Biological Journal of the Linnaean Society (in press)

Fertility as a Constraint on Group Size in African Great Apes

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Abstract

Gorillas and chimpanzees live in social groups of very different size and structure. I here test the hypothesis that this difference might reflect the way fertility maps onto group demography as it does in other Catarrhines. For both genera, birth rates and the number of surviving offspring per female are quadratic (or ∩-shaped) functions of the number of adult females in the group, and this is independent of environmental effects. The rate at which fertility declines ultimately imposes a constraint on the size of social groups that can be maintained in both taxa. The differences in group size between the two genera seem to reflect a contrast in the way females buffer themselves against this cost. Gorillas do this by using males as bodyguards, whereas chimpanzees exploit fission-fusion sociality to do so. The latter allows chimpanzees to live in much larger groups without paying a fertility cost (albeit at a cognitive cost).

Key words: Chimpanzees, gorillas, fertility, group size, fission-fusion, bodyguard hypothesis

Short title: Fertility in African great apes

Introduction

The factors that limit social group size in animals have usually been viewed as a trade-off between, on the one hand, predation risk or competition for access to resources from conspecifics (between-group competition, BGC) acting centripetally to promote group-living and, on the other hand, within-group competition (WGC, reflecting either access to resources or the effects of social stress on fertility) acting centrifugally to limit group size (Sterck et al. 1997; Dunbar et al. 2009; Schülke & Ostner 2012; Markham et al. 2015). Ultimately, however, these effects must all be reflected in either fertility or mortality rates (van Schaik 1983).

There is increasing evidence that fertility declines with group size in primates (primates in general: van Schaik 1983; Harcourt 1987; Majolo et al. 2008; colobines: Dunbar 1988; Srivastava & Dunbar 1996; Borries et al. 2008; baboons: Dunbar & Sharman 1983; R. Hill et al. 2000; Smuts & Nicholson 1989; Altmann & Alberts 2003; Garcia et al. 2006; gorillas: Watts 1990; chimpanzees: Pusey & Schroepfer-Walker 2013: humans: Ji et al. 2013; Pettay et al. 2016) as well as other mammals (equids: Rubenstein 1986; carnivores in general: Moehlman & Hofer 1997; suricates: Creel et al. 1992; Young et al. 2006; rodents: Downhower & Armitage 1971; Huck et al. 1988). At least in Old World monkeys, this seems to impose limits on the size of group that a species can maintain. Importantly, these demographic effects on fertility appear to be independent of any effects that environmental conditions may have (R. Hill et al. 2000; Majolo et al. 2008; Markham et al. 2015; Dunbar et al. 2018).

In the case of baboons (genera *Papio* and *Theropithecus*), fecundity (or birth rate) is a ∩-shaped function of the number of females in the group, and this seems to set upper limits on the size of groups that these species can maintain (Dunbar 2018; Dunbar et al. 2018a). Takahata et al. (2006) have also noted that birth rates may be a ∩-shaped function of both group size and the number of females in ringtailed lemurs (*Lemur catta*). suggesting that this phenomenon might be more widespread among the primates. A quadratic relationship of this kind usually indicates a tradeoff between two linear relationships that correlate in opposite directions with the independent variable (a positively correlated benefit and a negatively correlated cost). Baboon group sizes seem to be constrained within a set of non-overlapping demographic oscillators within which group size oscillates. These represent alternative solutions to the trade-off between predation risk (with group size providing the benefit) and fertility (providing the cost): populations living in high predation risk habitats adopt a larger oscillator than populations living in low predation risk regimes (Dunbar et al. 2018a; Dunbar & MacCarron 2019).

Because of their larger body size, the African great apes (gorillas and chimpanzees) differ significantly from monkeys in terms of both lifehistory and ecological adaptations. They thus provide a strong test of the hypothesis that group sizes are constrained by fertility patterns. Gorillas live in small, moderately cohesive groups (typically 5-20 animals in size), whereas chimpanzees live in large communities (typically 30-80 animals) that normally forage in dispersed parties of 3-8 animals (a social arrangement usually known as fission-fusion sociality). Models of their ecology indicate that, in the limit, both genera’s biogeography is ecologically constrained, although most populations in fact live well below these limits (Lehmann et al. 2007, 2008a,b). However, chimpanzees are only able to occupy as wide a range of habitats as they do compared to gorillas because of their capacity to fission into semi-independent foraging parties (Lehmann et al. 2007, 2008b). Indeed, but for the fact that they can manage the cognitive demands of a fission-fusion system, it is unlikely that they would exist in most of the habitats they currently occupy: fission-fusion allows them to reduce the travel costs that would otherwise very quickly become prohibitive if the whole community foraged as a single group (Lehmann et al. 2007, 2008b). These models did not, however, consider the impact that fertility might have on a taxon’s ability to survive in a given habitat.

Here, I ask whether fertility is a function of group size in the African great apes and, if so, whether this can explain the striking differences in group size and social organisation between these genera. I first examine the distribution of group size in the two genera to determine whether these are unimodal normal or consist of a set of distinct modes representing different demographic oscillators. I then examine fertility in relation to group size and the number of females in the group and ask (1) whether this is a linear or quadratic (i.e. ∩-shaped) function of demography and (2) whether this might explain the differences in grouping pattern between the two genera.

Methods

I obtained gorilla group sizes (N=135) from six studies of well-habituated animals where multiple groups have been under continuous study for several years. The chimpanzee sample is based on 19 habituated communities. In each case, the data are as provided in the relevant papers. Census data normally refer either to a specific time point or to average composition over a period of time (e.g. a year). The data are given in online *Dataset S1*. I use *k*-means cluster analysis to determine whether the distribution of group sizes for each genus is unimodal or has a natural fractal structure (and, if so, whether there is a consistent scaling ratio).

