

Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*)

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Abstract Over the past few decades, socioecological models have been developed to explain the relationships between the ecological conditions, social systems, and reproductive success of primates. Feeding competition, predation pressures, and risk of infanticide are predicted to influence how female reproductive success (FRS) depends upon their dominance rank, group size, and mate choices. This paper examines how those factors affected the reproductive success of female mountain gorillas (*Gorilla beringei beringei*) of the Virunga Volcanoes, Rwanda from 1967–2004. Reproductive success was measured through analyses of interbirth intervals, infant survival, and surviving infant birth rates using data from 214 infants born to 67 females. Mountain gorillas were predicted to have “within-group scramble” feeding competition, but we found no evidence of lower FRS in larger groups, even as those groups became two to five times larger than the population average. The gorillas are considered to have negligible “within-group contest” competition, yet higher ranked mothers had shorter interbirth intervals. Infant survival was higher in multimale groups, which was expected because infanticide occurs when the male dies in a one-male group. The combination of those results led to higher surviving birth rates for higher ranking females in multi-

male groups. Overall, however, the socioecological factors accounted for a relatively small portion of the variance in FRS, as expected for a species that feeds on abundant, evenly distributed foliage.

Keywords Mountain gorilla · Female reproductive success · Dominance rank · Group size · Feeding competition · Socioecological model

Introduction

Over the past few decades, conceptual models have been developed to explain the links between ecological conditions, the social systems of primates, and reproductive success of their individuals (Wrangham 1980; Isbell 1991; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002). This socioecological model indicates that social groups are shaped primarily in response to the abundance and distribution of food (Wrangham 1980; Isbell 1991), predation pressures (van Schaik 1989), and infanticide risks (Sterck et al. 1997). The abundance and distribution of food can influence female reproductive success (FRS) through contest or scramble feeding competition (Table 1), which can occur within or between groups (Janson and van Schaik 1988; van Schaik 1989; Sterck et al. 1997; Koenig 2002).

Scramble competition occurs when consumption by any one individual reduces net energy intake of all others. Within-group scramble competition (WGS) is expected when limiting food resources occur in large patches, or when such food is highly dispersed and/or quickly depleted (e.g., Thomas langurs, Steenbeek and van Schaik 2001). Larger groups may need to travel farther for food (Janson and Goldsmith 1995), increasing the energetic costs and reducing reproductive success for all females (Srivastava

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Table 1 Summary of predictions for each type of feeding competition

| Type of competition | Within-group contest (WGC) | Within-group scramble (WGS) | Between-group contest (BGC) | Between-group scramble (BGS) |
|--------------------------|----------------------------|-----------------------------|-----------------------------|------------------------------|
| Food distribution | Small clumps | Dispersed | Large clumps | Any |
| Higher FRS for | Higher rank | Smaller groups | Larger groups | Lower density |
| Predictions for gorillas | Little or none | In large groups | None | Low |

Type of food distribution in which the competition is expected, and the conditions that will favor higher female reproductive success (FRS). Predictions for the intensity of each type of competition in mountain gorillas are based upon their abundant, evenly distributed food and low population density.

and Dunbar 1996; Hill et al. 2000). Alternatively, larger groups may avoid additional travel by increasing group spread, at the potential cost of increasing predation risks (see below) and reduced social cohesion (Chism and Rowell 1988; Dias and Strier 2003; Smith et al. 2005).

Within-group contest competition (WGC) is expected when limiting food resources are clumped into patches that are small enough to be monopolized or usurped by a fraction of the group, possibly by a single individual (e.g., see references in Vogel 2005). Such competition typically leads to despotic, nepotistic dominance relationships, with better reproductive success for higher ranked females (Harcourt 1987; Ellis 1995) as seen with baboons (Altmann and Alberts 2003; Wasser et al. 2004), mandrills (Setchell et al. 2002), and Japanese macaques (Gouzoules et al. 1982; but see Takahata et al. 1999). The average rank declines in larger groups, so if FRS correlates with rank under WGC, then the average FRS in a group should also decline at larger sizes (Fig. 1a). Thus, the most precise way to separate those effects of WGC versus WGS is through multivariate analysis of FRS versus both group size and ordinal rank (Fig. 1b).

The effects of group size on FRS can be further complicated by between-group contest competition (BGC), which is expected when food patches are large enough to accommodate all members of one group, but still small enough that one group can exclude others. Such competition favors larger groups, so FRS is expected to increase with group size (Robinson 1988). The fourth permutation of feeding competition, between-group scramble competition (BGS), is expected at high population density because foraging efficiency can suffer when many groups use the same area (van Schaik 1989). It is not expected to directly affect female relationships (van Schaik 1989) because the competing females may not even meet, but a reduction in relative food abundance could intensify the other types of feeding competition (Isbell 1991).

Studies of net energy intake and reproductive success have shown that these four types of feeding competition can occur in a variety of combinations such as WGS combined with WGC and/or BGC (Sterck et al. 1997; Packer et al. 2000;

Koenig 2000, 2002; Altmann and Alberts 2003; Schülke 2003; Izar 2004). Studies of the socioecological model may also be complicated by temporal or spatial variations in food availability (Hill et al. 2000; Gillespie and Chapman 2001). Some species can quickly adjust group sizes to match food availability, thus, keeping WGS relatively constant (Dias and Strier 2003). In other species, the effects of feeding competition can depend upon seasonal or longer term fluctuations in ecological conditions (Koenig 2000; Wasser et al. 2004; Pazol and Cords 2005).

In addition to the effects of feeding competition, FRS may depend upon causes of mortality such as predation and infanticide. Larger groups are generally expected to improve FRS by reducing the risk of predation due to better detection of predators and a lower probability that any particular individual will be killed (Hill and Lee 1998; Rogovin et al. 2004; but also see Zuberbühler and Jenny 2002). However, small-bodied and/or nocturnal species may fare better in smaller groups if concealment is more important than detection (Janson and Goldsmith 1995; Hill and Lee 1998; Hebblewhite and Pletscher 2002).

