



The Infertility Trap: The Fertility Costs of Group-Living in Mammalian Social Evolution

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Mammal social groups vary considerably in size from single individuals to very large herds. In some taxa, these groups are extremely stable, with at least some individuals being members of the same group throughout their lives; in other taxa, groups are unstable, with membership changing by the day. We argue that this variability in grouping patterns reflects a tradeoff between group size as a solution to environmental demands and the costs created by stress-induced infertility (creating an infertility trap). These costs are so steep that, all else equal, they will limit group size in mammals to ~15 individuals. A species will only be able to live in larger groups if it evolves strategies that mitigate these costs. We suggest that mammals have opted for one of two solutions. One option (fission-fusion herding) is low cost but high risk; the other (bonded social groups) is risk-averse, but costly in terms of cognitive requirements.

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INTRODUCTION

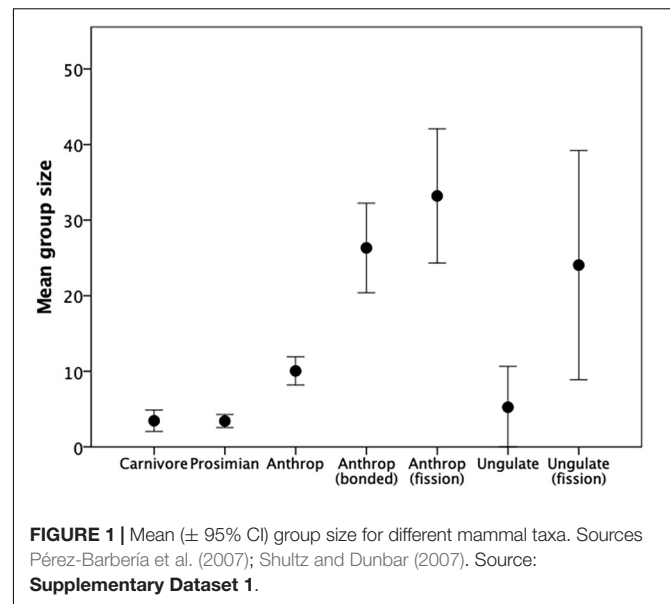
For most social animals, the group provides a buffer between the individual and its environment. In mammals, groups vary in size and structure from family groups centred around monogamous pairs (most canids, miniature antelope, some primates) to small harems of 10–20 individuals (usually but not always with one breeding male: some antelope, lion, some primates), large stable groups (some primates, dolphins, elephants) and very large, unstable herds (many herding antelope and deer) (Clutton-Brock, 2016). Parallel categorisations are recognised for birds and fish, although in this case most species fall into either the pairbonded (the vast majority in the case of birds) or large unstable social groupings (many seabirds and other flocking species) categories, or both (colonial nesters) (Ligon, 1999; mating system Taborsky and Wong, 2017), with just a few birds having small, stable primate-like groups (notably parrots, babblers and mousebirds). We focus in this paper on mammals.

Cutting across these categories is an important distinction between *aggregations* (unstable herds and flocks whose composition is variable and largely anonymous) and *congregations* (stable groups in which individuals usually remain for life and have personalised relationships) (Allee, 1927; Morris et al., 1992; Parrish et al., 1997). The distinction hinges on the stability of groupings through time, and hence on the extent to which individuals are motivated to remain with specific individuals. Herds are typically anonymous and their membership is relatively unstable (even though there may be small stable cores such as female-offspring subgroups); bonded groups have stable memberships created by a core of members who have personalised affiliative relationships.

Aggregations tend to convene and disperse on the scale of hours or days, as individual animals or subsets of animals come together or drift apart as environmental circumstances dictate. They typically form either on rich localised food patches (dispersing once the patch has been exhausted: e.g., deer, antelope, geese, many shorebirds) or as a temporary anti-predator strategy in high risk habitats (e.g., stingray: Semeniuk and Dill, 2005). Social relationships are typically casual and avoidant (such that individuals usually maintain a distance from each other), with interactions rarely involving more than dyads. Group size is adjusted on a moment-by-moment basis through individuals joining or leaving (as joiner/leaver models describe: Krause and Ruxton, 2002). In contrast, congregations are stable over time (on the scale of years, subject to the flux of births and deaths); individuals know each other as individuals and usually devote a significant amount of time to affiliative behaviours (social grooming, sitting in physical contact) with some, but never all, of their group members. These species are often distinguished by engaging in social play as juveniles (Fagen, 1981; Lewis, 2000; Iwaniuk et al., 2001). Congregations typically have a stable core (often only one sex disperses) with groups changing size mainly through group fusion (rare) or group fission (Dunbar, 1988; Dunbar et al., 2009). Unlike aggregations, these kinds of groups are based on individual bonds between individuals that are built up through social grooming or other forms of affiliative behaviour (Dunbar and Shultz, 2010; Massen et al., 2010).

Living in bonded groups increases the costs of group-living because individuals are not free to pursue their own activities when they want to, but instead must coordinate their activities with the rest of the group. The 'flexible herd' strategy minimises these costs: animals that have converged to form a herd simply drift apart, mainly because of differences in activity scheduling (Ruckstuhl and Kokko, 2002; Ruckstuhl and Neuhaus, 2002; Calhim et al., 2006; Dunbar and Shi, 2008; King and Cowlishaw, 2009). However, they do so at the risk of individuals being caught alone or in groups of sub-optimal size should a predator appear. Living in stable groups avoids this problem and can be viewed as a risk averse strategy that allows animals to be sure that they will always have conspecifics with them. However, it does so at the cost of incurring stresses that are not easily mitigated: these costs will naturally limit group size unless solutions can be found (Dunbar and Shultz, 2021). The intensity of bonding can vary, but in the limit the inertia created by social bonds means that these groups can only adjust their size through group fission (as opposed to individuals drifting away on their own), a process that can take many months, sometimes even years. The need to ensure that both the daughter groups are large enough to cope with the local predation risk means that groups can only undergo fission when their size is double this minimum: this results in a trajectory of group size over time that has the form of a non-linear oscillator between limits set by the environment, with the group under stress at either end of the cycle (Dunbar et al., 2009, 2018a; Dunbar and MacCarron, 2019).

This dichotomy has profound implications for the size of groups that mammals can achieve, as **Figure 1** illustrates. Groupings on the scale of seabird breeding colonies or pelagic fish shoals simply do not occur, other than during brief periods



of migration in some ungulates (wildebeest, saiga antelope) and some rodents (lemmings). With a handful of exceptions (e.g., spotted hyaena), most carnivores, the smaller ungulates and the prosimians forage solitarily (all felids except the lion, all galagines), are pairbonded (some canids, many small-bodied ungulates, medium-sized prosimians) or live in groups of 5–15 individuals (large-bodied canids, the social lemurs) (Shultz and Dunbar, 2007). Many of the larger-bodied ungulates, in contrast, live in large, unstable herds characterised by fission-fusion sociality that allows the animals to maintain flexible group sizes (Jarman, 1974; Shultz and Dunbar, 2007). Although very large herds can form (e.g., during mass migrations), typical herd size is actually in the region of 20–30 individuals (**Figure 1**). Anthropoid primates contrast with all three of these Orders: groups of 10–15 are their default social units (many New World monkeys and Old World colobines), but groups can be as large as 25–30 if they have strongly bonded relationships (cercopithecines), and >50 if they operate some form of fission-fusion sociality in addition (gelada and hamadryas baboons: Dunbar and MacCarron, 2019; chimpanzees: Lehmann et al., 2007a). This also seems to apply to a small number of other (mainly species-poor) mammalian orders (elephants, delphinids, equids, camelids), all of which share with anthropoid primates the capacity for females to form bonded coalitions (Shultz and Dunbar, 2010).

Most small-bodied mammals, in contrast, are nocturnal and solitary, coming together only for mating (or, in a few cases, while infants are being reared: e.g., prairie voles), although some form stable breeding pairs while foraging separately (e.g., elephant shrews) (Müller and Thalmann, 2000). Many of the smaller ungulates are also *de facto* solitary in that, even if they occupy a joint territory as a monogamous pair, they forage and rest alone (e.g., duiker, dikdik, suni, oribi). With the latter exceptions, most of these smaller mammal species are solitary: interactions outside the breeding season are largely antagonistic, such affiliative signalling as there is associated only with mating,

and most social signals likely to be olfactory (distance signals such as scent marking) rather than behavioural (close signals). This form of sociality appears to be ancestral to mammals (Müller and Thalmann, 2000).

Ultimately, the limit on group size is set by the point at which the costs of group-living exceed the benefits, or more strictly the point at which the tradeoff between the costs and benefits results in fertility dropping below replacement rate. The costs of group-living are conventionally viewed as being a consequence of density-dependent, within-group competition for resources (Clutton-Brock et al., 1983; Chapman, 1990; Molvar and Bowyer, 1994; Andersen and Linnell, 1998; Pettorelli et al., 2002; Nilsen et al., 2004; Shi and Dunbar, 2005; Thompson et al., 2007; Borowik and Jwdrzejewska, 2018). The effects of these costs are usually reflected in increased foraging competition, higher rates of aggression, longer day journeys, and elevated time budget allocations to foraging (Dunbar et al., 2009; Markham et al., 2015), all of which typically increase monotonically with the number of individuals in the group (Dunbar et al., 2009). These factors, in particular competition for access to food, are conventionally assumed to be responsible for reduced fertility when this is observed.

This assumption, however, is open to question. Although both excessive exercise (primates: Williams et al., 2001; humans: Bullen et al., 1985; Frisch, 1987; Ellison, 1990; Warren and Perlroth, 2001) and lack of food (Clutton-Brock et al., 1983; ungulates: Albon et al., 1983; mongoose: Creel et al., 2013; primates: Williams et al., 2007; Gesquiere et al., 2018; humans: Dean, 1949; Stein and Susser, 1975; Arends et al., 2012) can adversely affect fertility, this usually happens only in cases involving significant weight loss (typically > 15% of body mass, or close to starvation). In a within- and between-population study of red deer living in thermally stressful environments at high latitudes, Albon et al. (1983) found that conception rates were significantly reduced only for females in the lower tercile of normal adult body weight (i.e., those already on the margin for survival).

A more serious problem with this assumption is that models of the time constraints operating on group-living anthropoid primates (representing all the ape and African Old World monkey genera, and one New World monkey genus) and one group-living ungulate (feral goats) suggest that these species only reach the limits of their respective carrying capacities on the fringes of their biogeographic distributions (Dunbar et al., 2009, 2019; Dunbar and Shi, 2013; Korstjens et al., 2018). In every case, observed group sizes are considerably smaller than those that their local habitat would allow. This suggests that while ecological constraints undoubtedly do set limits on the grouping patterns of these taxa, this only becomes an issue toward the periphery of the taxon's biogeographic distribution. For most of their populations, something else is limiting group size at well below the local carrying capacity.

An alternative, and largely overlooked, possibility is the effect that the stresses of group-living have on female fertility independent of environmental quality or nutrient throughput. Birth rates have been reported to decline with either group size or the number of females in a group across a wide range of mammalian taxa (mammals in general: Rubenstein et al.,

2016; equids: Rubenstein, 1986; Medill, 2018; babirusa: Clayton and Macdonald, 1999; most canids: Moehlman and Hofer, 1997; hyaena: Holekamp et al., 1996; badgers: Woodroffe and Macdonald, 1995; marmots: Allainé, 2000; mongoose: Creel et al., 1992; meerkats: Young et al., 2006; rodents: Huck et al., 1988; Lacey, 2004; Schradin and Pillay, 2005; Kinahan and Pillay, 2008; Wey et al., 2013). In primates, fertility has been reported to decline with either female rank (baboons: Dunbar, 1980; Smuts and Nicholson, 1989; Altmann and Alberts, 2003; Garcia et al., 2006; chimpanzees: Pusey and Schroepfer-Walker, 2013) or group size (great apes: Dunbar, 2019; baboons: Dunbar and Sharman, 1983; Huchard and Cowlishaw, 2011; colobines: Srivastava and Dunbar, 1996; Borries et al., 2008; Dunbar, 2018a; lemurs: Schülke, 2003). In humans, female fertility is lower in polygamous households than in either monogamous households (Muhsam, 1956; Smith and Kunz, 1976; Bean and Mineau, 1986; Ji et al., 2013) or polygamous families where wives occupy separate dwellings (Chojnacka, 1980; Borgerhoff Mulder, 1989). Lutz et al. (2006) showed that human fertility declines as population density increases both across countries and, within countries, over time.

