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Group Size as a Trade Off Between Fertility and Predation Risk:

Implications for Social Evolution

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19   **Abstract**

20   Cluster analysis reveals a fractal pattern in the sizes of baboon groups, with peaks at

21   ~20, ~40, ~80 and ~160. Although all baboon species individually exhibit this pattern,

22   the two largest are mainly characteristic of the hamadryas and gelada. We suggest that

23   these constitute three pairs of linear oscillators (20/40, 40/80 and 80/160), where in

24   each case the higher value is set by limits on female fertility and the lower by

25   predation risk. The lower pair of oscillators form an ESS in woodland baboons, with

26   choice of oscillator being determined by local predation risk. Female fertility rates

27   would naturally prevent baboons from achieving the highest oscillator with any

28   regularity; nonetheless, hamadryas and gelada have been able to break through this

29   fertility 'glass ceiling' and we suggest that they have been able to do so by using

30   substructuring (based partly on using males as 'hired guns'). This seems to have

31   allowed them to increase group size significantly so as to occupy higher predation risk

32   habitats (thereby creating the upper oscillator).

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35   **Key words:** social organisation, fission, fertility, predation risk, bodyguard

36   hypothesis

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40 **Introduction**

41   Groups are of fundamental importance in an evolutionary context for two

42 reasons. First, they provide the demographic context in which animals play out their

43 individual social and reproductive strategies. The size and demographic structure of

44 the group in which an individual lives determines its behavioural and strategic

45 options: if you don't have a sister, you cannot form an alliance with sisters, even

46 though this may be the optimal thing to do (Altmann & Altmann 1979; Dunbar 1979).

47 Second, group size is the key interface between the animal and its environment and,

48 because primates, in particular, solve many of their ecological challenges socially,

49 group size will often be a crucial feature of their ecological success. Understanding

50 the factors that determine the size of groups that individuals live in is thus essential if

51 we are to fully understand the processes that lie behind primate evolutionary history,

52 and the particular behaviour of extant species. Despite this, the determinants of group

53 size for any primate species have not been a significant focus of interest for several

54 decades, and our understanding remains disappointingly poor and often very informal.

55   For all animals, group size is ultimately a tradeoff between costs and benefits.

56 For primates (and most cursorial mammals), the principal benefits arise from

57 protection against predation (Altmann & Altmann 1970; Cowlishaw 1994; Shultz et

58 al. 2004; Cheney et al. 2004; Adamczak & Dunbar 2008; Lehmann & Dunbar 2009a;

59 Willems & Hill 2009; Shultz & Finlayson 2010; Bettridge & Dunbar 2012). The costs

60 arise from a combination of indirect costs (increased day journey length and foraging

61 demand: Dunbar et al. 2009) and direct costs (competition between group members,

62 and in particular the consequences this has for female fertility: Dunbar 2018). In this

63 paper, we explore how these play out to influence social group size in baboons.

64   Predation by cursorial predators (principally lion, leopard and hyaena) is a

65   serious problem faced by baboons (Altmann & Altmann 1970; Cowlishaw 1994;

66   Bettridge & Dunbar 2012), especially at night when these predators are most active

67   and primates are vulnerable due to their poor night vision. Not only do the densities of

68   predators place constraints on the biogeographic distributions of all terrestrial

69   primates (Lehmann & Dunbar 2009a), they also dictate minimum group size (Dunbar

70   et al. 2009; Bettridge & Dunbar 2012). Some evidence of the significance of this for

71   baboons is provided by a rare case of group fusion: two groups in the Mikumi

72   National Park (Tanzania) whose sizes had progressively declined over time to 11 and

73   13 due to high mortality rates fused to create a group of 24 individuals (Hawkins

74   1999). Not only were both of the original groups below the size for demographic

75   viability (~17 individuals: Dunbar et al. 2018), but they were also below the minimum

76   group size (16.3) predicted for this site by the local predator density (Bettridge et al.

77   2010). Fusing placed both groups in the demographic 'safe zone'.

78   In contrast, the substantive costs of group-living seem to arise from the impact

79   that this has on female fertility, rather than access to resources *per se*. In mammals,

80   female reproductive endocrinology is extremely sensitive to stress: even low levels of

81   stress can destabilise it, resulting in increased levels of infertility, and in some cases

82   even the complete suppression of puberty (Bowman et al. 1978; Abbott et al. 1981,

83   1986, 1988; Seifer & Collins 1990). The mechanism for this is well understood

84   pharmacologically: high levels of ß-endorphins produced in response to social or

85   physical stress block the production of GnRH in the hypothalamus, with the result that

86   the pituitary fails to produce the lutenising hormone (LH) surge required to trigger

87   ovulation, leading to anovulatory (and hence infertile) menstrual cycles (Zacur et al.

88   1976; Seifer & Collins 1990; Laatikainen 1991; von Borell et al. 2007; Einarsson et

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89   al. 2008). A decline in fertility with either rank (Dunbar 1980; Smuts & Nicholson

90   1989; Altmann & Alberts 2003; Garcia et al. 2006; Pusey & Schroepfer-Walker 2013)

91   or group size (van Schaik 1983; Dunbar 1989; Srivastava & Dunbar 1996; Hill et al.

92   2000; Borries et al. 2008) has been widely documented in primates, and seems to be

93   characteristic of mammals as a whole (Dunbar 2018). Since the same

94   endocrinological mechanism underpins human and primate infertility (An et al. 2013;

95   Schliep et al. 2015; Pettay et al. 2016), and stress has been an identified factor in

96   human infertility (An et al. 2013; Schliep et al. 2015; Pettay et al. 2016), similar

97   effects have also been noted in humans: fertility declines with harem size in

98   ethnographic societies (Muhsam 1956; Smith & Kunz 1976; Chojnacka 1980; Bean &

99   Mineau 1986; Borgerhof Mulder 1989).

100   Ecologists have invariably attributed the decline in fertility with rank or group

101   size to reduced food intake as a result of scramble competition. In fact, starvation

102   itself triggers the endorphin system and thereby precipitates infertility (Dobson et al.

103   2012, Clarke 2014), so the effect may be due to stress rather than shortage of nutrients

104   *per se*. While lack of food can certainly cause the reproductive system to shut down,

105   this usually happens only in cases where extreme starvation or excessive exercise (e.g.

106   athletes) results in insufficient fat reserves to support pregnancy (Smith 1947; Dean

107   1949; McClure 1968; Warren & Perlroth 2001; Kirchengast & Huber 2001). Even

108   then, it seems to be the hypothalamic pathway that regulates this, rather than nutrition

109   itself (Kalra & Kalra 1996; Schwartz & Seeley 1997). Indeed, experimental studies of

110   domestic stock have shown that stocking rate (in effect, social group size) is

111   responsible for this, independently of any effect due to food availability or nutrition

112   (von Borell et al. 2007; Einarsson et al. 2008; Dobson et al. 2012; Clarke 2014). In

113   short, it seems that the same endorphin/HPA pathway is involved in both social and

114   ecological routes, perhaps explaining why it can be difficult to distinguish between

115   their respective effects. In short, it seems that living in large groups can adversely

116   affect female fertility irrespective of how rich the foraging conditions may be.

117   For species that live in loose associations (herds), these costs can easily be

118   defused by leaving the group and joining a smaller one – as is widely exemplified in

119   non-primate mammals. However, for species like primates that live in bonded social

120   groups (Dunbar & Shultz 2010; Shultz & Dunbar 2010; Massen et al. 2010),

121   individuals cannot easily leave one group to join another because entry by strangers is

122   often aggressively resisted (Dunbar 1984; Kahlenberg et al. 2008). Since predation

123   risk militates against leaving groups to forage alone (Dunbar et al. 2009), the only

124   way a group can lose members is to fission into two independent groups large enough

125   to survive on their own. Fission has been documented in many primate species (e.g.

126   Dunbar 1988; Ménard & Vallet 1993; Henzi et al. 1997; van Horn et al. 2007). An

127   important constraint is that if minimum group size is set by the local predation risk

128   (Dunbar et al. 2009; Bettridge & Dunbar 2012), groups need to be at least twice this

129   size at fission in order to allow both daughter groups to be above the specified

130   minimum (see also Dunbar & Sosis 2017).

131   We use a comprehensive dataset of baboon group sizes to investigate the

132   structural patterns that these exhibit, and explore likely reasons for the patterns in

133   terms of predation risk and fertility. We take baboons to refer to the large terrestrial

134   primates of Africa ('baboons' *sensu* Jolly 2007). For present purposes, we include the

135   genera *Papio* (the baboons of conventional usage) and *Theropithecus* (the gelada). We

136   exclude *Mandrillus* (drills and mandrills) because their groups are still poorly

137   understood and have yet to be reliably censused. There are some grounds for

138   considering *Lophocebus* and *Rungwecebus* as allies of the baboons, but as these are

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139   arboreal and hence likely to be subject to very different selection pressures as a result

140   (arboreal habitats are typically much less predator risky), we exclude them as well.

141   We ask three questions: (1) Is there a typical or natural size for baboon

142   groups? (2) Why do baboons have the range of group sizes that they do? and (3) How

143   can we explain the structural differences that distinguish some species (specifically,

144   hamadryas and gelada with their multilevel harem-based social systems) from others

145   (the remaining four species of *Papio* which lack a harem structure).

146

147   **Methods**

148   We comprehensively searched the literature for census data on baboon group

149   sizes, providing such censuses were part of a systematic attempt to count the size and

150   composition of individual baboon groups at a given location. We take group (or troop)

151   size to be that defined by the field worker. For *Papio anubis*, *P. cynocephalus* and *P.*

152   *ursinus*, the group is fairly obvious, since animals forage and sleep together in stable

153   social groups that maintain a degree of demographic coherence and stability over time

154   as well as spatial separation from neighbouring groups. Exactly what counts as a

155   group in *Papio papio* has been the subject of some debate because of this species'

156   rather more flexible form of sociality, but all field workers on this species agree on

157   the existence of some form of stable social group, at least as defined by animals that

158   share a common range area (Dunbar & Nathan 1972; Boese 1975; Sharman 1981;

159   Patzelt et al. 2011). For *P. hamadryas* and *Theropithecus gelada*, we equate the social

160   group with the band (a collection of single male reproductive units, or harems, that

161   share a common home range and frequently forage together: Kummer 1968; Mac

162   Carron & Dunbar 2016). In all three latter cases, we use the group (or band) as

163   defined by the fieldworker concerned. However, in order to ensure that we were

164 comparing like with like, we excluded publications (e.g. Zinner et al. 2001) which

165 provided only mean group sizes for a location or did not provide clear evidence for

166 differentiating between grouping levels in the case of those species (*P. hamadryas*

167 and *T. gelada*) which have multilevel societies.

168 In populations that were subject to longterm study with repeated censuses of

169 the same social groups, we counted a census as being new only providing it had been

170 carried out at least five years after the previous census of that group. In either case, we

171 always used the original (i.e. earliest) census and at most one later census. This

172 yielded a total of 444 groups across 53 study sites in 13 countries for five species of

173 *Papio* and the one extant species of *Theropithecus*. There are insufficient data

174 available for *P. kindae*, which has only recently been elevated to species status

175 (Zinner et al. 2013) and has not been well studied in the field. The data are given in

176 Table S1.

177 We first determined whether the distribution of group sizes is unimodal. If the

178 distribution is not normal, our task is to find the most appropriate distribution that

179 does describe the data. We used maximum-likelihood methods (Clauset et al. 2009) to

180 fit the following common distributions: power law, truncated power law, geometric,

181 negative binomial, exponential, stretched exponential, normal, lognormal, and a

182 compound Poisson distribution. The first eight of these assume that the data are non-

183 normal (i.e. skewed) distribution with a single definable mode. The last assumes that

184 the observed distribution is in fact the product of several separate distributions, each

185 with their own modes, that have been pooled together. That might occur because each

186 species has a single modal (or typical) value, but the values for the various species

187 differ significantly. However, more interestingly, such a pattern might occur when a

188 group's size oscillates within sets of defined limits, with the particular limits being set

189   by some key aspect of the animals' ecology; in these cases, individual species may be

190   found in a wide range of group sizes (or group size "types").

191   As the dataset consists of discrete integers, we used the discrete approach as

192   described by Clauset et al. (2009). We numerically maximised the log-likelihood of

193   each candidate distribution to obtain its parameter estimates, using the *optimize*

194   module of Python's *scipy* (v0.17.1) library, and identified the most likely model using

195   the Akaike Information Criterion (AIC). In the case of the compound Poisson, we

196   treated the data as being made up of 1 to *n* Poisson distributions; the AIC for each *n* is

197   calculated successively, stopping when a local minimum is reached to give the

198   optimal *n*. This is the only distribution tested that is multimodal; the rest have a single

199   peak and, except for the normal distribution, all are right skewed.

200   Because models with more parameters are always more likely to fit the data,

201   we applied a clustering algorithm to see if a different approach gives the same result.