Although sexual selection favors infanticide by males who had not sired the infant, this strategy has obvious negative impacts on FRS (e.g., van Schaik and Kappeler 1997; Harcourt and Greenberg 2001; Broom et al. 2004; van Schaik et al. 2004). For example, infanticide risks for mountain gorillas have been lower in multimale groups, which tend to be larger than one-male groups (Watts 2000). This is because in mountain gorillas, infanticide typically occurs when a new silverback takes over a one-male group after the death of its former silverback. In contrast, infanticide losses have been greater in larger groups of Thomas langurs and red howlers even when larger groups of the latter species were multimale (Sterck 1997; Crockett and Janson 2000; Steenbeek and van Schaik 2001).

This paper examines the impact of socioecological factors on the reproductive success of female mountain gorillas in the Virunga Volcano region from 1967–2004. Mountain gorillas feed on abundant, evenly distributed herbaceous vegetation (Watts 1984, 1985). As the socioecological model predicts, females have been characterized

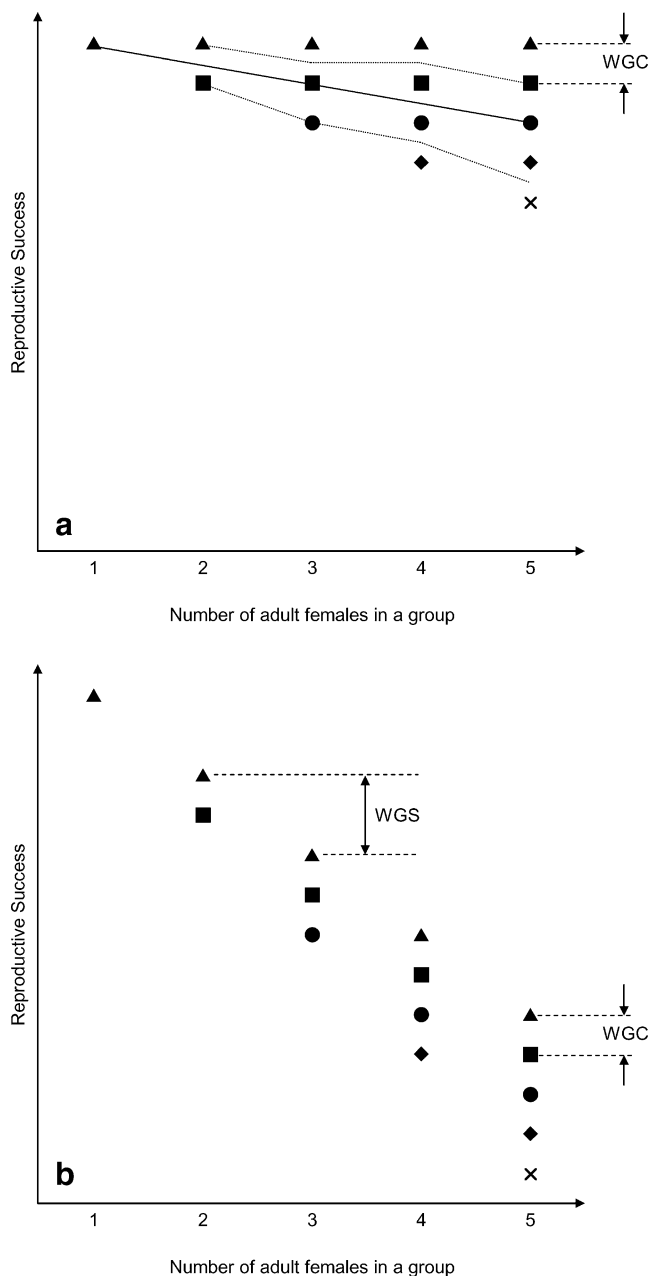


Fig. 1 Reproductive success (RS) versus group size. *Triangles* represent the top-ranked female, *squares* the 2nd rank, *circles* 3rd, etc. Under pure, within-group contest competition (**a**), the RS of each female depends upon the number of females above her who can control her access to food. The RS of each female is independent of the number of females below her because she can control their access to food. Larger groups have a lower average rank, so their average RS is lower too (*solid line*). The average RS also declines for broad dominance classifications such as high/low rank (*dotted lines*), but the RS at each ordinal rank is independent of group size. When WGS is present (**b**), it is most precisely measured by the effect of group size at a constant ordinal rank. The graphs assume no between-group competition or ecological variations among groups. Adapted from van Schaik 1989; Janson and van Schaik 1988; Koenig 2002

as having weak or unclear dominance relationships (Stewart and Harcourt 1987; Watts 1994, 2001). Recently, however, a meta-analysis suggested that their dominance relationships may be stronger and more stable than previously reported, though still not as strong as nepotistic species such as baboons and macaques (Robbins et al. 2005). A statistical analysis of the relationship between dominance rank and FRS has not been published, but birth rates are reportedly 9–14% higher for mothers ranked above average (Table 3 of Sterck et al. 1997).

Mountain gorillas have been cited as a species with WGS (Sterck et al. 1997; Koenig 2002). Feeding time was significantly longer in larger groups, although such increases were considered to be very small (Watts 1988). Birth rates have shown a not significant decline with group size (Watts 1990a; Watts 1996). The mean day journey length was relatively constant over a wide range of group sizes, but it was predicted to increase rapidly as groups became very large (Watts 1998a). The study groups used in that analysis were already twice the average size (8–11 gorillas) for this population, yet they have subsequently grown by another 50–100%. These extremely large groups should provide the clearest evidence of any correlation between FRS and group size in this species.

Mountain gorillas are unlikely candidates for BGC, again because their food is evenly distributed. In contrast with many other primates (e.g., Hanuman langurs, Koenig 2000; see also Isbell 1991), female mountain gorillas do not compete during intergroup encounters in which aggression is mainly limited to mating competition among silverbacks (Sicotte 1993, 2001). The gorillas currently have no natural predators, but leopard attacks had been reported in earlier decades (Schaller 1963). In addition to facing less risk of infanticide, females in multimale groups reportedly have an earlier age of first parturition and higher birth rates (Gerald 1995; Gerald-Steklis and Steklis 2001), so we look for other reproductive advantages such as lower overall infant mortality or shorter interbirth intervals. Based on those collective considerations, we predict that FRS will be lower in the very large groups due to WGS, which may be offset by higher offspring survival when those groups are multimale, with little or no influence from dominance rank.

