Does a Trade off between Fertility and Predation Risk Explain Social Evolution in Baboons?

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Abstract

The distribution of group sizes in woodland baboons forms a pair of demographic oscillators that trade fertility off against predation risk. Fertility rates, however, set an upper limit on group size of around 90-95 animals. Despite this, two species of baboons (hamadryas and gelada) have groups that significantly exceed this limit, suggesting that these two species have been able to break through this fertility constraint. We suggest that they have done so by adopting a form of social substructuring that uses males as 'hired guns' to minimise the stresses of living in the unusually large groups required by high predation risk habitats.

Key words: social organisation, fission, fertility, predation risk, bodyguard hypothesis

Introduction

While most baboons (*genus Papio*) live in coherent, stable groups that average 40-50 individuals, two Ethiopian endemics (*Papio hamadryas* and *Theropithecus gelada*) live in much larger groups (bands) that are sub-structured into 10-25 semi-independent reproductive units (harems). Harems typically consist of 5-15 individuals, normally with a single breeding male but occasionally (perhaps 20% of cases) with additional younger or older follower males. These congregate in bands but have the flexibility to be semi-independent. The reasons why these two species have this unique form of social system has been debated since the 1960s, but no fully convincing explanation has ever been found.

In a previous analysis, Dunbar et al. (2018) showed that the distribution of group sizes in baboons (genus *Papio*) exhibits a fractal pattern that is best explained as a pair of demographic oscillators that optimise fertility against local predation risk. Each oscillator defines limits between which group size oscillates as a result of natural growth rates followed by fission. However, this analysis considered only the four species of "woodland" baboons (*Papio anubis*, *P. cyncephalus, P. papio* and *P. ursinus*) that live in stable, medium-sized social groups. Here we extend this analysis to the other two well-studied species that live in large multilevel groupings (hamadryas and gelada) in order to ask whether the principles underlying woodland baboon demography might also explain these species' unusual form of sociality. Background details of the social organisation and ecology of hamadryas and gelada are given in the *SI*.

We first ask whether the distribution of group sizes across the taxon, and then for the two species individually, is unimodal (i.e. simply represents natural variation around a characteristic mean value), or, if not unimodal, what form the distribution

actually has. In our analysis of woodland baboons, we found that the distribution of group sizes was best explained by four separate Poisson distributions whose modes are fractally related. We then ask how this distribution of group sizes relates to variations in predation risk and fertility, and whether this provides a principled explanation for the substructuring of hamadryas and gelada groups.

Methods

We used the comprehensive database collated by Dunbar et al. (2018) for the four woodland *Papio* species, with additional group size data for hamadryas (N=13) and gelada (N=25) bands provided by various field studies. This yielded a total of 448 groups across 54 study sites in 14 countries. We used the fertility rate data for woodland baboon populations given by Dunbar et al. (2018) and added to this data for four hamadryas and three gelada bands. For further details on taxonomic definitions and data sources, see *SI*. The data are given in full in Datasets S1 and S2.

To determine the underlying patterns in the distribution of group sizes, we followed Dunbar et al. (2018) and used Maximum Likelihood Estimation and confirm this with the Jenks natural breaks algorithm (for details, see *SI*). These use different algorithms to find the optimal number of clusters into which a dataset can be divided so as to minimise the differences from the local mean.

Results

Group size

The distribution of group sizes is highly skewed, with a mean of 49.3±44.2SD and a range of 3-262 (Fig. 1: note that, for illustrative purposes, the X-axis is $\log_{10}$-transformed). Applying maximum likelihood estimation (MLE) to the raw data in Fig.

1 indicates that the distribution is most likely made up of 4 separate Poisson distributions (Table 1). The Jenks algorithm yields similar results (Table 2; see also *SI*). The mean cluster sizes, averaged across the two methods, are indicated by the dashed vertical lines, with values at 18.7, 41.0, 79.1 and 180.3. Overall, the mean scaling ratio for the MLE analysis is 2.1 and 2.3 for the Jenks series, suggesting a fractal pattern indicative of binary fission.

This pattern is also present in each of the six species separately, with the exception of the largest cluster (~180) for *Papio anubis* and the smallest cluster (~20) for *P. papio*, *P. hamadryas* and the gelada (Table 2). The set of 14 pairwise scaling ratios for the individual species in Table 2 is not significantly different from a value of 2.0 ($t=0.26$, $df=13$, $p=0.799$), but is significantly different from scaling ratios of 1 or 3 ($p<0.0001$) (Fig. S1).

We suggest that these cluster values make up a set of three sequential linear oscillators, with attractors at ~20 and ~40, ~40 and ~80, and ~80 and ~160 respectively: within each oscillator, natural fertility causes groups to increase in size until they fission at the upper value to return to the lower value, and begin the cycle all over again. An analysis of the distribution of group sizes for the 27 *Papio* sites with at least five censused groups indicates that all but five have a group size distribution that is unimodal normal and falls mainly into just one of the oscillators (Fig. S2). In all five exceptions (Amboseli NP, Gilgil, Mt Assirik, Nairobi NP and Giants Castle), the bimodality is created by a small number of very large ($N>100$) outliers, with the bulk of the groups normally distributed within one or other of the two smaller oscillators. In effect, each population is characterised by a single oscillator.

Optimising group size in different habitats

To determine whether the different oscillators correspond to habitats with different predation risk, we plot population mean group size as a function of predator density and tree cover (the two main factors that influence predation risk for baboons: Cowlishaw 1997a,b) (Fig. 2). Group size is low when there are plenty of trees available as refuges, but in habitats with few trees groups are large (in some cases, very large) *if* predator density is high. A general linear model indicates that, while there is only a weak effect (in the predicted direction) for predation ($F_{1,20}$=0.75, p=0.199), mean group size is significantly higher in less forested habitats ($F_{1,20}$=3.77, p=0.033) and there is a significant forest*predator interaction ($F_{1,20}$=3.52, p=0.038). (We here test a set of explicit directional hypotheses based on Cowlishaw [1997a,b], so all statistical tests are necessarily 1-tailed, since converse results would disprove the hypothesis in each case.)

To further illustrate this, Fig. 3 plots mean population group size against a composite index of predation risk. The predation risk index is the sum of the standardised deviate of predator density and the standardised deviate of habitat openness (defined as 100 minus percent tree cover). There is a significant relationship between mean group size and the composite index of predation risk (r=0.506, N=24, p=0.006 1-tailed). Tree cover (an index of the density of refuges) is significantly lower in hamadryas and gelada habitats than the habitats of the other *Papio* species (Fig. S3), which may explain why these two species have such large group sizes.

Fertility

Fig. 4 plots mean birth rate against ecological group size for 25 *Papio* groups and three gelada herds (i.e. the group sizes in which the animals typically forage). The

woodland baboon data (excluding *Papio papio*) are clearly best explained by a quadratic regression ($b=0.149+0.0145N-0.000135N^2$, where b = annual birth rate per female and N = group size; $F_{2,14}=6.35$, $r^2=0.476$, $p=0.011$; linear: $F_{1,15}=0.52$, $r^2=0.034$, $p=0.479$). The quadratic relationship holds individually across all three woodland species (Dunbar et al. 2018), and when the Guinea baboon datapoints are included ($F_{2,16}=9.64$, $r^2=0.547$, $p=0.002$). It seems that fertility increases monotonically with group size to a maximum of about 0.52 births/year at a group size of ~50, and then declines again at a similar rate. These results are not confounded by environmental quality: for the woodland baboons at least, the results are exactly the same if we plot residuals from a regression of fertility on mean ambient temperature against group size (Fig. S4), indicating that, irrespective of the effect that habitat quality has on fertility, birth rates are independently a quadratic function of group size.