202   Since most clustering algorithms are meant for a high number of dimensions (Jain

203   2010), we used the Jenks natural breaks algorithm as this is more appropriate for data

204   with only one dimension (Jenks 1967). Jenks is very similar to *k*-means clustering in

205   one dimension and works by minimising the variance within different numbers of

206   clusters. In order to choose the optimal number of clusters, we calculated a goodness

207   of fit for each number of clusters. Since a goodness of fit of 1.0 can only be attained

208   when there is no within-class variation (typically when the number of clusters is the

209   same as the sample size), we follow Coulson (1987) and take a value of 0.85 as the

210   threshold.

211   Female fertility rates for 15 individual baboon troops are taken from Hill et al.

212   (2000), with additional data from more recent studies for one group each for *P. anubis*

213   (Higham et al. 2009) and *P. ursinus* (Cheney et al. 2004), two groups for *P.*

214   *hamadryas* (Swedell & Saunders 2006; Chowdhury et al. 2015), and three bands for

215   *T. gelada* (from Ohsawa & Dunbar 1984). In addition, we give two population means

216   for *P. papio* (Boese 1975; Sharman 1981) based on the number of immatures

217   (prepuberty individuals, less than ~ 4 years of age) in a group. In plotting fertility rate

218   against group size, we use the mean size of the foraging group in the case of the

219   multilevel hamadryas and gelada since this is the social context in which animals

220   spend most of their time and it is this that affects female fertility. For hamadryas, we

221   identify this as the band; for gelada, we identify this as the herd. Mean population

222   group size, climatic and forest cover data for these habitats are from Bettridge et al.

223   (2010). The data are provided in Table S2.

224

225   **Results**

226   *Group size*

227   The distribution of baboon group sizes is highly skewed, with a mean of

228   48.5±43.4SD and a range of 3-262 (Fig. 1). Analysis of variance indicates that group

229   sizes vary significantly across the six species (Fig. 2: $F_{5,438}=32.25$, $p<<0.0001$).

230   Scheffé post hoc tests suggest that the data fall into two clusters that differ

231   significantly from each other ($p<0.001$). These are: (1) *Papio anubis* (mean group size

232   = 40.3±26.4, N=104), *P. cynocephalus* (mean group size = 51.7±34.5, N=105) and *P.*

233   *ursinus* (mean group size = 30.4±21.9, N=166) and (2) *P. papio* (mean group size =

234   91.6±69.4, N=34), *P. hamadryas* (mean group size = 93.5±62.4, N=13) and

235   *Theropithecus gelada* (mean = 115.7±71.7, N=22). For convenience, we label the first

236   set as the 'woodland' species, a term that has no taxonomic implications but refers to

237   the fact that they mostly occupy savannah woodland habitats that are rather different

238   to the kinds of habitats occupied by the hamadryas and gelada.

239   Applying maximum likelihood estimation to the raw data in Fig. 1 indicates

240   that the distribution is most likely made up of 4 Poisson distributions (Table 1) with

241   means 19.1, 42.6, 83.3 and 189.4. Excluding gelada gives virtually the same results

242   (means at 18.7, 41.0, 79.1 and 180.3). The Jenks algorithm also suggests that four

243   clusters is optimal for all *Papio* combined (means of 19.8, 45.6, 85.4 and 184.4), but

244   opts for just three clusters when gelada are included (means 27.1, 77.0 and 190.1). All

245   four series have a mean scaling ratio of ~2.1 (2.7 for the last case), suggesting a

246   fractal pattern indicative of binary fission.

247   We also analysed each species separately: Jenks identifies three or four as the

248   optimal number of clusters for all six species, with cluster means that are all close to

249   those found for the sample as a whole and scaling ratios close to 2 (Table 2). More

250   importantly, with the exception of the largest cluster (~160) for *Papio anubis* and the

251   smallest cluster (~20) for *P. papio*, *P. hamadryas* and *Theropithecus gelada*, all

252   clusters are present in all species.

253   We suggest that these cluster values make up a set of linear oscillators, with

254   attractors at ~20 and ~40, ~40 and ~80, and ~80 and ~160 respectively. In effect,

255   group size oscillates between the limits set by a given oscillator (i.e. 20/40, 40/80 or

256   80/160). Within an oscillator, natural growth rates cause groups to increase in size

257   until they fission at the upper value to return to the lower value, and begin the cycle

258   all over again.

259   It seems that most populations have a characteristic group size that sits

260   comfortably within one of these oscillators. Analysis of the distribution of group sizes

261   for the 27 sites with at least five censused groups indicates that only five are not

262   (unimodal) normally distributed. In these five cases (Amboseli NP, Gilgil, Mt Assirik,

263   Nairobi NP and Giants Castle), the bimodality is created by a small number of very

264 large (N>100) outliers, with the bulk of the groups normally distributed within one or

265 other of the two smaller oscillators. This may reflect the fact that these sites are

266 typically associated with a mosaic of habitat types. The rest all have a group size

267 distribution that falls mainly into one of the oscillators. Fig. 3 plots the proportion of

268 groups in the smallest (20/40) oscillator in each of these populations. The data exhibit

269 a clear bimodal pattern: about half the populations have all or most their groups in the

270 20/40 oscillator and half have all or most of their groups within the 40/80 or 80/120

271 oscillators. There is a conspicuous absence of groups with an even split.

272   This raises three questions: (1) Why are there distinct oscillators rather than a

273 continuous series of optimal values tracking some environmental variable like

274 rainfall? (2) Why do different populations seem to opt for different oscillators? (3)

275 What are the structural consequences of the oscillators? We suggest that the trade off

276 between fertility and predation risk is the key to answering these questions.

277

278 *Optimising group size in different habitats*

279   Fig. 4 plots population mean group size as a function of predator density and

280 tree cover (the two main factors that influence predation risk for baboons: Cowlishaw

281 1997a,b). Predator density is the sum of the densities of the baboons' two main

282 predators (leopard and lion: Cowlishaw 1994), each predicted from species-specific

283 climate envelope models using data from 59 locations distributed across sub-Saharan

284 Africa (Bettridge et al. 2010). Tree cover (percent of ground covered by tree canopy)

285 is estimated from satellite imagery for the *Papio* populations (see Bettridge et al.

286 2010) and from ground transects for the gelada populations (Iwamoto & Dunbar

287 1983). Tree cover is significantly lower in hamadryas and gelada habitats than the

288 habitats of the other *Papio* species (Fig. S1). Essentially, group size is low when there

289   are plenty of trees available as refuges, but, in habitats with few trees, groups are large

290   (in some cases, very large) *if* predator density is high. A general linear model

291   indicates that, while there is no main effect for predation in the predicted direction

292   ($F_{1,20}$=0.75, p=0.199), mean group size is significantly higher in less forested habitats

293   ($F_{1,20}$=3.77, p=0.033) and there is a significant forest*predator interaction ($F_{1,20}$=3.52,

294   p=0.038). (We here test a set of explicit directional hypotheses based on Cowlishaw

295   [1997a,b], so all statistical tests are necessarily 1-tailed.)

296   To further illustrate this, Fig. 5 plots mean population group size against a

297   composite index of predation risk. The predation risk index is the sum of the

298   standardised deviate of predator density and the standardised deviate of habitat

299   openness (defined as 100 minus percent tree cover). There is a significant relationship

300   between mean group size and the composite index of predation risk (r=0.506, N=24,

301   p=0.006 1-tailed). In other words, resort to large group sizes (and hence the higher

302   oscillators) appears to be driven by high predation risk.

303   Finally, we use Bettridge et al.'s (2010) baboon time budget model to

304   calculate minimum and maximum ecologically tolerable group sizes as a function of

305   climatic conditions. Minimum group size is a simple function of the density of

306   baboons' two main predators (leopard and lion) (Bettridge et al. 2010). Maximum

307   group size is determined by first calculating the amount of time that animals need to

308   devote to feeding, moving and resting using the equations given by Bettridge et al.

309   (2010) that relate each of these to climate variables; we then subtract the sum of these

310   from 100% (i.e. all daytime) to give the maximum amount of time available for social

311   grooming; finally, we use the regression equation relating required grooming time to

312   group size in primates (Dunbar 1991; Lehmann et al. 2007a) to determine the largest

313   group size that the animals' time budget could support at that locality (for details, see

314   Dunbar et al. 2009; Bettridge et al. 2010).

315   To simplify the presentation of these results, we transformed the eight climate

316   variables used in the model into functions of a single variable (mean annual rainfall)

317   (using the data given in Bettridge et al. 2010; linear regressions: $0.366 \leq r \leq 0.892$,

318     $p \leq 0.078$ 2-tailed) and use these to plot minimum and maximum group sizes across the

319   full range of rainfall regimes (0-2000 mm per annum) found in Africa (Fig. 6).

320   Rainfall is a reliable index of forest cover (tree density) in Africa. Minimum group

321   size declines slowly as rainfall increases (i.e. as tree density increases), with a mean

322   value of ~20.7 (range 18.6-25.9). Maximum tolerable group size increases with

323   rainfall, rising from a base of ~55 to a maximum of ~110 in the wettest (i.e. richest)

324   habitats. Maximum group size sets an absolute upper limit and groups cannot exceed

325   this value without paying a price in terms of group cohesion or energy intake because

326   they will not be able to balance their time (and hence energy/nutrient) budget. The

327   space between the minimum and maximum lines in Fig. 6 represents the genus's

328   realisable niche space: groups will be in ecological balance only if they lie between

329   the two lines (Dunbar et al. 2009). Although groups can stray outside these limits,

330   they should be able to do so only to a limited extent and, usually, only for a limited

331   period of time.

332   Notice that the lines on Fig. 6 represent the two conventional components of

333   fitness (fertility and survivorship). In any given habitat, animals will reduce predation

334   risk, and hence maximise survivorship (albeit at the expense of fertility), by living in

335   the largest groups they can (i.e. closest to the upper dashed line); conversely, they will

336   maximise fertility (at the expense of increased predation risk, and hence reduced

337   survivorship) by living in the smallest groups they can (i.e. closest to the lower solid

338   line). Where they choose to position themselves in this state space should depend on

339   how intrusive predation risk is for them.

340   The mean group sizes for 19 populations of *Papio* for which detailed climate

341   data are available are plotted onto Fig. 6 as a function of their actual local rainfall

342   regime. All except one of the datapoints lie within or close to the minimum and

343   maximum lines. The exception (Laikipia, Kenya) which lies just outside the upper

344   limit is a site with a particularly low density of tree cover (10%) and a high predicted

345   density of predators (and, within the last century, an unusually high actual density of

346   leopard). More importantly, there appears to be a phase shift in group size at

347   ~1000mm rainfall: populations seem to switch from maximising group size in dry

348   habitats to minimising group size in wet habitats. This likely reflects the availability

349   of trees that can act as refuges when a group encounters predators during foraging: the

350   heavy sigmoid line plots the percentage of tree cover as a function of rainfall. The

351   switch point seems to correspond to a phase transition in the degree of forest cover,

352   with a value of ~30% tree cover (i.e. quite heavily wooded habitats) demarcating this

353   transition point. In more open habitats, baboons rely on maximising group size to

354   deter predators (at the expense of reduced birth rates), whereas more wooded habitats

355   allow them to live in smaller groups so as to maximise fertility.

356

357   *Fertility*

358   Next, we ask how fertility is affected by group size. Fig. 7 plots mean birth rate

359   against group size for 25 baboon study sites (including three for gelada). The

360   woodland baboon data are clearly best explained by a quadratic regression

361   ($b=0.149+0.014N-0.00016N^2$, where b = annual birth rate per female and N = group

362   size; $F_{2,12}=6.82$, $r^2=0.532$, $p=0.011$; linear: $F_{1,13}=0.30$, $r^2=0.022$, $p=0.594$). The

363   quadratic relationship holds individually across all three woodland species (Dunbar et

364   al. 2018a), and when the Guinea baboon datapoints are included ($F_{2,14}$=5.38, r^2=0.434,

365   p=0.019). It seems that fertility increases monotonically with group size to a

366   maximum of about 0.54 births/year at a group size of ~55, and then declines again at a

367   similar rate.

368   Hill et al. (2000) found that *Papio* birth rates are also independently

369   determined by mean ambient temperature (an index of habitat quality: Dunbar et al.

370   2009). However, for the woodland baboons at least, the results are exactly the same if

371   we plot residuals from a regression of fertility on rainfall against group size (Fig. S2),

372   indicating that, irrespective of the effect that habitat quality has on birth rates, birth

373   rates are independently a quadratic function of group size.

374   In contrast, the hamadryas and gelada datapoints lie well outside the 95%

375   confidence intervals for the woodland species. Their data also fit a quadratic

376   regression ($F_{2,8}$=10.66, r^2=0.727, p=0.006; linear: $F_{1,19}$=1.09, r^2=0108, p=0.323) that is

377   very similar in form, but with a significantly lower intercept (meaning that the graph

378   is displaced to the right compared to that for the woodland baboons). For the

379   hamadryas and gelada, a quadratic relationship gives a maximum birth rate at groups

380   of N≈125 (i.e. slightly more than twice that for the woodland species). This result

381   holds even when we use the maximum group sizes for hamadryas (sleeping troops)

382   and gelada (the band) (Fig. S3).

