variance in siring rate among breeding males, the relative importance of non-breeders declined.

When the siring rate was based upon offspring survival to age one, N_{MATE} accounted for 62% of its variance among breeders (Table 2), which was larger than the contributions from female fertility (49%) and offspring survival (15%). Those G′ values indicate (for example) that if each male had the mean values for female fertility and offspring survival and the observed variation in N_{MATE} was the only difference among males, then the variance in the siring rate would be only 62% of its observed value. The G′ values do not add up to 100% due to covariance among the components. Males with more mates had significantly higher siring rates when based on all three age criteria for offspring survival. However, when the criterion for offspring survival was extended to ages three and four, N_{MATE} accounted for only 43% and 26% of the variance in the siring rate. Offspring survival became the largest source of variance in the siring rate, explaining 54% of that variance among breeders (Fig. 3). Males with higher offspring survival had significantly higher siring rates at all three age criteria.

zHypothetically, the large contribution from variance in offspring survival could be an artifact of this study because it contains some males that have died and others that have not. Offspring mortality is expected to increase when a silverback dies in a one-male group because his infants become more vulnerable to predators and infanticide by other males. Accordingly, nine of 11 infants (82%) died following the death of the silverback in their group, versus only 31 of 64 infants (48%) when the silverback remained alive (Fisher's exact test: p=0.053). Four of the nine deceased infants were less than 6 months old, one was between 2.0 and 2.5 years old, and the other four infants were between 3.0 and 3.5 years old (Fig. 1). Overall, infant mortality was similar to one-male groups of mountain gorillas, which face a higher infanticide risk than their multi-male groups (Table 4).

To test whether silverback mortality was responsible for the influence of offspring survival upon variance in

Table 2 Components of the siring rate (*SR*): the number of mates per male (N_{MATE}), the female birth rate (*BR*), and offspring survival (*SV*)

Dataset Age criterion	All adult males One	All adult males Three	All adult males Four	Long/complete observations Four
Brown partition contributions (G′)				
N_{MATE}	62%	43%	26%	43%
BR	49%	26%	19%	17%
SV	15%	54%	54%	56%
Spearman rank correlations				
*SR*versusN_{MATE}	0.638	0.809	0.732	0.848
*SR*versus*BR*	0.299	-0.146	-0.078	-0.763
*SR*versus*SV*	0.519	0.670	0.841	0.996
*H*versus*SV*	0.235	0.469	0.510	0.880
*P*values for the Spearman rank correlations				
*SR*versusN_{MATE}	0.0030	0.0003	0.0017	0.0074
*SR*versus*BR*	0.2032	0.5640	0.7658	0.0240
*SR*versus*SV*	0.0167	0.0034	0.0001	0.0001
*H*versus*SV*	0.3156	0.0532	0.0405	0.0067

The Brown partitions show the contribution of each component to the variance in the siring rate (the G′ values from upward partitioning as presented in Table 27.1 of Brown 1988). Results are shown for all breeding adult males at each criterion for offspring survival (ages one, three, and four) and for males who were observed for their entire adulthood or at least 10 years (long/complete observations)

Table 3 Contributions of breeders versus non-breeders to the variance in siring rates among all adult males (surviving offspring per male-year, SR_{a})

Dataset Age criterion	All adult males One	All adult males Three	All adult males Four	Long/complete observations Four
Number of males				
Breeders	20	17	17	9
Non-breeders	18	18	15	2
Total	38	35	32	11
%Non-breeders	47%	51%	47%	18%
Siring rate among all males (SR_{a})				
Mean	0.34	0.19	0.20	0.27
Standard deviation	0.45	0.32	0.36	0.37
Standardized variance	1.77	2.75	3.46	1.79
Siring rate among breeders (SR_{b})				
Mean	0.64	0.40	0.37	0.33
Standard deviation	0.43	0.36	0.43	0.38
Standardized variance	0.46	0.83	1.39	1.30
Contributions to variance among all males				
%Between	51%	38%	25%	12%
%Within	49%	62%	75%	88%
Total	100%	100%	100%	100%

The "%non-breeders" represents the proportion of adult males that were non-breeders. For both breeders and all males, the standardized variance equals the variance divided by the mean squared. The "%within" represents the proportion of variance in SR_{a} that arose among breeders, and "% between" is the proportion that arose between breeders versus non-breeders (Eq. 3). Results are shown for all adult males at each criterion for offspring survival (ages one, three, and four) and for males who were observed for their entire adulthood or at least 10 years (long/complete observations)