To determine whether fertility is a function of demography, I consider two different measures, namely birth rate (fecundity) and the average number of immatures (infants and juveniles) per female (fertility). Since group composition can change dramatically over time, we ideally want to determine the instantaneous reproductive rate (usually approximated by the annual birth rate). This was possible only for two chimpanzee populations: Mahale (Nishida et al. 2003) and Tai (Boesch & Boesch 2000). However, a small number of other chimpanzee studies also provide mean birth rates averaged over several years for a number of different locations. I analyse chimpanzee birth rates first across study sites using population averages, and then separately through time for the two populations that provide these data on an annual basis. Birth rate data for individual gorilla groups at the same study site are available for only two gorilla populations: Mbeli Bai (Stokes et al. 2003) and Karisoke (A. Robbins et al. 2006). Those for Karisoke are long term averages for individual groups over lengthy study periods (on average 13.5 years, range 5-26) during which group compositions obviously changed considerably, whereas those for Mbeli Bai cover a much shorter period (mean of 2.97 years, range 1-6.4). I use average group composition for the Karisoke groups as given in A. Robbins et al. (2006); I have used only interbirth intervals following the survival of the previous offspring. For Mbeli Bai, Stokes et al. (2003) give initial composition plus the number of each age-sex class immigrating and emigrating over the study period, so I adjusted the Mbeli Bai initial group compositions by half the difference between the number of immigrations and emigrations. In practice, except for Mad Max's group, the adjusted group compositions did not differ by more than one individual from the initial values. Because some of the Mbeli Bai groups were sampled for quite short periods, I set a minimum criterion for inclusion of 4 female-years sampled (reflecting the average birth interval of ~4 years given by A. Robbins et al 2006) to allow for at least one complete reproductive cycle so that birth rates were not subject to erratic small sample effects. The data are provided in online *Dataset S2.*

Average values for group size (all ages and sexes combined), number of adult males (silverbacks only in the case of gorillas), number of adult (breeding age) females and number of dependent immatures (juveniles plus infants, defined as individuals aged less than 6 years old: Weber & Vedder 1983) are available for 13 populations of gorillas (representing all three species: *G. gorilla*, *G. berengei* and *G. graueri*) and 15 populations of chimpanzees (representing both *P. troglodytes* and *P. paniscus*). I take group size to be community size for *Pan* (cf. Lehmann et al. 2007). I use these data to calculate average fertility (number of immatures per adult female) for each population. The number of groups sampled per site varies between 1 and 31 for gorillas; no chimpanzee study provides data on more than one community. Data on mean foraging party size were also collated for those chimpanzee populations where this was provided. Mean annual rainfall and mean temperature data for the chimpanzee sites are from Lehmann et al. (2008a).

These data are provided in online *Datasets S3*.

A population will inevitably go extinct if females produce an average of less than two surviving offspring in a lifetime (the criterion for demographic viability). To provide a benchmark for how many immatures an average female should have at any one time to meet this criterion, I calculated the number of dependent immatures that a female would need to have alive during the time window bounded by birth and the end of the juvenile period (taken to be 6 years for gorillas and 7 for chimpanzees, and averaged at 6.5 years, following the values given by Harcourt et al. 1981; K. Hill et al. 2001; Emery-Thompson et al. 2017) as a proportion of her reproductive lifespan (based on an age at first reproduction of ~10 years and an average age at death of 34.7 for the Karisoke gorillas [A. Robbins et al. 2006] and 29 for five chimpanzee populations [K. Hill et al. 2001, Table 2]). Taking an average reproductive lifespan for both species of ~20 years, an adult female would need to have $(2/20)*6.5=0.65$ immatures at any given time, assuming all offspring survived to maturity. If mortality rates are such that the chances of surviving to adulthood are 50% (K. Hill et al. 2001; Nishida et al. 2003; for other large primates, see also Altmann et al. 1979; Sigg et al. 1982; Dunbar 1980), then we should scale this up by the geometric mean of the mortality rate to an average of ~0.85 live offspring aged 0-6.5 years. Groups, or populations, with fertility below these values will inexorably decline to extinction.

This paper complies with all relevant legal and ethical requirements. The author declares no conflicts of interest.

Results

Distribution of group sizes

I first test for a fractal structure to the distribution of group sizes for each genus. Fig. 1 plots the distribution of group sizes. For neither genus is the distribution normal (one sample Kolmogorov-Smirnov tests using sample mean and variance: chimpanzees: $p<0.001$; gorillas: $p=0.040$). A $\log_{10}$-transform of group size does, however, yield distributions that are not significantly different from normal (both genera: $p=0.200$), suggesting that group size has a Poisson distribution in both cases (as is, in fact, typical of other taxa and primates as a whole: Dunbar et al. 2018a,b). A k-means cluster analysis suggests that the chimpanzee data has a significant fit to $k=3$ clusters (Fig. 1a: $F_{2,15}=28.0$, $p<0.0001$), with cluster means at 32.3, 58.6 and 107.5 and a mean fractal, or scaling, ratio of 1.82. Decreasing the number of clusters simply combines the two smallest, while increasing the number of clusters results in too many clusters with a single datapoint (which is undesirable). In the gorilla case, goodness of fit (indexed by the F-ratio) is maximised at $k=4$ clusters (Fig. 1b: $F_{3,131}=413.6$, $p<<0.0001$), with cluster means at 5.8, 12.4, 21.7 and 39.9 and a mean scaling ratio of 1.91. Scaling ratios close to 2 are usually indicative of some kind of fission process. The difference between scaling ratios for the two genera is not large enough to be considered significant.

Fertility and group size

Birth rate data for individual social groups (averaged over several years) are available for gorillas at Karisoke (A. Robbins et al. 2006) and Mbeli Bai (Stokes et al. 2006), and for five individual chimpanzee communities. A multivariate regression of birth rate on $\log_{10}$-transformed group size and $\log_{10}$-transformed number of adult females (with quadratic terms in both) yields significant effects only for the female terms (Table 1). There are too few chimpanzee data to run the equivalent analysis, although group size and number of females both yield significant individual quadratic equations. The results for number of females are shown in Fig. 2. The best fit equations (with regressions set through the origin since groups of size zero must have zero birth rates) are:

$$\text{Gorilla: Birthrate} = 0.812^* \log_{10}(\text{Females}) - 0.626^* \log_{10}(\text{Females})^2$$

$$\text{Chimpanzee: Birthrate} = 0.356^*\log_{10}(\text{Females}) - 0.162^*\log_{10}(\text{Females})^2$$

(gorillas: $r^2=0.803$, $F_{2,15}=30.66$, $p<<0.0001$; linear, $r^2=0.000$, $F_{1,16}=0.002$, $p=0.970$; chimpanzees: $r^2=0.996$, $F_{2,4}=504.24$, $p<<0.0001$; linear, $r^2=0.882$, $F_{1,5}=5.34$, $p=0.082$; with the linear regressions negative in both cases). Note that, in both cases, most of the data points lie on the right hand downward slope of the relationship. Differentiating the regression equations and setting Birthrate=0 indicates that fecundity is maximised at 4.5 and 12.6 females for the two genera, respectively.

Annual birth rates over an extended period are available for two individual chimpanzee communities (Mahale and Tai). In both cases, there is a spike in mortality towards the end of the series: community sizes were in the order of 80-100 at Mahale and 60-80 at Tai, but fell rapidly to 30-40 in both cases following the spike in mortality. Since the synchronised mortality of infants and juveniles is likely to cause females to return to oestrus prematurely, thereby changing birth rates over the immediately ensuing years, I exclude the last four years in each case. Fig. 3 plots birth rate in a given year against the number of adult females in the community in the *preceding* year (i.e. the period when any interference effects are likely to affect conception). In both cases, the data are best described by a ∩-shaped quadratic relationship (regression set through the origin; Mahale: $r^2=0.913$, $F_{2,14}=71.6$, $p<<0.0001$; Tai: $r^2=0.951$, $F_{2,8}=78.2$, $p<<0.0001$). Once again, most of the data points lie on the right hand downward slope.