383   Fig. 7 indicates that no population has a birth rate below 0.3 per annum. With

384   a ~13-year reproductive lifespan, a minimum fertility of ~0.15 births per year is

385   required for replacement (i.e. two offspring at the end of a lifetime). Since

386   survivorship to puberty averages ~50% in wild baboons (Altmann et al. 1977; Sigg et

387   al. 1982), this would require a minimum birth rate of 0.3 for demographic stationarity

388   (i.e. for a population to avoid extinction). This being so, the regression equation for

389   the woodland baboon populations would set an upper limit to group size at 95 for

390   demographic viability. This value includes 92.4% of all baboon groups in the sample

391   in Fig. 1 (or 93.1% of the groups for the three woodland species: Table S1). Note that

392   this is only just above the mean group size (91.6) for Guinea baboons, suggesting that

393   they are on the edge of viability. Groups larger than this will not be reproducing fast

394   enough to compensate for natural mortality, and will therefore oscillate perpetually

395   around this value until they fission. In contrast, the fertility data for hamadryas and

396   gelada predict a limiting group size of ~180 (2.2 times the equivalent for the other

397   species), just above the uppermost attractor in Fig. 1.

398   The quadratic form of this equation also implies a minimum limit on group

399   size: in woodland species, groups smaller than ~15 would have birth rates below the

400   limit for demographic viability, and so would be in terminal decline. Only 8.6% of all

401   groups in the savannah sample are smaller than this. Note that baboons thus have a

402   lower limit on group size that is substantially larger than the size of groups

403   characteristic of most primate species (~60% of primate species have a mean group

404   size of <15 individuals: Dunbar et al., 2018b). In contrast, hamadryas and gelada

405   would have a lower limit on group size of 38. The smallest hamadryas band recorded

406   in the present sample is in fact 38 (Table S1), while the mean size for gelada teams

407   (the natural grouping for this species, and the set of harems that stay together most

408   closely) is 34 (Mac Carron & Dunbar 2016).

409

410   **Discussion**

411   The regular patterning in the distribution of baboon group sizes suggests a

412   fractal sequence with attractors at ~20, ~40, ~80 and ~160 that are particularly

413   common. Since these values have a scaling ratio of ~2.0, they are likely to be the

414   product of a binary fission process, as also seems to be the case in the gelada (Mac

415   Carron & Dunbar 2016). At the same time, very small groups of the size common in

416   many other primates (<15 members) are rare (Fig. 1). In fact, 60% of groups with

417   N<15 in the baboon sample were from South African *Papio ursinus* populations

418   living in high latitude, high altitude (i.e. poor quality, thermally challenging) habitats

419   with extremely low predator densities and environmental conditions that impose

420   severe limits on group size. There are no census data available for *Papio kindae*, but

421   the count of 83 for one group given by Weyher et al. (2014) is within the range for the

422   middle oscillator and similar to the group sizes reported from *Papio cynocephalus*

423   populations. Since minimum group size is determined by female body mass in

424   addition to predation risk (smaller species live in bigger groups: Bettridge & Dunbar

425   2012), we would expect *P. kindae* to live in larger groups than any of the other

426   species in comparable habitats.

427   If groups of ~20 are the minimum viable size, then the corresponding

428   minimum size at fission will need to be around 40-45 – or above if groups do not

429   fission into equal halves. While predation risk and fission processes seem to provide a

430   natural explanation for a fractal pattern of group sizes, they do not of themselves

431   explain why fission should typically occur at the group sizes where seems to,

432   especially as these are well below the limiting group size for baboons set by their

433   carrying capacity in most habitats (Bettridge et al. 2010).

434   The impact of social competition on fertility is clearly an issue for group-

435   living primates, as it is for all social mammals. The fact that, in both monkeys and

436   humans, the fertility decline can be attributed directly to the number of females in the

437   group rather than to the number of males or total group size (Dunbar 1980; Hill et al.

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438 2000; Ji et al. 2013), and does so even in captivity where food is abundant (Garcia et

439 al. 2006), points to the importance of a social, rather than ecological, explanation –

440 even though competition for food may sometimes provide the context for this. These

441 costs appear to be so strong that they effectively limit group size to ~15 individuals in

442 most primates (Dunbar 2018). Cercopithecine primates seem to have evolved female

443 coalitions as a mechanism for mitigating these costs in order to make larger groups

444 possible (Dunbar 2012, 2018; Dunbar & Shultz 2017). Female baboons with larger

445 grooming-based coalitions experience less harassment (Dunbar 1980, 2018), have

446 lower cortisol titres (Crockford et al. 2008; Wittig et al. 2008), produce more

447 offspring and live longer (Silk et al. 2003, 2009, 2010).

448   We have suggested that woodland baboon species are constrained by the

449 fertility curve in Fig. 7 to groups between ~20 and ~80 in size, and that this gives rise

450 to a pair of linear oscillators (20/40 and 40/80). We have shown elsewhere (Dunbar et

451 al. 2018b) that the two lower oscillators (20-40 and 40-80) are an evolutionary stable

452 strategy (ESS) for the woodland baboon species. The estimated lifetime reproductive

453 outputs of the average female in the two oscillators, given the fertility rates in Fig. 7,

454 are equal only when the phase shift between them occurs at a group size of ~40. Phase

455 transitions set either side of this value will result in one or other of the oscillators

456 being disproportionately favoured: if the switch over occurs at smaller group sizes

457 (groups in the range 25-35), then females in the larger oscillator do significantly

458 better, while the reverse is true if the switch over occurs at larger group sizes (45-75).

459 This seems to be due to the fact that a phase transition at the group size that

460 maximises fertility results in females doing equally well either way, the difference

461 simply being whether they experience maximum fertility early or late in their

462 reproductive lives. In other words, these two oscillators seem to represent an optimal

463   partition for females trying to maximise their fitness under different predation risk

464   conditions. Although predation risk might favour a quantitative response, the fertility

465   costs result in a qualitative switch between states (i.e. oscillators).

466   That the upper values in each case are fission points is indicated by evidence

467   that *Papio ursinus* groups living in a low predation risk habitat in South Africa

468   typically fission at a size of ~32 (for a mean population group size of 22.4, N=61)

469   whereas *P. cynocephalus* groups living in a high predation risk habitat in East Africa

470   do so at ~65 (mean population group size 50.7, N=51) (Henzi et al. 1997). These are

471   likely to be facultative responses to environmental conditions, so populations can be

472   expected to switch between these oscillators as environmental circumstances change.

473   Some evidence for this is provided by the fact that, over a period of four decades, the

474   *Papio anubis* population at Gombe switched from a 20/40 range to a 40/80 range and,

475   subsequently, back again (Tony Collins, pers. comm.), though the circumstances that

476   prevailed on them to do so remain unclear.

477   We are left with the question of why hamadryas and gelada have opted for an

478   oscillator that lies outside this range. Part of the answer may lie in the fact that these

479   two species live in much more open (hence even more predator risky) habitats than

480   those typically occupied by other baboons (Fig. 5). This does not necessarily mean

481   that they have higher predator densities, but it does mean that the availability of large

482   trees to act as refuges is very limited. It is the virtual absence of large trees that

483   obliges hamadryas to congregate at night on rocky outcrops and gelada to seek refuge

484   on sheer cliff faces.

485   The problem for both these two species is that they can only increase group

486   size significantly to compensate for the higher predation risk providing they can find

487   some way of circumventing the fertility trap. To illustrate the magnitude of this trap

488   we can use the regression equation for fertility from Fig. 7 to model the change in

489   group size over time for groups with initial sizes of 15, 17, 20 and 25, subject to an

490   annual mortality rate that varies randomly across a normal distribution with a mean of

491   10% and a range of 4-16% (based on data from 3 long term study sites: Moremi,

492   Amboseli and Gombe; Cheney et al. 2004; Bronikowski et al. 2002). Reproductive

493   females are assumed to constitute ~30% of the group, as is typical of both *Papio*

494   baboons in particular (Fig. S4) and primates in general (Dunbar et al. 2018a). Note

495   that the point of this model is simply to observe the consequences of the particular

496   demographic configuration implied by the fertility rates in Fig. 3.

497   Fig. 8 plots the results. Groups whose initial size is <17 animals will always

498   go extinct (grey shaded region) because their fertility rates are too low to offset

499   mortality. Groups with an initial size >17 grow slowly for a number of years and then

500   accelerate until they reach an asymptotic value of ~100, where they will stay

501   indefinitely. When group size exceeds this value, fertility drops and excess mortality

502   reduces group size; this allows fertility to increase, which in turn allows the group to

503   grow again until fertility once more drops below mortality. Left to their own devices,

504   populations will have natural limits at ~20 and ~100, and groups will often be stuck at

505   these values for some considerable time (in the first case, until random fluctuations in

506   mortality and female cohort size allow them to break out of the lower cycle; in the

507   second case, until fission radically reduces group size).

508   The contrast between hamadryas and gelada and the woodland species

509   (including the Guinea baboon) is striking. The decline in fertility at group sizes above

510   50 is sufficiently steep that it will place groups of >100, as occur regularly in

511   hamadryas and gelada, under significant demographic pressure with birth rates below

512   the level for demographic replacement. Fig. 8 suggests that, all else equal, it should be

21

513   extremely difficult, if not impossible, for these two species to increase group size to

514   the levels that they have been able to do. Yet they have both clearly managed to do so.

515   They have somehow been able to shift their fertility schedule to the right such that

516   they can live in much larger groups (Fig. 7).

517   Hamadryas live in a poor quality semi-desert habitat, with very few large trees

518   to act as refuges (even along watercourses) and predator densities similar to those

519   faced by woodland baboon populations. In a habitat virtually devoid of large trees,

520   they are obliged to congregate at night in very large herds (typically several bands) on

521   the few rocky outcrops large enough to provide safe night time refuges (Kummer

522   1968; Sigg & Stolba 1981; Schrier & Swedell 2012b). That predation is a concern for

523   them is indicated by the fact that, during the day, hamadryas bands (which normally

524   disperse over a wide area when foraging) will bunch defensively when predators are

525   heard or sighted (Schrier & Swedell 2012a), just as savannah baboons do (Altmann &

526   Altmann 1970).

527   Although the gelada live in a cool, high altitude habitat with rich grassy

528   swards that allow very large herds to congregate (at least during the wet season: Mac

529   Carron & Dunbar 2016), they also face a significant level of predation risk

530   (historically from leopard, but more recently hyaena in large numbers) in a

531   completely treeless habitat that can be nutritionally challenging for them during the

532   dry season (Dunbar 1984; Mac Carron & Dunbar 2016). As with the hamadryas, large

533   groups remain a crucial adaptation for minimising predation risk if gelada are to

534   forage on the plateau tops away from the safety provided by the cliff faces of the

535   gorge systems. Where gelada remain on the cliff faces, they have much smaller bands

536   (typically 40-70 animals) and individual harems often forage on their own (Dunbar &

537   Dunbar 1975; Dunbar 1984; Dunbar & Mac Carron 2016).

538   The dietary adaptations of these two species (Dunbar & Boese 1991) and the

539   dynamics of their social relationships (Dunbar 1983b) are radically different and

540   unlikely to be the cause of this substructuring. The only aspect of behaviour or

541   ecology that is common to the two species is the subdivision of groups (bands) into

542   harems. If so, this provides a principled explanation for why hamadryas and gelada

543   have such different social systems to the other baboons (and the other large-bodied

544   cercopithecines like the mangabeys and macaques). It is perhaps worth noting that

545   when habitat conditions dictate foraging groups significantly smaller than band size in

546   gelada, the harems are sufficiently independent to be able to separate out and forage

547   alone (e.g. Bole valley: Dunbar & Dunbar 1975; Bale Mountains: Mori et al. 1999).

548   One plausible suggestion, then, is that the hamadryas and gelada have

549   achieved this transition by exploiting a form of alliance-based substructuring (i.e.

550   harems) so as to buffer females against the stresses of living in very large groups. It

551   may be no coincidence that both these species have adopted a harem-based form of

552   sociality in which groups of closely related females (Dunbar 1984; Swedell 2002;

553   Städele et al. 2016) are attached to a male rather than dispersing in small, unstable

554   foraging parties, as happens in chimpanzees (Lehamnn et al. 2007b) and spider

555   monkeys (Korstjens et al. 2006) under similar circumstances. In both hamadryas and

556   gelada, the substructuring is reinforced (more so in the first case, less so in the

557   second) by forms of male herding behaviour that are not observed in the other species,

558   but functionally the consequences are that groups of (usually related) females

559   associate with a male capable of providing additional support during altercations

560   without creating the fertility problems associated with associating with more females.

561   In this respect, they are rather similar to gorilla groups, where the male also provides

562   what amounts to a bodyguard service (Harcourt & Greenberg 2001).