In a few cases, however, \cap -shaped relationships between fertility and group size have been reported (lemurs: Takahata et al., 2006; baboons: Dunbar et al., 2018a; Dunbar and MacCarron, 2019; apes: Dunbar, 2019). In ecology, quadratic relationships of this kind usually signal a tradeoff between two or more variables that influence the dependent variable in opposite ways. Most authors test only for a linear regression when analysing data on birth rates against demographic variables, and these invariably yield little evidence for any relationship (e.g., Stokes et al., 2003). Inspection of the data in these cases, however, often suggests that the data have an obvious quadratic form (a reminder, perhaps, of the importance of looking at plots of data rather than simply relying on statistical packages).

So far, we have made two general points: first, mammals vary in both the size and dynamics of their groups; second, birth rates are a negative (or in some cases quadratic) function of group size or reproductive female cohort size. Given this, the questions that motivate this article are: (1) how widespread is the \cap -shaped pattern compared to a simple linear decline, (2) what causes the decline (on the right-hand side in the quadratic case), and (3) does the difference between the linear and quadratic forms explain the differences in group size and structure that we find in mammals? We deal with each of these questions in turn in the following three sections.

DEMOGRAPHIC DETERMINANTS OF FERTILITY

The data, along with their sources, are given in *Online Data Sheets 1–5*. The statistical methods and analytical strategy are described in the **Supplementary Material**. Our analyses focus on the genus, with individual group or population means as the unit of analysis. For primates, we follow previous studies in treating a genus as an ecological species because populations belonging to the same genus invariably fall on the same curve and are more

strongly influenced by environmental conditions than phylogeny (Dunbar et al., 2009; Strier et al., 2014). Following longstanding convention in the primate literature, however, we treat *Papio hamadryas* separately from other *Papio* baboons because it has a very different social system and fertility regime (more akin to that of *Theropithecus*: see Dunbar and MacCarron, 2019; Dunbar and Shultz, 2021).

Most comparative analyses use phylogenetic methods in order to control for the inflation in the degrees of freedom that occurs when closely related species inherit a trait from a common ancestor. We do not use phylogenetic methods in our analyses for three reasons. First, all our analyses are at the level of the genus: in primates, within-genus variation in the variables of interest is much greater than the between-genus variation (**Supplementary Figure 1**). More importantly, there is no phylogenetic signal for any of the variables we consider (**Supplementary Table 1**), making the need for phylogenetic controls less necessary. Second, phylogenetic methods are important when testing causal hypotheses (to show that one variable has driven another during the course of evolution). We do not here directly test any causal hypotheses when testing between genera; all tests of causal hypotheses are within-genus. Rather, when we compare genera, we search for patterns in the distributions of variables: for this we use cluster analysis that simply looks for natural breaks in a distribution, and hence does not suffer from the problem of inflated degrees of freedom. Third, even if this was a problem, there are in fact no phylogenetic methods for analysing univariate distributions of this kind. For further details, see **Supplementary Material**. The data for non-primate mammals are few in number and come from different orders, so that taxonomic relationships are not an issue.

To avoid confusion, we use the term *fertility* to refer to reproductive output in general (precise index unspecified). We use *birth rate* to refer to the number of births (or litters) per female per year, and *reproductive output* to refer to the average number of immatures alive at any given time per female (see **Supplementary Material**).

Within-Taxon Variation in Fertility

We located data on birth rates as a function of demographic structure in eight non-primate and 12 primate mammalian genera that live in definable, stable groups (for details, see **Supplementary Material**). Despite an extensive literature search, few data are available for non-primate taxa, mainly because most species are solitary or, if social, live either in monogamous pairs or in large, unstable herds (Shultz and Dunbar, 2007, 2010). We distinguish three demographic variables: total group size (individuals of all ages and sexes living together), number of adult (i.e., post-puberty) females and number of adult (i.e., fully mature) males. In primates, there is in addition usually a class of subadult males that do not compete for breeding opportunities but do contribute to total group size (and hence the ecological pressure the group places on the its home range). Since some of the non-primate species produce litters of more than one infant, we use litters per female per year for those species that

have multiple births in order to be able to compare more directly across genera.

Data on birth rates are for individual groups of known composition (where possible belonging to the same population for each genus, thus holding ecological conditions constant). In some primate taxa (e.g., *Papio*, *Pan*), only one group is ever studied in any given population, and in these cases we use data from separate populations: for at least some of these genera, demography is known to influence fertility independently of environmental effects (Dunbar and Sharman, 1983; Hill et al., 2000; Dunbar, 2018a, 2019; Dunbar et al., 2018a).

Except for taxa where males do not associate with females outside the breeding season, we analysed fertility rates separately against group size, number of adult males and number of adult females. Since the patterns are essentially the same (see **Supplementary Material**), we show only the analyses for female cohort size here since, for many non-primate genera, female number and group size are synonymous. However, in most cases where data are available, the statistical fit is better for females only than for the other two variables. To avoid creating graphs that are so cluttered as to be uninterpretable, we present these results graphically in three separate figures: non-primates with clear linear relationships (**Figure 2**), non-primates with clear quadratic relationships (**Figure 3**) and primates (all but one of which exhibit quadratic relationships) (**Figure 4**). Analyses of birth rate as a function of group size and number of males are given in **Supplementary Table 2**.

The five mammal species in **Figure 2** all exhibit a simple linear decline in birth rate as the number of females in the group

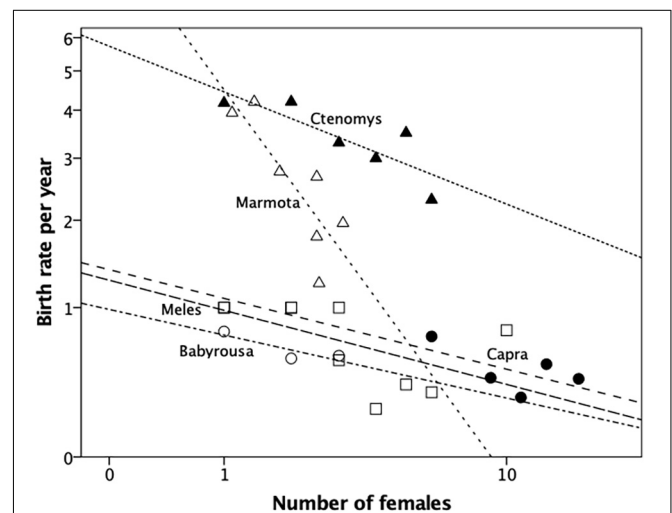


FIGURE 2 | Mean fecundity (litters per female per year) for groups of different size for a carnivore (European badger, *Meles meles*: squares), two rodents (tuco-tuco, *Ctenomys sociabilis*: filled triangles; yellow-bellied marmots, *Marmota flaviventra*: unfilled triangles) and two ungulates (babirusa, *Babyrousa babyrousa*: unfilled circles; feral goats, *Capra hircus*: filled circles). All datapoints are individual groups sampled from the same population. Sources: Downhower and Armitage (1971), Woodroffe and Macdonald (1995), Clayton and Macdonald (1999); goat data from RIMD. Source: **Supplementary Dataset 2**.

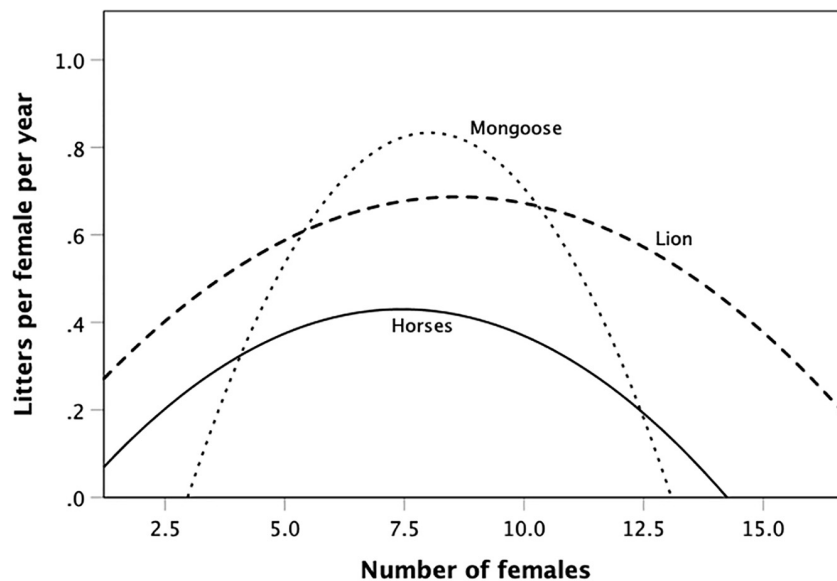


FIGURE 3 | Mean fertility (litters per female per year) for groups of different size for banded mongoose (*Mungos mungo*), averaged across three separate years from the same population (De Luca and Ginsberg, 2001); lion (*Panthera leo*), Serengeti: the plotted curve is the equation given by Mosser and Packer (2009) with territory quality held constant; feral horses (*Equus caballus*), Shackleford Banks, N. Carolina, United States (Rubenstein, 1986). For individual data distributions, see **Supplementary Figure 2**. Source: **Supplementary Dataset 2**.

increases. This set of regressions is significantly more negative than would be expected by chance if there was no underlying trend (Fisher's meta-analysis with 1-tailed p -values in a negative direction: $\chi^2 = 30.23$, $df = 2 \times 5 = 10$, $p = 0.0008$), with a mean correlation of $r = -0.698$ and a mean slope of $b = -0.109$. None of these distributions are better explained by a quadratic regression

(as indexed by goodness-of-fit). With the possible exception of *Capra*, this steepness of the decline in fertility would limit group size to between 2.5 and 7.0 reproductive females, since anything above that would result in birth rates falling below replacement rate, and hence in negative population growth and, thus, group extinction. In all these genera, fertility is maximised if females live on their own (i.e., in groups of just one female, with or without males and/or dependent young).

In contrast, fertility rates for banded mongoose, lion and feral horses all exhibit \cap -shaped distributions (**Figure 3**; the original data and analyses are given in **Supplementary Figure 2**). For the banded mongoose, the overall quadratic equation is significant (quadratic $r^2 = 0.420$ vs. linear $r^2 = 0.179$, $N = 6$; Fisher's log-likelihood meta-analysis combining the individual quadratic regressions for the three separate years shown in **Supplementary Figure 2**: quadratic: $\chi^2 = 23.03$, $df = 6$, $p = 0.0008$; linear negative slope: $\chi^2 = 0.84$, $df = 6$, $p = 0.991$). Double differentiating the regression equation to find the maximum indicates that optimal fertility occurs at ~ 8 females. The regression for the lion data is the statistically significant ($p < 0.001$) quadratic regression for female reproductive success in lion prides given by Mosser and Packer (2009), holding other significant predictors (territory quality, takeover rate) constant (see **Supplementary Material**). Double-differentiating indicates that fertility is maximised in groups with 8.6 females. The quadratic regression for feral horses is also significant ($r^2 = 0.308$, $F_{2,22} = 4.89$, $p = 0.017$; linear: $r^2 = 0.099$, $p = 0.125$). Optimal fertility occurs in bands with 6–7 females, at exactly the transition point between territorial and non-territorial males in this population – raising the possibility that territoriality results in males attempting to corral females when it is not actually in the females' reproductive interests.

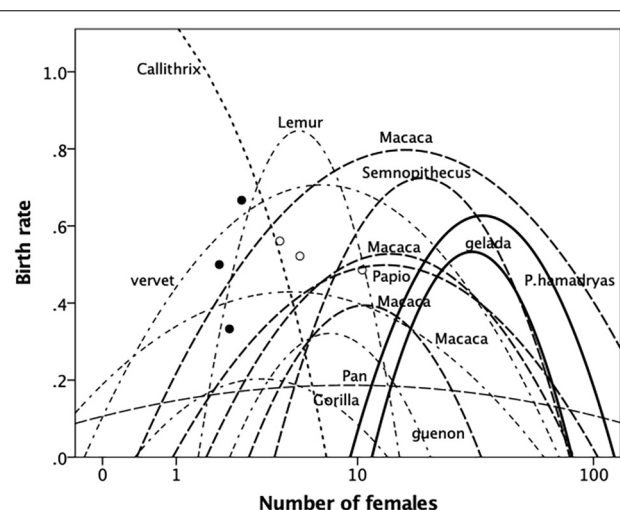


FIGURE 4 | Best-fit quadratic regressions for birth rate (births per female per year) regressed on female group size for different genera of primates. Guenon = *Cercopithecus*; vervet = *Chlorocebus*; gelada = *Theropithecus*. Filled symbols: *Eulemur*; unfilled symbols: *Trachypithecus*. Lines in different format indicate clustering of regressions (for further details, see text and **Supplementary Material**). Source: **Supplementary Dataset 3**.