In contrast, the hamadryas and gelada datapoints lie well outside the 95% confidence intervals for the woodland species. Nonetheless, their data also fit a quadratic regression ($b=0.08+0.00749N-0.000031*N^2$; $F_{2,4}=4.29$, $r^2=0.682$, $p=0.051$ 1-tailed; linear: $F_{1,5}=0.60$, $r^2=0.107$, $p=0.474$) that is very similar in shape, but with a significantly lower intercept ($t_{20}=44.33$, $p<0.00001$), meaning that the graph is displaced to the right compared to that for the woodland baboons. For the hamadryas and gelada, a quadratic relationship gives a maximum birth rate at groups of $N\approx125$ (i.e. slightly more than twice that for the woodland species, and midway between the limits for the upper oscillator). This result holds even when we use the maximum group sizes for hamadryas (sleeping troops) and gelada (the band) (Fig. S5).

Fig. 4 indicates that no population has a birth rate below 0.3 per annum. With a ~13-year reproductive lifespan, a minimum fertility of ~0.15 births per year is required for replacement (i.e. two surviving offspring at the end of a lifetime). Since

survivorship to puberty averages ~50% in wild baboons (Altmann et al. 1977; Sigg et al. 1982), this would require a minimum birth rate of 0.3 for demographic stationarity (i.e. for a population to remain stable and avoid extinction). This being so, the regression equation for the woodland baboon populations would set an upper limit to group size at 95 for demographic viability. This value includes 92.4% of all baboon groups in the sample in Fig. 1 (or 93.1% of the groups for the three woodland species: Dataset S1). Groups larger than this will not be reproducing fast enough to compensate for natural mortality, and will therefore oscillate indefinitely around this value (see below, Fig. 5) until they fission. In contrast, the fertility data for hamadryas and gelada predict a limiting group size of ~180 (2.2 times the equivalent for the woodland species), just where the uppermost attractor is in Fig. 1.

The quadratic form of the fertility equation also implies a minimum limit on group size: in woodland species, groups smaller than ~15 would have birth rates below the limit for demographic viability, and so would be in terminal decline. Only 8.6% of all groups in the woodland sample are smaller than this. In contrast, hamadryas and gelada would have a lower limit on group size of 38. The smallest hamadryas band recorded in the present sample is in fact 38 (Dataset S1), while the mean size for gelada teams (the set of harems that stay together most closely and the natural stable grouping for this species) is 34 (Mac Carron & Dunbar 2016).

To illustrate the magnitude of this fertility trap we used the regression equation for fertility from Fig. 4 to model the change in group size over time for groups with initial sizes of 15, 17, 20 and 25, subject to an annual mortality rate that varies randomly across a normal distribution with a mean of 10% and a range of 4-16% (based on data from 3 long term study sites: Moremi, Amboseli and Gombe; Cheney et al. 2004; Bronikowski et al. 2002) (for details, see *SI*). Fig. 5 indicates that

groups whose initial size is <17 animals will always go extinct (grey shaded region) because their fertility rates are too low to offset mortality. That this may represent a minimum viable group size is suggested by a case where two *Papio cynocephalus* groups of 11 and 13 at Mikumi (Tanzania) in 1994 fused to form a group of 24 (Hawkins 1999). Groups with an initial size >17 grow slowly for a number of years and then accelerate until they reach an asymptotic value of ~100, where they will stay indefinitely: when group size exceeds this value, fertility drops below mortality, reducing group size, which then allows fertility to increase, which in turn allows the group to grow again until fertility once more drops below mortality. The decline in fertility at group sizes above 50 is sufficiently steep that, all else equal, it will be extremely difficult, if not impossible, for any species to increase group size above ~95.

Discussion

The regular patterning in the distribution of baboon group sizes suggests a fractal sequence with attractors at ~20, ~40, ~80 and ~160. Since these attractors have a scaling ratio of ~2.0, they are most likely to be the product of a binary fission process, as also seems to be the case in the gelada (Mac Carron & Dunbar 2016). We suggest that these form a set of three consecutive linear oscillators at 20-40, 40-80 and 80-160, thus adding a third oscillator to the two already identified for woodland baboons (Dunbar et al. 2018). Within each oscillator, groups increase in size from the lower value as a result of natural recruitment until they reach the upper value, at which point they fission. Allowing group size to exceed the upper attractor before fissioning is, of course, possible but only at a cost of reduced fertility. That the 20-40 and 40-80 oscillators are distinct is indicated by evidence from two longterm study

populations: *Papio ursinus* groups living in a low predation risk habitat in South Africa typically fissioned at a size of ~32 (12 fission events, for a mean population group size of 22.4, N=61), whereas *P. cynocephalus* groups living in a high predation risk habitat in East Africa did so at ~65 (mean population group size 50.7, N=51) (Henzi et al. 1997). For the South African population, neither time devoted to foraging nor bite rate nor speed of travel while foraging were related to group size, suggesting that ecological stresses were probably not responsible for group fission.

Dunbar et al. (2018) suggested that the lower pair of oscillators (20-40 and 40-80) are the consequence of a trade off between predation risk and fertility and constitute an evolutionary stable strategy (ESS) for woodland baboon populations that is driven by predation risk. The estimated lifetime reproductive outputs of the average female in the two oscillators, given the fertility rates in Fig. 4, are equal only when the phase shift between them occurs at a group size of ~45. Phase transitions set either side of this value result in one or other of the oscillators being disproportionately favoured. With a phase transition at the group size that maximises fertility, females do equally well either way, the difference simply being whether they experience maximum fertility early or late in their reproductive lives. Although predation risk might favour a quantitative response, the fertility costs result in a qualitative switch between states (i.e. oscillators). These results confirm the suggestion by that fertility was an additional, orthogonal constraint on social group size in addition to more conventional foraging costs (see Dunbar et al. 2009). Since the way fertility mapped onto group size was not then known, it had not been possible to include it in any of the dozen or so primate time budget models.

Given that these oscillators set an upper limit to group size at 90-95 individuals, we are left with the question of why hamadryas and gelada have opted for

an oscillator that lies outside this range and how they have broken through the glass ceiling created by the fertility trap to achieve this. The answer to the first part seems to lie in the fact that these two species live in habitats that have very low densities of large trees that can function as refuges than those typically occupied by other baboons (Fig. 3). This does not necessarily mean that they experience higher predator densities, but it does mean that trees that are tall enough to act as safe refuges are very limited and hence predation *risk* is higher.

The problem for both these species is that they can only increase group size beyond the upper limit set by the lower two oscillators *if* they can find some way of circumventing the fertility trap (Fig. 5). That they have in fact done so can only be because they have found a solution to the fertility constraint. The habitats and dietary adaptations of these two species (Dunbar & Bose 1991), as well as the dynamics of their social relationships (Dunbar 1983a; Grueter et al. 2012), are radically different (see *SI*) and hence unlikely to explain the similarity in their fertility phase transition. Indeed, their patterns of fissioning are completely opposite: hamadryas harems fission to forage during the day and coalesce for safety at night, whereas gelada harems coalesce to forage during the day and fission to sleep at night. The only feature that is common to both species is the substructuring of groups into harems: in both species, groups of closely related females (Dunbar 1984; Johnson et al. 2014; Schnider-Mackler et al. 2014; Swedell 2002; Städele et al. 2016) are attached to a male rather than dispersing in small, unstable foraging parties, as happens in chimpanzees (Lehmann et al. 2007b), spider monkeys (Korstjens et al. 2006) and perhaps Guinea baboons (Patzelt et al. 2011) under similar circumstances. In both species, the substructuring is reinforced (more so in hamadryas, less successfully so in gelada) by male herding behaviour.