Materials and methods

Data were evaluated for the mountain gorilla population of the Virunga Volcano region of Rwanda, Uganda and Democratic Republic of Congo from 1967–2004. Since the late 1960s, a few groups of gorillas have been habituated by the Karisoke Research Center (Table 2), providing data about their births, deaths, dispersal patterns, and other life history events (Harcourt et al. 1981; Watts

Table 2 Summary of study groups

| Group | Years observed | | Total size | | | Adult females | | | Silverbacks | | | Female | Total | Surviving |
|---------------|----------------|------|------------|-----|---------|---------------|-----|---------|-------------|-----|---------|--------|--------|-----------|
| | First | Last | Min | Max | Average | Min | Max | Average | Min | Max | Average | Years | Births | Births |
| Amok's Grp | 1969 | 1971 | 1 | 2 | 1.1 | 0 | 1 | 0.1 | 1 | 1 | 1.0 | 0.2 | 0 | 0 |
| Beetsme's Grp | 1985 | 2004 | 8 | 27 | 19.0 | 1 | 10 | 6.0 | 1 | 5 | 2.6 | 111.6 | 27 | 19 |
| Group 4 | 1967 | 1979 | 3 | 14 | 11.0 | 0 | 7 | 4.0 | 1 | 3 | 1.3 | 45.8 | 12 | 6 |
| Group 5 | 1967 | 1993 | 10 | 36 | 17.4 | 3 | 14 | 6.5 | 1 | 4 | 2.2 | 165.3 | 44 | 31 |
| Group 8 | 1967 | 1974 | 1 | 6 | 3.8 | 0 | 2 | 0.6 | 0 | 3 | 1.6 | 3.9 | 1 | 0 |
| Nunkie's Grp | 1972 | 1985 | 1 | 18 | 9.2 | 0 | 7 | 4.3 | 0 | 1 | 1.0 | 54.6 | 15 | 9 |
| Pablo's Grp | 1993 | 2004 | 19 | 52 | 37.6 | 8 | 17 | 14.8 | 2 | 4 | 2.8 | 157.9 | 42 | 24 |
| Samson's Grp | 1971 | 1976 | 1 | 2 | 1.6 | 0 | 1 | 0.6 | 1 | 1 | 1.0 | 2.8 | 1 | 0 |
| Shinda's Grp | 1993 | 2004 | 16 | 25 | 20.9 | 5 | 7 | 5.9 | 1 | 8 | 3.4 | 62.9 | 18 | 7 |
| Susa Grp | 1978 | 2004 | 2 | 37 | 25.3 | 0 | 13 | 8.6 | 1 | 5 | 2.3 | 217.5 | 53 | 36 |
| Tiger's Grp | 1982 | 1987 | 1 | 3 | 1.6 | 0 | 1 | 0.4 | 0 | 1 | 1.0 | 2.2 | 1 | 0 |
| Total | | | | | | | | | | | | 824.6 | 214 | 132 |

Minimum, maximum, and average values are tallied from monthly counts for each group.

1990b, 1991a; Gerald 1995; Robbins 1995, 2001; Sicotte 2001). Another 12 groups have been habituated for tourism, and demographic data from one of those groups (Susa) were available and are included in our dataset. The gorillas have been monitored daily, except for 1997–1998 when research was interrupted due to civil unrest in the region. In this study, gorillas <3 years old are considered infants, and females >8 years old are considered adults. Males between 8–12 years are called blackbacks, and those >12 years old are called adult males or silverbacks (Williamson and Gerald-Steklis 2003). Groups are classified as one-male, multi-male, or all-male, based on their adult composition only.

The dependent variables in this analysis involved three measures of reproductive success: interbirth intervals with surviving offspring (IBI), infant mortality, and surviving birth rates. We examined each of these measures from two perspectives: treating each birth separately and looking at overall values for each mother (Table 3). For example, we performed some analyses in which each IBI was a separate data point and other analyses in which the dependent variable was the average IBI of each mother. The first approach can find relationships that would be masked if each female experienced the same range of conditions, but it would be less reliable if data points for each birth were less independent than for each mother. To test for interdependence among births, we look for relationships between consecutive births by the same mother, which seem like the most probable instances in which one birth could influence another.

For each dependent variable, the “main” independent variables were dominance rank, group size, and group type (Table 3). We also tested for influences from five “secondary” independent variables: the age and parity of the mother (Robbins et al. 2006), the identity of each

mother, the identity of her group, and the date of observation. Details for those secondary variables are beyond the scope of this paper, so we mention results only when relevant to our discussion of the socioecological model (i.e., if a main variable is significant only after accounting for a secondary variable, or if a secondary variable is significant in place of a main variable). For example, lower reproductive success has been reported for primiparous mothers (Robbins et al. 2006), and rank improves with age (Robbins et al. 2005), so we examine whether primiparous mothers are responsible for any apparent effects of rank. The mother's identity variable is used to test for inter-female differences, and the last two secondary variables are used as proxies for spatial and temporal variations in ecological conditions. Those proxies

Table 3 Summary of socioecological influences on female reproductive success

| | Higher rank | Smaller groups | Multimale group |
|-----------------------------|-------------|----------------|-----------------|
| Shorter IBI | | | |
| Each birth separately | + | ns | ns |
| Average per mother | ns | ns | ns |
| Lower infant mortality | | | |
| Each birth separately | ns | ns | + |
| Frequency per mother | + | ns | + |
| Higher surviving birth rate | | | |
| Each birth separately | ns | ns | ns |
| Per mother | + | ns | + |

The header for each column indicates the condition that is predicted to promote higher female reproductive success (FRS), as defined by the variables in each row. The results for each combination show whether the FRS was higher (+), lower (–), or not significant (ns).

are admittedly weak, so whereas significant results may indicate ecological influences, nonsignificant results do not disprove such effects.