Fisher's meta-analysis for the three genera, indicates a consistent quadratic pattern underlying all three genera ($\chi^2 = 15.16$, $df = 2 \times 3 = 6$, $p = 0.019$). In all three cases, optimal fertility occurs in groups with 7–8 breeding females.

To maintain comparability with **Figures 2–4** plots the best-fit regressions for birth rate against the number of adult females in the group for the 12 primate genera. (The data plots and regression equations for individual genera are given in **Supplementary Figure 3** and **Supplementary Table 2**). Overall, quadratic regressions yield much a better fit than linear relationships (**Supplementary Table 3**). There are, however, some exceptions. A linear relationship clearly provides a better fit for *Callithrix*. The callitrichids are, as a group, exceptional among the anthropoid primates in that they live in small, often unstable, groups of 1–5 females with a variable number of males (Digby et al., 2007). The only other exceptions are *Eulemur* and *Trachypithecus*, both of which have only three datapoints available. The data for the first fit neatly on the up-slope for the closely related genus *Lemur* (to which genus *Eulemur* formerly belonged); those for the second are either a weak negative relationship or arguably straddle the \cap -relationship within the same *Lemur* arc. Including *P. hamadryas* with the rest of the *Papio* species does not change the fact that, overall, a quadratic regression is a significantly better fit for this genus (linear: $r^2 = 0.038$, $N = 21$, $p = 0.396$; quadratic: $r^2 = 0.310$, $N = 21$, $p = 0.035$); however, combining them obscures the fact that the data for the other *Papio* species in fact form a distinct quadratic relationship on their own account.

To explore the primate patterns on a broader taxonomic scale and with a larger sample, we used census data on reproductive output, indexed as the average number of immatures (i.e., pre-pubertal young) per female for a given population. We located reliable census data for a sample of 277 populations representing 23 genera for which at least three populations had been sampled (mean number of populations sampled per genus = 12.3 ± 11.1 SD). We use the number of surviving dependent offspring over a 2–5 year period (depending on species life history) since this can easily be determined from group census data. While a proxy for birth rate, it obviously also includes some discounting due to postnatal mortality. Each data point is the mean fertility and mean group composition for an individual population, averaged across several groups.

Plots for individual genera are given in **Supplementary Figure 4**, with regression analyses in **Supplementary Table 4**. A quadratic regression gives a significantly better fit than a linear regression for all three predictor variables for most genera. In this case, the differences between the three demographic variables as the predictor are less clear cut (**Supplementary Table 5**), although the overall fit is better for number of females (see **Supplementary Material**). **Figure 5** plots the summary quadratic (or linear, where this gives a better fit) regressions for the individual genera (based on the assessments given in the **Supplementary Material**).

The \cap -shaped relationships in **Figures 4** and **5** imply that there is an optimal group size that maximises reproductive rate. These values ought to predict mean taxon group size if species are trying to behave optimally, as evolutionary theory would predict.

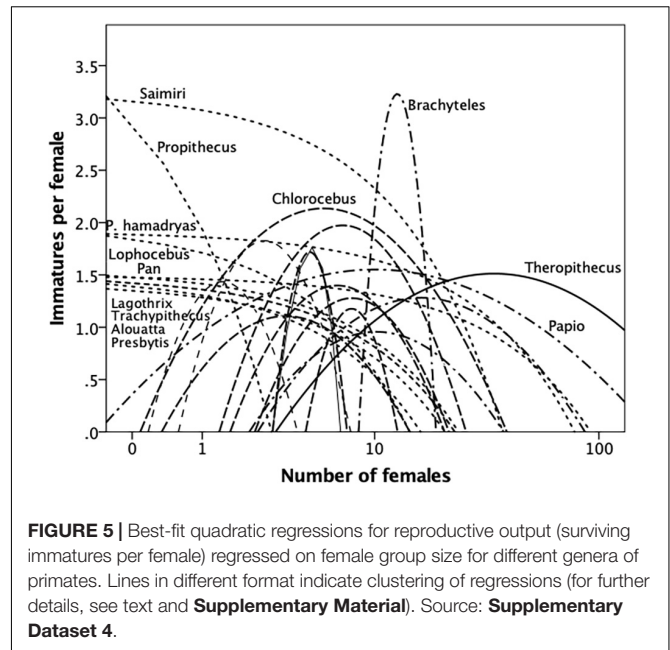


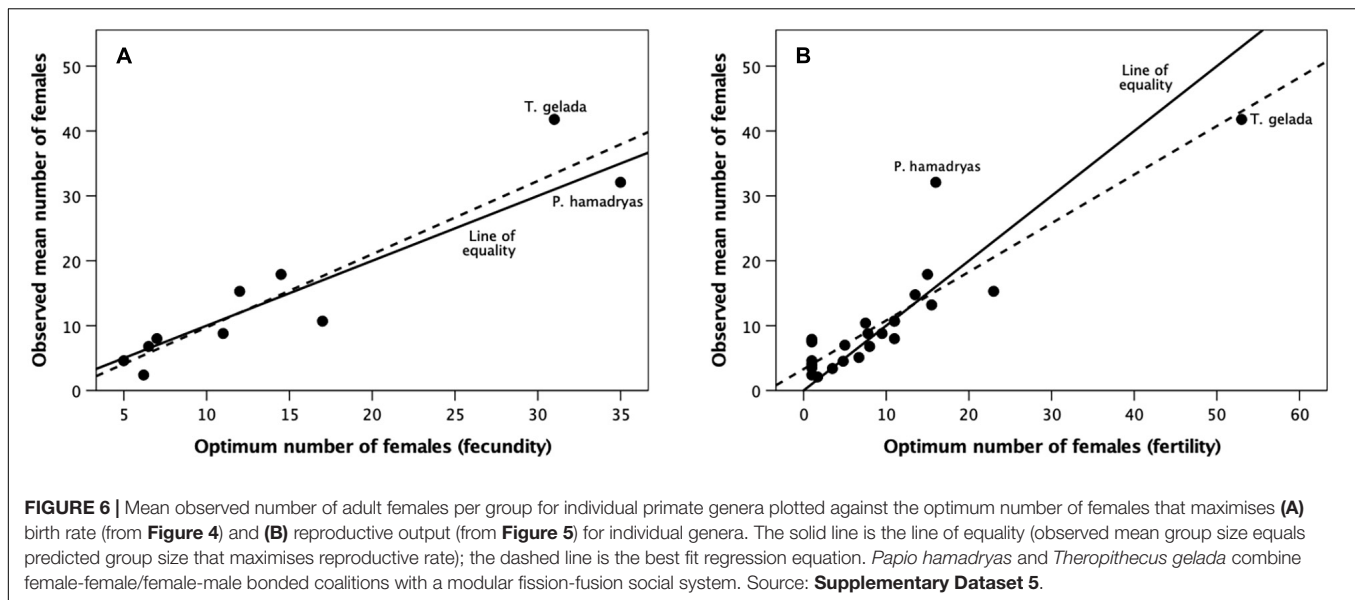
FIGURE 5 | Best-fit quadratic regressions for reproductive output (surviving immatures per female) regressed on female group size for different genera of primates. Lines in different format indicate clustering of regressions (for further details, see text and **Supplementary Material**). Source: **Supplementary Dataset 4**.

To determine the optimal number of females that maximised fertility, we set the second derivative of the quadratic equation to 0 and solve for X (the number of females) for those genera where there was a clear quadratic distribution; for those genera where a quadratic regression did not provide a better fit than a linear regression, we identified the optimal number of females as that corresponding to the highest observed fertility value (for details, see **Supplementary Material**). The optimal number of females in each case is given in **Table 1** for each dataset.

Figure 6 plots the resulting optimal female cohort size against the observed mean number of females per group (from Dunbar et al., 2018b) for each genus. We plot the regressions line for the data in each case not to test a causal relationship, but simply to illustrate how close the data lie to the line of equality. We are here concerned simply with whether the observed and predicted values match in each individual case. Matched pairs t -tests indicate that the two indices do not differ significantly from each other (birth rate, $t = -0.211$, $N = 10$, $p = 0.837$; reproductive output: $t = 0.287$, $N = 23$, $p = 0.777$). In other words, species' mean female cohort size is very close to that which optimises fertility (however, we measure this). Notice that even *Papio hamadryas* and *Theropithecus gelada* (who live in very large modular fission-fusion herds) sit quite close to the line of equality: these two species seem to have managed to increase group size well beyond the normal range for primates without sacrificing fertility; they seem to achieve this by exploiting the capacity to substructure their groups so completely that the subcomponents are semi-independent, thereby exploiting the advantages of fission-fusion herding without losing the benefits of bonded groups.

Endogenous Determinants of Within-Taxon Variation in Fertility

A quadratic relationship usually implies a tradeoff between benefit and cost functions that correlate in opposite directions



with the independent variable. To determine which variables give rise to the tradeoff, we ran separate multivariate regressions for each primate genus, with the three demographic variables (group size, number of adult males, number of adult females) as predictors. **Figure 7A** plots the distributions for the standardised slope coefficients for the 12 primate genera from **Figures 4, 7B** plots the same for the 23 genera from **Figure 5**. The multiple regression models and statistics for individual genera are given in **Supplementary Table 6**. The slopes differ significantly across factors in both cases (**Figure 7A**: $F_{2,37} = 4.88$, $p = 0.013$; **Figure 7B**: $F_{2,51} = 15.84$, $p < 0.0001$). In both cases, the slope for group size is consistently positive and that for number of females consistently negative, whereas the slope for number of males overlaps zero.

A multiple regression analysis for the mongoose data (**Figure 3**) with group size and number of females as predictor variables (male numbers were not given) also yields a significant regression that is positive in group size and negative in adult female cohort size:

$$\text{Fecundity} = 0.087 + 0.037 \cdot \text{Group} - 0.066 \cdot \text{Females}$$

($r^2 = 0.475$, $F_{2,12} = 5.43$, $p = 0.021$; group, $p = 0.010$, females $p = 0.014$, 1-tailed). The lion data (**Figure 3**) mirror these results, with a significant positive effect due to pride size and no effect due to male numbers ($p > 0.05$) (Mosser and Packer, 2009). Mosser and Packer (2009) note that increasing pride size correlated significantly with greater success in conflicts with neighbouring prides ($p \approx 0.001$), fewer injuries to females ($p \approx 0.005$) and lower female mortality rates ($p \approx 0.015$).

Both **Figures 4** and **5** suggest that the primate data partition into separate clusters that occupy non-overlapping sections of the X-axis state space. To determine whether this is so, and if so which genera fit in which cluster, we ran a k -means cluster analysis across the range $2 \leq k \leq 6$ on the data for all 20 primate and non-primate genera combined for the birth rate dataset and

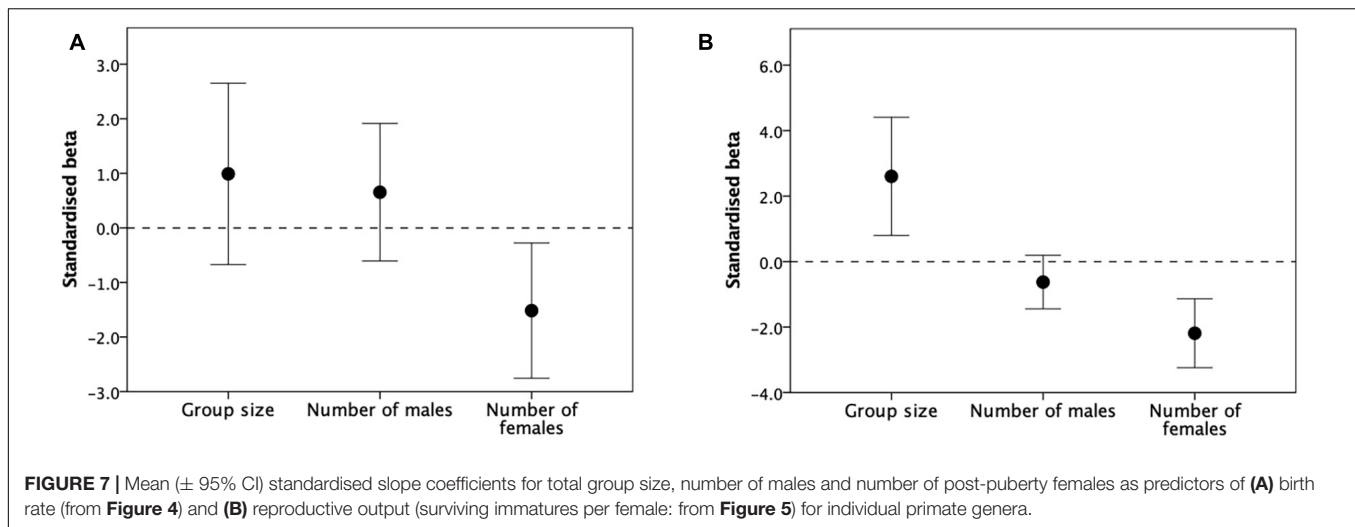
all 23 genera for the primate reproductive output dataset. We use the change in goodness-of-fit (indexed by the F -ratio) to identify the optimal number of clusters. The rate of change in F -ratio peaks at $k = 4$ for the birth rate data (**Supplementary Figure 5A**) and at $k = 5$ for the reproductive rate data (**Supplementary Figure 5B**). However, in the latter case, cluster 5 contains a single genus (*Theropithecus*); since clusters with a single member are considered undesirable, we combine clusters 4 and 5 in this case and consider $k = 4$ to be the optimal solution for both datasets. In other words, the data consist of four superimposed normal distributions whose peaks differ.