Grueter et al. (2012) suggested that this substructuring may be a defence against infanticide risk. However, infanticide occurs in both hamadryas (Swedell & Tesfaye 2003) and gelada (Dunbar 1984; Moos et al. 1985; Beehner & Bergman 2008), where it is specifically associated with male takeovers. While we agree that infanticide risk is a problem and that harem males may well reduce this risk (Opie et al. 2014), males clearly do not solve this problem completely since infanticide occurs after takeovers anyway. More importantly, it does not explain how females have managed to buffer their fertility rates. Aside from the fact that high rates of infanticide would normally result in elevated birth rates (females usually conceive again rapidly after losing an infant), the intervals between takeovers (Dunbar 1984) are simply too long to give rise to the observed reduction in fertility. In any case, it is clearly the number of females in the group that is the problem, not the number of males (Hill et al. 2000).

Instead, we suggest that this substructuring has allowed the females of both species to buffer themselves against the undoubted stresses of living in very large social groups in a context where these have been forced on the animals by local predation risk conditions. The only way of increasing fertility may be to add a male who can act as a 'hired gun' to protect a group of females from conflict with neighbours, but who doesn't himself compete with the females (the 'bodyguard hypothesis': Mesnick 1997; Wilson & Mesnick 1997; Harcourt & Greenberg 2001). The effectiveness of this is evident in gelada. Conflicts between neighbouring harems are usually initiated by one, occasionally two, females; if the conflict escalates, more females will become involved, until eventually the harem males are drawn into the dispute and force the separation of the two groups of females (Dunbar 1983b, 2018). Whether females associate with a male voluntarily (as seems to be the case in gelada:

Dunbar 1984) or because males force them to remain close (as is the case in hamadryas: Kummer 1968) is immaterial: functionally, the outcome is the same in that both mechanisms provide a male who will protect the females against neighbours. This structuring, of course, has one consequential benefit: it allows a fission-fusion response to local ecology, thereby giving these species extra flexibility in habitats they might otherwise not have been able to occupy. Once again, the issue of interpretation is one of functional causes versus evolutionary consequences.

In sum, it seems that the lower pair of oscillators represents an evolutionarily stable strategy set driven by local predation risk and explains the pattern of group sizes observed in woodland baboon species. While baboon sociality can cope with the two lower oscillators without significant stress, the upper oscillator (characteristic of hamadryas and gelada) is only possible if the animals shift the fertility schedule to the right. This seems to have involved formal substructuring created by attaching the natural matrilineal coalitions characteristic of baboons and other cercopithecines to a male who effectively increases coalition size without increasing competition among the members. At least in the case of the hamadryas, this seems to have required some degree of genetic underpinning in terms of male herding behaviour (Nagel 1973; Bergman et al. 2008), a pattern that seems crucial in enforcing their harem-based system (given that both anubis and hamadryas females seem able to adapt to either social system: Kummer 1968). However, even gelada males herd their females away from rivals (Dunbar 1984), although they do not do so as effectively as hamadryas do.

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Legends to Figures

Figure 1. Distribution of social group sizes in baboon (*Papio* and *Theropithecus*) populations. Note that the X-axis is log10-transformed for illustrative purposes. White bars: woodland baboons (genus *Papio*); grey bars: hamadryas baboons; black bars: gelada. Dashed vertical lines demarcate the optimal group sizes of 18.7, 41.0, 79.1 and 180.3, averaged for the two the clustering methods (see text for details). Source: Dataset S1.

Figure 2. Mean (±1se) population mean group size as a function of predator (lion + leopard) density (filled symbols: >0.25 /km^2; unfilled symbols: <0.25/km^2) and percentage tree cover. Predator density is estimated as the sum of the location-specific densities of the baboons' two main predators (leopard and lion: Cowlishaw 1994), each predicted from species-specific climate envelope models using data from 59 locations distributed across sub-Saharan Africa (Bettridge et al. 2010). Tree cover (percent of ground covered by tree canopy) is estimated from satellite imagery for the *Papio* populations (see Bettridge et al. 2010) and from ground transects for the gelada populations (Iwamoto & Dunbar 1983). Source: Dataset S2.

Figure 3. Mean population group size plotted against a composite index of predation risk (standard deviation of predator density plus standard deviation of converse of tree cover [i.e. 100 - % tree cover]). Circles: woodland baboon populations; triangles: hamadryas and gelada populations. Data: Dataset S2.

Figure 4. Mean fertility (births per adult female per year) for individual baboon groups, plotted against group size. Filled circles: woodland baboons; open circles: Guinea baboons; solid triangles: hamadryas; open triangles: gelada. The best fit regression for the three woodland species combined has a quadratic form (solid line, with 95% CI indicated by dotted lines). A separate regression (dashed line) is set through the hamadryas and gelada datapoints, with a quadratic again being the best fit.

Figure 5. Growth in group size over succeeding time units (years), modelled using the birth rates shown in Fig. 4 for woodland species and an annual mortality rate varying across a normal distribution with a mean of 10% and varying between 4-16%, for different initial group sizes (N=15: dotted line; N=17: short dash; N=20: long dash; N=25: solid). The lines are mean values for 10,000 simulations in each case. Grey zone: region within which a group will inevitably go extinct because its death rate will always exceed its birth rate.

Table 1. AIC values for the model tested for the distribution of baboon group sizes. The best-fit model (that with the lowest AIC value) is shown in bold.

Distribution	AIC
Power law	4632.7
Exponential	4006.5
Truncated power law	4099.1
Weibull	3978.1
Gaussian	4061.6
Log-normal	3914.6
Geometric	4045.3
Negative binomial	3967.5
Poisson (single)	12829.6
Compound Poisson*	**3207.0**

* A compound Poisson composed of four Poisson distributions with different means

Table 2. Optimal number of clusters, and the resulting cluster means and mean scaling ratios between successive clusters, for each of the species separately, compared to that for the pooled sample, using the Jenks algorithm.

Species	Cluster means *				Mean scaling ratio
All species	27.1 (308)		77.2 (114)	189.3 (26)	2.65
All *Papio* species	19.8 (202)	45.6 (138)	79.1 (66)	184.4 (17)	2.12
P. anubis	22.1 (58)	49.3 (33)	94.1 (13)	-	2.06
P. cynocephalus	20.7 (32)	46.6 (41)	80.0 (28)	176.0 (4)	2.06
P. ursinus	17.8 (99)	37.1 (49)	64.9 (10)	99.8 (8)	1.79
P. papio	-	42.0 (19)	113.0 (9)	216.3 (6)	2.30
P. hamadryas	-	52.7 (7)	88.0 (3)	190.0§ (3)	1.91
Theropithecus gelada	-	54.8 (10)	116.4 (7)	205.0 (8)	1.94

* Numbers in parentheses in the body of the table are the number of groups assigned to the cluster by the algorithm.

§ Jenks gives four clusters, but the two largest contain only one and two groups, respectively, with cluster means of 150 and 210. The weighted average is 190.