To check whether a broader range of populations exhibit similar patterns, average fertility (mean number of immatures per female) was regressed against the mean number of adult females in a group for a larger sample of study populations, with values averaged across all groups in the population. As with birth rates, a multivariate regression in both group size and number of females yields significant quadratic partial effects only for number of females in the case of the gorillas (Table 1). For chimpanzees, the equation that gives the highest r^2 with all parameters significant is one in positive group size and negative number of females, with no quadratic terms (Table 1). The difference in fit compared to a quadratic in female number (see below) is, however, marginal.

Fig. 4 plots these fertility data against number of adult females, with each data point being the mean for a study population across several groups. The best fit equations set through the origin are:

$$\text{Gorilla: Fertility} = 3.071 * \log_{10}(\text{Females}) - 2.036 * \log_{10}(\text{Females})^2$$

$$\text{Chimpanzee: Fertility} = 2.994 * \log_{10}(\text{Females}) - 1.590 * \log_{10}(\text{Females})^2$$

(gorillas: $r^2=0.972$, $F_{2,11}=191.51$, $p<<0.0001$; linear, $r^2=0.142$, $F_{1,12}=0.23$, $p=0.643$; chimpanzees: $r^2=0.966$, $F_{2,14}=196.69$, $p<<0.0001$; linear, $r^2=0.714$, $F_{1,15}=14.55$, $p=0.002$; with both linear regressions again being negative). Note that the slope parameters are quite similar between the two genera. Fertility is maximised in groups with 5.7 females in gorillas (and perhaps bonobos) and 8.7 females in chimpanzees.

The horizontal line in Fig. 4 gives the minimum fertility required to maintain demographic viability (0.85 living immatures per female). Populations will be in positive growth when mean fertility lies above this line, and conversely will decline towards extinction when they lie below the line. All populations except one gorilla population (the Karisoke population as of 2001, following a period of low growth or even decline: Williamson & Gerard-Steklis 2001; Kalpers et al. 2003) lie above the line. The chimpanzee (but not the gorilla) data again fall mainly on the right hand downward slope. The limit on group size is set by where the regression line on the right hand side crosses the viability criterion: it does so at 15 females for gorillas and 40 females for chimpanzees. Since females consistently account for 30% of group size across primates (Dunbar et al. 2018a,b), these would be equivalent to group sizes of 50 and 133, respectively.

Comparison of the variance in fertility between groups from the same gorilla population (study site) yields similar results. There are four populations with $N \geq 5$ regularly censused groups: Kahuzi ($N=18$), Mbeli Bai ($N=16$), Mt Mikeno ($N=10$) and Virunga ($N=19$). In all four cases, fertility is a significant ∩-shaped function of the number of adult females ($0.416 \leq r^2 \leq 0.808$, $p \leq 0.023$; linear regressions: $0.012 \leq r^2 \leq 0.500$, $0.033 \leq p \leq 0.682$, with two positive and two negative slopes).

To check whether these results might be better explained by differences in habitat quality rather than demography, I plotted population fertility against the location's mean annual rainfall and mean temperature, since these are usually considered reliable predictors of habitat quality (Dunbar et al. 2009). Neither of these (on their own or in combination) predict fertility (both genera combined: $r^2=0.117$, $F_{2,22}=1.46$, $p=0.255$). However, including temperature (but not rainfall) in a multiple regression with $\log_{10}$-females does yield a significant independent effect of temperature:

$$\text{Fertility} = 0.025*\text{Temp} + 0.525*\log_{10}(\text{Females}) - 0.850*\log_{10}(\text{Females})^2$$

(both genera combined: $r^2=0.962$, $F_{3,22}=185.8$, $p<<0.0001$; with significant partial effects for all three variables: $p=0.015$, $p=0.003$ and $p=0.003$, respectively). Fertility increases in wetter (i.e. more forested, and hence richer) habitats. However, the standardised ß for temperature (0.476) is considerably smaller than those for logged females (1.335 and -0.895, respectively), indicating that its impact on fertility is more modest. The quadratic relationship with number of females is thus independent of any environmental effects on fecundity (as is also the case in baboons: Hill et al. 2000; Dunbar et al. 2018a). In other words, even if climatic variables (as proxies for habitat quality) explain some of the variance in fertility, this does not obviate the fact that fertility is independently determined by demographic variables.

Discussion

These analyses yield two main findings. First, group sizes in both genera are fractally structured rather than unimodal normally distributed. Nonetheless, 72% of gorilla groups are <12 in size and 68% of chimpanzee communities are <50. Second, birth rates is a quadratic function of the number of females in the group, with group size and mean ambient temperature having only modest independent positive effects. Importantly, the latter effect implies that the issue is fecundability (the capacity to conceive) rather than anything to do with the more conventional influence of habitat quality on infant survival. Can we explain the first as a function of the second, as seems to be the case in colobines and baboons (Dunbar 2018; Dunbar et al. 2018a; Dunbar & MacCarron 2019)?

The distribution of gorilla group sizes (Fig. 1b) can best be interpreted as a pair of demographic oscillators (6-12 and 12-22), with a few large outliers. In baboons at least, most populations are characterised by a single oscillator (determined by local environmental conditions: Dunbar et al. 2018a; Dunbar & MacCarron 2019), and group size oscillates up and down within the limits defined by the local oscillator. In most group-living primates, group size increases steadily with natural growth and then collapses catastrophically as a result of fission to begin the cycle again (Dunbar et al. 2009; Dunbar et al. 2018a; Dunbar & MacCarron 2019). Although fission has been observed in gorilla groups (e.g. group 5 at Karisoke: M. Robbins 1995; Kyagurillo group at Bwindi: Nsubuga et al. 2008), many females transfer between groups during intergroup interactions or following group disintegration after the death of the silverback (Sicotte 1993; A. Robbins et al. 2009; Harcourt & Harcourt 2009; Forcina et al. 2019). In both the Mbeli Bai and the Virunga populations, for example, female emigration was positively correlated with group size: larger groups lost females, while smaller groups gained them (Stokes et al. 2003; A. Robbins et al. 2009). This strongly suggests that females may be trying to mitigate costs as group size increases (A. Robbins et al. 2009). Notwithstanding the different processes involved, emigration and group disintegration have the same *functional* consequence of reducing group size as conventional fission does in other species.