Maternal dominance data came from 15 hierarchies involving all of the major groups except one (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). Although the ordinal rankings are theoretically preferred to distinguish between the effects of WGC versus WGS (Fig. 1b), broader classifications may be needed to detect any effect of dominance if those ordinal ranks are not sufficiently precise (as used in Janson and van Schaik 1988; Borries et al. 1991; Pusey et al. 1997; and van Noordwijk and van Schaik 1999; but see Packer et al. 2000). Dominance relationships for mountain gorillas are considered relatively weak and unclear (Watts 1994; Sterck et al. 1997), so we focused on the broader classifications. Ordinal ranks below the median were considered “low”, and all others were “high”. Maternal dominance data are not available for all births, so those analyses used a subset of the larger database (Table 4). When a mother had the same classification both before and after a time when data were not available, we used that classification throughout the missing time. If her classification changed while data were unavailable, we assumed it was unknown throughout that time. When treating each birth separately, we excluded those births with unknown rank. When looking at overall values for each mother, we used a continuous variable to indicate the percentage of her known data that were at high rank, even though they did not cover her entire adulthood.

Table 4 Summary of the full dataset and the subset for females with known dominance classifications

| Data set | Full | Known rank |
|---|------|------------|
| Number of births | | |
| Survived | 132 | 77 |
| Died | 53 | 27 |
| Censored | 29 | 6 |
| Total | 214 | 110 |
| Number of mothers | 66 | 37 |
| Female-years | 827 | 425 |
| Group-years | 121 | (38) |
| Group conditions (averaged from the time of each birth) | | |
| Total size | 24.6 | 22.3 |
| Adult females | 9.3 | 8.7 |
| Silverbacks | 2.5 | 2.3 |

For the subset, the dominance group-years does not include years in which we could interpolate a dominance classification for at least some females in a group (see “Materials and methods”). Censored births represent offspring who were not (yet) observed until they died or reached age three.

Measures of group size included both the total number of gorillas and the number of adult females. Those two variables were significantly intercorrelated, and results were generally similar, so we describe only those for the number of adult females. Nonlinear patterns have been predicted for the effects of group size (e.g., Figure 3 in Sterck et al. 1997; Hill et al. 2000), so we also evaluated a quadratic term for those variables, but those results were not significant and are not reported. When treating each birth separately, we used a dichotomous variable to indicate whether the group type was one-male or multimale. When looking at overall values for each mother, we used a continuous variable to indicate the percentage of her data that were in a multi-male group.

The analyses of IBI are limited to intervals in which the former offspring survived for at least 3 years, the age at which offspring are typically weaned. This approach excludes intervals that were shortened by the death of the former infant. We also limited the analyses to IBI in which the birth dates of both the former and latter offspring are known to within 15 days. During the civil unrest, births could have been missed when very young infants died, so we exclude three cases that might be combining two consecutive IBI into one deceptively long interval. Conditions for each birth interval are taken from the time of the former birth and were analyzed using general linear models (GLM).

We used a dichotomous variable for infant mortality, which indicates whether an offspring survived to age three (0=no, 1=yes). Our dataset uses records through 1/1/2004, so infant mortality analyses were limited to births before 1/1/2001 because we could not determine survival for all subsequent offspring. When explicitly stated, we excluded infants who were killed by poaching or infanticide to see whether the remaining data would provide a clearer perspective on feeding competition. We used logistic regressions when treating each birth separately and GLM when evaluating the overall offspring survival percentage of each mother. To convert those survival percentages into a more normalized distribution, we used an empirical logit transformation, which allows us to model an s-shaped relationship (Sokal and Rohlf 1995). The dependent variable for each mother equaled $\ln[(N_{\text{live}}+0.5)/(N_{\text{die}}+0.5)]$, in which N_{live} and N_{die} represent the number of her offspring that lived and died. Data for the linear regression were weighted by the total number of births for each mother because the survival percentages become more reliable and less prone to demographic stochasticity when they are based upon a larger number of births.

The analysis of surviving birth rates involved pooling the data in a separate fashion for each independent

variable. We used three different types of analysis: (1) To evaluate the effects of group size, we tallied the number of surviving births at each size and divided by 12 times the number of female-months observed at that size (e.g., Watts 1990a). We then performed a univariate regression of those birth rates versus size, weighting each data point according to the number of observed female-months that it represents. In this particular example, the duration of observations at each group size ranged from 17–562 female-months. A birth rate is obviously less reliable when it is calculated from 17 rather than 562 female-months, so a weighting factor helps to provide an appropriate perspective for evaluating each data point (Chatterjee and Price 1991). (2) To evaluate the effects of group type, we pooled all of the female-months and surviving births from one-male groups and compared the results with pooled data from multimale groups. We calculated the expected number of births at each group type based on the null hypothesis that those births would be distributed proportionally to the number of female-months observed. We then used Chi square goodness of fit calculations to compare the expected versus the actual number of births (Altmann and Altmann 1977). We performed similar calculations in which the data were pooled according to rank. (3) In addition to those “population-wide” analyses of surviving birth rates, we also examined sources of variance among females. We pooled all of the female-months and surviving births for each mother and calculated her overall surviving birth rate per year throughout the observations. We used GLM analyses to look for relationships between the surviving birth rate of each female and the mean value of the other independent variables from each month of her observations. In those analyses, we weighted the data points according to the number of months that each mother was observed, again because the birth rates become more reliable and less prone to demographic stochasticity when they are based upon longer observations. Statistical analyses were performed using Systat 11 (2004, SYSTAT Software, Richmond, CA).