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565   But why should such substructuring take the form of harems associated with a

566   single breeding male (and sometimes an associated follower male)? One possible

567   explanation might be that the size of coalitions is limited by matriline size, and this

568   itself may set a limit on the point at which fertility is maximised by woodland

569   baboons in Fig. 7. Matriline size is likely to be limited by lifehistory processes, since

570   matrilines typically fission once their matriarch dies. If this sets an upper limit to

571   matriline size, then their ability to buffer females against the stresses of group-living

572   will set a corresponding limit to group size. Some evidence to suggest this is given by

573   the fact that, across cercopithecine primates, mean grooming clique size (commonly a

574   matrilineal grouping) correlates with species mean group size (Kudo & Dunbar 2001;

575   Lehmann & Dunbar 2009b). Perhaps the only way of increasing coalition size beyond

576   this may be to add a male who can act as a 'hired gun' to protect the females from

577   harassment, but who doesn't himself compete with the females (the 'bodyguard

578   hypothesis': Mesnick 1997; Wilson & Mesnick 1997; Harcourt & Greenberg 2001).

579   The effectiveness of this is evident in gelada. Conflicts between neighbouring harems

580   are usually initiated by one, occasionally two, females; if the conflict escalates, more

581   females will become involved, until eventually the harem males are drawn into the

582   dispute in defence of their females (Dunbar 1983a, 2018).

583   In many ways, Guinea baboons (*Papio papio*) face similar problems: the

584   density and height of the ground level vegetation throughout most of their range in

585   West Africa, combined with a relatively flat landscape and a low overall density of

586   large trees away from the major rivers, makes their habitats particularly predator-

587   risky. The density and height of the ground-level vegetation, for example, means that

588 Guinea baboons have little advance warning of the approach of cursorial predators,

589 thus making them especially vulnerable (pers. obs.; see also Cowlishaw 1997b). The

590 Guinea baboon social system is not well understood, although most authors agree that

591 some form of loose multi-level grouping seems to be involved. Patzelt et al. (2011)

592 provide some evidence (albeit based only on association patterns between individual

593 males) that this species has a three tier social system that consists of parties, gangs

594 and communities. They identify the gang (defined as the set of animals that share the

595 same home range) of around ~60 animals (at their study site) as the equivalent of the

596 baboon troop (and hamadryas band), with the party being a group of females loosely

597 associated with a male. The *Papio* time budget model (Bettridge et al. 2010) gives a

598 maximum ecologically tolerable group size of 88.5 for baboons in the habitats

599 occupied by Guinea baboons in southeast Senegal – almost exactly the observed mean

600 group size for the censussed Guinea baboon populations from this area (Fig. 2). This

601 suggests that this species is attempting to maximise its group sizes, presumably to

602 cope with high predation risk, but, in contrast to the hamadryas, does so at the

603 expense of reduced fertility and social coherence because it has not mnaged to evolve

604 the behavioural and cognitive mechanisms (e.g. the male herding behaviour observed

605 in both hamadryas and gelada) that would allow it to substructure these groups

606 effectively. This might explain their seemingly somewhat chaotic social structure.

607 These analyses provide principled answers to the questions we posed in the

608 light of the fractal distribution of baboon group sizes, namely why there are distinct

609 oscillators rather than a series of optimal values, why different populations prefer

610 different oscillators and what the structural consequences of the oscillators are. It

611 seems that the oscillators represent an evolutionarily stable strategy set driven by local

612 predation risk. While baboon sociality can cope with the two lower oscillators without

613   significant stress, the upper oscillator (characteristic of hamadryas and gelada) is only

614   stable if the animals can introduce structural adaptations that allow the fertility

615   schedule to be shifted sufficiently to the right. This seems to have involved formal

616   substructuring that has involved an intensification of the natural matrilineal coalitions

617   characteristic of baboons and other cercopithecines and then attaching these

618   subgroups to a male who acts as a 'hired gun'. At least in the case of the hamadryas,

619   this seems to have required some degree of genetic underpinning in terms of male

620   herding behaviour (Nagel 1973; Bergman et al. 2008), a pattern that seems crucial in

621   enforcing their harem-based system (given that both anubis and hamadryas females

622   seem able to adapt to either social system: Kummer 1968). However, even gelada

623   males herd their females away from rivals (Dunbar 1984), although they do not do so

624   as effectively as hamadryas males do.

625   There are several predictions that follow from this model of baboon

626   demography. First, the oscillator should change when baboons migrate into a more, or

627   less, predator risky habitat, or there are changes in, for example, tree density due to

628   deforestation or longterm climatic change influencing habitat structure and tree

629   composition (as has happened at Amboseli: Altmann et al. 1985). Second, individual

630   groups should show cyclic changes in average female fertility over time, following

631   the patterns in Fig. 7. These changes should be upwards (followed by rapid collapse)

632   for baboon groups in the 20-40 oscillator, and downwards (followed by rapid

633   improvement) in populations in the 40-80 oscillator.

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645 **References**

646 Abbott, D.H., Hodges, J.K. & George, L.M. (1988). Social status controls LH

647 secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*).

648 *Journal of Endocrinology* 117: 329-339.

649 Abbott, D. H., McNeilly, A. S., Lunn, S. F., Hulme, M. J. & Burden, F. J. (1981).

650 Inhibition of ovarian function in subordinate female marmoset monkeys

651 (*Callithrix jacchus jacchus*). *Journal of Reproduction and Fertility* 63: 335-

652 345.

653 Abbott, D.H., Keverne, E.B., Moore, G.F. & Yodyinguad, U. (1986). Social

654 suppression of reproduction in subordinate talapoin monkeys, *Miopithecus*

655 *talapoin*. In: Else, J. & Lee, P.C. (eds.) *Primate Ontogeny*, pp. 329-341.

656 Cambridge: Cambridge University Press.

657 Adamczak, V. & Dunbar, R.I.M. (2008). Variation in the mating system of oribis and

658 their ecological determinants. *African Journal of Ecology* 45: 197-206.

659 Altmann, J. & Alberts, S.C. (2003). Variability in reproductive success viewed from a

660 life-history perspective in baboons. *American Journal of Human Biology* 15:

661 401-409.

662 Altmann, J., Hausfater, G. & Altmann, S.A. (1985). Demography of Amboseli

663 baboons, 1963-1983. *American Journal of Primatology* 8: 113-125.

664 Altmann, S.A. & Altmann, J. (1970). *Baboon Ecology*. Basel: Karger.

665 Altrnann, S.A. & Altmann, J. (1979). Demographic constraints on behavior and social

666 organization. In: Bernstein, I.S. & Smith, E.O. (eds) *Primate Ecology and*

667 *Human Origins*, pp. 47-63. New York: Garland.

668 Altmann, J., Altmann, S.A., Hausfater, G. & McCuskey, S.A. (1977). Life history of

669 yellow baboons: physical development, reproductive parameters, and infant

670   mortality. *Primates* 18: 315-330.

671   An, Y., Sun, Z., Li, L., Zhang, Y. & Ji, H. (2013). Relationship between

672   psychological stress and reproductive outcome in women undergoing in vitro

673   fertilization treatment: psychological and neurohormonal assessment. *Journal*

674   *of Assisted Reproduction and Genetics* 30: 35-41.

675   Bean, L.L., & Mineau, G.P. (1986). The polygyny-fertility hypothesis: a reevaluation,

676   *Population Studies* 40: 67-81.

677   Bergman, T.J., Phillips-Conroy, J.E., & Jolly, C.J. (2008). Behavioral variation and

678   reproductive success of male baboons (*Papio anubis×Papio hamadryas*) in a

679   hybrid social group. *American Journal of Primatology* 70: 136-147.

680   Bettridge, C. & Dunbar, R.I.M. (2012). Predation as a determinant of minimum group

681   size in baboons. *Folia Primatologica* 83: 332-352.

682   Bettridge, C., Lehmann, J. & Dunbar, R.I.M. (2010). Trade-offs between time,

683   predation risk and life history, and their implications for biogeography: a

684   systems modelling approach with a primate case study. *Ecological Modelling*

685   **221**, 777-790.

686   Boese, G.K. (1975). Social behaviour and ecological considerations of West African

687   baboons (*Papio papio*). In: *Socioecology and Psychology of Primates* (ed.

688   R.H. Tuttle) pp. 205-230. The Hague: Mouton.

689   von Borell, E., Dobson, H. & Prunier, A. (2007). Stress, behaviour and reproductive

690   performance in female cattle and pigs. *Hormones and Behavior* 52: 130-138.

691   Borgerhoff Mulder, M. (1989). Marital status and reproductive performance in

692   Kipsigis women: Re-evaluating the polygyny-fertility hypothesis. *Population*

693   *Studies* 43: 285-304.

694   Borries, C., Larney, L., Lu, A., Ossi, K. & Koenig, A. (2008). Costs of group size:

695   lower developmental and reproductive rates in larger groups of leaf monkeys.

696   *Behavioral Ecology* 19: 1186-1191.

697   Bowman, L.A., Dilley, S. & Keverne, E.B. (1978). Suppression of oestrogen-induced

698   LH surges by social subordination in talapoin monkeys. *Nature* 275: 56-58.

699   Bronikowski, A.M., Alberts, S.C., Altmann, J., Packer, C., Carey, K.D. & Tatar, M.

700   (2002). The aging baboon: comparative demography in a non-human primate.

701   *Proceedings of the National Academy of Sciences, USA* 99: 9591–9595.

702   Cameron EZ, Setsaas TH, Linklater WL. 2009 Social bonds between unrelated

703   females increase reproductive success in feral horses. *Proceedings of the*

704   *National Academy of Sciences, USA S* 106, 13 850–13 853.

705   Cheney, D.L., Seyfarth, R.M., Fischer, J., Beehner, J., Bergman, T., Johnson, S.E.,

706   Kitchen, D.M., Palombit, R., Rendall, D. & Silk, J.B. (2004). Factors affecting

707   reproduction and mortality among baboons in the Okavango Delta, Botswana.

708   *International Journal of Primatology* 25: 401-428.

709   Chojnacka, H. (1980), Polygyny and the rate of population growth. *Population*

710   *Studies* 34: 91-107.

711   Chowdhury, S., Pines, M., Saunders, J. & Swedell, L. (2015). The adaptive value of

712   secondary males in the polygynous multi-level society of haramyas baboons.

713   *American Journal of Physical Anthropology* 158: 501-513.

714   Clarke, I.J. (2014). Interface between metabolic balance and reproduction in

715   ruminants: Focus on the hypothalamus and pituitary. *Hormones and*

716   *Behavior* 66: 15-40.

717   Clauset, A., Shalizi, C.R., & Newman, M.E.J. (2009). Power-law distributions in

718   empirical data. *SIAM Review* **51**, 661-703.

719   Coulson, M.R. (1987). In the matter of class intervals for choropleth maps: with

720   particular reference to the work of George F. Jenks. *Cartographica* **24**, 16-39.

721   Cowlishaw, G. (1994). Vulnerability to predation in baboon populations.

722   *Behaviour* 131: 293-304.

723   Cowlishaw, G. (1997a). Trade-offs between foraging and predation risk determine

724   habitat use in a desert baboon population. *Animal Behaviour* 53: 667-686.

725   Cowlishaw, G. (1997b). Refuge use and predation risk in a desert baboon

726   population. *Animal Behaviour* 54: 241-253.

727   Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M. & Cheney, D.L. (2008).

728   Social stressors and coping mechanisms in wild female baboons (*Papio*

729   *hamadryas ursinus*). *Hormones and Behavior* 53: 254-265.

730   Dean, R.F.A. (1949). Women war captives in Russia. *British Medical Journal* 1: 691-

731   695.

732   Dobson, H., Fergani, C., Routly, J.E. & Smith, R.F. (2012). Effects of stress on

733   reproduction in ewes. *Animal Reproduction Science* 130: 135-140.

734   Dunbar, R.I.M. (1979). Population demography, social organisation and mating

735   strategies. In: I. Bernstein & E.O. Smith (eds) *Primate Ecology and Human*

736   *Origins*, pp. 65-88. New York: Garland.

737   Dunbar, R.I.M. (1980). Determinants and evolutionary consequences of dominance

738   among female gelada baboons. *Behavioural Ecology and Sociobiology* 7: 253-

739   265.

740   Dunbar, R.I.M. (1983a). Structure of gelada baboon reproductive units. IV. Organisation

741   at group level. *Zeitchrift fur Tierpsychologie* 63: 265-282.

742   Dunbar, R.I.M. (1983b). Structure of social relationships in nonsavannah baboons. In:

743   R.A. Hinde (ed) *Primate Social Relationships*, pp. 299-307. Oxford: Blackwells,.

744   Dunbar, R.I.M. (1984). *Reproductive Decisions: An Economic Analysis of Gelada*

745   *Baboon Social Strategies*. Princeton NJ: Princeton University Press.

746   Dunbar, R.I.M. (1988). Habitat quality, population dynamics and group composition in

747   colobus monkeys (*Colobus guereza*). *International Journal of Primatology* 9:

748   299-329.

749   Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia*

750   *Primatologica* 57: 121-131.

751   Dunbar, R.I.M. (2012). Bridging the bonding gap: the transition from primates to

752   humans. *Philosophical Transactions of the Royal Society, London,* 367B:

753   1837-1846.