Figure 1

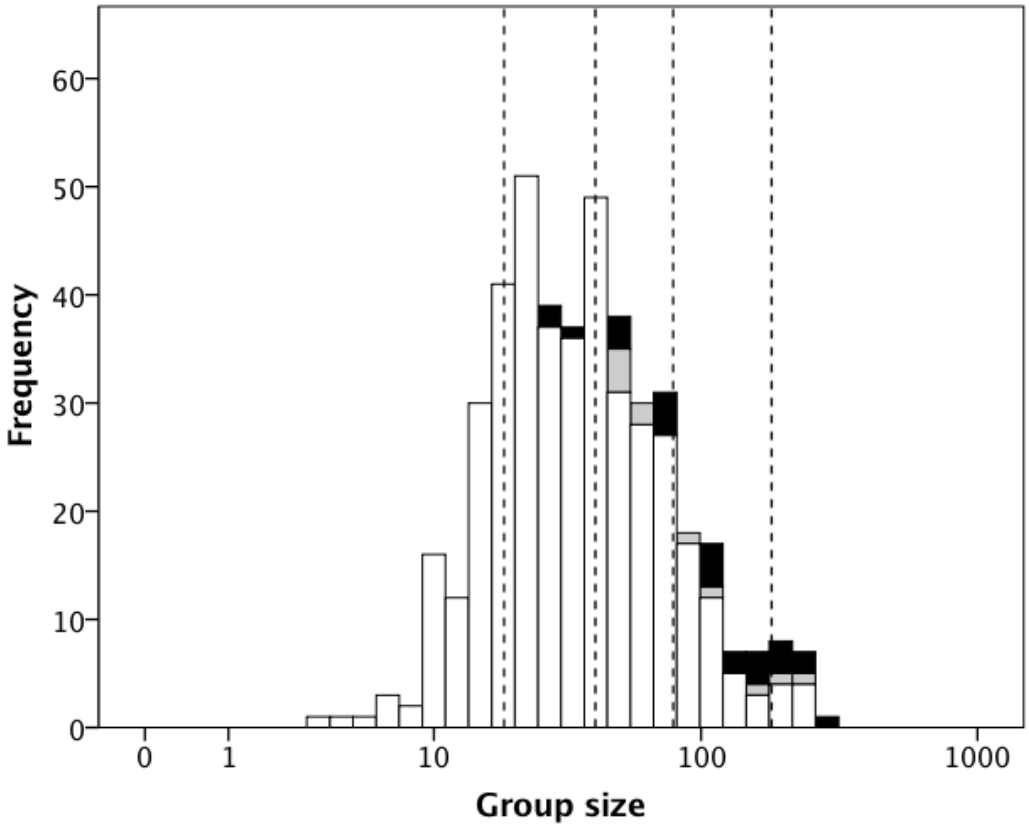


Figure 2

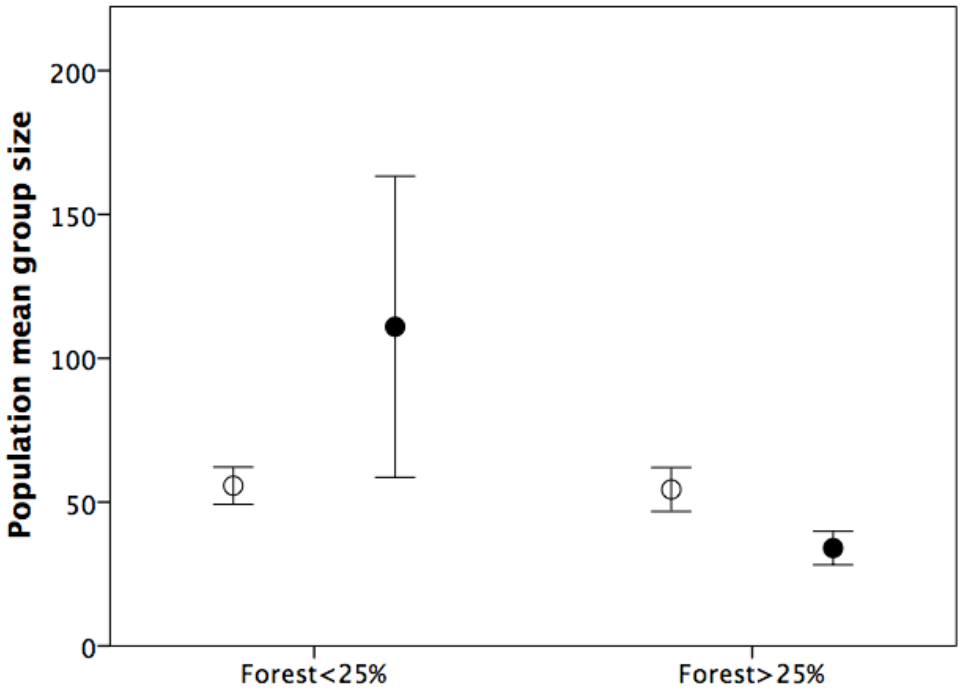

Population mean group size
200
150
100
50
0
Forest<25%
Forest>25%

Figure 3

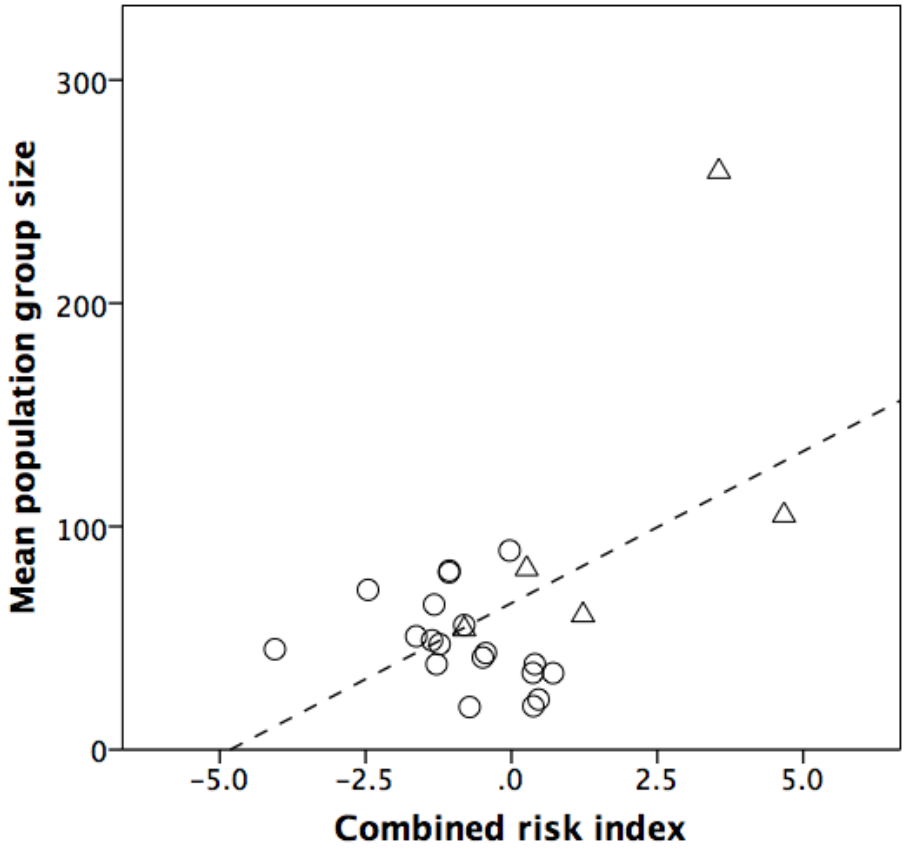

Mean population group size
300
200
100
0
-5.0
-2.5
.0
2.5
5.0
Combined risk index