Results

Interbirth intervals (IBI)

Among the 39 females with at least one IBI that meets our criteria for analysis, the average length per female ranged from 39–73 months (mean=48.9, SD=7.7). In univariate GLM analyses, the average IBI per female was not significantly correlated with their proportion of IBI in multimale groups ($R^2=0.02$, $F_{37,1}=0.70$, $p=0.41$), their average group size ($R^2<0.001$, $F_{37,1}=0.03$, $p=0.87$), or

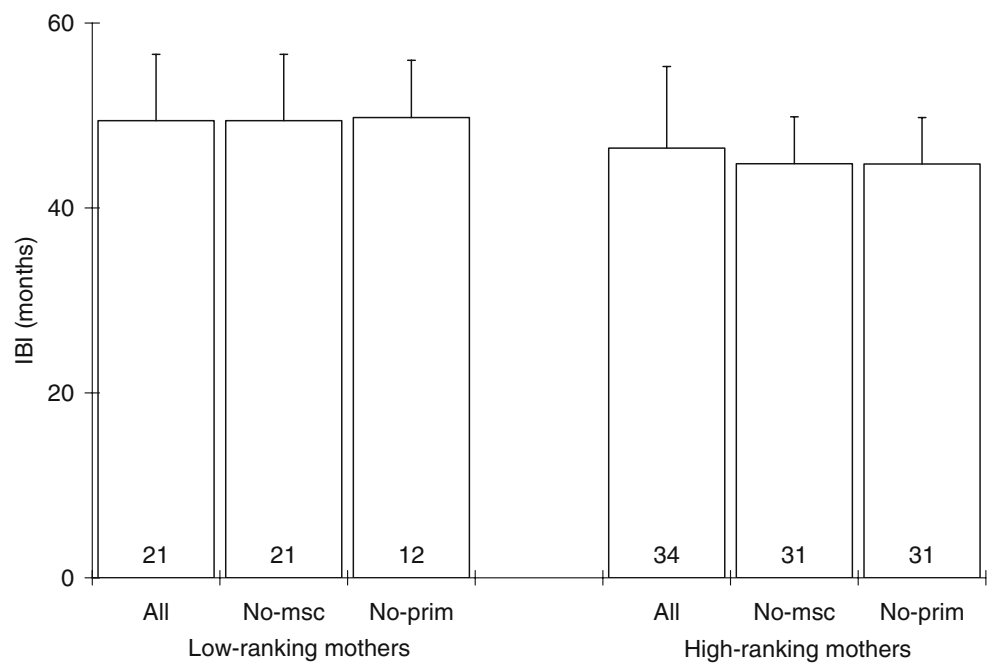
their proportion of IBI while high ranked ($R^2=0.01$, $F_{23,1}=0.33$, $p=0.57$). In multivariate GLM analyses, those three “main” variables were not significant in combinations with each other, or with the “secondary” independent variables tested (average age and parity of the mother, average date of observations, etc).

When treating each birth separately, the 88 IBI in the full dataset ranged from 27–87 months (mean=47.8, SD=9.0). The length of an IBI did not depend upon the length of the previous IBI by the same mother ($R^2=0.01$, $F_{35,1}=0.32$, $p=0.58$). Those results give no indication that one birth can influence another, so they support the reliability of the analyses that treat each IBI as an independent data point. In a univariate GLM using the full dataset, IBI in one-male groups averaged 48.4 ± 7.9 SD months, which is not significantly longer than 47.6 ± 9.4 SD in multimale groups ($t=0.32$, $df=86$, $p=0.75$). Group size accounted for only 1% of the variance in IBI ($R^2=0.014$, $F_{86,1}=1.2$, $p=0.28$). In multivariate GLM analyses, those two variables were not significant in combination with each other, nor with the “secondary” independent variables tested.

In the data subset with known maternal rank, IBI were significantly shorter when mothers were high-ranking (Fig. 2), but only after removing one or two outliers ($p=0.20$, 0.017, and 0.043 after removing zero, one, or two outliers, respectively). Those outliers are the two longest IBI in the data subset, both by primiparous mothers, and the first one contains a miscarriage. The effect of rank was also significant if we excluded all miscarriages ($R^2=0.13$, $F_{50,1}=7.5$, $p=0.009$) or all primiparous births ($R^2=0.16$, $F_{41,1}=7.6$, $p=0.009$), but even in the latter of those analyses, the IBI with low ranking mothers were only 11% longer (49.8 ± 6.2 SD months, versus 44.8 ± 5.0 SD for high-ranking). The variables for group size and group type were not significant when added to that analysis.

In post-hoc tests to determine whether inter-female differences could account for the apparent effects of dominance, we focused on the nine mothers who had IBI at both high and low rank and used the mothers’ identity as a category variable (neither of the outliers was among the 23 IBI with those mothers). The mothers’ identity and rank were both significant in the multivariate GLM ($p=0.050$ and 0.035, respectively), collectively accounting for 67% of the variance in those IBI. The variables for group size and group type were not significant when added to that analysis. In two separate univariate GLM analyses using the same data subset, the mothers’ identity and rank accounted for 54 and 12% of the variance, respectively, but neither variable was significant in those tests. So, although inter-female differences show a major influence on IBI, they do not account for the effects of dominance, which remained significant even after adjusting for the mothers’ identity.

Fig. 2 IBI (months) of high versus low ranking mothers. Datasets examined included all IBI with mothers having known rank (*All*), or excluded IBI with miscarriages (*No-msc*), or excluded IBI by primiparous mothers (*No-prim*). Sample sizes are shown above each label. Error bars represent one standard deviation



Offspring survival to age three

In addition to the 39 females with at least one IBI that meets our criteria for analysis, another 19 females are included in the analyses for offspring survival (e.g., females who were observed for only one birth). Among these 58 females, the offspring survival percentage per mother was positively correlated with the percentage of their births that were in multimale groups (GLM: $R^2=0.11$, $F_{56,1}=6.8$, $p=0.012$). Group size was not significant when added to that analysis, nor in a univariate analysis ($R^2<0.01$, $F_{56,1}=0.29$, $p=0.59$), nor in combination with the other variables tested.

Among the 35 females with known dominance ranks, the offspring survival percentage per mother was positively correlated with the percentage of their births that were in multimale groups and with their percentage of births when high ranking (multivariate GLM: $R^2=0.25$, $F_{32,2}=5.4$, $p=0.010$ for the overall model; $p=0.027$ and 0.015 , respectively, for the effects of rank and group type within the model). When we excluded primiparous births, the R^2 value improved for the overall model, but the p value worsened for the effect of rank within the model (multivariate GLM: $R^2=0.33$, $F_{26,2}=6.4$, $p=0.005$ for the overall model; $p=0.073$ and 0.007 , respectively, for the effects of rank and group type within the model). The percentage for multimale groups could not be replaced with the average group size in those analyses, even though those two independent variables were positively correlated ($R=0.56$, $N=58$, $p<0.001$).