754   Dunbar, R.I.M. (2018). Social structure as a strategy to mitigate the costs of group-

755   living: a comparison of gelada and guereza monkeys. *Animal Behaviour* 136:

756   53-64.

757   Dunbar, R.I.M. & Bose, U. (1991). Adaptation to grass eating in gelada baboons.

758   *Primates* 32: 1-7.

759   Dunbar, R.I.M. & Dunbar, P. (1975). *Social Dynamics of Gelada Baboons*. Basel:

760   Karger.

761   Dunbar, R.I.M., Mac Carron, P. & Robertson, C. (2018a). Tradeoff between fertility

762   and predation risk drives a geometric sequence in the pattern of group sizes in

763   baboons. *Biology Letters* 14: 20170700.

764   Dunbar, R.I.M., Mac Carron, P. & Shultz, S. (2018b). Primate social group sizes

765   exhibit a regular scaling pattern with natural attractors. *Biology Lett*ers 14:

766   20170490.

767   Dunbar, R.I.M. & Nathan, M. (1972). Social organisation of the Guinea baboon, *Papio*

768   *papio*, in Senegal. *Folia Primatologica* 17: 321-334.

769   Dunbar, R.I.M. & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147: 775-803.

770   Dunbar, R.I.M. & Shultz, S. (2017). Why are there so many explanations for primate
771   brain evolution? *Philosophical Transactions of the Royal Society, London,*
772   244B: 201602244.

773   Dunbar, R.I.M. & Sosis, R. (2017). Optimising human community sizes. *Evolution*
774   *and Human Behavior* 39: 106-111.

775   Dunbar, R.I.M., Korstjens, A.H. & Lehmann, J. (2009). Time as an ecological
776   constraint. *Biological Reviews* 84: 413-429.

777   Dunbar, R.I.M., Mac Carron, P. & Shultz, S. (2018). Fractal patterning of social
778   group size in primates. *Biology Letters* 14: 20170490.

779   Einarsson, S., Brandt, Y., Lundeheim, N. & Madej, A. (2008). Stress and its influence
780   on reproduction in pigs: a review. *Acta Veterinaria Scandinavica* 50: 1-48.

781   Garcia, C., Lee, P.C. & Rosetta, L. (2006). Dominance and reproductive rates in
782   captive female olive baboons, *Papio anubis*. *American Journal of Physical*
783   *Anthropology* 131: 64-72.

784   Harcourt, A.H. & Greenberg, J. (2001). Do gorilla females join males to avoid
785   infanticide? A quantitative model. *Animal Behaviour* 62: 905-915.

786   Hawkins, D. (1999). *Behaviour and Ecology of Baboons in the Mikumi National*
787   *Park, Tanzania.* PhD thesis, University of Liverpool.

788   Henzi, S.P., Lycett, J.E., Piper, S.E. (1997). Fission and troop size in a mountain
789   baboon population. *Animal Behaviour* 53: 525-535.

790   Higham, J.P., Warren, Y., Adanu, J., Umaru, B.N., MacLarnon, A.M., Sommer, V. &
791   Ross, C. (2009). Living on the edge: life-history of olive baboons at Gashaka-
792   Gumti National Park, Nigeria. *American Journal of Primatology* 71: 293-304.

793   Hill, R.A., Lycett, J. & Dunbar, R.I.M. (2000). Ecological determinants of birth intervals
794   in baboons. *Behavioral Ecology* 11: 560-564.

795   van Horn, R.C., Buchan, J.C., Altmann, J. & Altberts, S.C. (2007). Divided destinies:

796   group choice by female savannah baboons during social group

797   fission. *Behavioural Ecology and Sociobiology* 61: 1823-1837.

798   Jain, A. K. (2010). Data clustering: 50 years beyond K-means. *Pattern Recognition*

799   *Letters* 31: 651-666.

800   Jenks, G.F. (1967). The data model concept in statistical mapping. *International*

801   *Yearbook of Cartography* 7: 186-190.

802   Ji, T., Wu, J.J., He, Q.Q., Xu, J.J., Mace, R. & Tao, Y. (2013). Reproductive

803   competition between females in the matrilineal Mosuo of southwestern China.

804   *Philosophical Transactions of the Royal Society, London,* 368B: 20130081.

805   Jolly, C.J. (2007). Baboons, mandrills, and mangabeys: Afro-papionin socioecology

806   in a phylogenetic perspective. In: C. Campbell, A. Fuentes, K. MacKinnon, S.

807   Bearder & R. Stumpf (eds.) *Primates in Perspective*, pp. 240-251. Oxford:

808   Oxford University Press.

809   Kahlenberg, S.M., Thompson, M.E., Muller, M.N. & Wrangham, R.W. (2008).

810   Immigration costs for female chimpanzees and male protection as an

811   immigrant counterstrategy to intrasexual aggression *Animal Behaviour* 76:

812   1497-1509.

813   Kalra, S.P. & Kalra, P.S. (1996). Nutritional infertility: the role of the interconnected

814   hypothalamic neuropeptide Y–galanin–opioid network." *Frontiers in*

815   *Neuroendocrinology* 17: 371-401.

816   Kirchengast, S. & Huber, J. (2001). Fat distribution patterns in young amenorrheic

817   females. *Human Nature* 12: 123-140.

818   Korstjens, A.H., Verhoeckx, I. & Dunbar, R.I.M. (2006). Time as a constraint on group

819   size in spider monkeys. *Behavioural Ecology and Sociobiology* 60: 683-694.

820   Krause, J. & Ruxton, G. (2002). *Living in Groups*. Oxford: Oxford University Press.

821   Kudo, H. & Dunbar, R.I.M. (2001). Neocortex size and social network size in primates.

822   *Animal Behaviour* 62: 711-722.

823   Kummer, H. (1968). *Social Organisation of Hamadryas Baboons.* Basel: Karger.

824   Laatikainen, T.J. (1991). Corticotropin-releasing hormone and opioid peptides in

825   reproduction and stress. *Annals of Medicine* 23: 489-496.

826   Lehmann, J. & Dunbar, R.I.M. (2009a). Implications of body mass and predation for

827   ape social system and biogeographical distribution. *Oikos* 118: 379-390.

828   Lehmann, J. & Dunbar, R.I.M. (2009b). Network cohesion, group size and neocortex

829   size in female-bonded Old World primates. *Proceedings of the Royal Society,*

830   *London*, 276B: 4417-4422.

831   Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. (2007a). Group size, grooming and

832   social cohesion in primates. *Animal Behaviour* 74: 1617-1629.

833   Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. (2007b). Fission-fusion social

834   systems as a strategy for coping with ecological constraints: a primate case.

835   *Evolutionary Ecology* 21: 613-634.

836   Linklater, W.L., Cameron, E., Minor, E.O. & Stafford, K.J. (1999). Stallion

837   harassment and the mating system of horses. Animal Behaviour 58: 295-306.

838   Mac Carron, P. & Dunbar, R.I.M. (2016). Identifying natural grouping structure in

839   gelada baboons: a network approach. *Animal Behaviour* 114: 119-128.

840   McClure, T.J. (1968). Malnutrition and infertility of cattle in Australia and New

841   Zealand. *Australian Veterinary Journal* 44: 134-138.

842   Markham, A.C., Guesquiere, L.R., Alberts, S.C. & Altmann, J. (2015). Optimal group

843   size in a highly social mammal. *Proceedings of the National Academy of*

844   *Sciences, USA,* 112: 14882-14887.

845   Massen, J.J.M., Sterck, E.H.M. & de Vos, H. (2010). Close social associations in

846   animals and humans: functions and mechanisms of friendship. *Behaviour* 147:

847   1379–1412.

848   Ménard, N., & Vallet, D. (1993). Dynamics of fission in a wild Barbary macaque

849   group (*Macaca sylvanus*). *International Journal of Primatology* 14: 479-500.

850   Mesnick, S.L. (1997). Sexual alliances: evidence and evolutionary implications. In:

851   P.A. Gowaty (ed.) *Feminism and Evolutionary Biology*, pp. 207–60. London:

852   Chapman & Hall.

853   Mori, A., Iwamoto, T., Mori, U. & Bekele, A. (1999). Sociological and demographic

854   characteristics of a recently found Arsi gelada population in Ethiopia.

855   *Primates* 40:365-381.

856   Muhsam, H.V. (1956). Fertility of polygamous marriages. *Population Studies* 10: 3-

857   16.

858   Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons and their

859   hybrids at a species border in Ethiopia. *Folia Primatologica 19*: 104-165.

860   Nuñez, C.M.V., Adelman, J.S. & Rubenstein, D.I. (2015). Sociality increases juvenile

861   survival after a catastrophic event in the feral horse (*Equus caballus*).

862   *Behavioral Ecology* 26: 138–147.

863   Ohsawa, H. & Dunbar, R.I.M. (1984). Variations in the demographic structure and

864   dynamics of gelada baboon populations. *Behavioural Ecology and*

865   *Sociobiolology* 15: 231-240.

866   Patzelt, A., Zinner, D., Fickenscher, g., Dieghou, S., Camara, B., Stahl, D. & Fischer,

867   J. (2011). Group composition of Guinea baboons (*Papio papio*) at a water

868   place suggests a fluid social organization. *International Journal of*

869   *Primatology* 32: 652-668.

870   Pettay, J.E., Lahdenperä, M., Rotkirch, A. & Lummaa, V. (2016). Costly reproductive

871   competition between co-resident females in humans. *Behavioral Ecology* 27:

872   1601-1608.

873   Pusey, A.E. & Schroepfer-Walker, K. (2013). Female competition in

874   chimpanzees. *Philosophical Transactions of the Royal Society, London,* 36B8:

875   20130077.

876   van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour* 87:

877   120-144.

878   Schliep, K.C., Mumfored, S.L., Vladutiu, C.J., Ahrens, K.A., et al. (2015). Perceived

879   stress, reproductive hormones, and ovulatory function: a prospective cohort

880   study. *Epidemiology* 26: 177-184.

881   Schreier, A.L. & Swedell, L. (2012a). Ecology and sociality in a multilevel society:

882   ecological determinants of spatial cohesion in hamadryas baboons. *American*

883   *Journal of Physical Anthropology* 148: 580-588.

884   Schreier, A. & Swedell, L. (2012b). The socioecology of network scaling ratios in the

885   multilevel society of hamadryas baboons. *International Journal of*

886   *Primatology* 33: 1069-1080.

887   Schwartz, M.W. & Seeley, R.J. (1997). Neuroendocrine responses to starvation and

888   weight loss. *New England Journal of Medicine* 336: 1802-1811.

889   Seifer, D.B. & Collins, R.L. (1990). Current concepts of β-endorphin physiology in

890   female reproductive dysfunction. *Fertility and Sterility* 54: 757-771.

891   Sharman, M. (1981). *Feeding, Ranging and Social Organization of the Guinea*

892   *Baboon*. PhD thesis, University of St. Andrews.

893   Shultz, S. & Dunbar, R.I.M. (2010). Encephalisation is not a universal

894   macroevolutionary phenomenon in mammals but is associated with sociality.

Proceedings of the National Academy of Sciences, USA, **107**, 21582-21586.

Shultz, S. & Finlayson, L.V. (2010). Large body and small brain and group sizes are associated with predator preferences for mammalian prey. *Behavioral Ecology* 21: 1073-1079.

Shultz, S., Noe, R., McGraw, S. & Dunbar, R.I.M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society, London,* 271B: 725-732.

Sigg, H. & Stolba, A. (1981). Home range and daily march in a hamdryas baboon troop. *Folia Primatologica* 36: 40-75.

Sigg, H., Stolba, A., Abegglen, J.-J. & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates* 23: 473-487.

Silk, J.B., Alberts, S.C. & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science* **302**, 1232-1234.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., et al. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society, London,* 276B: 3099-3104.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., et al. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology* 20: 1359-1361.

Smith, C.A. (1947). The effect of wartime starvation in Holland upon pregnancy and its product. *American Journal of Obstetrics and Gynecology* 53: 599-608.

919 Smith, J.E., &. Kunz, P.R. (1976) Polygyny and fertility in nineteenth century
920   America. *Population Studies* 30: 465-480.

921 Smuts, B.B. & Nicholson, N. (1989). Dominance rank and reproduction in female
922   baboons. *American Journal of Primatology* 19: 229-246.

923 Srivastava, A. & Dunbar, R.I.M. (1996). The mating system of hanuman langurs: a
924   problem in optimal foraging. *Behavioural Ecology and Sociobiology* 39: 219-
925   226.

926 Städele, V., Pines, M., Swedell, L. & Vigilant, L. (2016). The ties that bind: maternal
927   kin bias in a multilevel primate society despite natal dispersal by both Sexes.
928   *American Journal of Primatology* 78: 731-744.

929 Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio
930   hamadryas hamadryas*). *International Journal of Primatology* 23: 1205-1226.

931 Swedell, L. & Saunders, J. (2006). Infant mortality, paternity certainty, and female
932   reproductive strategies in hamadryas baboons. In: L. Swedell & S. Leigh (eds)
933   *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life
934   History Perspectives*, pp. 19-51. New York: Springer.