Figure 8A plots the cumulative distribution of the optimal number of females for the birth rate sample. The cluster divisions (numbered I–IV) are identified by the sideways step-changes in the rising cumulative curve. The mean number of females for the four clusters are 1.0, 6.9, 13.6, and 32.0, respectively. Cluster I contains only non-primate mammals from **Figure 2**; the remaining non-primate mammal genera (from **Figure 3**) group with some primates in cluster II, but only primates occur in the two largest clusters (III and IV). **Figure 8B** plots the cumulative distribution for the reproductive output sample (primates only). In this case, cluster means occur at 3.2, 9.1, 14.8, and (for the combined clusters IV and V) 29.0 females.

Table 1 gives the cluster allocations for the individual genera generated by the two fertility indices. For genera in common in the two primate datasets, the allocation of genera to clusters is significantly correlated (Kendall's $\tau = 0.732$, $N = 10$, $p = 0.005$ 1-tailed). To obtain a consensus classification, we averaged the cluster allocations of the two k -means analyses (rounding up, as appropriate), and these are given in **Table 2**.

Extrinsic Determinants of Within-Taxon Variation in Fertility

The fact that the slope parameters for the effect of group size on fertility are so consistently and strongly positive in the primate



sample allows us to rule out within-group competition for resources as the cause of declining fertility: this pattern implies that living in groups provides a fertility benefit for females, with the benefit increasing monotonically with group size. This could either be because larger groups are better able to defend resources against neighbouring groups (Markham et al., 2015), or because group size is an effective buffer against predation risk (Dunbar, 1988; Shultz et al., 2004; Shultz and Finlayson, 2010), or because groups provide females with protection from infanticidal males (van Schaik and Dunbar, 1990; Harcourt and Greenberg, 2001; Opie et al., 2017). In the case of lion, hunting success correlates with pride size, suggesting a direct foraging benefit, but this is unlikely to apply in the case of any other taxa in this sample. Infanticide can probably be discounted because the burden of the evidence clearly points to living in groups as an increased, rather than decreased, risk factor for infanticide (Opie et al., 2017). In fact, the single most important driver for increasing group size in mammals, birds and fish is probably predation risk (van Schaik, 1983; Cowlshaw, 1994; Molvar and Bowyer, 1994; Shultz et al., 2004; Creel et al., 2007; Adamczak and Dunbar, 2008; Shultz and Finlayson, 2010; Kelley et al., 2011). Most animals minimise predation risk by passive defence (bunching or grouping), and very rarely, if ever, by the much riskier strategy of active defence (engaging with a predator).

We test between the first two options using two indices of predation risk and one index of intergroup competition, with consensus cluster (as defined in Table 2) as the independent variable. As indices of predation, we use observed rates of predation from field studies (for a limited sample of primates, provided by Cheney and Wrangham, 1987) and an estimate of exposure to predation risk based on the habitats a genus occupies and the kinds of predators common in those habitats. To test whether group size is driven by the risk of encountering and competing with neighbours (Grueter, 2015; Ashton et al., 2020), we use overlap in the ranges of neighbouring groups (from Grueter, 2015).

Habitat predation risk reflects background risk in the habitat, and would predict a positive correlation with fertility cluster

(and hence group size). Predation rate, in contrast, reflects the residual predation risk that a species has not been able to control by its anti-predator strategies (i.e., by increasing group size) (Hill and Dunbar, 1998). In this case, a positive correlation would imply that the animals' anti-predator strategies were not working; a negative correlation would imply that shifting cluster so as to increase group size enables species to reduce predation risk. If range overlap reflects background risk of encountering neighbours, then we would predict a positive correlation between range overlap and fertility cluster (females need to live in bigger groups when there is greater risk of encountering neighbours). A negative correlation might imply that, when animals live in large groups, they reduce range overlap in order to minimise encounter rates (and the mortality risks these entail). The latter implies that animals reduce range overlap because they live in large groups (for some other reason), whereas the former implies that they live in large groups because range overlap is high (for some other reason). For these analyses, we use Kendall's correlation test, since this was specifically recommended by Kendall for use with categorical data (Maxwell, 1961). Note that the fertility clusters in Table 2 contain a complete mix of taxonomic groupings, and thus cannot have a significant phylogenetic signal.

Figure 9A suggests that, at least in primates, predation rate is uncorrelated with cluster (and hence group size) (Kendall's $\tau = 0.088$, $N = 12$, $p = 0.714$, all tests 2-tailed). However, habitat riskiness correlates significantly and positively with fertility cluster (Figure 9B: $\tau = 0.702$, $N = 25$, $p < 0.001$), suggesting that being able to live in larger groups while maintaining fertility does allow species to occupy habitats that are more predator-risky. An analysis of partial correlations holding the alternative predation variable constant yields a slight increase in the correlation with habitat predation risk (Spearman $r_{\text{bivariate}} = 0.760$ vs. $r_{\text{partial}} = 0.833$, $p = 0.001$), and a strong (albeit not significant) negative correlation with predation rate ($r_{\text{bivariate}} = 0.104$ vs. $r_{\text{partial}} = -0.384$, $p = 0.244$), reinforcing the suggestion that the fertility clusters are related to the animals' need to reduce exposure to predation.

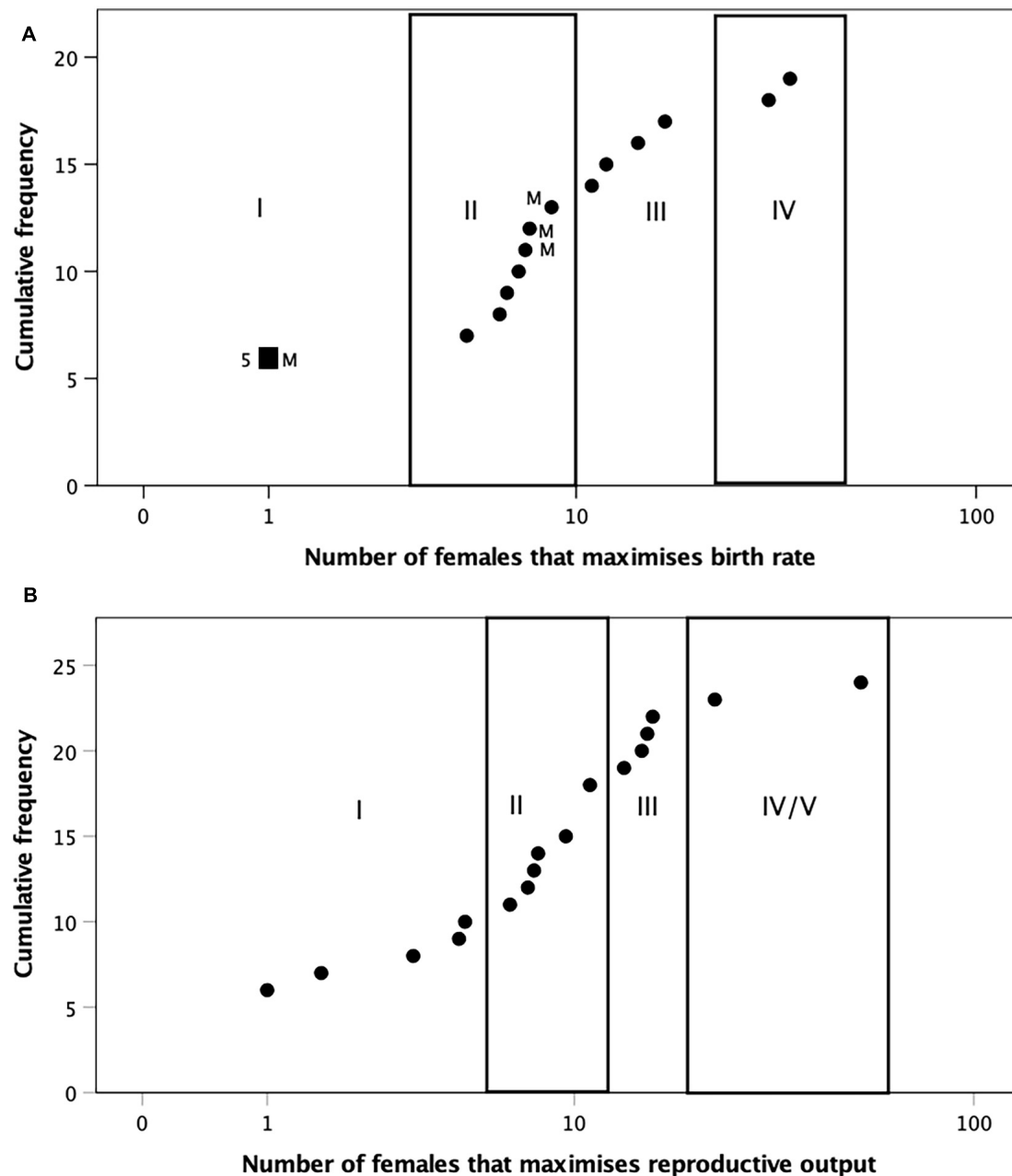


FIGURE 8 | Cumulative distributions of the number of females that maximise (A) birth rate in mammal genera (from **Figures 2–4**) and (B) reproductive output in primate genera (from **Figure 5**). The clusters identified by a *k*-means cluster analysis in each case are identified by the Roman numerals. In (A), M denotes non-primate mammals; the large square with the adjacent numeral 5 denotes five non-primate mammal genera at the same position.

The alternative suggestion (that species live in large groups to buffer themselves against attack by neighbours) is not supported (**Figure 9C**: $\tau = 0.027$, $N = 25$, $p = 0.862$). This last result is, perhaps, not too surprising: competition is usually most intense in species with small groups and small defensible ranges, whereas species that have large groups and live in large undefensible ranges tend to have more relaxed relationships when they meet (Mitani and Rodman, 1979; Lowen and Dunbar, 1994), in part because they meet less often and in

part because they have more alternative feeding places to go to if they do meet.

An exploratory multiple regression with cluster as the dependent variable and the three indices as predictors confirms these results. The overall model is significant ($F_{3,7} = 6.96$, $p = 0.017$), but only habitat riskiness has a significant independent effect (predation rate: $t = -0.322$, $p = 0.756$; habitat riskiness: $t = 4.43$, $p = 0.003$; range overlap: $t = 0.485$, $p = 0.642$).

TABLE 1 | Cluster allocations by *k*-means cluster analysis.

Genus	Optimal females [fecundity]	Fecundity cluster	Optimal females [reproductive output]	Reproductive cluster	Mean cluster	Consensus cluster*
Non-primate mammals:						
<i>Babyrousa</i>	1.0	1			1	I
<i>Capra</i>	1.0	1			1	I
<i>Ctenomys</i>	1.0	1			1	I
<i>Marmota</i>	1.0	1			1	I
<i>Meles</i>	1.0	1			1	I
<i>Mungos</i>	8.0	2			2	II
<i>Panthera</i>	8.6	2			2	II
<i>Equus</i>	7.5	2			2	II
Primates:						
<i>Alouatta</i>			1.0	1	1	I
<i>Ateles</i>			11.0	2	2	II
<i>Brachyteles</i>			13.5	3	3	III
<i>Callithrix</i>	1.0	1			1	I
<i>Cebus</i>			4.8	1	1	I
<i>Cercopithecus</i>			7.8	2	2	II
<i>Chlorocebus</i>	7.0	2	11.0	2	2	II
<i>Colobus</i>			3.5	1	1	I
<i>Eulemur</i>			1.7	1	1	I
<i>Gorilla</i>	6.5	2	8.0	2	2	II
<i>Lagothrix</i>			7.5	2	2	II
<i>Lemur</i>	6.2	2			2	II
<i>Lophocebus</i>			5.0	1	1	I
<i>Macaca</i>	17.0	3	11.0	2	2.5	III
<i>Nasalis</i>			1.0	1	1	I
<i>Pan</i>	12.0	3	23.0	4	3.5	IV
<i>Papio</i>	14.5	3	15.0	3	3	III
<i>Papio hamadryas</i>	35.0	4	16.0	3	3.5	IV
<i>Ptilocolobus</i>			15.5	1	1	I
<i>Presbytis</i>			1.0	1	1	I
<i>Propithecus</i>			1.0	1	1	I
<i>Saimiri</i>			1.0	1	1	I
<i>Sapajus</i>			6.4	2	2	II
<i>Semnopithecus</i>	12.0	3	9.5	2	2.5	III
<i>Theropithecus</i>	31.0	4	53.0	4	4	IV
<i>Trachypithecus</i>	11.0	2	1.0	1	1.5	II

*Equivalent to mean cluster, rounding up.