The explanation for the two gorilla oscillators may lie in the way fertility maps onto group size. The transition point between them (a group size of 12-13 with ~4 breeding females) lies at the peak in fertility (compare Fig. 1b with Fig. 2a). As with *Papio* baboons, this suggests that females optimise their fertility schedule with respect to group size: those opting for the lower oscillator do best at the end of the demographic cycle (i.e. just before group fission), whereas those opting for the upper oscillator do best at the beginning of the cycle (just after group fission or, in the gorilla case, group formation) (Dunbar et al. 2018a). Which option is best is likely to depend, in part, on the rate at which groups grow and how long a group survives without fissioning relative to the average interbirth interval. Groups in the upper oscillator will usually have shorter durations than groups in the lower oscillator simply because, having more females, they will inevitably grow faster. If the average interval between successive fissions for a large group is shorter than the interbirth interval (as may well the case in a species like gorillas with a slow lifehistory), it will be better to be in a small group; if longer, then large groups may be better if they provide other benefits (such as protection). In baboons, populations are more likely to maximise group size (i.e. adopt the higher oscillator) when the local predation risk is high (see Dunbar et al. 2018a; Dunbar & MacCarron 2019). The fact that, in gorillas, the upper oscillator is much less common than the lower one may reflect the widespread impression that predation risk is generally low for these animals (though not completely absent: Klailova et al. 2012) and the frequency of fission or fragmentation is high. Data on predation risk (*not* predation rates: Hill & Dunbar 1998) will be needed to evaluate this. The reason why a small number of gorilla groups are significantly larger even than the upper oscillator is also in need of further investigation.

Although the dataset is small, the distribution of chimpanzee group sizes is best described by a single oscillator at 30/60, with a small number of outliers that have very large groups (Fig. 1a). The Gombe chimpanzee community famously underwent fission between 1971 and 1973 when it numbered around 55 individuals (Feldblum et al. 2018). Feldblum et al. (2018) conclude that the fission appears not to have been driven by any ecological factors, and the same conclusion has been drawn for fissions in two different baboon populations (Henzi et al. 1997; van Horn et al. 2007). Feldblum et al. suggest that although a glut of males competing with each other was unlikely to have caused the Gombe fission, a skewed operational sex ratio might have intensified male-male competition. The data presented here, however, suggest an alternative hypothesis: the problem may have been the stresses imposed on female fertility as the number of females in the community increased (even if this was exacerbated by intensifying male-male competition).

Why the two outliers in the chimpanzee dataset have communities that are so much larger than other populations remains to be answered, though both are well within the absolute fertility-determined upper limit on group size (Fig. 4). It is possible they represent a second, much less common oscillator at 60/120. Of these two unusually large communities, that at Ngogo was strongly substructured into two subnetworks (Mitani 2006), which is often a prelude to fission; it is no surprise, therefore, that the Ngogo community has since undergone fission (Watts 2019). The other (Mahale) underwent demographic collapse in 1992 (Nishida et al. 2003); community fission could not be ruled out (and, indeed, was originally assumed to be the cause, especially as community size dropped from ~100 to ~50), but no obvious cause could be identified. Again, fertility may have been the issue, but this was not considered.

While there is evidence that fertility may be negatively related to social group size in a taxonomically wide range of mammals (as briefly reviewed in the Introduction), the present analyses suggest that chimpanzee and gorilla birth rates, and fertility more generally, are better explained as a quadratic function of the number of adult females in the group. These results parallel those reported for baboons (Dunbar et al. 2018a; Dunbar & MacCarron 2019) and lemurs (Takahata et al. 2006). Quadratic relationships generally imply a trade-off between two factors that correlate in opposite ways with the independent variable. This raises two questions. First, what underlying factors explain these ∩-shaped patterns? Second, if gorillas suffer rapidly declining fertility once groups have more than 5 females, how is it that chimpanzees do not, and instead seem to be able to defer this effect so as to allow much larger group sizes?

Three points may be noted. First, the similarity in the pattern for the two genera suggests that the underlying causes must be the same. Second, these effects cannot simply be a consequence of differential offspring survival (which would conventionally imply ecological factors like food availability): because the pattern for both birth rates and fertility is the same, the cause must be more fundamental in terms of females' ability to conceive (or at least carry foetuses to term). Third, since small gorilla groups generally have only a single adult (silverback) male, the explanation for the rising left hand side of the relationship must reflect the benefits that derive from having either a larger group or more females in the group rather than an increase in the number of males. These benefits might include reduced predation risk, reduced risk of infanticide or improved competitiveness against neighbouring groups.

Despite their size, neither gorillas (Fay 1995; Klailova et al. 2012) nor chimpanzees (Boesch 1991; Tsukahara 1993; Henschel et al. 2005; D'Amour et al. 2006; Lehmann & Dunbar 2009; Nakazawa et al. 2013) are immune to predation, so this remains a likely benefit of living in larger groups. For large-bodied animals, very small differences in group size are sufficient to reduce predation risk to acceptable levels (Bettridge & Dunbar 2012). The second possibility, infanticide, is an issue for gorillas in particular (Harcourt & Harcourt 2007) and, to a lesser extent, for chimpanzees as well (Arcadi & Wrangham 1999; Takahata 1985; Watts 1989; Watts & Mitani 2000; Watts et al. 2002; Lowe et al. 2019). Since its main effect is to increase the apparent birth rate when females lose infants, infanticide risk would have to increase with the number of females if it was to explain the rising left hand side. In fact, infanticide, though common in gorillas, does not appear to be related to either group size or the probability of group disintegration (A. Robbins et al. 2013), and may instead simply be a constant risk when males take over groups or females join new (usually smaller) groups. The third possibility is that larger groups may be able to repulse neighbours more effectively during intergroup conflicts and/or monopolise better territories or food patches (cf. Markham et al. 2015). This may be especially beneficial for chimpanzees, but its value for the more folivorous gorilla is less clear (Harcourt & Harcourt 2007). In western populations at least, gorilla groups often feed together without conflict (Bradley 2004; Forcina et al. 2019). Either way, if this was a major benefit, we might expect its advantages to be a function of group size rather than female numbers alone – yet it isn't. On balance, then, predation risk would seem to be the most likely explanation.

The declining right hand side implies that competition adversely influences fertility. Table 1 suggests that this is solely due to relationships between the females, and not due to the total number of animals in the group. Combined with the fact that the same pattern is observed in groups occupying very different environments (Figs. 3 and 4), this would seem to rule out ecological competition leading to nutritional shortfalls. This concurs with Koenig's (2002) conclusion that there is little evidence to support the suggestion that ecological factors limit reproduction in female primates and that other factors beyond conventional feeding competition are likely to be the explanation. Although, there is an effect of temperature (an index of habitat quality) on fertility in the present case, it is independent of the impact of female numbers, as is also the case in baboons (see Hill et al. 2000; Dunbar et al. 2018a). Rather, it appears to be the stresses that females place on each other, directly or indirectly, that are the root cause of the fertility decline. In baboons, female-female aggression increases around the time of mating, and has explicitly been identified as a cost of sociality, most likely mediated by reproductive suppression (Huchard & Cowlishaw 2011). In gelada, these effects accumulate on lower ranking females because there are more higher ranking females to target them, especially so when they are in oestrus (Dunbar & Dunbar 1977).