935 Warren, M.P. & Perlroth, N. E. (2001). The effects of intense exercise on the female
936   reproductive system. *Journal of Endocrinology* 170: 3-11.

937 Willems, E. & Hill, R.A. (2009). Predator-specific landscapes of fear and resource
938   distribution: effects on spatial range use. *Ecology* 90: 546–555.

939 Wilson, M. & Mesnick, S.L. (1997). An empirical test of the bodyguard hypothesis.
940   In *Feminism and Evolutionary Biology* (ed. P.A. Gowaty) pp. 000-000.
941   London: Chapman & Hall.

942   Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M. & Cheney,
943   D.L. (2008). Focused grooming networks and stress alleviation in wild female
944   baboons. *Hormones and Behavior* 54: 170-177.

945   Zacur, H.A., Chapanis, H.P., Lake, C.R., Ziegler, M. & Tyson, J.E. (1976).
946   Galactorrhea-amenhorrea: psychological interaction with neuroendocrine
947   function. *American Journal of Obstetrics and Gynecology* 125: 859-862.

948   Zinner, D., Peláez, F. & Torkler, F. (2001). Group composition and adult sex-ratio of
949   hamadryas baboons (*Papio hamadryas hamadryas*) in central
950   Eritrea. *International Journal of Primatology* 22: 415-430.

951   Zinner, D., Wertheimer, J., Liedigk, R., Groeneveld, L.F. & Roos, C. (2013). Baboon
952   phylogeny as inferred from complete mitochondrial genomes. *American
953   Journal of Physical Anthropology* 150: 133-140.

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956 **Legends to Figures**

957

958 Figure 1. Distribution of social group sizes in baboon (*Papio* and *Theropithecus*)

959 populations. Dashed vertical lines demarcate the optimal group sizes of 18.7,

960 41.0, 79.1 and 180.3, averaged for the two the maximum likelihood estimates

961 (see text for details).

962

963 Figure 2. Mean (±2 se) group size for individual species. Samples size are: *P. anubis*

964 = 102, *P. cynocephalus* = 109, *P. ursinus* = 165, *P. hamadryas* = 13; *P. papio*

965 = 34 groups; *Theropithecus gelada* = 22 groups.

966

967 Figure 3. Proportion of groups in populations with >4 censused groups that fell into

968 the lowest oscillator (20/40) for all six species.

969

970 Figure 4. Mean (±1se) population mean group size as a function of predator (lion +

971 leopard) density (filled symbols: >0.25 /km^2; unfilled symbols: <0.25/km^2)

972 and percentage tree cover. Data: *ESM* Table S2.

973

974 Figure 5. Mean population group size plotted against a composite index of predation

975 risk (standard deviation of predator density plus standard deviation of

976 converse of tree cover [i.e. 100 - % tree cover]). Unfilled symbols: woodland

977 baboon populations; filled symbols: hamadryas and gelada populations. Data:

978 Table S2.

979

980   Figure 6. Mean group size for individual baboon populations, plotted against annual

981   rainfall. Filled circles: woodland baboon populations; open circle: Guinea

982   baboon population; triangles: hamadryas populations. The solid line gives the

983   maximum ecologically tolerable group size (N_{max}) determined by the time

984   budget model, and the dashed line gives the minimum group size (N_{min})

985   determined by predation risk, using the equations from Bettridge et al. (2010)

986   and converting all climatic variables into functions of annual rainfall (using

987   regression equations based on data given by Bettridge et al. 2010). Heavy

988   solid line plots percentage of tree cover, based on data given for baboon study

989   sites by Bettridge et al. (2010). See text for details.

990

991   Figure 7. Mean fertility (births per adult female per year) for individual baboon

992   groups, plotted against group size. Filled circles: woodland baboons; open

993   circles: Guinea baboons; solid triangles: hamadryas; open triangles: gelada.

994   The best fit regression for the three woodland species combined has a

995   quadratic form (solid line, with 95% CI indicated by dotted lines). A separate

996   regression (dashed line) is set through the hamadryas and gelada datapoints,

997   with a quadratic again being the best fit.

998

999   Figure 8. Group size over succeeding time units (years), given the birth rates shown in

1000   Fig. 7 for woodland species and an annual mortality rate varying across a

1001   normal distribution with a mean of 10% and varying between 4-16%, for

1002   different initial group sizes (N=15 = dotted line; N=17 = short dash; N=20 =

1003   long dash; N=25 = solid). The lines are mean values for 10,000 simulations in

1004   each case. If a group fissions at a size of ~60, it might do so into daughter

1005   groups of 20 and 40 (heavy arrows) or two groups of 30. Grey zone: region

1006   (N<17) within which a group will inevitably go extinct because its death rate

1007   will always exceed its birth rate.

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1011   Table 1. AIC values for the model tested for the distribution of baboon group sizes.

1012   The best-fit model (that with the lowest AIC value) is shown in bold.

1013

1014   Distribution   AIC

1015   --

1016   Power law   4632.7

1017   Exponential   4006.5

1018   Truncated power law   4099.1

1019   Weibull   3978.1

1020   Gaussian   4061.6

1021   Log-normal   3914.6

1022   Geometric   4045.3

1023   Negative binomial   3967.5

1024   Poisson (single)   12829.6

1025   **Compound Poisson***   **3207.0**

1026   ---

1027   * A compound Poisson composed of four Poisson distributions with different

1028   means

1029

1030   Table 2. Optimal number of clusters, and the resulting cluster means and mean scaling

1031   ratios between successive clusters, for each of the species separately,

1032   compared to that for the pooled sample, using the Jenks algorithm.

1033

Species	Cluster means *				Mean scaling ratio
All *Papio* species	19.8 (202)	45.6 (138)	79.1 (65)	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)	131.0 (8)	237.3 (4)	2.11

1045   * Numbers in parentheses in the body of the table are the number of groups assigned
1046   to the cluster by the algorithm.

1047   § Jenks gives four clusters, but the two largest contain only one and two groups,
1048   respectively, with cluster means of 150 and 210. The weighted average is 190.
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Figure 1