Figure 4

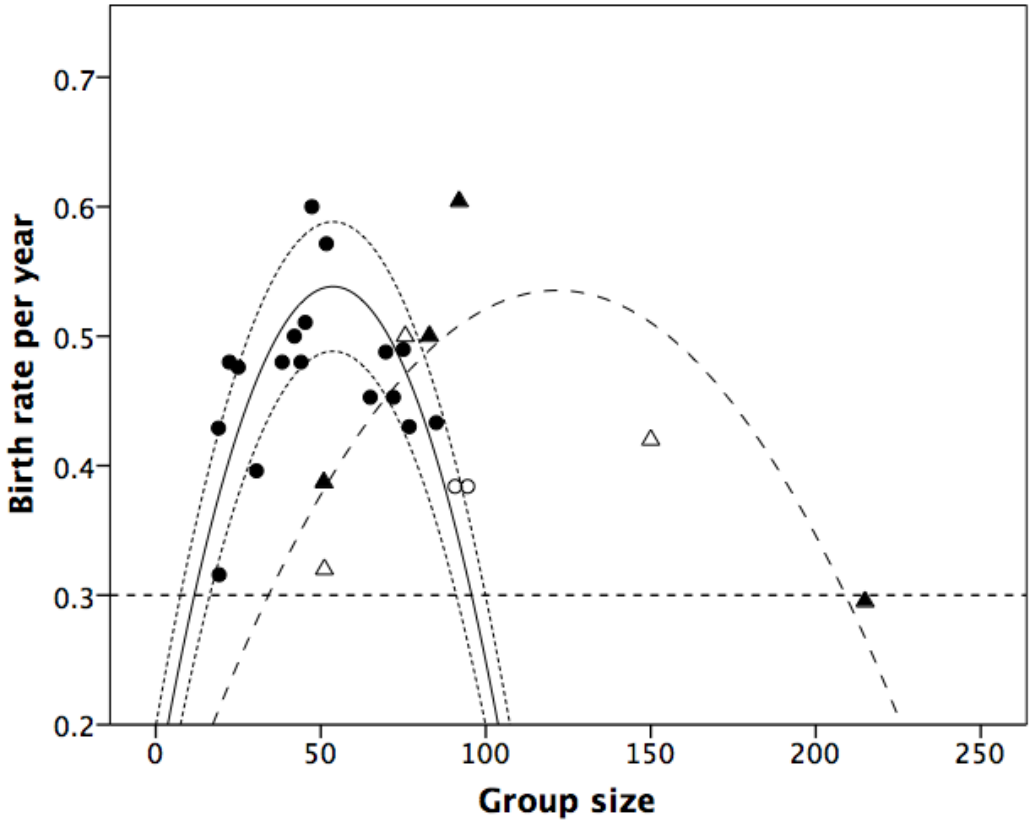
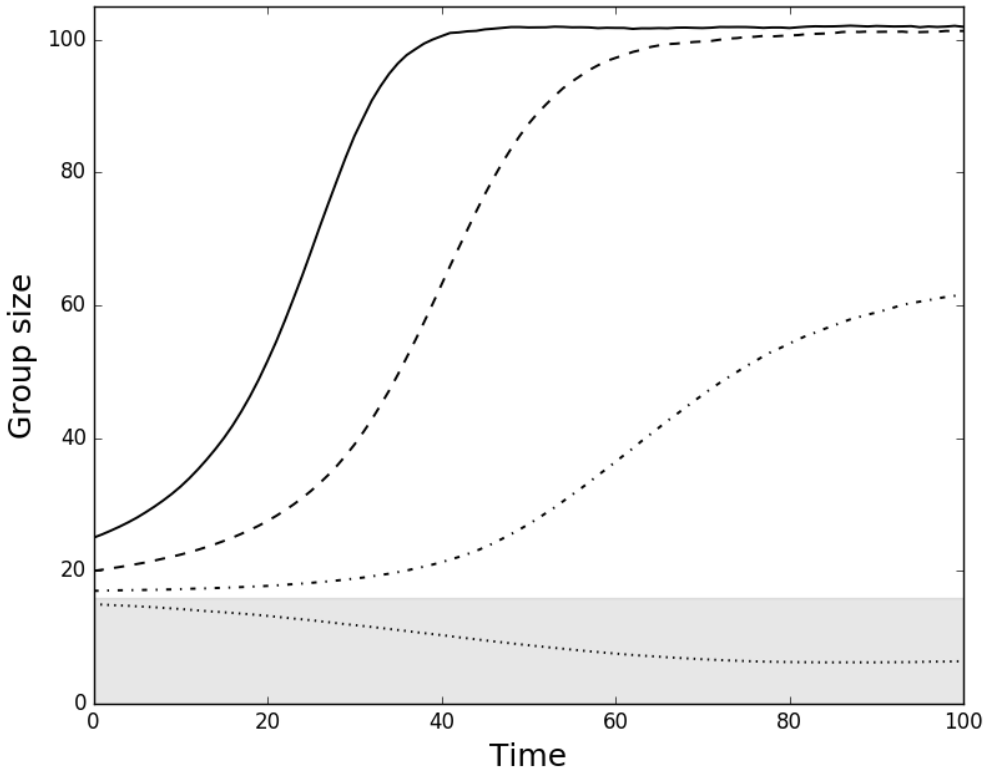

Birth rate per year
0.7
0.6
0.5
0.4
0.3
0.2
0
50
100
150
200
250
Group size

Figure 5



Does a Trade off between Fertility and Predation Risk Explain Social Evolution in Baboons?

R.I.M. Dunbar and Padraig Mac Carron

Supplementary Information

Behavioural ecology of hamadryas and gelada baboons

Hamadryas are frugivore/omnivores like all *Papio*, live in poor quality desert-edge habitats in lowland Ethiopia where there are very few large trees (even along watercourses) to act as refuges, but with predator densities similar to those faced by woodland baboon populations. In a habitat virtually devoid of large trees, they are obliged to congregate at night in very large herds (typically several bands) on the few rocky outcrops large enough to provide safe night time refuges (or very occasionally groves of trees). These 'sleeping troops' disperse during the day while foraging in a resource poor environment, with each band fanning out into its own territory. Even the harems of a band can become scattered over distances as large as a kilometre, albeit without losing contact with each other (Kummer 1968; Sigg & Stolba 1981; Schreier & Swedell 2012a). That predation is a concern for hamadryas is indicated by the fact that, during the day, hamadryas bands will bunch defensively when predators are heard or sighted (Schreier & Swedell 2012a), just as woodland baboon groups do (Altmann & Altmann 1970). As with all baboons (Cowlishaw 1994), their main predators are likely to be lion, leopard and hyaena, though only the last is now at all common in their Ethiopian habitats. These are also most dangerous at night, when primates are at a disadvantage with their poor night vision.