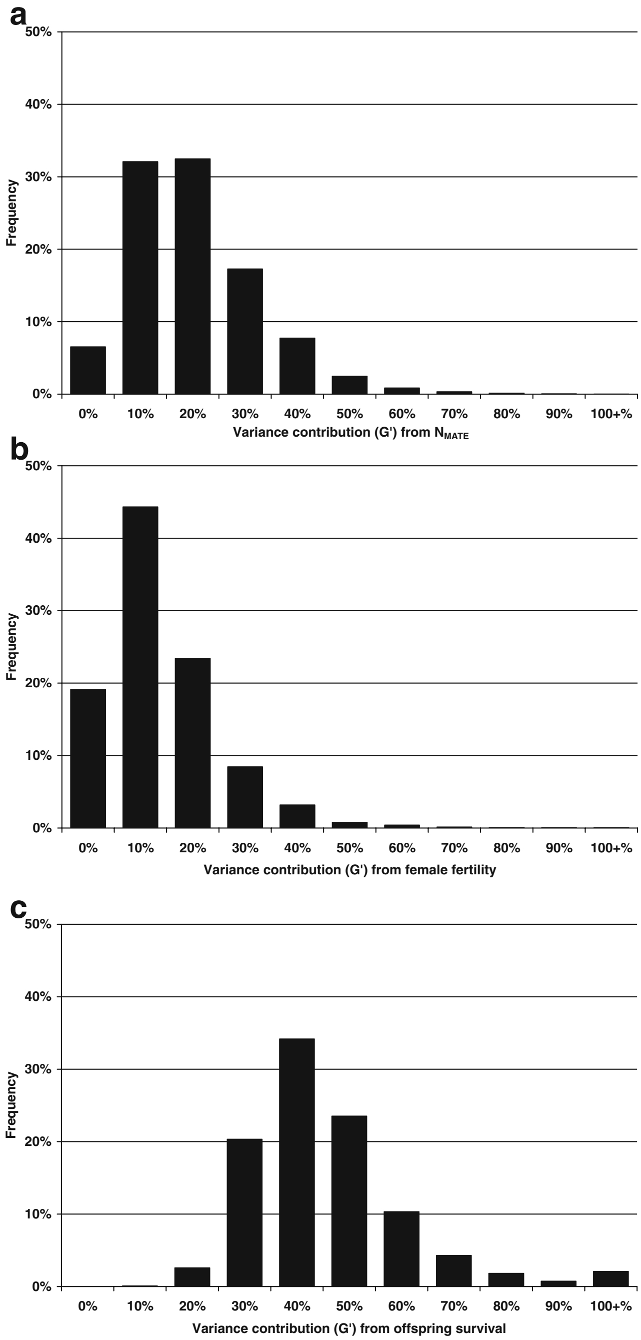

Fig. 3 Estimated bootstrap sampling distributions for variance contributions to the rate of siring offspring that survived to reach age four. The G′ values were calculated from upward partitioning as presented in Table 27.1 of Brown (1988). The approximate 95% confidence intervals were 7–53% for the number of mates per male (N_{MATE}, **a**), 5–44% for female fertility (**b**), and 30–91% for offspring survival (**c**). For each graph, the numbers on the *x*-axis indicate the minimum value for G′ that was tallied in each bar. The *y*-axis shows the proportion of the 10,000 bootstrap iterations that predicted each G′ value. For example, 7% of the iterations predicted a G′ value for N_{MATE} that was at least 0% but less than 10% (the first bar in **a**)

siring rates, we repeated the Brown partitioning while excluding males who had infants when they died. In that analysis, offspring survival accounted for 57% of the variance in siring rate, which is essentially identical to the corresponding value of 54% from the full dataset (both analyses are based on offspring survival to age four). Offspring survival also accounted for 56% of the variance in siring rate in the data subset of males with long/complete observations, where the death of a silverback would affect a smaller proportion of his observed offspring. Thus, the large contribution of offspring survival to the variance in siring rate does not seem to be an artifact of whether males had unprotected infants during the study.

Observed tenure length

Males with higher siring rates will not necessarily have higher lifetime reproductive success, if they have shorter reproductive lifespans due to the increased competition of defending a larger harem. To begin investigating this possibility, we looked for a potential tradeoff between their observed tenure length and their average harem size. The observed tenure length has averaged 5.9±3.7 years (range, 0.8–12.3; $n=24$ tenures). Males with a higher average harem size had significantly longer observed tenures, which is in the opposite direction of any tradeoff between having a few mates for a long time versus many mates for a short time ($r_{\mathrm{S}}=0.58$, $p=0.0029$, $n=24$ tenures). In addition, the observed tenure length was positively correlated with the siring rate to age four and the cumulative number of weaned offspring per male (siring rate, $r_{\mathrm{S}}=0.74$, $p<0.001$; number of offspring, $r_{\mathrm{S}}=0.78$, $p<0.001$; $n=24$ tenures). Thus, males with longer observed tenures had higher reproductive success.