Two key questions remain: what is responsible for this decline in fecundity and, given that it exists, how do the females in some taxonomic groups manage to overcome it in order to live in larger groups? We consider each questions of these in turn.

A MECHANISM FOR REPRODUCTIVE SUPPRESSION

We noted above that, for individual taxa, a negative impact of female numbers on fertility seems to occur widely across populations in both rich and poor quality habitats, as well as in captivity where food is unlikely to be an issue. Using long term lifetime data from the Gombe chimpanzee population,

Pusey and Schroepfer-Walker (2013) report that high rank females live longer and have shorter interbirth intervals than low ranking females, despite there being no evidence that they have differential access to food resources. Similarly, Garcia et al. (2006) found that the low rank females in a captive population of baboons were less fertile than high rank ones despite unlimited access to food. Huchard and Cowlshaw (2011) concluded that declining fertility as a function of group size in a baboon population was unrelated to access to food resources and was most likely a consequence of reproductive conflict between females.

Similar findings have emerged from studies of domestic stock, where infertility at high stocking densities even when food is abundant has been a longstanding problem. Careful experimental

TABLE 2 | Consensus cluster allocations of mammalian genera by *k*-means cluster analysis of optimal number of females to maximise fecundity and fertility (see **Supplementary Table 5**) for species with stable social groups (congregations).

Consensus cluster			
I	II	III	IV
Unstable groups, Unbonded*	Stable groups, Weakly bonded	Strongly bonded, Structured networks	Modular bonded
1–5 females†	5–10 females	10–15 females	> 15 females
Non-primates[§]			
<i>Babyrousa</i>	<i>Mungos</i>		
<i>Ctenomys</i>	<i>Equus</i>		
<i>Marmota</i>	<i>Leo</i>		
<i>Meles</i>			
<i>Capra</i>			
Primates			
<i>Eulemur</i>	<i>Lemur</i>	<i>Brachyteles</i>	<i>Papio hamadryas</i>
<i>Propithecus</i>	<i>Ateles</i>	<i>Semnopithecus</i>	<i>Theropithecus</i>
<i>Alouatta</i>	<i>Lagothrix</i>	<i>Macaca</i>	<i>Pan</i>
<i>Callithrix</i>	<i>Sapajus</i>	<i>Papio</i>	
<i>Cebus</i>	<i>Trachypithecus</i>		
<i>Saimiri</i>	<i>Cercopithecus</i>		
<i>Colobus</i>	<i>Chlorocebus</i>		
<i>Ptilocolobus</i>	<i>Lophocebus</i>		
<i>Nasalis</i>	<i>Gorilla</i>		
<i>Presbytis</i>			

Source of data: **Supplementary Dataset 5**.

*Unstructured groups have more casual relationships, with a membership that can change through individual immigration/emigration, usually by both sexes; weakly bonded groups have a more stable membership (only one sex disperses), typically lack network structure, and can reduce size only by group fission; strongly bonded groups have more intense, focussed relationships and a clear network structure, and manage group size by fission; modular bonded groups have similar strongly bonded relationships, but with highly structured networks such that stable subgroups are able to disperse as need arises without sacrificing their longer term associations with each other, creating a form of fission-fusion sociality.

[§]Non-primate mammals based on **Figures 2, 3**.

[†]Optimal number of females to maximise fertility.

testing eventually identified social stress due to crowding as the cause (Dobson and Smith, 2000; Pierce et al., 2008; Dobson et al., 2012). Williams et al. (2001) showed that, although mild social and energy stresses on their own did not disrupt the menstrual cycles of female monkeys, their occurrence in combination did, indicating that mild stress can disrupt menstrual endocrinology even without any weight loss providing the system as a whole is under stress. In a study of lemurs (*Lemur catta*) on Madagascar, cortisol titres driven by seasonal stresses in nutrient throughput were lower in groups of intermediate size (10–15 individuals) than in smaller (5–9) or larger (19–26) groups (Pride, 2005).

The fact that, in primates at least, fertility is strongly influenced by the number of females in the group across groups within the same population (where environmental effects, while not absent, are at least minimised; **Figure 4**) as well as across different populations (where environmental effects will be maximised; **Figure 5**) argues against an environmental driver. This suggests that the effect must, at least in part, be driven

by something to do with group demography. **Figure 7** points to the number of females in the group as the likely cause. Socially induced stress arising from direct or indirect interactions between females seems the most likely explanation.

In primates, stress levels are known to be influenced by purely social events that are unrelated to ecological conditions. Levels of the stress hormone glucocorticoid (GC) were elevated in wild female baboons during periods of social and demographic instability resulting from both predation events (Engh et al., 2006) and conflict among males (with its attendant risks of infanticide) (Wittig et al., 2008). Similarly, intergroup encounters (and the risks they entail of injury and even death) result in elevated cortisol levels in wild chimpanzees (Wittig et al., 2016). Levels of salivary alpha-amylase (another marker of physiological stress) were also elevated in captive bonobos during stressful situations such as the transfer of individuals between groups (Behringer et al., 2012).

Taken together, these studies, combined with the data in **Figure 7**, point to stress induced by female-female interactions as the likely immediate cause of infertility, even if this sometimes arises as a consequence of competition over access to resources (Muller, 2002; Rubenstein, 2007; Creel et al., 2013) or conflict between males. There are two possible mechanisms that might produce this effect: (1) stress resulting in the suppression of ovulation or (2) stress obstructing implantation and/or early foetal development (leading to resorption or abortion of the embryo). There is evidence to support both routes.

The reproductive endocrinology of female mammals is extremely sensitive to stress: females subjected to even modest levels of social stress experience reduced levels of fertility across a wide range of taxa (rodents: Geraghty et al., 2015; ungulates: von Borell et al., 2007; Einarsson et al., 2008; primates: Rowell, 1970; Bowman et al., 1978; Abbott, 1984; humans: Zacur et al., 1976; Ferin, 1984; Seifer and Collins, 1990; Laatikainen, 1991; Schenker et al., 1992; Sanders and Bruce, 1997; Sheiner et al., 2003; An et al., 2013; Schliep et al., 2015; Pettay et al., 2016). In some cases, this can even result in complete reproductive suppression, including even the suppression of puberty (callitrichid primates: Abbott et al., 1981; most canids: Moehlman and Hofer, 1997; suricates: Young et al., 2006; mole rats: Faulkes et al., 1990; Bennett, 1994). In most species, harassment and aggression typically accumulate down the female hierarchy (Dunbar, 1980; Creel et al., 2013), resulting in low-ranking females being under increasing levels of stress. Directed aggression, however, is not necessarily the only cause; more generalised levels of stress (frequent predator alarms, spatial compression, conflict with neighbouring groups) will impact on all group members more or less equally.

Whether reduced fertility affects all females in the group equally, or only younger or lower ranked females, is an open question. We cannot differentiate between these two options with the present data. There is, however, experimental (primates: Bowman et al., 1978; Abbott, 1984) and observational (meerkats: Young et al., 2006; primates: Dunbar, 1980; Abbott et al., 1984) evidence that the fertility of subordinate females is differentially suppressed as a result of harassment by dominant females in at least some species. Where females do not form strong dominance hierarchies, however, it may be more likely for all females to be

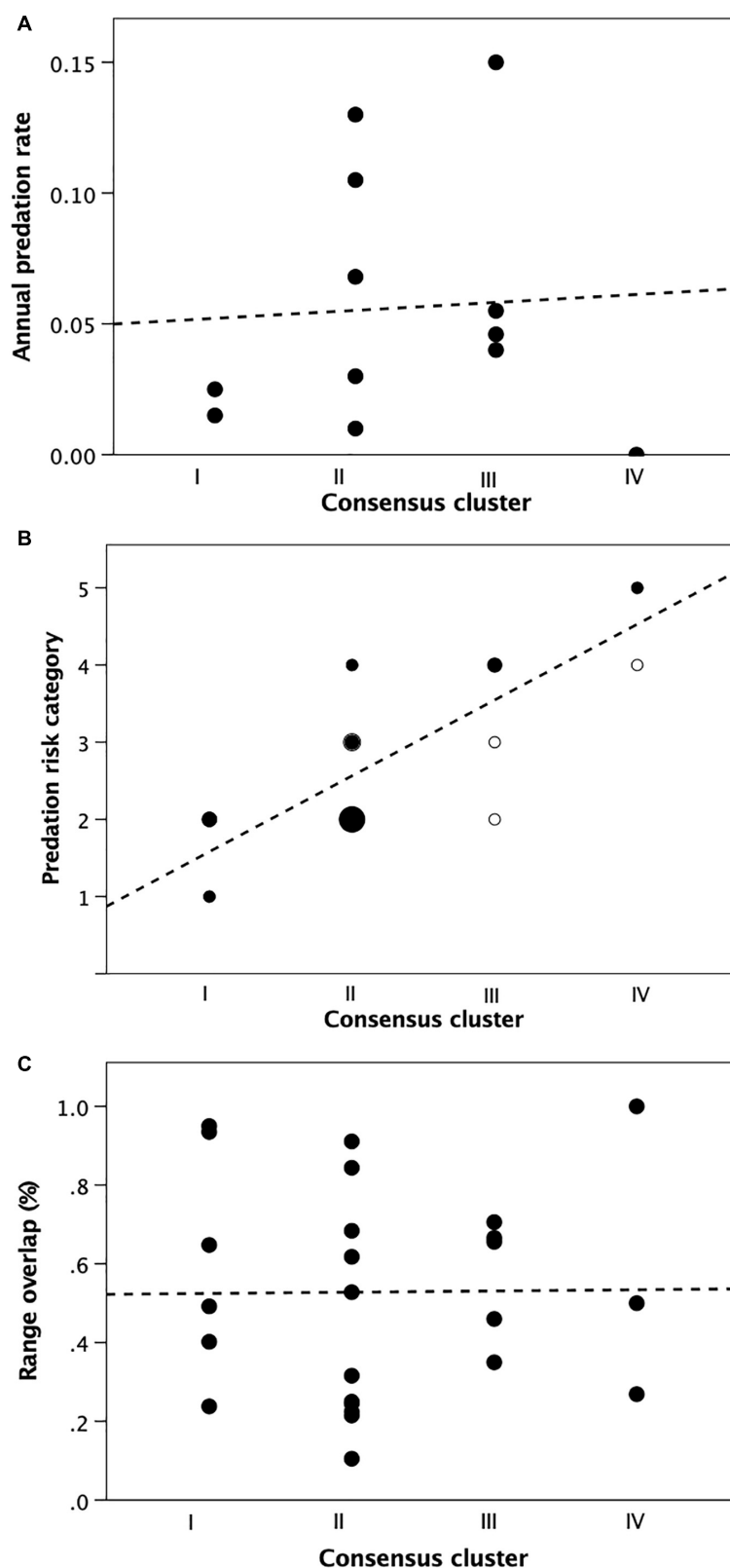


FIGURE 9 | External threats experienced by primate genera as a function of cluster membership from **Table 1**: **(A)** Observed predation rate; **(B)** Predation risk of habitats typically occupied by genus: 1 (low risk) = small-bodied, arboreal forest; 2 = large-bodied, arboreal forest; 3 = terrestrial forest; 4 = terrestrial woodland; 5 (high risk) = open country; small unfilled symbol: 1 datapoint; small filled symbol: 2 datapoints; medium filled symbol: 3 datapoints; large symbol: 7 datapoints; **(C)** mean proportion of overlap with the ranges of neighbouring conspecific groups (as an index of risk of conflicts). Source: **Supplementary Dataset 5**.

affected equally. Average group fertility would, however, decline either way, and some females would be motivated to leave in order to be in a smaller group – which, for present purposes, is all we are interested in.

There is some evidence to suggest that, independently of any glucocorticoid involvement, endorphin up-regulation in response to any social or physical stress inhibits the GnRH, thereby blocking the LH surge needed to precipitate ovulation (Howlett and Rees, 1986; Ziegler et al., 1990; Gordon et al., 1992; McNeilly et al., 1994; Kalra and Kalra, 1996; McNeilly, 2001; Son et al., 2012; Iwasa et al., 2017). In rats, even the stress induced by being physically constrained for short periods can be sufficient to block the cyclic release of gonadotrophins necessary for ovulation (Euker and Riegle, 1973).