The graminivorous gelada live in cool, high altitude Ethiopian habitats where rich grassy swards allow very large herds to congregate (at least during the wet season: Mac Carron & Dunbar 2016). They also face a significant level of predation risk (historically from leopard, but more recently hyaena in large numbers) in a completely treeless habitat that are nutritionally challenging for them only during the last few months of the dry season (Dunbar 1984; Mac Carron & Dunbar 2016). Their main source of refuge is the massive cliff faces (some as much as 1000m high) that adorn the gorges that intersect the 2000-4000 m altitude Amhara and Bale plateaux where they live. Gelada usually forage on the plateau tops during the day, but always retreat down onto the cliffs at night, with individual harems typically sleeping alone or in small scattered groups. The capacity to form large herds is a crucial adaptation for minimising predation risk if gelada are to forage on the plateau tops away from the

safety provided by the escarpment and gorge faces. Here, harems from one or several bands (Dunbar & Mac Carron 2016) congregate in some of the largest casual groupings (herds) of any primate species (sometimes in excess of 500 animals). Where gelada forage on the cliff faces, they typically do so in much smaller bands (typically 40-70 animals) (Dunbar & Dunbar 1975; Dunbar 1984; Dunbar & Mac Carron 2016); indeed, individual harems often forage on their own when resource conditions are poorest at low altitudes (e.g. Bole valley: Dunbar & Dunbar 1975; Bale Mountains: Mori et al. 1999), a behaviour that is almost unknown in hamadryas.

In effect, gelada disperse to sleep at night on very large, abundant cliff faces and converge into herds to forage in predator-risky habitats during the day, whereas hamadryas disperse to forage during the day and converge to sleep on modest-sized, rather scarce kopjes (although where large clumps of tall trees are available, they will use these). Hamadryas night time roosts are often very crowded, whereas the gelada social units are well spaced out at night. A further important contrast between the two species is that while hamadryas habitat (typically described as sub-desert) is genuinely poor quality by *Papio* standards, typical gelada habitat has high rainfall and low temperatures (both positive indicators of habitat quality), and as a result gelada can maintain populations densities many times those of any *Papio* population, never mind the hamadryas. This is not, of course, to say that both species are not ultimately constrained by their ecologies: this much is clear from the time budget models for both genera (Dunbar 1992; Bettridge et al. 2010). Longstanding claims to the contrary notwithstanding, it seems that whatever may have driven the evolution of their rather similar kind of harem-based fission-fission sociality in hamadryas and gelada, adaptation to poor quality habitat cannot be the reason since this does not apply to gelada.

Supplementary Methods

We take baboons to refer to the large terrestrial primates of Africa ('baboons' *sensu* Jolly 2007). For present purposes, we include the genera *Papio* (the baboons of conventional usage) and *Theropithecus* (the gelada). We exclude *Mandrillus* (drills and mandrills) because their groups are still poorly understood and have yet to be reliably censused. There are some taxonomic grounds for considering *Lophocebus* and *Rungwecebus* as allies of the baboons; however, as these are arboreal and hence subject to very different selection pressures (arboreal habitats are typically much less predator risky: Shultz et al. 2004), we exclude them as well.

We take group (or troop) size to be that defined by the field worker: in most cases, this grouping is fairly obvious, since the animals forage and sleep together, and maintain a degree of demographic coherence and stability as well as spatial separation from other similar groups. For both *Papio hamadryas* and *Theropithecus gelada*, we follow convention and take the band to be the homologue of the *Papio* troop – a set of

animals that share the same home range (Kummer 1968; Dunbar 1984). Exactly what counts as a group in *Papio papio* has been the subject of debate because of this species' rather flexible form of sociality (Dunbar & Nathan 1972; Boese 1975; Sharman 1981), but all field workers on this species agree on the existence of some form of stable social group, at least as defined by animals that share a common range area (Patzelt et al. 2011). The data are provided in *Dataset* S1.

To identify patterns in the distribution of group sizes, we follow the method used by Dunbar et al. (2018a,b). We first determine whether the distribution of group sizes is unimodal, and if so what form it takes. To do this, we use maximum-likelihood methods (Clauset et al. 2009) to fit a set of common distributions (power law, truncated power law, geometric, negative binomial, exponential, stretched exponential, normal, and lognormal), using the discrete approach as described by Clauset et al. (2009). We then test whether the distribution can be better explained as a set of independepent unimodal Poisson distributions mapped on top of each other. Since most data of this kind are highly skewed, we use a compound Poisson distribution of different magnitudes, and seek the set that best describes the data. We numerically maximised the log-likelihood of each candidate distribution to obtain its parameter estimates, using the optimize module of Python's scipy (v0.17.1) library. We identified the most likely model using AIC. In order to choose the optimal number of clusters for the compound Poisson, we calculated a goodness of fit for each number of clusters and take a value of 0.85 as the threshold (following Coulson 1987). Because models with more parameters are always more likely to fit the data, we applied the Jenks natural breaks clustering algorithm (Jenks 1967) to check that a different approach gives the same result.

Female fertility rates (birth per year) for 15 individual baboon troops are taken from Hill et al. (2000), with additional data from more recent studies for one group each for *P. anubis* (Higham et al. 2009) and *P. ursinus* (Cheney et al. 2004), two groups each for *P. cynocephalus* (Hawkins 1999) and *P. hamadryas* (Swedell & Saunders 2006; Chowdhury et al. 2015), and three bands for *T. gelada* (from Ohsawa & Dunbar 1984). Although Roberts et al. (2017) provide data on fertility in gelada, they do not provide mean herd or band sizes. In addition, we give two population means for *P. papio* (Boese 1975; Sharman 1981) based on the number of immatures (prepuberty individuals, less than ~4 years of age). The data are given in *Dataset* S2.

In most cases, fertility rates are based on observed mean birth rate or mean interbirth interval. In a few cases (notably the two estimates for *Papio papio*), birth rates were estimated from the number of immatures per female in a group. Immatures are defined as animals that are pre-puberty, with puberty occurring at around 4 years of age (Altmann et al. 1977). In the case of the gelada, we have used mean herd size rather than band size as the appropriate social grouping for comparison with the other *Papio* species: this is because not all the units of a gelada band forage together on any given day: herd sizes vary from a single harem to upwards of 50 harems from several

bands (~500 individuals) (MacCarron & Dunbar 2016). Given that the driver of functional infertility is the number of individuals who are foraging or resting together at any given time (see Dunbar 2018), mean herd size seems the most appropriate measure. As a check on this, however, we also analyse the fertility data for both species against the largest groupings in which they typically occur (sleeping troops for hamadryas; bands for gelada).

Supplementary Results

Optimal clustering

The Maximum Likelihood Estimate (MLE) method gave a compound Poisson distribution with four clusters as optimal for the combined data, with cluster means at 19.1, 42.7, 83.6 and 188.5. Excluding gelada gives virtually the same results for all *Papio* combined (means at 18.7, 41.0, 79.1 and 180.3). The Jenks algorithm also suggests that four clusters is optimal for all *Papio* combined (means of 19.8, 45.6, 85.4 and 184.4), but opts for just three clusters when gelada are included (means 27.1, 77.2 and 189.3), effectively combining the two smallest clusters.

Scaling ratio

Table 2 suggests that the scaling ratio between cluster means approximates 2.0. We test whether the 14 values from Table 2, taken together, differ significantly from a theoretical scaling ratio that varies between 0 and 4 using a one sample t-test using the sample standard error of the mean. The results are shown in Fig. S1. All values except that for a scaling ratio of 2 differ significantly from expectation ($p<0.05$). All scaling ratio values <1.82 and >2.22 would be significantly different from an expected value of 2.0.