Discussion

The standardized variance was 1.0–1.2 for the number of mates per male (N_{MATE}) versus 1.8–3.2 for the rates of siring offspring that survived to reach ages one to four. The difference between those two measurements mainly reflects variance in offspring survival, which became increasingly important as we incorporated a greater proportion of infancy into the analyses. Thus, access to mates and offspring survival were both major sources of variance in male reproductive success, while differences in female fertility were less important. Preliminary results showed higher reproductive success for males with longer observed tenures as harem holders.

Table 4 Observed infant mortality to age three within different gorilla populations in relation to group type

Gorilla population	Group type	References	Mortality	*N*	χ^2	*df*	*p*
Western	Omg	This study	43%	79			
Mountain	Both	Robbins et al. (2007)	27%	181	5.7	1	0.017
Mountain	Omg	Robbins et al. (2007)	42%	48	<0.1	1	1.000
Eastern lowland	Both	Yamagiwa and Kahekwa (2001)	26%	46	2.9	1	0.089

Chi-square statistics are based on three separate 2×2 tables of deceased versus surviving infants in this study versus each of the other populations

N the number of infants, *Omg* one-male group, *both* one-male and multi-male groups

Harem size and number of mates per male

Males with larger harems had higher siring rates, which is consistent with higher reproductive success for such males in mountain gorillas (Watts 2000; Robbins and Robbins 2005; Bradley et al. 2005) and many other species such as red deer, elephant seals, and Soay sheep (Clutton-Brock et al. 1988; Le Boeuf and Reiter 1988; Coltman et al. 1999). Larger harems are expected to lead to higher male reproductive success unless the benefits of increased mating opportunities are offset by costs such as increased feeding competition (Sterck et al. 1997), greater infanticide risk (Crockett and Janson 2000; Steenbeek and van Schaik 2001), or shorter tenures (Dunbar 1984; Packer et al. 1988). Similar to gorillas, the group sizes of Thomas's langurs (*Presbytis thomasi*) are determined by female dispersal, which is related to the ability of a male to protect females and offspring (Steenbeek et al. 2000). In this study, males with larger harems had lower offspring mortality with no apparent reduction in female fertility or observed tenure length (see below), so the factors that are limiting harem size remain unclear.

Up to 58% of the variance in access to mates arose from the difference between harem holders versus non-harem holders (Table 1), which is consistent with theoretical predictions that such differences can be important (Wade and Shuster 2004). Single season assessments of the variance in harem size will underestimate the contribution of non-harem holders if males typically become more successful as they age, and it will overestimate that contribution if aging males typically become less successful (ibid). Rather than consistently increasing or decreasing with age, however, male competitive ability has been considered to follow an inverted-U shaped trajectory in many species (e.g., Alberts et al. 2003; Robinson et al. 2006). A nonlinear pattern may explain why the single season estimates of variance were fairly consistent with longer-term calculations in this study.

Female fertility

Female fertility is often lumped together with harem size to make the siring rate a single component of male reproductive success (e.g., Brown 1988), but separating the two parameters can help to investigate evidence of feeding competition among or within groups. Of the parameters that we examined, female fertility had the least influence upon variance in male siring rates. This is not surprising because fertility is mainly expected to depend upon food availability, and male gorillas do not seem to compete for resources for their group (Sicotte 1993; Robbins and Sawyer 2007; but see Bermejo 2004). In that regard, western gorillas differ from species such as chimpanzees whose males defend territories, and black and white colobus monkeys whose males are the main participants in feeding competition between groups (Fashing 2001; Williams et al. 2004; Harris 2006). Like those species, western gorillas have some clumped foods, but they also feed on more evenly distributed foliage, which may be sufficiently abundant to minimize competition among groups (Stokes 2004). More quantitative ecological comparisons would be needed to fully determine why those species differ from western gorillas and to determine whether female fertility is a greater source of variance in their male reproductive success.

Female fertility was not significantly lower in larger groups, which is consistent with other studies that found little or no influence of feeding competition upon the birth rates, inter-birth intervals, offspring survival, and dispersal patterns of female gorillas (Watts 1990; Stokes et al. 2003; Robbins et al. 2007, 2009b). Similarly, studies of other folivorous species have not consistently found evidence for greater feeding competition within larger groups, possibly because females may reduce the impact of such competition by increasing group spread, or because their food is relatively abundant, and/or because larger groups may have better habitat (Isbell 1991; Janson and Goldsmith 1995; Gillespie and Chapman 2001; Borries et al. 2008).