The mediating mechanism appears to be endorphins and the KNDy neuron complex (Ferin, 1984; Schedlowski et al., 1995; Kalra and Kalra, 1996; Li et al., 2010; Dobson et al., 2012). This is confirmed by the fact that both naloxone (an endorphin antagonist) and disengaging the hypothalamus (a key source of endorphins) reinstate the hormone cascade from the pituitary, thereby re-engaging the ovulatory mechanism (Li et al., 2010; Geraghty et al., 2015). Endorphins seem to form a key component of the organism's global defensive response to stress, acting to buffer the system against short-term physiological and behavioural consequences. However, as with many adaptive physiological processes, chronic overactivation has deleterious consequences (Amir et al., 1980).

What role glucocorticoids play in this remains unclear. Although it is possible that they play a mediating role (Geraghty et al., 2015; Ralph et al., 2016), the consensus is either that they are an indirect by-product of stress (mainly because the primary function of cortisol is energy homeostasis) (Wagenmaker et al., 2009) or that they themselves trigger the endorphin system, thereby indirectly instigating infertility (Ayrout et al., 2019). Maeda and Tsukamura (2006) and Wagenmaker et al. (2009) provide experimental evidence that glucosteroids protect the LH surge independently of cortisol titres when stress has suppressed the GnRH surge. In humans, endorphins are known to suppress the release of cortisol through a noradrenergic pathway (Howlett and Rees, 1986). Stress has the same effect in males (Kirby et al., 2009), though this is less likely to be reflected in conception rates, and hence population dynamics and the risk of group extinction, since only one male is needed to fertilise many females.

Starvation can trigger the endorphin system (in response either to the pain caused by hunger pangs or to the physiological stresses that hunger causes), thereby precipitating infertility in mammals (sheep: Dobson et al., 2012; pigs: Clarke, 2014). However, it appears to be the hypothalamic-pituitary-adrenal (HPA) pathway that regulates this, rather than nutrition *per se* (Kalra and Kalra, 1996; Schwartz and Seeley, 1997). In other words, the same endorphin→HPA pathway is involved in both social and ecological routes, perhaps explaining why the effects of one are easily mistaken for the other.

The second possible route is *via* the effects of stress on implantation or early foetal development. There is experimental and clinical evidence to suggest that stress can affect post-conception processes (Arck, 2001). In sheep, stress is known to

cause pregnant females to abort (Howarth and Hawk, 1968) and, in rats, even the stress of being handled can result in reduced litters sizes through foetal resorption (Geraghty et al., 2015). It has been estimated that 34% of all cases of functional infertility in humans (i.e., where there is no congenital or anatomical cause) is due to the effects of stress (Berga and Loucks, 2005). In placental mammals generally, successful implantation is only possible if inflammation due to the conceptus implanting can be suppressed. Failure to do so results in resorption or abortion of the conceptus or, in the limit, a marsupial-like form of gestation. Glucocorticoids play an important role in suppressing this natural rejection response by the immune system (Arck, 2001).

It is natural to assume that this ought to be an easy problem to solve through selection. However, most biological processes are not simple cause-effect mechanisms that can be adjusted in isolation. They invariably form part of a complex system with feedback loops: altering one inevitably has consequences elsewhere in the system. One important function of the endorphin-HPA-ovulation inhibitory mechanism is to impose lactational amenorrhoea so as to prevent the female becoming pregnant again while bearing the burden of lactating for the previous infant (a particular problem for primates with their long reproductive cycles and heavy investment in lactation). Since the costs of lactation are very high (both maternal and infant mortality are demonstrably higher if successive infants are born too close together: red deer: Albon et al., 1983; Clutton-Brock et al., 1983; humans: Blurton Jones, 1986; Borgerhoff Mulder, 1989; Nath et al., 1994; Lindstrom and Berhanu, 2000; Fotso et al., 2013; Houle et al., 2013; Kozuki and Walker, 2013), this is probably one of those constraints that cannot easily be solved by genetic tinkering with the mechanism itself without incurring even more serious downstream consequences. Instead, it may have been more effective to manage the problem behaviourally.

MANAGING FERTILITY DECLINE

The second issue to consider is the why some species exhibit a simple negative relationship between female number and fertility whereas others have a quadratic relationship created by a positive effect of group size on fertility such that the negative effect of female cohort size is deferred. **Figures 2–5** suggest that, in the first case, fertility is maximised when females live singly (irrespective of the number of males with them) whereas, in the second case, fertility is maximised at some value of female cohort (and hence overall group) size that is significantly larger than can be achieved by the first group. The steepness of the relationship with fertility is typically such that, all else equal, group size is limited to 5–7 females. Since, at least in primates, adult females consistently make up 30% of total group size (Dunbar et al., 2018a,b), this effectively limits groups to 15–20 individuals. If females need to live in groups larger than this in order to gain an ecological benefit, then they must first find a way of deferring the fertility decline so that it occurs at larger group sizes.

Figure 1 and **Table 2** suggest that there are two ways mammals solve this problem. One is to adopt a fission-fusion form of sociality; the other is to evolve bonded relationships. The first

defuses the stresses by allowing females to forage in smaller groups while making it possible for large groups to form on the few occasions when these are needed. The second enables females to form coalitions that buffer them against the stresses created by living permanently with other females, thereby allowing the community to forage as a single, stable group.

Because it is not necessary to know who individual herd members are, the first strategy (the formation of casual herds, or aggregations) is the easier to achieve since it does not require any specialised social or cognitive skills. At worst, simple association learning of whom to avoid is all that is required, and, since herd membership is inconsistent over time, this is probably best learned anew each time a herd forms. In such cases, herds naturally form when predation risk is momentarily high, but drift apart once the crisis has passed. Similarly, in cases where herds form on a rich resource patch, they will disperse as soon as food intake falls below some threshold just as optimal foraging theory predicts (Krause and Ruxton, 2002). In those species that forage in herds, groups readily fragment when differences in individuals' activity scheduling cause their activity cycles to become desynchronised (Ruckstuhl and Kokko, 2002; Ruckstuhl and Neuhaus, 2002; Dunbar and Shi, 2008; King and Cowlishaw, 2009). The disadvantage of this solution is that an individual runs a significant risk of being on its own (or in too small a group) on the one critical occasion when an external threat (a predator or a rival group) manifests itself.

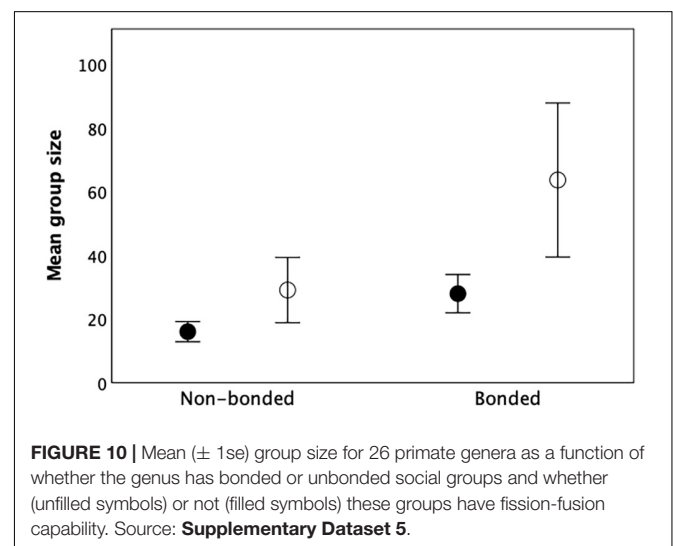
In contrast, bonded groups (stable congregations) have the advantage that the individual's sources of support against external threats are always present and so can be guaranteed to be there on the unpredictable occasions when it really matters. There is considerable evidence that bonded relationships ("friendships": Silk, 2002; Dunbar and Shultz, 2010; Massen et al., 2010) also offer significant additional fitness benefits. Female baboons that have more grooming partners (i.e., allies) experience less harassment (Dunbar, 2018a), and have lower cortisol titres (Crockford et al., 2008; Wittig et al., 2008), higher wound healing (Archie et al., 2014) and lower infection rates (Balasubramaniam et al., 2016) and live longer (Silk et al., 2003, 2009, 2010; Cheney et al., 2016), and in addition produce more offspring that in turn have higher survival rates. Similar results have been reported for chimpanzees (Wittig et al., 2016), macaques (Young et al., 2014; McCowan et al., 2016; Brent et al., 2017), feral horses (Cameron et al., 2009; Nuñez et al., 2015) and dolphins (Frère et al., 2010), as well as humans (for whom there is a substantial epidemiological literature demonstrating very significant effects of the number of close friends on both psychological and physical health and wellbeing, as well as longevity: Holt-Lunstad et al., 2010; Dunbar, 2018b; Santini et al., 2020).

The potential role of protective alliances based on bonded relationships raises the question as to whether the negative effects of female numbers on fertility is due solely to agonistic interactions involving only a female's immediate neighbours (the members of her social or grooming subgroup) or to more general disturbance effects due to the total number of females in the group (in effect, a crowding effect, reflecting the fact that fights or squabbles elsewhere in the group stress everyone). The first implies that group size (or, in this case, female group size) itself

is irrelevant (with some other factor setting the limit on group size). **Supplementary Figure 6** suggests that a localised effect is unlikely to be the answer: the slope coefficient for the female parameter in the multiple regression rises to an asymptotic value close to zero as female cohort size increases across genera. More importantly, the genera on the right hand side of **Supplementary Figure 6** are precisely those with bonded social groups that provide females with alliances that buffer them against the costs of living in a large group.

Bonded groups come at a considerable cost: individuals (especially females) cannot easily move from one group to another because entry by strangers is often aggressively resisted once bonded relationships have evolved (Dunbar, 1984; Payne et al., 2003; Kahlenberg et al., 2008; Teichroeb et al., 2009; Pusey and Schroepfer-Walker, 2013). While species that live in fission-fusion social systems (e.g., most herding bovids and cervids) can dissipate the stresses of group-living relatively easily by facultatively adjusting group (or herd) size on a day-to-day basis, bonded groups cannot shed individuals as soon as the group exceeds optimum size. They can only do so by fission, and then only providing the smaller subgroup created by fission exceeds the minimum size set by local habitat predation risk (Dunbar et al., 2009, 2018a; Dunbar and MacCarron, 2019). Smaller groupings will likely suffer from higher stress levels due to elevated predation risk as well as increased likelihood of being displaced by larger conspecific groups. As a result, group size oscillates within a range around the target value, forcing the females, in particular, to live for some periods of time in groups that are less than optimal for them before the group manages to achieve a size at which it can safely fission (Dunbar et al., 2009, 2018a; Dunbar and MacCarron, 2019).

Figure 10 illustrates the point with the primate data. The differences in group size across the four categories in **Figure 10** are significant ($F_{2,19} = 6.69$, $p = 0.006$), with significant independent and equal effects of both bondedness ($F_{1,19} = 5.07$, $p = 0.036$, $\eta^2 = 0.211$) and fission-fusion sociality ($F_{1,19} = 6.82$, $p = 0.017$, $\eta^2 = 0.264$). It seems that when the ancestral state



is small unbonded groups, there are two equally good options for increasing group size: adopting a form of fission-fusion sociality that allows the fertility costs to be dissipated by spatial segregation or forming bonded groups that allow the costs to be deferred through protective coalitions. Once bonded groups have evolved, however, it is possible to increase group size still further by exploiting a fission-fusion structure based around bonded subgroups.

The behavioural mechanisms needed to create bonded groups so as to defer the infertility trap usually involve some form of social grooming or close physical contact. Bonded relationships of this kind are time consuming to maintain, accounting for up to 20% of an individual's daily time budget in the most social species of primates (Dunbar, 1998; Lehmann et al., 2007b; Sutcliffe et al., 2012). In addition, managing many social relationships simultaneously is cognitively demanding (Dunbar and Shultz, 2017, 2020, 2021). Not only is memory for individual group members required, but, far more importantly, animals need to be able to titrate relative status along two or more dimensions simultaneously (e.g., rank versus kinship: Cheney and Seyfarth, 1999; Bergman et al., 2003; Schino et al., 2006), as well as factor in the consequences of their actions for third party relationships (whether threatening B might elicit a response from B's ally C: Datta, 1983; Silk, 1999; Borgeaud et al., 2013). These depend on sophisticated metacognitive abilities, such as mentalising skills that allow animals to understand others' intentions (Devaine et al., 2017).