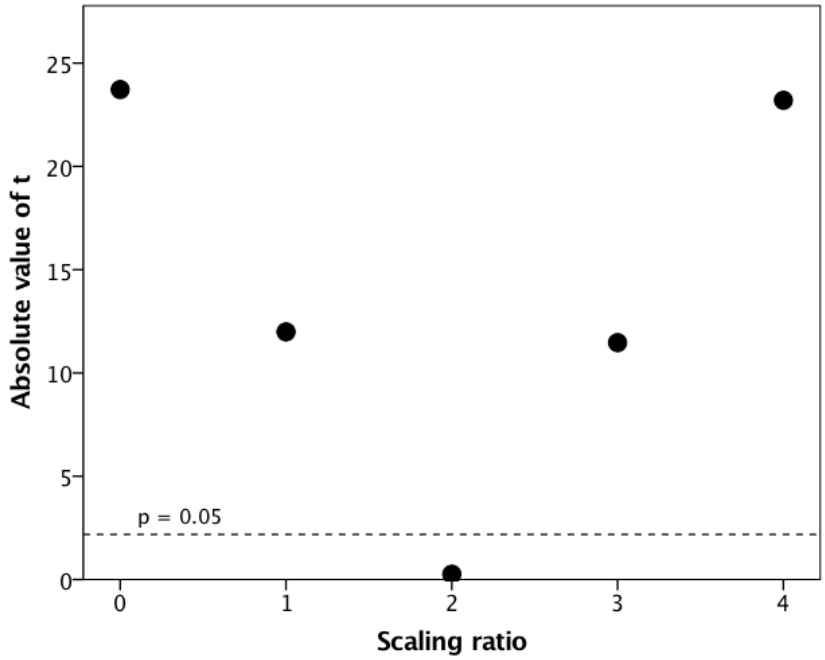


Figure S1

Absolute value for t in one sample t-test comparing the 14 pairwise scaling ratios in Table 2 to expected values ranging between 0 and 4. Values of t above the dotted line are significant at $p<0.05$ level.

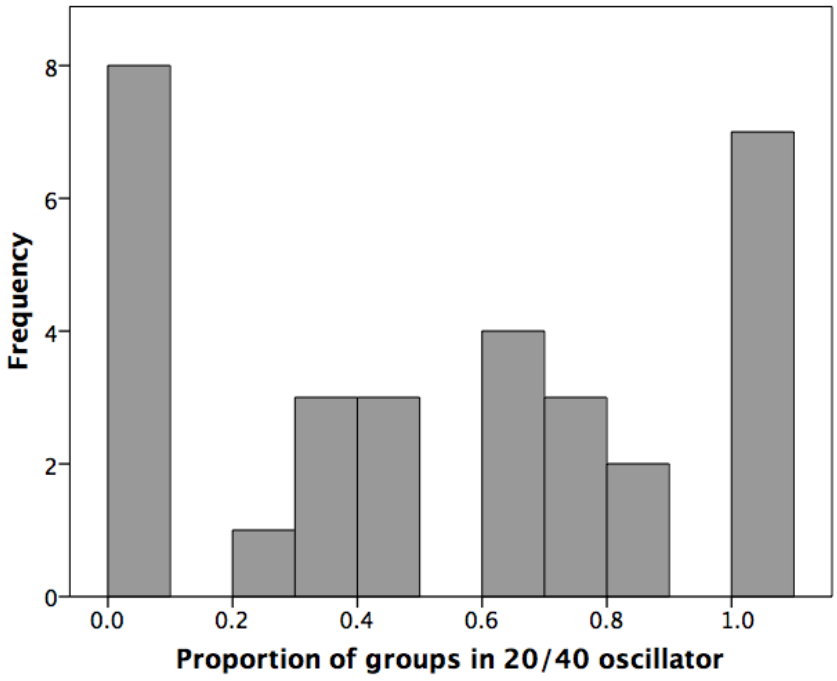


Figure S2

Proportion of groups in individual populations with >4 censused groups that fell into the lowest (20/40) oscillator (as opposed to the two larger oscillators: 40/80 and 80/160) for all six species. The distribution suggests that most populations' groups are within one or the other oscillators, with none that are evenly distributed across all the oscillators.

Oscillators are population-specific

For 22 of the 27 populations where at least five groups were censused, the groups fall predominantly within just one of the oscillators. To show this, we counted the number of groups in a given population that fell within the range of the lowest (20/40) oscillator as opposed to the two larger oscillators (40/80 and 80/160) combined. We plot the proportion of groups in the smallest (20/40) oscillator in each of these 27 populations in Fig. S2. The data exhibit a clear bimodal pattern: about half the populations have all or most their groups in the 20/40 oscillator and other half have all or most of their groups within the 40/80 or 80/120 oscillators. There is a conspicuous absence of populations with an even split between the smallest and the two larger oscillators.

Forest cover for habitats of different species

Fig. S3 plots the distribution of forest cover at sites listed by Bettridge et al. (2010) where the five *Papio* species have been studied in detail, with gelada habitats from Iwamoto & Dunbar (1983). For *Papio* species, forest cover is estimated from satellite imagery; those for the gelada sites are based on ground transects carried out by RD. Hamadryas and gelada live in habitats with especially low levels of forest cover. Note, however, that these data underestimate the contrast between hamadryas and gelada habitats and those occupied by other baboon species: the size of trees is much smaller in most hamadryas and gelada habitats than those in the habitats occupied by the other woodland baboon species. In gelada habitats, for example, few trees are over 5m in height.

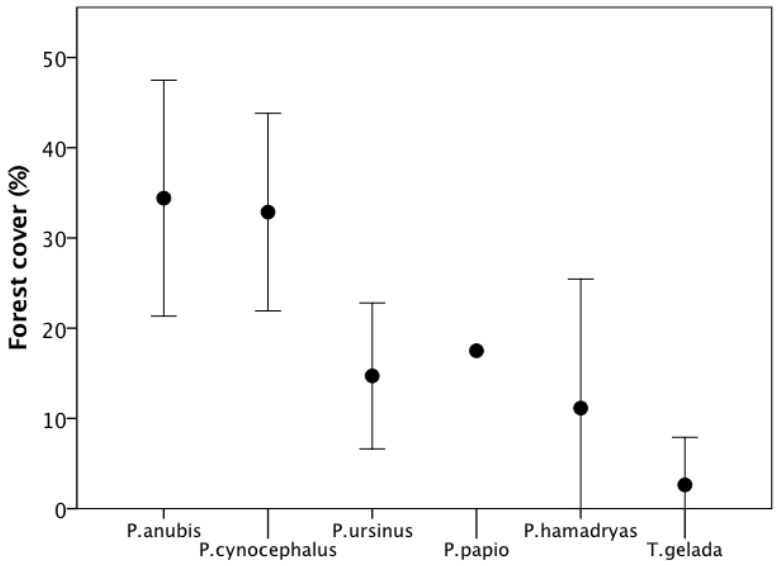


Figure S3

Mean (±2 se) forest cover (indexed as percentage of ground cover) for the six species. Sources: Bettridge et al. (2010) and Iwamoto & Dunbar (1983)

Fertility

Baboon fertility is independently predicted by both the number of adult females in the group and the mean ambient temperature of the habitat (an index of habitat quality) (Hill et al. 2000). To check whether environmental conditions might be a confound in our results, we regressed birth rate on mean habitat ambient temperature as a quadratic relationship (b = -0.672 + 0.104Temp - 0.00231*Temp^2: $F_{2,18}$=3.77, r^2=0.296, p=0.043; linear: $F_{1,19}$=0.01, r^2=0.000, p=0.933), and calculated residual birth rates from this regression. The results (Fig. S4) are identical to those shown in Fig. 2. Gelada were not included in this analysis because they inhabit a different (very high altitude) temperature regime to *Papio* baboons.