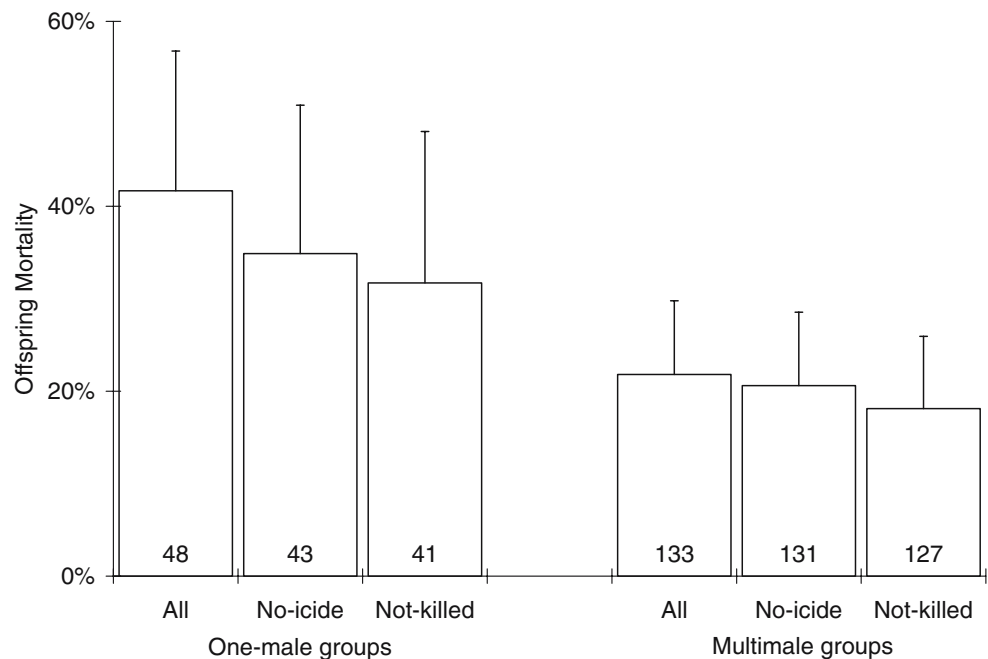
When treating each birth separately, infant mortality was 27% in the full dataset (49 of 181 infants, 95%CI=21–34%). The mortality data include 13 “killed” infants:

seven known cases of infanticide, five cases of possible infanticide, and one death from poaching. Only one case of mortality seemed related to lack of food for the offspring. And even in that case, the mother had trouble producing milk, but not any apparent trouble with access to her own food. Infant mortality did not depend upon whether the mother’s previous infant had died ($\chi^2=0.25$, $N=123$, $df=1$, $p=0.61$), which again supports the reliability of the analyses that treat each birth as an independent data point.

Mortality was 22% for infants born in multimale groups, which is significantly lower than the 42% mortality in one-male groups (Fig. 3; $\chi^2=7.1$, $N=181$, $df=1$, $p=0.008$). After excluding known cases of infanticide, mortality was 21% for infants born in multimale groups versus 35% in one-male groups ($\chi^2=3.6$, $N=174$, $df=1$, $p=0.058$). After excluding all killed infants, mortality was 18% in multimale groups versus 32% in one-male groups ($\chi^2=3.4$, $N=168$, $df=1$, $p=0.065$). Group size was not significant when added to those analyses, nor in univariate tests (e.g., when excluding killed infants, logistic $\chi^2=0.07$, $N=168$, $df=1$, $p=0.80$), nor in combination with the other variables tested.

In the data subset with known maternal rank, the effect of rank on infant mortality was not significant in univariate analyses, nor in combination with any other variables (including group type). Mortality was 24% for offspring when the mother had high rank, versus 28% when the mother had low rank ($\chi^2=0.19$, $N=103$, $df=1$, $p=0.66$). Excluding killed infants, offspring mortality was 19% for both high and low ranking mothers ($\chi^2=0.001$, $N=95$, $df=1$, $p=0.97$).

Fig. 3 Infant mortality in one-male versus multimale groups. Datasets examined included all infants (*All*), or excluded known cases of infanticide (*No-icide*), or excluded known and possible cases of infanticide, plus one death from poaching (*Not-killed*). Sample sizes are shown above each label. Error bars represent the upper 95% confidence limit



Surviving birth rates

In addition to the 58 females with at least one observed birth, another nine females did not give birth while observed during adulthood. Those nine females were observed for an average of 20 months (range=2–43). Four of those females were still alive and nulliparous when the observation period ended, and the other five died or disappeared during the observation period. Among the 67 females observed during adulthood, the surviving birth rate per female was positively correlated with their proportion of months in multimale groups (univariate GLM: $R^2=0.068$, $F_{65,1}=4.8$, $p=0.033$), but the best fit of this data was with their average date of observations (e.g., higher surviving birth rate in more recent years; $R^2=0.12$, $F_{65,1}=8.5$, $p=0.005$). Group size was not significant in a univariate analysis ($R^2=0.03$, $F_{65,1}=1.8$, $p=0.19$), nor in combination with the other variables tested. Among the 46 females with known dominance ranks, the surviving birth rate per female was positively correlated with proportion of months observed with high rank and with their average date of observations ($R^2=0.24$, $F_{44,2}=7.0$, $p=0.002$).

When treating each birth separately, the surviving birth rate was 0.189, based on 132 surviving births in 700 female-years. The rate was 0.196 surviving births per female-year when groups were multimale, which was not significantly different than the rate of 0.168 when they were one-male (goodness of fit $\chi^2=0.52$, $df=1$, $p=0.47$). The surviving birth rates per female-year were not significantly correlated with group size ($R^2=0.047$, $F_{15,1}=0.7$, $p=0.40$) and were essentially identical when females had high versus low rank (goodness of fit $\chi^2=0.001$, $df=1$, $p=0.97$).