These social cognitive abilities are significantly more costly in neural processing terms than conventional causal reasoning and memory processes (Powell et al., 2010; Lewis et al., 2017). They also require a large dedicated neural network (the combined mentalising/default mode neural network, comprising units in the frontal, parietal and temporal lobes, plus the limbic system: Sallet et al., 2013; Mars et al., 2016; Spreng et al., 2020) as well as specific brain regions such as the frontal pole (Brodmann Area 10) that are only found in anthropoid primates (Passingham and Wise, 2012). Neuroimaging studies of both humans (Bickart et al., 2011, 2012; Lewis et al., 2011; Kanai et al., 2012; Powell et al., 2012; von der Heide et al., 2014; Hampton et al., 2016; Sliwa and Freiwald, 2017; Krol et al., 2018; Kwak et al., 2018; Noonan et al., 2018; Spagna et al., 2018; Kiesow et al., 2020) and anthropoid primates (Sallet et al., 2011; Meguerditchian et al., 2020) indicate that the size of an individuals' personal social network (or living group) correlates with the volume of its mentalising and default mode networks and their associated white matter tracts.

In addition, species need mechanisms that will ensure that groups stay together during the day. This is not a trivial problem, as is indicated by the ease with which ungulate herds disperse during the course of foraging. Maintaining the integrity of groups depends on the capacity to inhibit prepotent responses so that individuals are willing to rest rather than feed when others want to rest, and feed rather than rest when others want to feed. The ability to inhibit prepotent responses (MacLean et al., 2014; Dunbar and Shultz, 2020, 2021) is crucial if synchronised time budgets are to be maintained (King and Cowlshaw, 2009). In some Old World monkeys, coordination during daily foraging is maintained by behaviours that allow subgroups to agree on a direction of travel or a geographical point at which the group will

converge later in case subgroups become completely detached during foraging (e.g., *Papio hamadryas*: Sigg and Stolba, 1981). In such cases, individuals often make explicit bids, or suggestions, about the direction of group travel (usually signalled by specific behaviours), with others then 'voting' on their preferences in order to arrive at a consensus (Sigg and Stolba, 1981; Sueur and Petit, 2010; Sueur et al., 2011). These kinds of signals depend on animals being able to infer the intentions of the signaller and interpret the meaning or significance ("go to waterhole X not waterhole Y") of a behavioural signal (i.e., mentalising capacities).

Both kinds of cognitive ability increase across primate taxa as a function of group (and brain) size (Dunbar and Shultz, 2021).

DISCUSSION

We have shown that, in mammals generally, fertility declines as the number of reproductive females in the group increases, but that in some taxa a trade off between the benefits of living in groups and these costs gives rise to a \cap -shaped relationship.

We argue that the negative relationship between fertility and number of females is most likely due to social stress created by female-female interactions and has little to do with access to food *per se*. All else equal, the steepness of the negative fertility effect sets a low limit on the size of group for mammals; this limits the size of groups to 5–7 reproductive females, which in turn sets an upper limit to total group size of a ~ 15 individuals. In such cases, females would always do best to live alone (with or without offspring and adult males). This seems to have been the ancestral condition for primates, and perhaps mammals in general (Müller and Thalmann, 2000; Shultz et al., 2011). However, this necessarily restricts females to living in low predation-risk habitats. Indeed, when primates switch from living in large groups to pairbonded monogamy (Shultz et al., 2011), it invariably seems to be associated with occupying low predation-risk niches (e.g., gibbons occupying a terminal branch niche).

If it is advantageous for a species to invade a high-risk habitat because of the foraging benefits these have to offer (Cowlshaw, 1997), then the only way this can be done is by finding ways to avoid the infertility trap. The options seem to be to adopt a form of fission-fusion sociality (a neurologically cheap behavioural solution) or to form bonded social groups (a neurologically expensive cognitive strategy that incurs additional costs due to increased foraging costs). Both strategies allow animals to live in larger groups (Figure 10), but they come with very different costs and benefits.

By combining bonded subgroups with a form of modular (or molecular) fission-fusion (Aureli et al., 2008), *Theropithecus* and *Papio hamadryas* seem to have been able to increase the sizes of their groupings significantly beyond those possible for species that have bonded groups (Figures 1, 10). To be able to do this, the two species have had to evolve an unusually radical form of sub-structuring in which groups of females attach themselves to a male who, in effect, acts as a "hired gun" (Mesnick, 1997; Wilson and Mesnick, 1997). The social dynamics that underpin the formation and stability of these subgroups is very different in the two species (Dunbar and MacCarron, 2019), but the

functional consequences are the same. In both cases, it allows the females to form small, stable, semi-independent groups that can operate a fission-fusion herd-like system that is very flexible in its response to environmental conditions. Although no satisfactory explanation has ever been given for these two species' unique social systems, it is conspicuous that both live in habitats that are unusually predator-risky because they lack the usual refuges (tall trees) that primates rely on to escape from predators (Dunbar and MacCarron, 2019). Other examples of species that exploit bondedness with a fission-fusion social system so as to increase group size include chimpanzees, elephants and dolphins. All share the distinction of having brains that are both absolutely and relatively much larger than is typical even for a large-bodied mammal (Dunbar and Shultz, 2021).

The evolution of bonded sociality comes at a significant cost in terms of the time demands of social bonding (Dunbar et al., 2009), which no doubt explains why this form of sociality is so rare in mammals (Sutcliffe et al., 2016). One constraint in this respect is the time costs associated with some diets. Folivores, for example, are obliged to devote significant quantities of time to resting in order to allow gut fermentation to occur because any form of activity suppresses the microbial activity responsible for fermentation (van Soest, 1994). This significantly reduces the time available for social bonding and directly limits group size as a result (Korstjens and Dunbar, 2007). Much may, therefore, depend on whether a species can switch to a dietary category (e.g., fruits) that allows higher nutrient throughput so as to minimise food processing time. Precisely such a transition has been documented in the African colobines: the more frugivorous *Procolobus* live in larger groups than the closely related folivorous *Colobus*, and the two species' social systems can be generated simply by switching the equations that govern foraging time (Korstjens and Dunbar, 2007).

In summary, we argue that the size and structure of mammalian social groups can best be understood as a tradeoff between the demands of external threats and demography-dependent infertility effects. We argue that, because of constraints imposed by mammalian reproductive endocrinology, the default condition is that fertility is a simple negative function of the number of cohabiting females; females would do best to live on their own, but if they need to form groups this will severely limit the size of their social groups. If environmental conditions require that they live in larger groups, they can only do so if they can find behavioural solutions that buffer them against these costs. Most mammals seem to do this either by a cognitively undemanding strategy (fission-fusion sociality) or by a cognitively expensive one (bonded sociality based on female-female coalitions). The only alternative is to avoid habitats

that make such demands. Our focus has been on mammals, because the mechanism we highlight is a consequence of the particular way in which mammalian reproductive endocrinology is arranged so as to manage lactational amenorrhea (which we take to be a uniquely mammalian phenomenon). It is not impossible that something similar occurs in birds or fishes: we leave that for others to pursue. There is some evidence in marine fish for density-dependent effects on fertility that are independent of environmental conditions (e.g., Samhouri, 2009; Forrester et al., 2011), but what evidence there is for birds perhaps suggests that fertility is more directly dependent on environmental quality and direct density-dependent effects on foraging success rather than on any social parameters (e.g., seabirds: Tavecchia et al., 2007), perhaps reflecting the particular foraging costs incurred by avian species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the data are all third-party archival data from the published literature.

AUTHOR CONTRIBUTIONS

Both authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.634664/full#supplementary-material>

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The Infertility Trap:

The Costs of Group-Living and Mammalian Social Evolution

R.I.M. Dunbar & Susanne Shultz

SUPPLEMENTARY INFORMATION

Supplementary Methods

Data

(1) *Group size*

Mean group size for individual species (Fig. 1) was sourced from Pérez-Barbería et al. (2007) for carnivores and ungulates, and Dunbar et al. (2018a) for primates. For all other analyses, demographic data are sourced from the primary sources.

(2) *Fertility data*

Demographers distinguish between *fecundability* (the capacity to conceive), *fecundity* (birth rate) and *fertility* (lifetime reproductive output, or completed family size [at the end of life]). Unfortunately, animal and human demographers disagree about the definitions: while agreeing about the definition of ‘fecundability’, they traditionally use ‘fecundity’ and ‘fertility’ in opposite senses. To avoid any confusion, we will use the term *fertility* to refer to reproduction in a general sense, *birth rate* to refer to the instantaneous rate of reproduction (births or litters per adult female per year), and *reproductive output* to refer to lifetime reproductive success (in this case, indexed as the number of surviving immatures at any given time).

Due to a long history of high quality, long term field studies, data are relatively abundant for primates. Useable data on birth rates for individual groups are extremely sparse for non-primate taxa, mainly for two reasons. First, the vast majority of ungulates are either pairbonded (monogamous) or herd-forming, while all felids (except lion) are solitary and all canids are monogamous breeders (even if they have helpers). This usually means there is little, if any, variation in breeding female cohort size. In herd-forming species, the instability of groups means that average herd size and fertility can be a highly misleading reflection of what individual females actually experience; for the analyses we envisage, we would need data for individual females on both birth rates and ‘typical [or experienced] group size’ (Jarman 1974) (or ‘crowding’: Reiczigel et al. 2008). Such data are never provided. Second, mammalogists seldom provide data on birth rates for individual social groups, since their interests are usually at the population or average female lifehistory level. All non-primate data in our sample are for group-living genera for this reason.

Birth rate data have been collated and published for some genera (notably *Papio*, *Theropithecus*, *Pan*, *Gorilla*), and we use these sources. Otherwise, we located mean birth rates for groups of different size from primary sources by a literature search on GoogleScholar with key terms: birth_rates, fertility and fecundity, in some cases listing specific taxa. Where possible, data are for individual groups within the same population so as to minimise the impact of environmental effects. For some primate genera, this was not possible because researchers study, and therefore provide data for, only a single group at a particular site. These usually concern species characterised by large social groups occupying very large home ranges (e.g. baboons, chimpanzees). In these cases, we use data from a single group belonging to different populations within the taxon's biogeographical range. The influence of environmental factors on fertility has been shown to be independent of the effects due to demography for a number of primate genera (*Colobus*, *Papio*, *Theropithecus*, *Pan*, *Gorilla*: Dunbar & Sharman 1983; Hill et al. 2000; Dunbar 2018, 2019; Dunbar et al. 2018b).

Data on average reproductive output (number of immatures per female) are widely available for primates since group census data are provided as standard by most studies, allowing us to examine a wider range of genera. Immatures include all individuals listed as infants or juveniles. Depending on genus, this refers to individuals that are less than 2-5 years old. With a few (species-poor) exceptions (equids, elephantids, delphinids), only primates live in multi-generational groups, and so only these are analysed for reproductive output. For these purposes, we use population mean values, averaged across all well-sampled groups in the population. Data on reproductive output were obtained from sources cited in two secondary compilations that list mean population structure for individual study sites for many genera (Smuts et al. 1987; Campbell et al. 2007), supplemented by a GoogleSearch for more recent studies with keywords as above. All data are population averages: the data points for each genus therefore represent different populations. Care was taken to ensure that samples were not duplicated from different publications.

For both fertility indices, the criteria for inclusion in the analysis were: stable social groups, censused from undisturbed populations, with a minimum of three data points per genus. Repeat censuses from the same population were allowed providing they were at least 5 years apart or significant demographic change had occurred between successive study periods.

Statistical methods

All statistical analyses were carried out using SPSS v.25.