Offspring survival

As we extended our criterion for offspring survival from age one to age four, it became the largest source of variance in siring rates among breeders (Table 2). At all age criteria, higher offspring survival led to significantly higher male siring rates. Offspring survival was higher in larger groups, though the relationship was significant only at age four. We consider three potential explanations that are not mutually exclusive. Firstly, females may prefer larger groups to reduce the risk of predation (Hamilton 1971; Elgar 1989; Caro 2005). Larger groups can detect predators more quickly, they may overwhelm a predator by mobbing or scattering, and their individuals may be safer due to dilution effects (ibid). If the risk of predation declines in larger groups, it could amplify the strength of selection for sexually dimorphic traits that enable males to acquire females, because males with more mates would have higher offspring survival. Such a conclusion must be considered tentative, however, because there are no confirmed cases of predation on infant gorillas in this population.

Secondly, females may aggregate around silverbacks with “good genes” (Zahavi 1975). Such female mate choices can lead to intersexual selection for extravagant secondary sexual traits (Andersson 1994). Harem size has been positively correlated with sexually dimorphic traits in comparative studies of pinnipeds, primates, and ungulates, although those traits may reflect a combination of both intersexual and intrasexual selection (Alexander et al. 1979; Lindenfors et al. 2002; Vanpé et al. 2008). Similarly, male western gorillas with larger sagittal crests and larger gluteal muscles have larger harems, higher offspring survival, and higher rates of siring offspring that reach weaning age (Breuer 2008; Caillaud et al. 2008). If silverbacks with those traits have good genes, they could sire higher quality offspring with increased survivorship (Moller and Alatalo 1999; Byers and Waits 2006). Conversely, extravagant sexual traits are often predicted to reduce survivorship while increasing the siring rates of the few males who survive (Lande 1981; Oufiero and Garland 2007).

Thirdly, females may aggregate around males who are good protectors. Female gorillas do not rely solely on “safety in numbers” to reduce the risk of predation to themselves and their offspring; they rely on a silverback who is twice their size with larger canines (Leigh and Shea 1995; Smith and Jungers 1997; Thoren et al. 2006). The dominant male plays the primary role in confronting threats from both predators and potentially infanticidal outsider males (Harcourt and Stewart 2007), so selection is likely to favor sexually dimorphic traits that enhance his ability to succeed in that role. For example, crest size may correlate with biting strength (Parnell 2002a; see also Anderson et al. 2008 for other correlates of biting power). Confronting predators is not typically considered an aspect of male mating competition, so it would not even fit within relatively broad definitions for sexual selection (Clutton-Brock 2004). In contrast, infanticide is often considered part of intrasexual selection because it can enable a male to reproduce more quickly with the mother of the infant that he kills (i.e., the sexual selection hypothesis: Hrdy 1974; van Schaik and Janson 2000).

There is still no proof of infanticide in this population, but several suspected cases have been reported including direct observations of one fatally wounded infant (Stokes et al. 2003). More conclusive evidence of infanticide has been reported for mountain gorillas, particularly after the silverback dies in a one-male group (Watts 1989). Similarly, when silverbacks in this study had infants at the time of their death, 82% of those infants died shortly thereafter. In this respect, gorillas are similar to lions (*Panthera leo*), which also have infanticide and year-round harem defense, and in which offspring survival is an important component of male reproductive success (Packer et al. 1988). Infanticide is considered a major influence upon the social systems of many species (Sterck et al. 1997; van Schaik and Kappeler 1997; van Schaik and Janson 2000). The potential for infanticide can vary considerably among species, depending on the probability that a mother will encounter males who could not have sired her offspring, and whether her interbirth interval will be shorter if her infant dies, and whether the infanticidal male would be likely to sire her next offspring (Harcourt and Greenberg 2001; van Schaik et al. 2004; Pradhan and van Schaik 2008; Boyko and Marshall 2009). Further study is needed to determine whether differences in the potential for infanticide contribute to differences in sexual dimorphism among species (Mitani et al. 1996; Lindenfors 2002; Thoren et al. 2006).

Observed tenure length

Silverbacks with larger harems had longer observed tenure lengths, so we found no evidence of a potential tradeoff between having a few mates for a long time versus many mates for a short time. In some species, male tenure is shorter in groups containing a large number of females (Packer et al. 1988; Steenbeek et al. 2000), which is probably due to the increased reproductive effort and higher risk of takeover by other males. In contrast, a lack of such a negative relationship (or the existence of a positive relationship) might be due to higher quality males attracting more females and simultaneously being able to maintain a long reproductive lifespan (McElligott and Hayden 2000). In this study, males with longer observed tenures had higher siring rates and a higher number of weaned offspring (see also Packer et al. 2001). Thus, the benefits of a long adulthood may be amplified because a longer tenure enables a silverback to fully protect a greater proportion of his offspring, which can further affect female preferences for younger and stronger males (Steenbeek et al. 2000). If so, then we expect that longevity and reproductive tenure may be a major source of variance in the lifetime reproductive success of male western gorillas, but it will not negate the importance of harem size or offspring survival as quantified by this study.

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