Discussion

Overall, we found evidence for greater reproductive success in females with higher rank and/or in groups with more than one silverback. However, those two variables generally accounted for only a small portion of the variance in female reproductive success (FRS), and neither was consistently significant throughout our analyses (Table 3). The inconsistent results illustrate the value of examining FRS from several perspectives (i.e., different measures of reproductive success, and treating each birth separately versus pooling values for each mother) because they provide a more complete picture than we would have obtained from any one analysis in isolation. Nonetheless, the complete picture indicates that any influence by socio-ecological factors is weak for this species, except for the infanticide that follows the disintegration of one-male groups and leads to lower FRS. That conclusion is further supported by the lack of any evidence that FRS declines in larger groups.

Dominance rank

In all three tests with significant results, higher rank was associated with better reproductive success: shorter IBI, a higher frequency of successfully rearing offspring, and a higher surviving birth rate per mother (Table 3). However, the effect of rank was not consistently significant for any of those three measures of FRS, nor from either of our two perspectives (treating each birth separately versus comparing overall values for each mother). The inconsistent results support the traditional view that dominance relationships

are weak or “egalitarian” for mountain gorillas (e.g., Sterck et al. 1997), especially in comparison with nepotistic species such as macaques (Rhine et al. 1989) and baboons (Hausfater et al. 1982; Samuels et al. 1987; Combes and Altmann 2001). Nonetheless, the few significant results still represent a degree of strength that had not been previously reported for this species. Significant correlations between rank and reproductive success have also been reported for chimpanzees (Pusey et al. 1997) and Hanuman langurs (Borries et al. 1991), which lack strong nepotistic dominance relationships. If such results continue to accumulate, they may eventually lead to more refined distinctions among species that are currently lumped together in the “egalitarian” category of the socioecological model (Koenig et al. 2004; Robbins et al. 2005).

Based upon the socioecological model, we did not expect to find any links between rank and FRS for mountain gorillas because their evenly distributed food (foliage) should not lead to within-group contest competition (WGC). In light of our few unexpected results, we should mention that mountain gorillas occasionally feed on clumped items, such as small patches of bamboo shoots (Fossey 1983; Watts 1984), and that even folivores may have WGC due to spatial variations in food quality (Koenig et al. 1998; see also Watts 1998a). Nonetheless, displacements are rare among female mountain gorillas, and aggression is largely ineffective in providing differential access to resources (Watts 1994). Therefore, our results may illustrate a cautionary lesson that links between rank and FRS are not necessarily related to WGC.

A more plausible explanation for the rank differences in FRS is that both measurements covary with the mother’s physical condition (Pusey et al. 2005). The physical condition of a female is generally expected to affect her reproductive success (Fig. 4). In nepotistic species, however, the physical condition of a female may have little effect on her rank, which is based instead upon the rank of her mother (Walters and Seyfarth 1987; Mori et al. 1989; Holekamp et al. 1996). But rank influences the physical condition of the female because it affects her access to food resources through WGC (Fig. 4a). Thus, rank indirectly affects FRS in nepotistic species. In individualistic species, rank may have little or no impact on the physical condition of the mother if WGC is weak (Fig. 4b). Conversely, the physical condition of the mother may affect her rank if dominance depends upon competitive abilities. Thus, reproductive success may be covariant with rank, but only because both parameters depend upon the physical condition of the female.

Differences in physical condition might be especially pronounced for primiparous mothers who may still be growing (Leigh and Shea 1996). Primipares have indeed shown lower FRS for this species and others, which could also arise from their relative inexperience or because they are

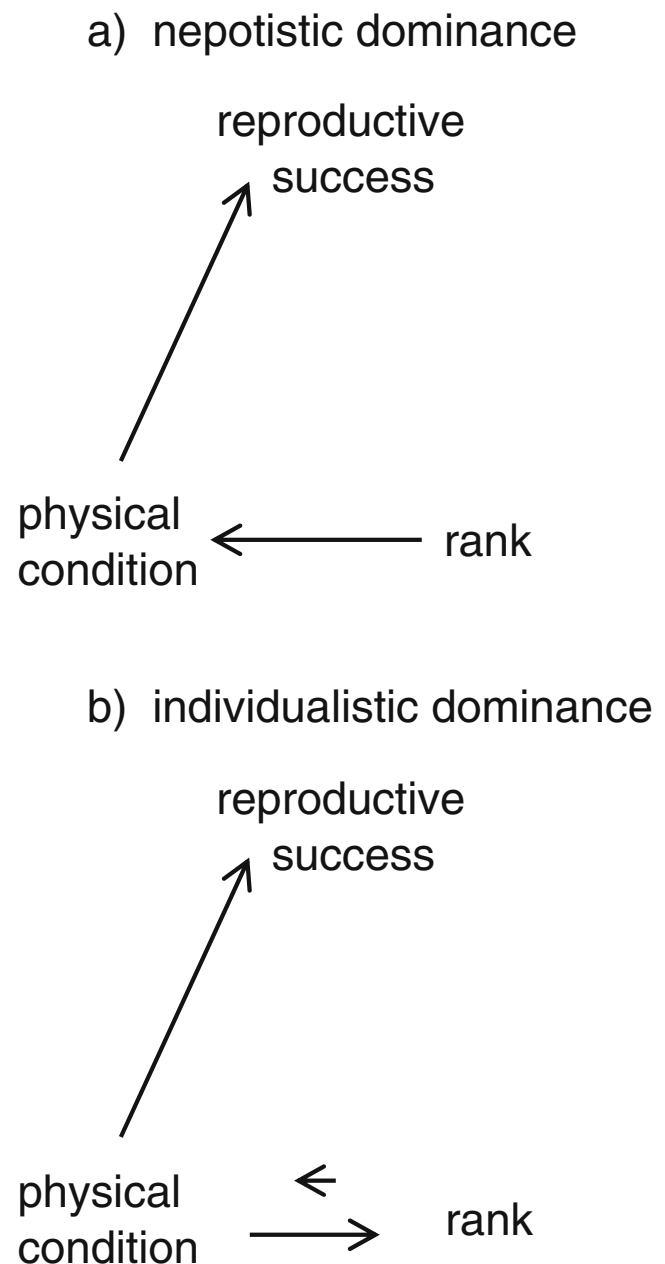


Fig. 4 Inter-relationships between physical condition, dominance rank, and female reproductive success for **a** nepotistic dominance systems and **b** individualistic dominance systems

investing in their own continued growth at the expense of their offspring (Robbins et al. 2006). Rank improves with age for female mountain gorillas (Robbins et al. 2005), so any apparent effect of rank could hypothetically reflect underlying correlations with age and/or parity. Yet, even after excluding primiparous births, the effect of rank remained significant for IBI. Furthermore, FRS subsequently starts declining with age for multiparous mountain gorillas (Robbins et al. 2006), so any covariation with age or parity does not seem to be a major factor in our results for rank.