Even though gorilla females harass and displace each other during feeding, such events seem to be relatively infrequent and to have limited consequences in terms of access to food (Harcourt & Harcourt 2007). Low level agonistic interactions of this kind do, nonetheless, increase dramatically in frequency with group size (and with the number of females in the group) (Watts 1985; see also Dunbar 2018). So it may be that simple stresses arising from spatial proximity when living in groups is the problem or that the females compete directly with each other for access to the silverback males (given that these function as “hired guns” or bodyguards: Harcourt & Greenberg 2001). One possible mechanism would be the impact that social stress has on the mammalian female menstrual system (and hence fecundity), the endocrinology of which is now well understood (Abbott 1984; Abbott et al. 1984; Gordon et al. 1992; McNeilly et al. 1994; McNeilly 2001a,b; von Borrel et al. 2007; Chatterjee & Chatterjee 2009; Son et al. 2012; Iwasa et al. 2017; see also Wasser & Barash 1983; Huchard & Cowlishaw 2011). To confirm this in the present case, endocrinological studies of gorillas and chimpanzees are needed.

The steepness of the downturn in both fecundity and fertility seems to limit gorilla group sizes to a maximum of ~15 females (Figs. 1a and 2), and hence a group size of 50. The largest gorilla groups ever recorded are of about this size (e.g. Pablo's group latterly at Karisoke; see also Fig. 1b). This is significantly larger than the limits imposed by fertility on group size in less socially complex monkeys like colobines: in colobines, fertility declines as a simple linear function of the number of females in the group, and this imposes a limit on group size at ~15 individuals (Dunbar 2018). The ∩-shaped function observed in gorillas resembles the pattern seen in cercopithecine monkeys, where female-female coalitions are used to buffer females against the stresses of group-living (Dunbar 2018; Dunbar et al. 2018a). Gorilla females do not form coalitions of this kind, but may instead have solved the problem by attaching themselves to a male who acts as a "hired gun" (Harcourt & Greenberg 2001), a social arrangement that has been suggested for a number of other species, including humans (Mesnick 1997; Wilson & Mesnick 1997; Dunbar 2010), chimpanzees (Kahlenberg et al. 2008), and gelada and hamadryas baboons (Dunbar & MacCarron 2019). Although Harcourt & Greenberg (2001) originally suggested this as a mechanism for protecting gorilla females from infanticide by males (which accounts for around 20% of infant mortality: Harcourt & Harcourt 2007; A. Robbins et al. 2013), it may equally protect them from more casual female-female harassment. Protection need not always involve active intervention: simply knowing that someone has a protector may be sufficient to deter others from harassing them (see also Datta 1983).

If males do act as bodyguards, it is likely that there will be an upper limit on the number of females for whom a male can be an effective bodyguard. This is suggested by a plot of the number of silverbacks in a group against the number of adult females. Although the two variables are significantly correlated (r^2=0.309, $F_{1,88}$=9.3, p=0.003), a LOESS regression suggests that the number of silverbacks does not change in a continuous fashion, but rather increases, at least initially, as a series of step changes at intervals of ~5 females (Fig. 5). Pawlowski et al. (1998) found that, across a wide range of primate species, 4-5 females was the limit that a dominant male could monopolise, after which he has to share sirings with subordinate males. In gorillas, a silverback may be able to keep rival males out of his group providing he has fewer than five females, but he may well have to contend with an element of female choice in larger groups because females may encourage additional silverbacks to join in order to be sure of having a bodyguard whose attentions are not too thinly distributed. One prediction might be that when females leave a group, it is ones that do not have close relationships with a silverback that are most likely to leave.

If fertility imposes what amounts to a glass ceiling on group size in gorillas, how have chimpanzees managed to shift their fertility pattern rightwards so as to allow much larger group sizes? The most obvious possibility has to be that a fission-fusion social system allows them to diffuse the tensions that would otherwise be created if the whole community foraged and travelled as a single group. The magnitude of the problem is indicated by Fig. 6, which plots fertility against residual foraging party size (adjusted for habitat mean temperature) for 10 chimpanzee populations for which these data are available. (A multivariate equation gives significant independent linear effects of temperature and party size on fertility: r^2=0.877, $F_{2,7}$=11.6, p=0.006; temperature: standardised β=0.885, p=0.005; $\log_{10}$ party size: β=-0.938, p=0.003.) The slope of this relationship is so steep that chimpanzees would not be able to live in communities larger than ~10 if the community foraged as a single group, which is significantly below the smallest observed size of ~20 (see Lehmann et al. 2008a). Interestingly, this slope appears to be steeper than is the case for gorillas, and might reflect the fact that chimpanzees are more aggressive than gorillas.

The slope and the maximum group size in Fig. 6 is actually not too different from that observed in colobine monkeys (Dunbar 2018), a genus that lacks any mechanism to diffuse the effects of stress on fertility. Instead, it seems that chimpanzees achieve this by being able to divide the community into smaller foraging parties, albeit at the significant cognitive cost of maintaining community cohesion (Amici et al. 2008, 2018). The suggestion being made here is not that chimpanzees adopt fission-fusion sociality to minimise fertility effects, but that they are able to exploit, for a reproductive benefit, a fission-fusion system that occurs for ecological reasons: in both chimpanzees and gorillas, travel time increases exponentially with group size and it is to mitigate *these* ecological costs that chimpanzees adopt a fission-fusion social system (Lehmann et al. 2007, 2008a,b).

In sum, fertility seems to be a quadratic function of the number of females in the group in both gorillas and chimpanzees (notwithstanding evidence that fertility increases with ambient temperature, at least in chimpanzees). As was shown to be the case in baboons, this seems to impose limits on the size of social groups that these species can live in. The two ape genera seem to use different strategies for managing the impact of female numbers on fertility – gorillas by forming alliances with the group's silverback, chimpanzees through fission-fusion sociality. These limit group size in different ways, and as a result affect the two taxa's biogeographical distributions (Lehmann & Dunbar 2009; Lehmann et al. 2010). Gorilla groups seem to occupy one of two alternative oscillators that constrain group sizes, with the choice of oscillator possibly determined by local predation risk. Chimpanzees, in contrast, are able to live in larger communities that seem to function within a single oscillator, which in turn allows them to occupy a wider range of habitats.

Acknowledgments

I thank Alexander Piel and an anonymous referee for their very helpful comments.