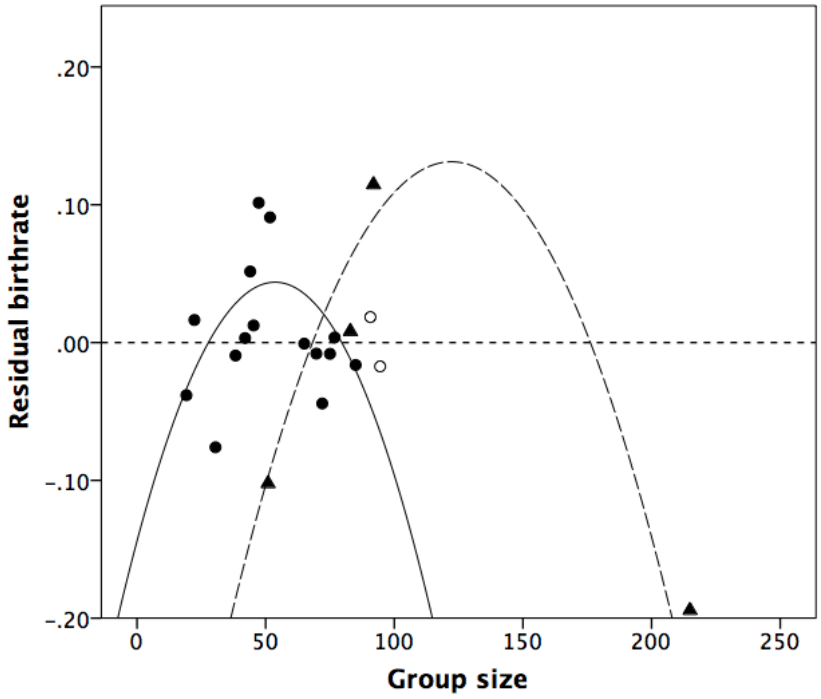


Figure S4

Residual of mean birth rate regressed on mean local temperature plotted against group size for individual populations. Filled circles: savannah baboons (P. anubis, P. cynocephalus and P. ursinus); unfilled circles: P. papio; triangles: P. hamadryas. Separate quadratic regressions set to data for savannah baboons and P. hamadryas, respectively. Gelada are not included.

Fig. S5 confirms that the results of Fig. 2 are invariant with social scale: the same U-shaped pattern emerges when birth rate is plotted against the largest social groupings observed in the two species that live in multi-level social groupings (hamadryas baboons and gelada). The fit, however, is better for Fig. 2, which uses foraging group size (bands for hamadryas, mean herd size for gelada), the groupings in which the animals spend most of their time (and hence where stress effects are likely to be most intense).

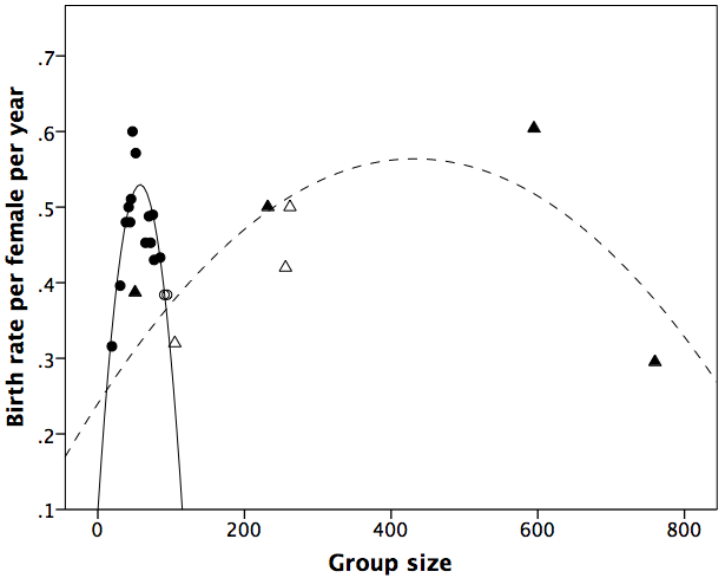


Figure S5

Birth rate plotted against highest level of social grouping (multi-band sleeping troop in the case of Papio hamadryas and band in the case of Theropithecus gelada. Filled circles: savannah baboons (P. anubis, P. cynocephalus and P. ursinus); unfilled circles: P. papio; solid triangles: P. hamadryas; unfilled triangles: T. gelada. Separate quadratic regressions set to data for savannah baboons and P. hamadryas, respectively.

Modelling group demography

We seek to model the natural growth pattern of a group, given the fertility schedule of Fig. 4 and natural mortality. For computational convenience, we consider mortality as a fixed cost unrelated to group size. We therefore use an annual mortality rate that varies randomly across a normal distribution with a mean of 10% and a range of 4-16% (based on data from 3 long term study sites: Moremi, Amboseli and Gombe; Cheney et al. 2004; Bronikowski et al. 2002). We consider four cases based on different initial group sizes, which we take to be 15, 17, 20 and 25 individuals so as to bracket the minimum viable group size as defined both by the fertility schedule in Fig. 4 and the distribution of group sizes in Fig. 1.

For computational convenience, reproductive females are assumed to constitute ~30% of the group, as is typical of both *Papio* baboons in particular (Fig. S6) and primates in general (Dunbar et al. 2018b). Overall, the average number of females in baboon groups in our fertility sample (*Dataset* S2) is 14.5±6.9, and average group size is 50.3±21.4 (N=16), for a ratio of 0.288. The mean ratio of females to total group size for these individual groups is 0.282±0.05 SD. Fig. S6 plots the data for these groups: the regression line has a slope of ~3.

The model calculation steps were as follows. For each year, we first determine the number of females in the group by multiplying current group size by the standard proportion of females in the group (30%): this figure is then multiplied by the group-specific fertility rate from Fig. 2 to give the number of births, and the resulting

number is added to the current group size. Mortality is then determined by a random number from the normal distribution given above, and group size reduced by this amount. The resulting group size is then carried forward to the next year, and the calculations repeated. These steps are repeated for as long as is necessary for group size to reach a stable state (constant size). For each starting group size, we ran 10,000 replicates.

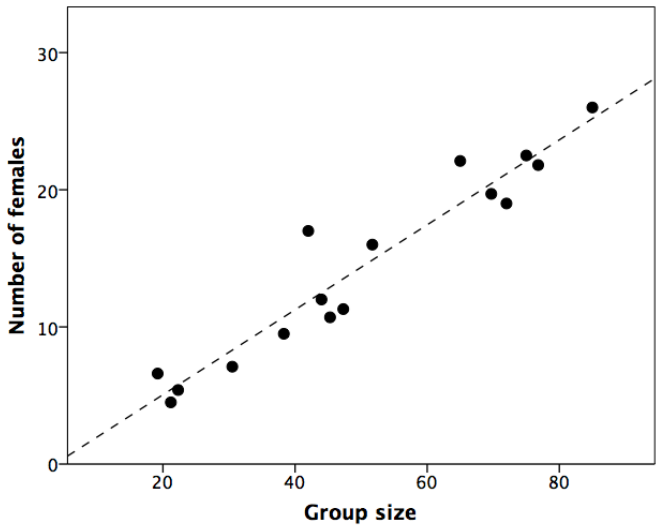


Figure S6
Number of females plotted against total group size for all the savannah baboon groups in the fertility sample. The dashed line is the best fit linear regression and has a slope of ~0.3.

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