Group size

Against our expectations, we found no evidence of lower FRS in larger groups, even as the groups have become three to five times larger than the population-wide average (Table 2). The extraordinary range of group sizes repeatedly explained less than 5% of the variance in FRS, as indicated by the R^2 values for IBI and surviving birth rates (both for births as independent events and average values per mother). Thus, rather than reflecting insufficient statistical power to detect an effect of group size, our results represent strong evidence that any such effect was negligible. Larger groups have a lower average rank, so under WGC, their average FRS should decline too (Fig. 1a). As we found no such effect, the results with group size support our conclusion that WGC is minimal for this population.

More surprisingly, the results also indicate that within-group scramble competition (WGS) is minimal. The costs of WGS may be negligible if groups increase their spread rather than their daily travel lengths or if females can easily compensate for the energetic costs of additional travel. Larger group sizes have not consistently led to greater travel for primates, especially among folivores, although such studies generally have not accounted for potential variations in food availability (Janson and Goldsmith 1995; Gillespie and Chapman 2001; Ganas and Robbins 2005). The daily travel of six gorilla groups was positively correlated with their size, and the travel of one group was positively correlated with food density (Watts 1991b), but further study would be needed for a multivariate analysis of travel costs versus both group size and food density. However, gorillas spend only about 6% of their time traveling (Watts 1988), and they “feed as they go”, so even if larger groups must travel farther, any impact on FRS could be too small to detect.

Although our results show no evidence of WGS, this conclusion has its caveats. As with many primate populations (Sterck 1998; Janson 2000), mountain gorillas have suffered from considerable human disturbances in recent decades. Due to poaching losses, the Virunga gorillas are reportedly well below their carrying capacity (McNeilage 1995), so the apparent lack of WGS may reflect an unusually low population density. Although the effects of population density are most directly represented by between group scramble competition (van Schaik 1989), a relative abundance of food could ease other types of competition such as WGS (Isbell 1991). Similarly, the study groups are reported to have the best habitat in the Virungas (McNeilage 1995), so the lack of WGS may not be representative of the broader region.

Furthermore, we cannot completely exclude the possibility that ecological improvements may have offset any cost of WGS, as the study groups have become larger and

more predominantly multimale in recent years. However, the most likely ecological improvements would have occurred after the cessation of cattle grazing in the 1970s, and there was no noticeable shift in IBI at that time (not shown), so it is unlikely to explain the success of large groups 25 years later. The date of observation was positively correlated with the surviving birth rate per female, which may merely reflect the initial prevalence of infanticide, but we found no correlation with date of observation in the other five analyses of FRS (average IBI and offspring mortality per female and all tests treating each birth separately). Resource availability, consumption, and rates of renewal were studied in the 1980s (Watts 1987, 1998b), so an updated analysis of those ecological conditions should show whether any subsequent improvements have occurred.

Group type (one-male versus multimale)

In the absence of strong feeding competition, the FRS of some species may be more sensitive to male reproductive strategies such as infanticide (Sterck 1997; Crockett and Janson 2000; Steenbeek and van Schaik 2001). In this study, infant mortality was significantly higher in one-male versus multimale groups, as expected based on infanticide losses from group disintegrations. Infanticide accounted for 37% of infant mortality through the 1980s (Fossey 1984; Watts 1989). Since then, the study groups have been predominantly multimale, and those known cases of infanticide now represent only 14% of all infant deaths, but an agent-based model suggests that the earlier values are more representative of the broader population (Robbins and Robbins 2004). Group type showed no significant effects on IBI, so any impact on surviving birth rates probably arose from infant mortality (Table 3). Surprisingly, we still found a trend toward higher infant mortality in one-male groups even after excluding killed infants from the analysis. Males play little role in raising offspring, and aside from infanticide protection, there is no obvious explanation for any inherent reproductive advantages in multimale groups. Thus, lower infant mortality in multimale groups would support our caveat that those groups may have had better ecological conditions in recent years.

Implications for female reproductive strategies

In species without clumped foods, WGC, or nepotistic dominance hierarchies; females can use intergroup transfers to reduce WGS and to associate with a high quality male (Sterck et al. 1997; Sicotte 2001). Transferring female mountain gorillas in these study groups have shown a preference for multimale groups, but no clear preferences regarding group size (Watts 2000; but see Harcourt 1978).

Those patterns are consistent with our results for higher offspring survival in multimale groups and the negligible costs of WGS as those groups become large. If anything, our results raise the question of why more females do not transfer to multimale groups, so further study is needed to evaluate any fitness costs of such transfers.

Our results also raise the question of why females engage in agonistic behaviors that are generally ineffective, especially if rank has no direct impact on FRS (Watts 1994, 2001). Current behavior may have evolved under different selection pressures if feeding competition and proximity to the dominant male had been more important while the gorillas were at a higher population density and under predation pressure from leopards (Schaller 1963). However, such conditions may also be more representative of western lowland gorillas where females transfer preferentially to smaller groups, and yet, preliminary studies suggest that their agonistic behavior is equally ineffective (Stokes et al. 2003; Stokes 2004). Therefore, the cost of such agonistic behavior may be sufficiently low to support its persistence in all gorilla populations, even if the benefits are small and infrequent. Interventions by the dominant male help to keep those costs and benefits low, which reduces the incentive for low ranking females to leave him (Watts 1994). Thus, in the absence of strong influences from ecological conditions, male reproductive strategies may play a key role in shaping female relationships within groups, just as the risk of infanticide may determine the preferences of females who transfer.

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