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Author contributions: The corresponding author declares sole authorship.

Conflict of Interest: The author declares no conflict of interest.

Legends to Figures

Fig. 1. (a) Distribution of community size for 19 individual chimpanzee communities. (b) Distribution of group size for 135 groups from six well-studied gorilla populations. Vertical lines demarcate cluster mean values identified for the optimal number of clusters in each case (three for chimpanzees, four for gorillas) by *k*-means cluster analysis.

Fig. 2. Mean birth rate (births per female per year) for (a) individual groups at Karisoke (filled symbols) and Mbeli Bai (unfilled symbols) and (b) individual chimpanzee communities, plotted against number of adult females in the group. Regressions are set through the origin.

Fig. 3. Annual birth rate (births per female per year) plotted against the number of adult females in the community in the preceding year (reflecting the year leading up to conception) for (a) the Mahale and (b) the Tai chimpanzee populations. Regressions are set through the origin.

Fig. 4. Fertility (indexed as mean number of immatures per female) for individual populations of gorillas (triangles), bonobos (black circles) and chimpanzees (shaded circles). Regressions (gorilla and chimpanzee only) are set through the origin. The horizontal line demarcates the minimum fertility for demographic viability (0.85 immatures per female).

Fig. 5. LOESS regression of number of silverback males plotted against number of adult females in the 135 groups sampled in Fig. 1b. The regression line plots the running-average mean number of silverbacks using an Epanechnikov kernal function set at 50%.

Fig. 6. Mean fertility (number of immatures per female) for individual chimpanzee communities as a function of residual $\log_{10}$-transformed foraging party size ($\log_{10}$ foraging

party size regressed on mean temperature of habitat). Filled symbols: bonobos; shaded symbols: chimpanzees. Horizontal line demarcates the minimum fertility for demographic viability (0.85 immatures per female). Solid line is the least squares regression.

Table 1. Slope parameters for multivariate least squares regression equation for fertility as a function of group size and number of females.

	Gorilla birth rates*			Gorilla fertility†			Chimpanzee fertility†		
Variable ‡	slope	t	p	slope	t	p	slope	t	p
Number of females	1.506	4.43	0.023	4.153	2.35	0.043	-2.628	-5.52	<0.0001
Females-squared	-1.817	-3.81	0.032	-3.657	-3.28	0.009			
Group size	0.453	1.80	0.170	-1.636	-1.40	0.196	2.582	7.70	<0.0001
Group-squared	-0.477	-1.96	0.144	1.496	2.57	0.030			
r^2	0.988			0.982			0.984		
F	188.5			41.1			215.9		
df	4,9			4,3			2,14		
p (2-tailed)	<0.0001			0.006			<<0.0001		

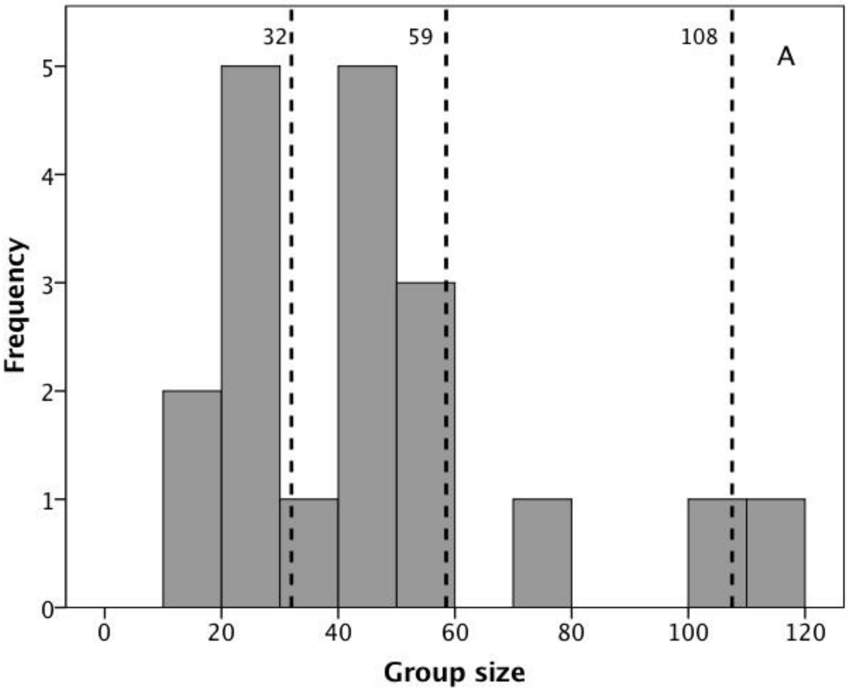
Regressions are set through the origin, since fertility must be zero when group size is zero

* Mean birth rate per female in individual groups from two study populations

† Average number of immatures alive at census per female for individual study populations

‡ All demographic variables are $\log_{10}$-transformed

Figure 1 (A and B)



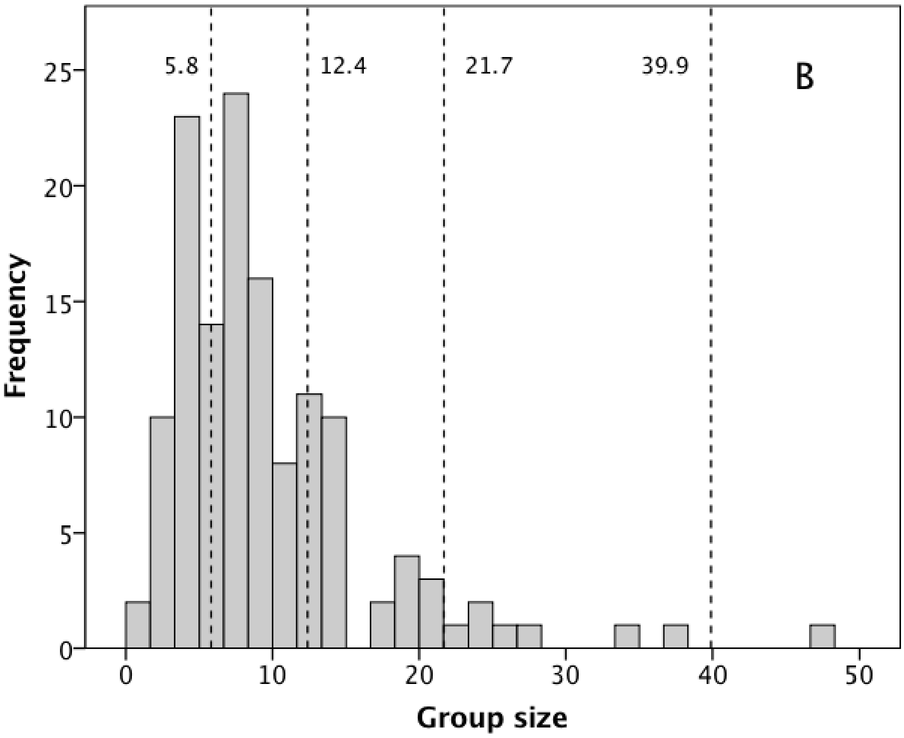


Figure 2 (A and B)