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Figure 2

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1073   **Figure 3**

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Figure 4

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Figure 5

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1102 **Figure 6**

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1106 **Figure 7**

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Figure 8

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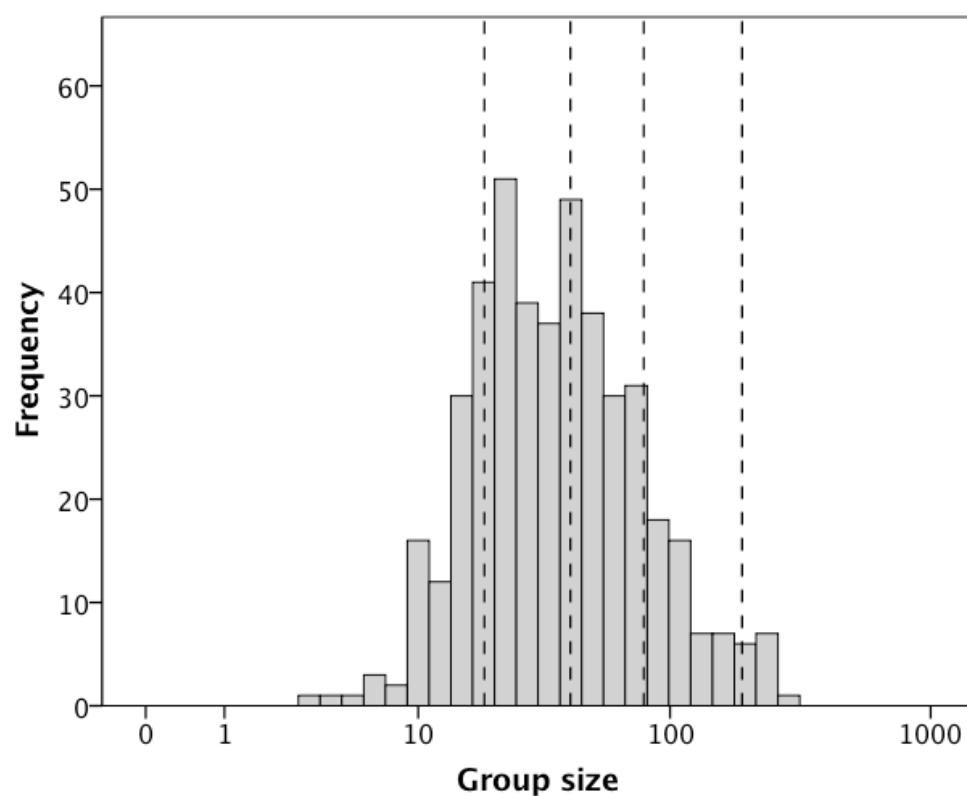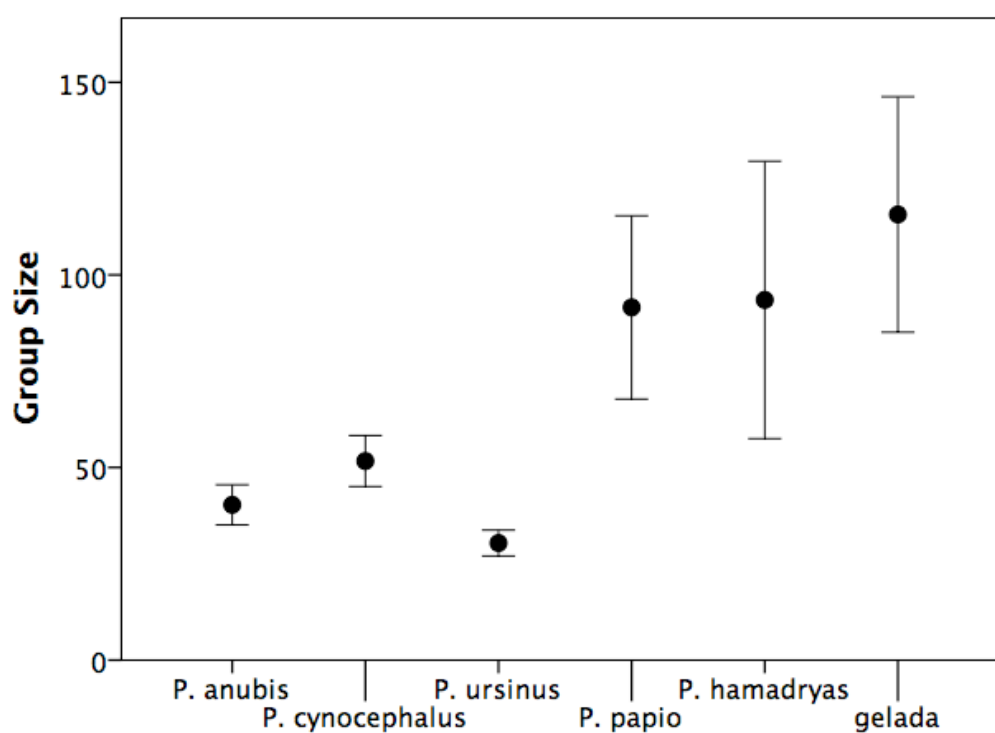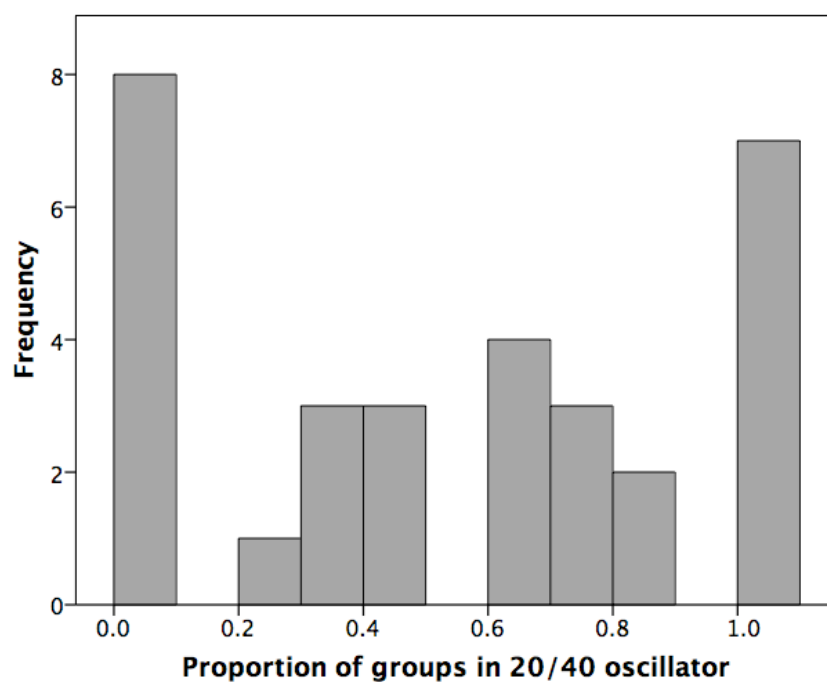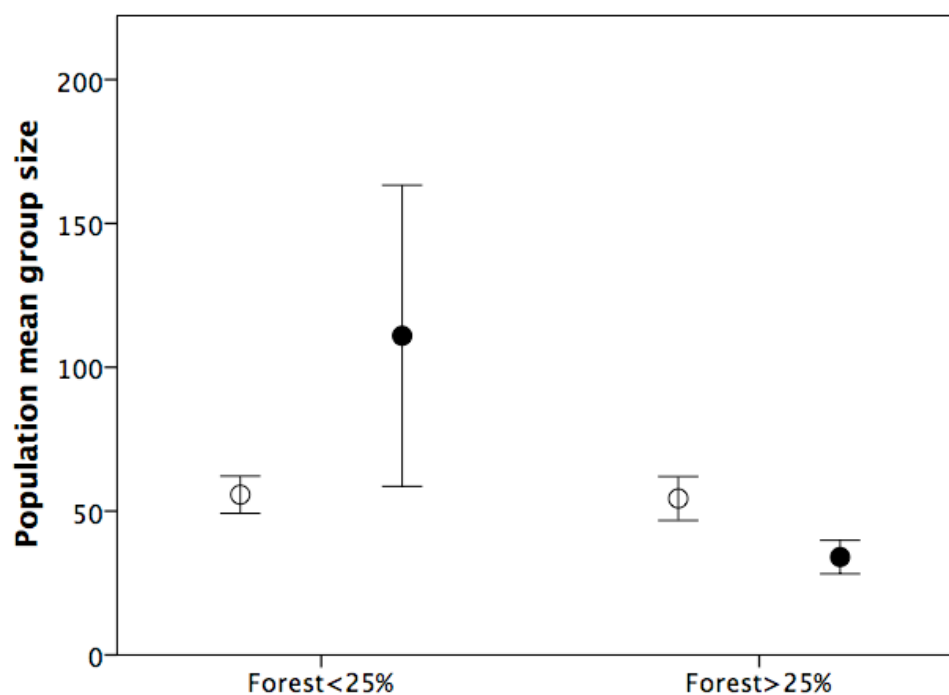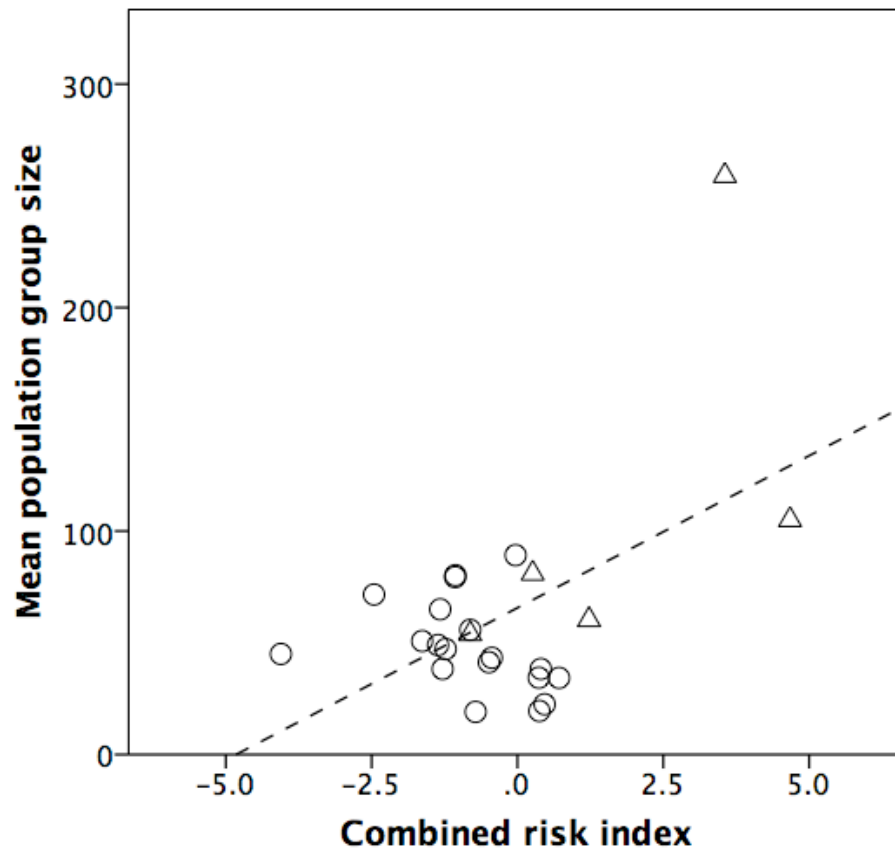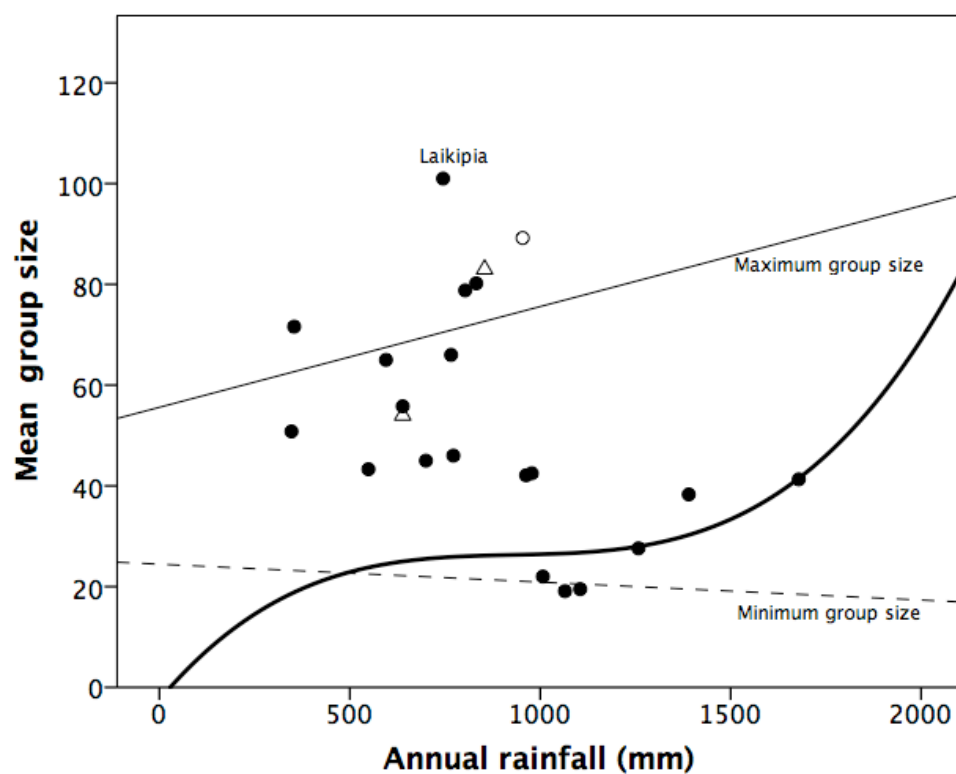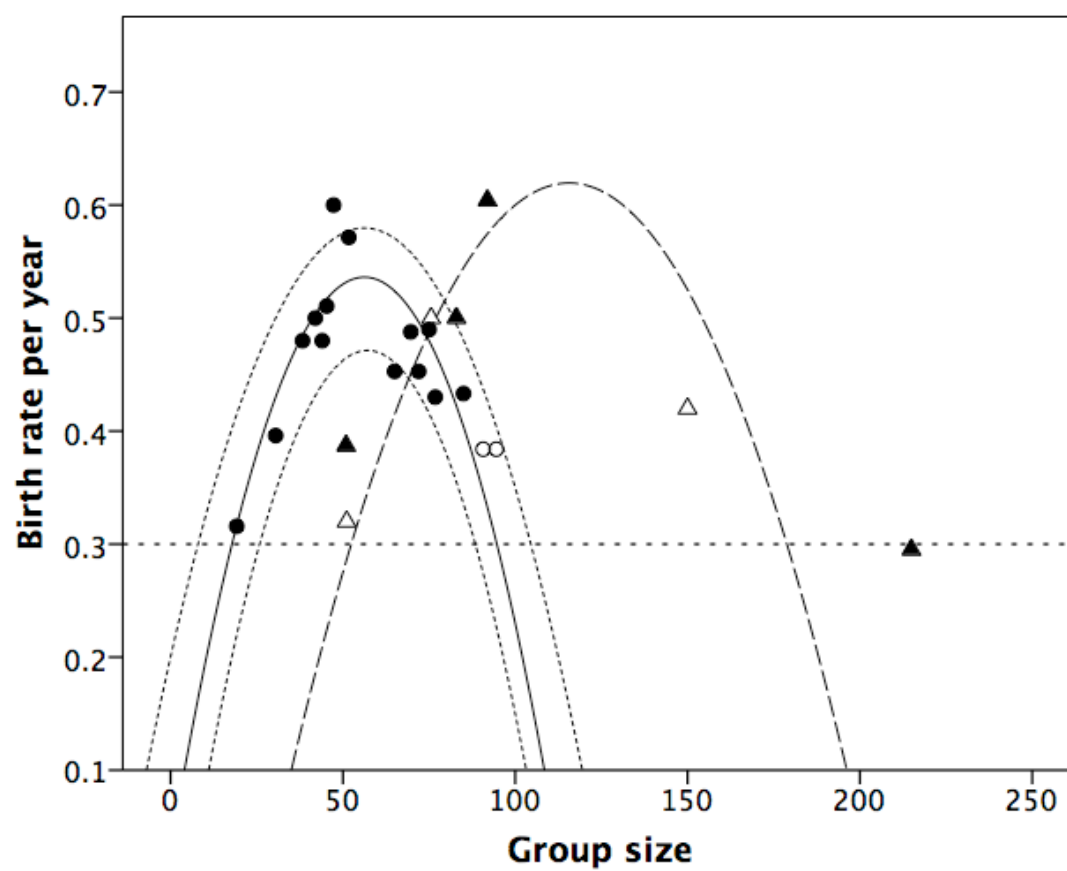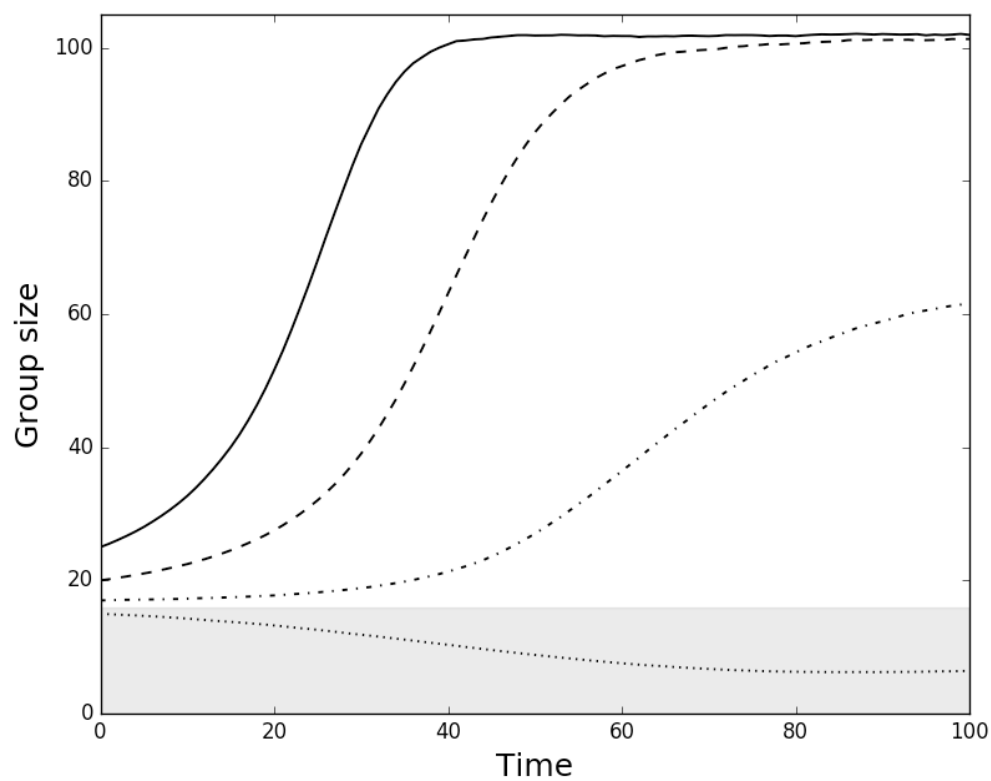
1116 **The Tradeoff Between Fertility and Predation Risk Drives a Fractal**

1117 **Pattern of Group Sizes in a Social Mammal (Baboons, Genus *Papio*)**

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1119 **R.I.M. Dunbar and Padraig Mac Carron**

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1121 **Supplementary Information**
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1124 *Supplementary Methods*

1125 We take group (or troop) size to be that defined by the field worker: in most cases,
1126 this grouping is fairly obvious, since the animals forage and sleep together, and
1127 maintain a degree of demographic coherence and stability as well as spatial separation
1128 from other similar groups. For *Papio hamadryas*, we follow convention and take the
1129 band to be the homologue of the *Papio* troop – a set of animals that share the same
1130 home range (Kummer 1968). Exactly what counts as a group in *Papio papio* has been
1131 the subject of debate because of this species' rather flexible form of sociality (Dunbar
1132 & Nathan 1972; Boese 1975; Sharman 1981), but all field workers on this species
1133 agree on the existence of some form of stable social group, at least as defined by
1134 animals that share a common range area (Patzelt et al. 2011). The data are provided in
1135 the *SI* Table S1.