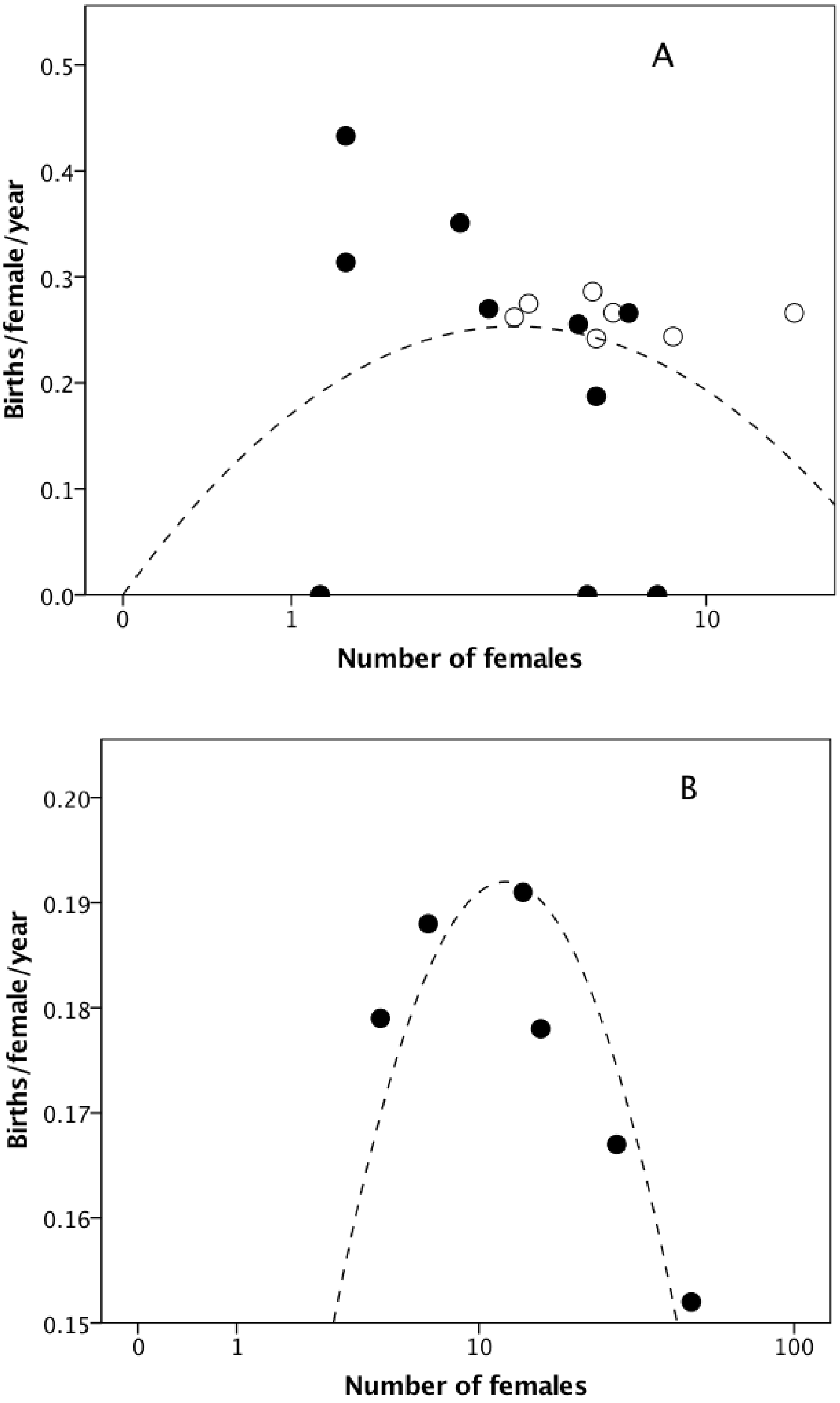


Figure 3 (A and B)

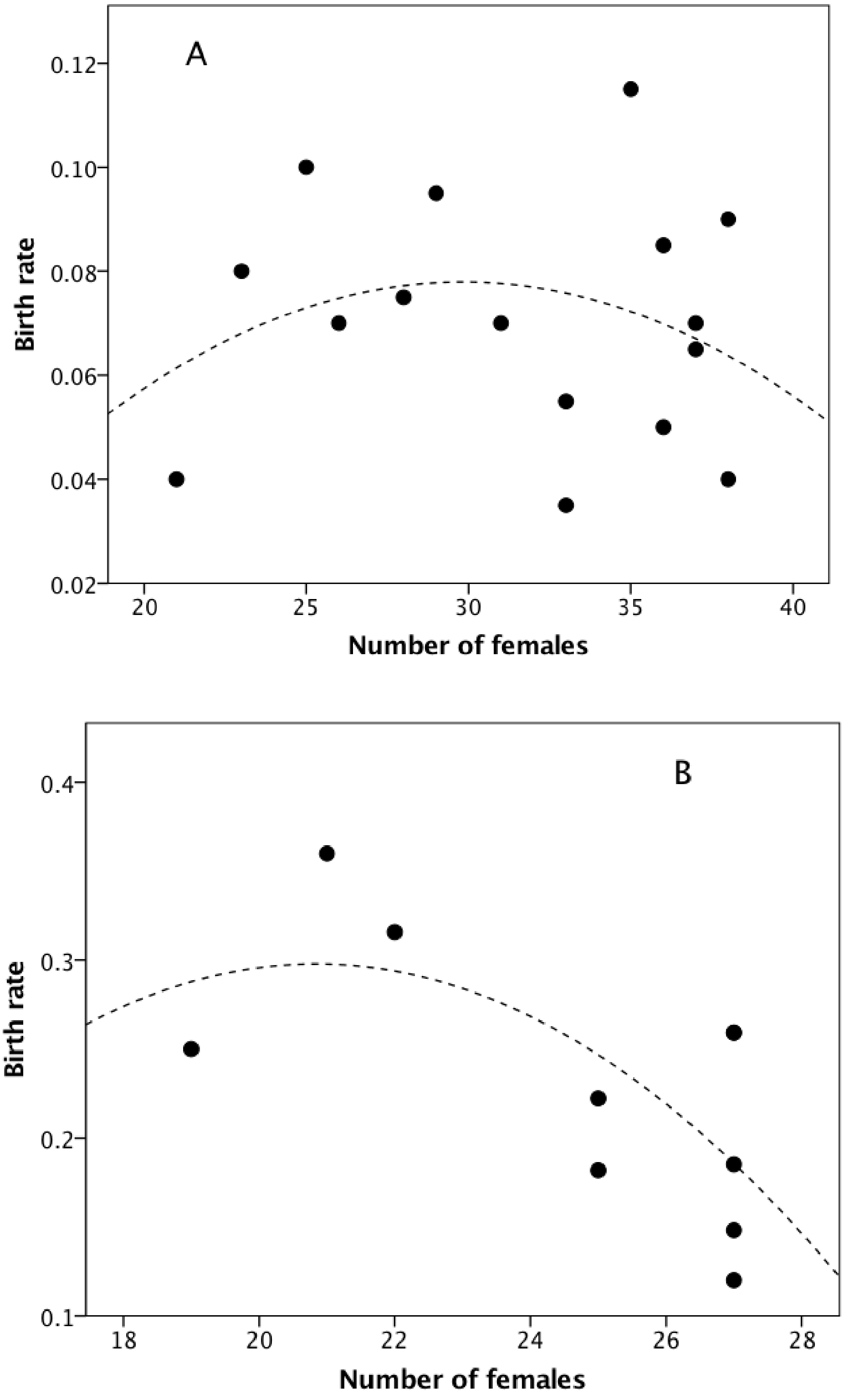


Figure 4

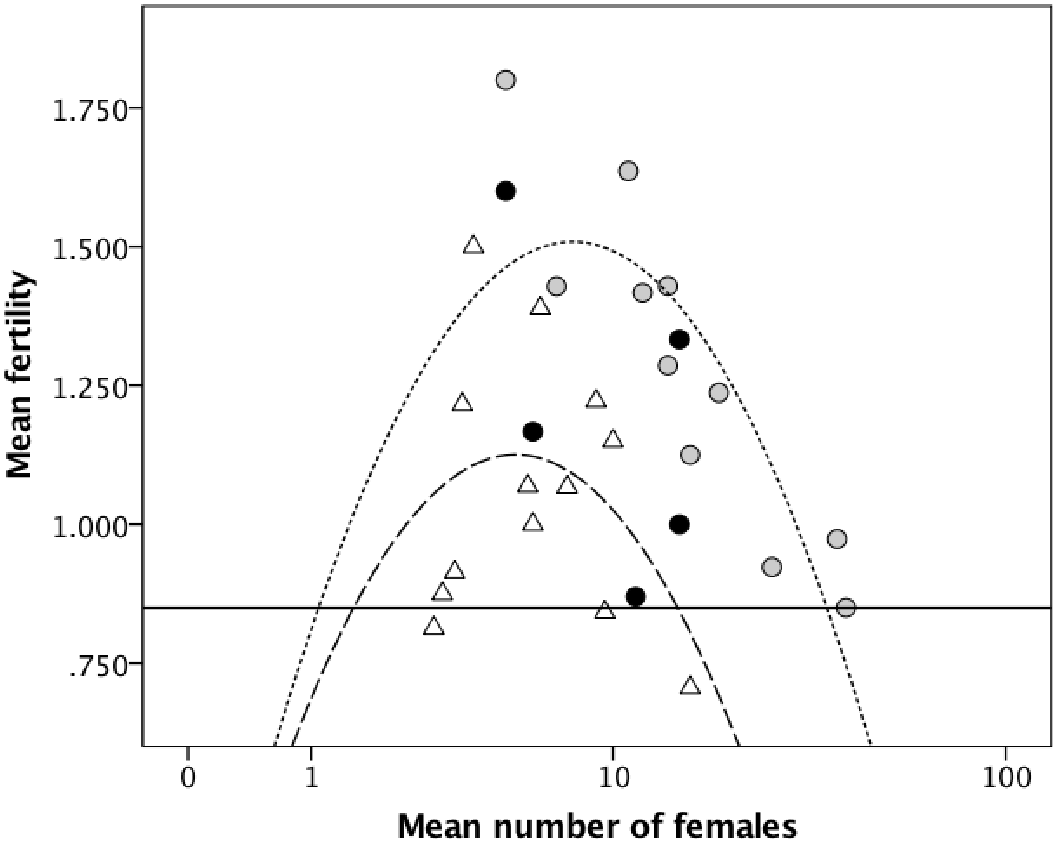

Mean fertility
1.750
1.500
1.250
1.000
.750
0
1
10
100
Mean number of females

Figure 5

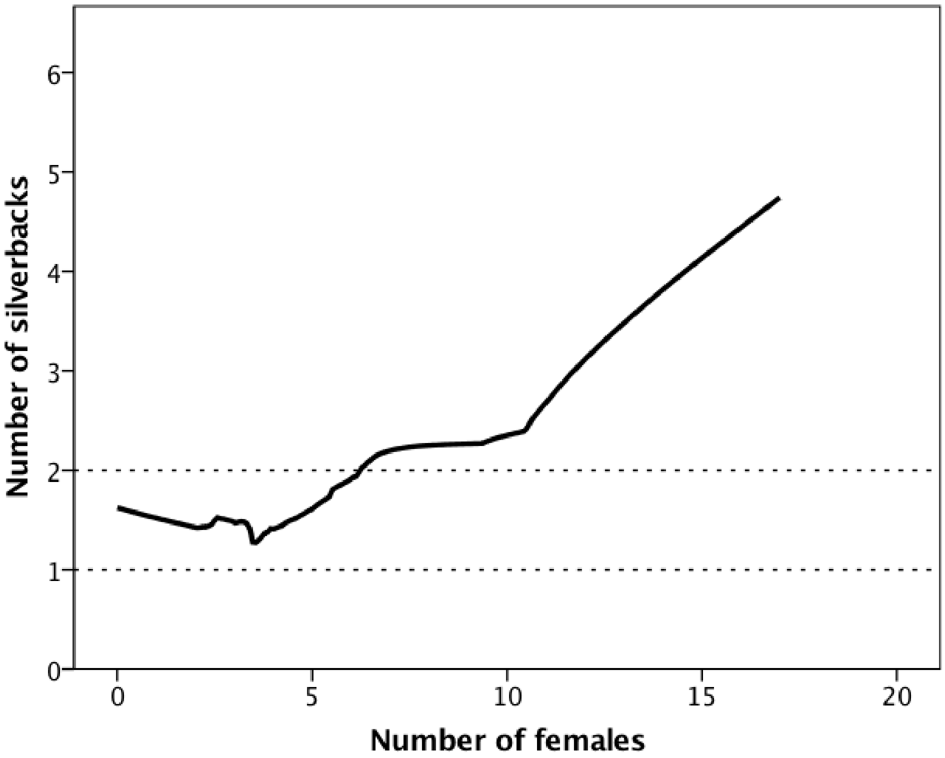


Figure 6