1136

1137 In most cases, fertility rates are based on observed mean birth rate or mean interbirth
1138 interval. In a few cases, birth rates were estimated from the number of immatures per
1139 female in a group. Immatures are defined as animals that are pre-puberty, with
1140 puberty occurring at around 4 years of age (Altmann et al. 1977). In the case of the
1141 gelada, we have used mean herd size rather than band size as the appropriate social
1142 grouping for comparison with the other *Papio* species: this is because gelada bands
1143 are probably not the homologue of baboon troops (MacCarron & Dunbar 2016) but
1144 rather are loose clusterings of harems that share a common range area. Not all the
1145 units of a band are found together on any given day (herd sizes vary from a single
1146 harem to upwards of 50 harems from several bands). Given that the driver of
1147 functional infertility is the number of individuals who are foraging or resting together
1148 at any given time, mean herd size seems the most appropriate measure.

1149
1150
1151 *Supplementary Results*
1152

1153 Fig. S1 plots the distribution of forest cover at sites listed by Bettridge et al. (2010)
1154 where the six species have been studied in detail, with gelada habitats from Iwamoto &

1155   Dunbar (1983). For *Papio* species, forest cover is estimated from satellite imagery; that
1156   those for the gelada sites are based on ground transects carried out by the authors.
1157   Hamadryas and gelada live in habitats with especially low levels of forest cover. Note,
1158   however, that these data underestimate the contrast between hamadryas and gelada
1159   habitats and those occupied by other baboon species: the size of trees is much smaller in
1160   most hamadryas and gelada habitats than those in the habitats occupied by the other
1161   woodland baboon species. In gelada habitats, for example, few trees are over 5m in
1162   height.
1163

1164
1165   *Fig. S1*
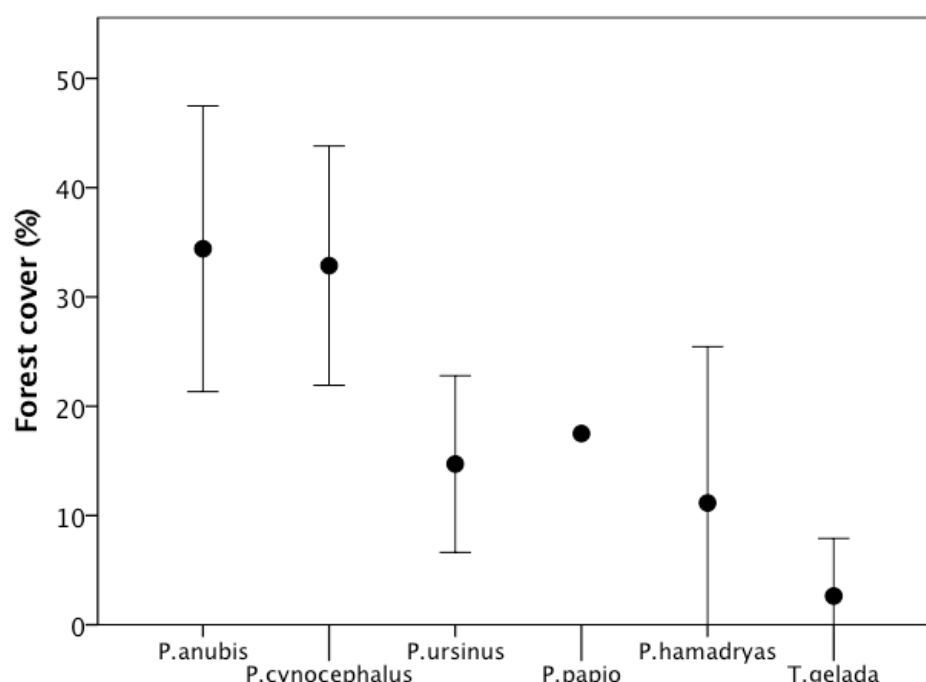
1166   *Mean (±2 se) forest cover (indexed as percentage of ground cover) for the six species.*
1167   *Sources: Bettridge et al. (2010) and Iwamoto & Dunbar (1983)*
1168
1169

1170   Baboon fertility is independently predicted by both the number of adult females in the
1171   group and the mean ambient temperature of the habitat (an index of habitat quality)
1172   (Hill et al. 2000). To check whether environmental conditions might be a confound in
1173   our results, we regressed birth rate on mean habitat ambient temperature as a
1174   quadratic relationship (b = -0.672 + 0.104Temp - 0.00231*Temp^2: $F_{2,18}$=3.77,
1175 r^2=0.296, p=0.043; linear: $F_{1,19}$=0.01, r^2=0.000, p=0.933), and calculated residual
1176   birth rates from this regression. The results (Fig. S2) are identical to those shown in
1177   Fig. 3. Gelada were not included in this analysis because they inhabit a different (very
1178   high altitude) temperature regime to *Papio* baboons.
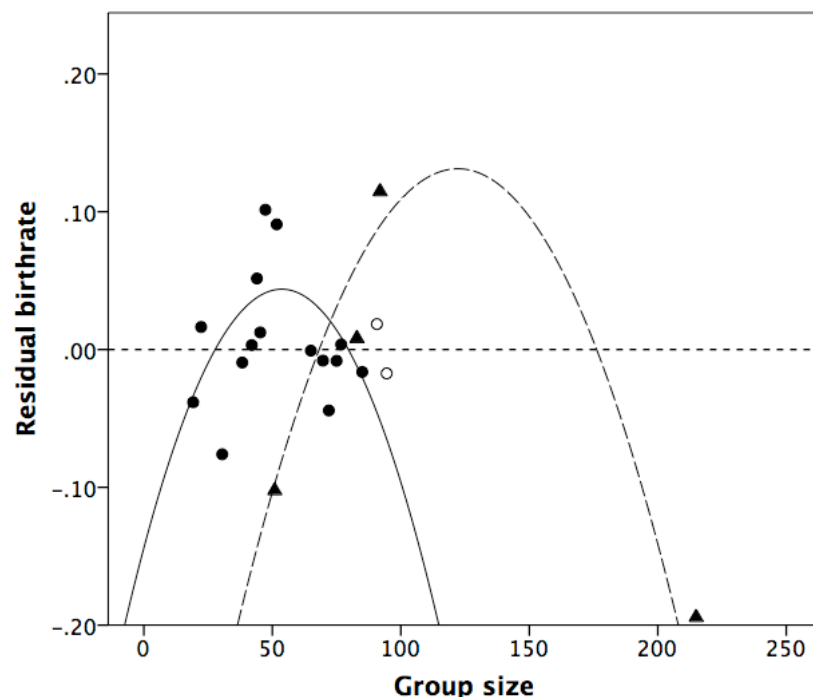
Figure S2

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 (see text).

Fig. S3 confirms that the results of Fig. 3 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. 3, 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).

Overall, the average number of females in baboon groups is 14.5±6.9, and average group size is 50.3±21.4 (N=16), for a ratio of 0.288. Fig. S5 plots the data for these groups: the regression line has a slope of ~3. The mean ratio of females to total group size for these individual groups is 0.282±0.05. In fact, this value seems to be characteristic across primates as a whole (data in Campbell et al. 2007).
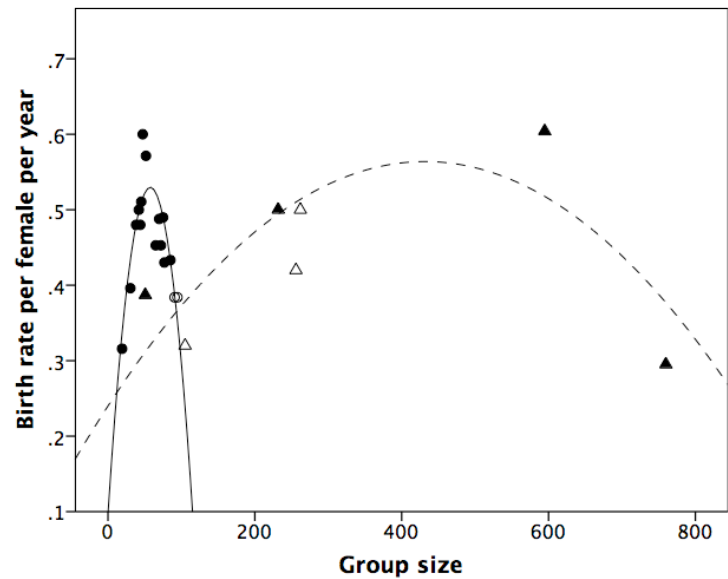
Figure S4

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. Separate quadratic regressions set to data for savannah baboons and P. hamadryas, respectively.
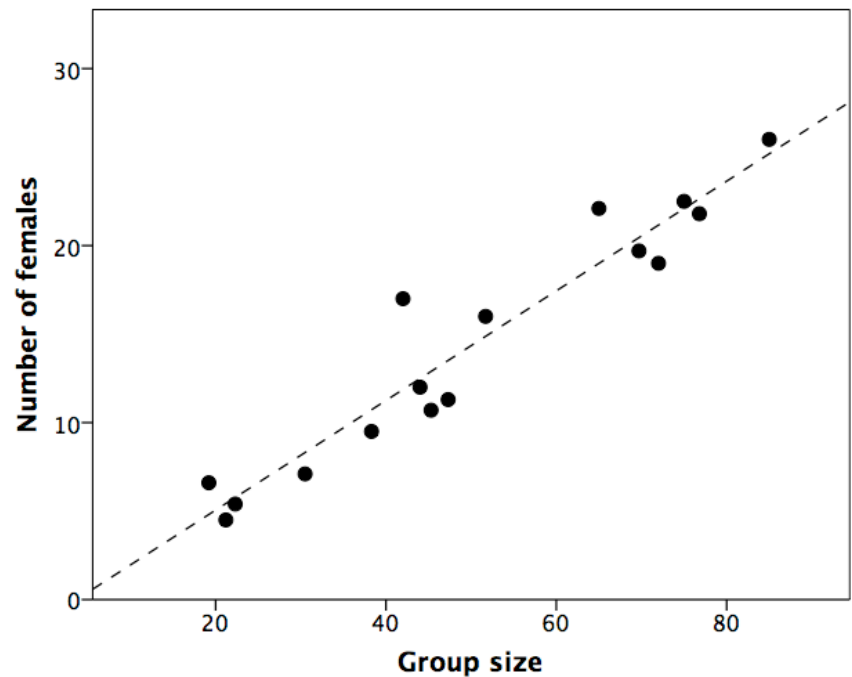

Figure S5

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.

REFERENCES

1219
1220

1221 Bettridge, C., Lehmann, J. & Dunbar, R.I.M. (2010). Trade-offs between time,
1222 predation risk and life history, and their implications for biogeography: a
1223 systems modelling approach with a primate case study. *Ecol. Modelling* 221:
1224 777-790.

1225 Boese, G.K. (1975). Social behaviour and ecological considerations of West African
1226 baboons (*Papio papio*). In: R.H. Tuttle (ed.) *Socioecology and Psychology of
1227 Primates*, pp. 205-230. The Hague: Mouton.

1228 Campbell, C.J., Fuentes, A., Mackinnon, K.C., Panger, M. & Bearder, S.K. (eds)
1229 (2007). *Primates in Perspective*. Oxford: Oxford University Press.

1230 Dunbar, R.I.M. & Nathan, M. (1972). Social organisation of the Guinea baboon, *Papio
1231 papio*, in Senegal. *Folia Primatologica* 17: 321-334.

1232 Hill, R.A., Lycett, J. & Dunbar, R.I.M. (2000). Ecological determinants of birth intervals
1233 in baboons. *Behavioural Ecology* 11: 560-564.

1234 Iwamoto, T. & Dunbar, R.I.M. (1983). Thermoregulation, habitat quality and the
1235 behavioural ecology of gelada baboons. *Journal of Animal Ecology* 52: 357-366.

1236 Kummer, H. (1968). *Social Organisation of Hamadryas Baboons*. Basel: Karger.

1237 MacCarron, P. & Dunbar, R.I.M. (2016). Identifying natural grouping structure in
1238 gelada baboons: a network approach. *Animal Behaviour* 114: 119-128.

1239 Patzelt, A., Zinner, D., Fickenscher, g., Dieghou, S., Camara, B., Stahl, D. & Fischer,
1240 J. (2011). Group composition of Guinea baboons (*Papio papio*) at a water
1241 place suggests a fluid social organization. *International Journal of
1242 Primatology* 32: 652-668.

1243 Sharman, M. (1981). *Feeding, Ranging and Social Organization of the Guinea
1244 Baboon*. PhD thesis, University of St. Andrews.

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