(1) Phylogenetic analysis

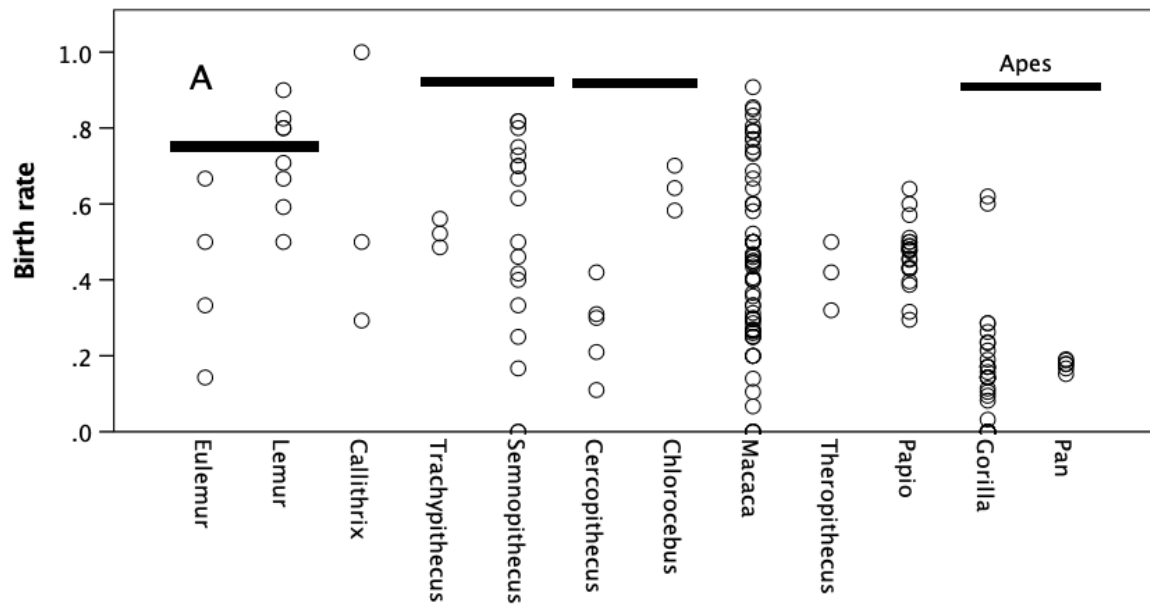
Following Dunbar et al. (2009, 2018b), all the primate data are analysed at genus level since, in primates at least, species largely represent ecological variants. In any case, in primates, demographic, behavioural and ecological indices have near-zero phylogenetic signals (Kamilar & Cooper 2013). Lifehistory variables exhibit higher levels of phylogenetic inertia when analysed at species level, but this is because most species within a genus share the same trait ('constraining traits', *sensu* Strier et al. 2014). Analysis of the phylogenetic signal at genus level for both the demographic and the lifehistory variables studied in this paper (calculated using the R package *Phytools* and the function *phylosig*) yields no detectable signal for either Blomberg's *K* (Blomberg et al. 2003) or Pagel's λ (Pagel 1999) (Table S1).

Table S1. Estimates of phylogenetic signal in the primate data*

Variable	K	P	Pagel's λ	logL	logL0	P
group	0.326	0.163	0.000048	-97.19457	-97.19453	1.000
females	0.221	0.734	0.000054	-87.50391	-87.50381	1.000
fecundity	0.396	0.356	0.000066	-35.01816	-35.01803	1.000
fertility	0.187	0.789	0.000066	-87.65898	-87.65866	1.000

* *Papio hamadryas* is not included in this analysis

More importantly, variation within genera far outweighs variation between genera (Fig. S1). Since our focus is at the group or population level, and all analyses are executed on a genus by genus basis, the question of phylogenetic inertia does not arise as a significant issue.



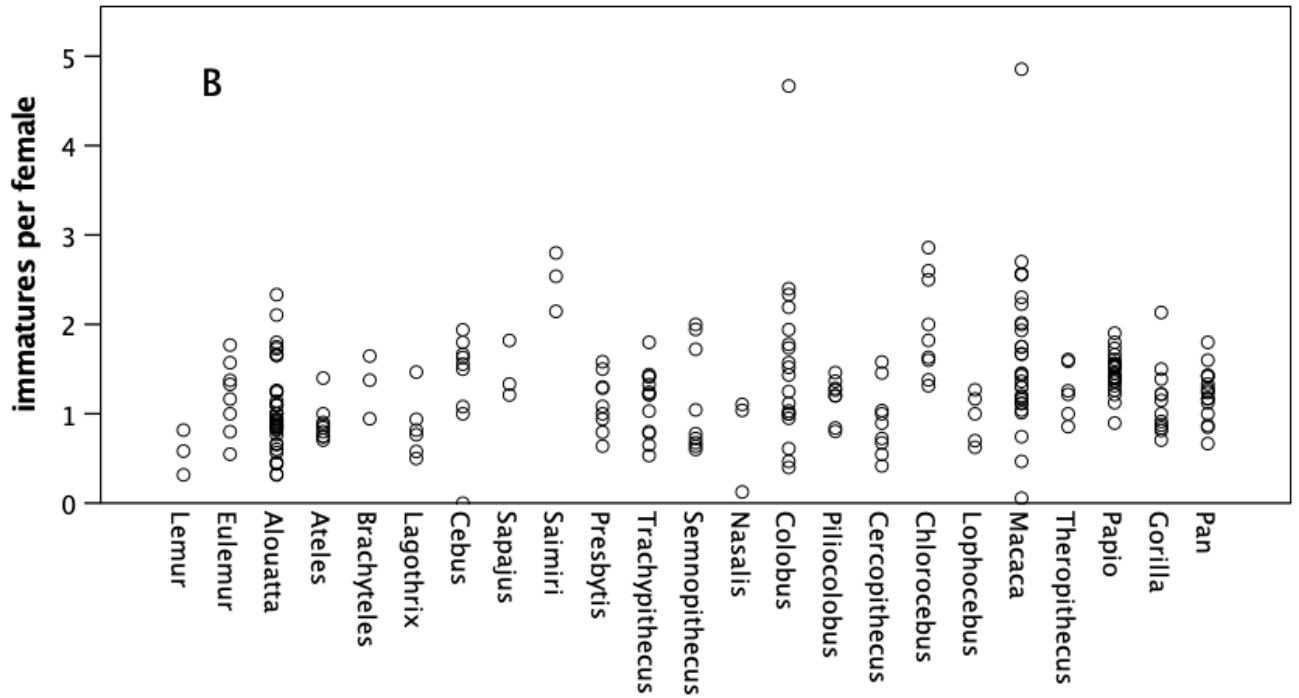


Figure S1

(a) Birth rate and (b) reproductive rate (immatures per female) for individual genera in the primate sample. In (a), closely related genera are indicated by the black bars. The apes are an order of magnitude larger in body size than the other genera (hence their lower birth rates). Variation within genera far outweighs variation between genera.

Perhaps the substantive issue, however, is that none of our analyses test functional hypotheses about the causal relationship between two variables – the context in which phylogenetic inertia has been identified as a problem. All our analyses focus on the numerical distribution of a single variable: we simply ask whether the distribution is best described by a single unimodal distribution or an overlapping set of such distributions. There are no phylogenetic methods available for analysing such data (Dunbar et al. 2018a).

In the case of the non-primate mammals sampled, all the data derive from a single species for any given taxonomic family.

(2) Statistical independence of data

Most of the data we use come in one of two forms: (i) data from different groups within the same population or (ii) population-level averages (i.e. across all sampled groups within a population) for a number of populations. The first form has the advantage of holding environmental conditions more or less constant (and is therefore preferred). Otherwise the data consist of single groups sampled from geographically separated populations, or (in the case of reproductive output) the averages for several groups from geographically separated populations.

Many field studies of primates involve long term studies of known individuals (Strier et al. 2014). In a few cases, we use data from the same population sampled some years apart. The definition of statistical independence (the autocorrelation problem) is that it should not be possible to predict, with better than random chance, the value(s) at time t2 from the values at time t1. This is simply a matter of the length of the interval between successive samples and the rate of change in the variable (Slatkin & Hausfater 1976). At least in studies of primates, it has been found that an interval of 5 years is usually sufficient to ensure that sufficient demographic change has occurred to make successive data points statistically independent when the variables are responsive to environmental conditions rather than being fixed species-specific values (Dunbar et al. 2009; see also Strier et al. 2014). We use a shorter interval in one case (*Theropithecus*), but only because there was significant demographic change in the population between two successive samples. This criterion has been extensively used in building highly predictive ecological models (see, for example, Dunbar et al. 2009).

(3) Hypothesis-testing and Methods

In some cases, we run a meta-analysis to determine the consistency in the patterns observed. Fisher showed that we can use the summed natural logarithm of the statistical significance levels (p-values) associated with a set of independent tests of the same underlying hypothesis to ask how likely it is that a set of results as extreme as those observed would occur by chance if there was no underlying relationship between the variables of interest. The tests do not have to be identical, or test exactly the same hypothesis. This gives us a log-likelihood test of the form:

$$\chi^2 = -2\sum \ln(p_i)$$

where p_i is the significance level (p-value) associated with the i^{th} independent test, with the degrees of freedom equal to twice the number of tests being combined (Sokal & Rolf 1969). Fisher's algorithm has the advantage that it is conceptually simple and robust to wide differences in study design and the statistical methods used, and was explicitly intended for use with small samples that are individually likely to provide weak statistical evidence for an effect. In most of these cases, we test a directional hypothesis (a significant negative relationship is as much evidence against a positive directional hypothesis as a non-significant result), and the associated p-value is therefore the signed 1-tailed p-value. In other words, when testing for a positive relationship, a 2-tailed p-value of 0.10 associated with a *negative* relationship has a 1-tailed value of $p^* = 1 - (0.5 * 0.1) = 0.95$ of significantly supporting a positive relationship. The genus is always the unit of analysis, and each genus is treated as an independent test of the underlying hypothesis.

Supplementary Results

Within-taxon variation in fertility (Main text: Figures 2-5):

To determine whether fertility is influenced by any of the demographic variables, we first plotted, for each genus separately, birth rate and reproductive rate against each of the three demographic variables (group size, number of adult males, number of adult females). For each

graph, we then ran a regression analysis to determine whether a linear or a quadratic regression provided the better fit. The plots differed little between the three demographic variables, though the high frequency of single male groups made for less clear patterns in the male case.

Fig. S2 plots the data for the three non-primate mammalian genera separately (main text Fig. 3), as well as the linear and quadratic regression lines. The data for mongoose are plotted separately for three successive years from the same population to emphasise the point that the same pattern emerges despite changes in the demography of the individual groups. The plot of the quadratic regression in Fig. 3 (main text) is that for these data averaged across groups of the same size (yielding 6 data points). The data for horses (all from the same population on the Shackleford Banks off the North Carolina mainland of the USA) are for individual harems, distinguishing those that are territorial from those that are non-territorial. A single combined regression line is set through all the data points.

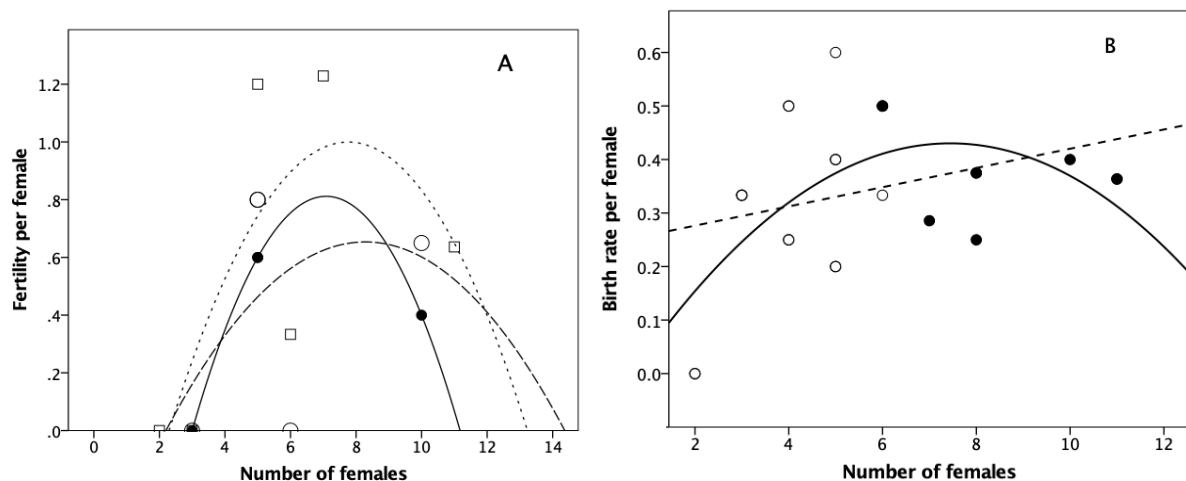


Figure S2

Plots of original data for (a) banded mongoose (*Mungos mungo*): the symbols, and separate quadratic regression lines, identify data for three separate years from the same population. Source: De Luca & Ginsberg (2001); (b) feral horses (*Equus caballus*), Shackleford Banks, N. Carolina, USA (unfilled: non-territorial groups; filled: territorial groups). Dashed line: best-fit linear regression; solid line: best-fit quadratic regression. Source: Rubenstein (1986)

The lion data are not shown, as the regression in Fig. 3 (main text) is based on the equation given by Moser & Packer (2009):

$$\text{Fertility} = 0.0911 + 0.131 \cdot \text{females} - 0.0076 \cdot \text{females}^2 - 0.2185 \cdot \text{Takeovers} + 0.0063 \cdot \text{TerritoryQuality}$$

with the takeover parameter set to 0, and the territory quality parameter set to 50 (the midpoint in the range).

The regression tables for the primate data are given in Table S2(a-c) below. The plots for female number, and the two respective regression lines, are graphed for each primate genus in

Fig. S3. In some cases, the quadratic fit is greatly improved if set through the origin. Arguably, this might be appropriate for all quadratic fits, since groups with no females must necessarily be zero when the number of females is zero.

Figure S3

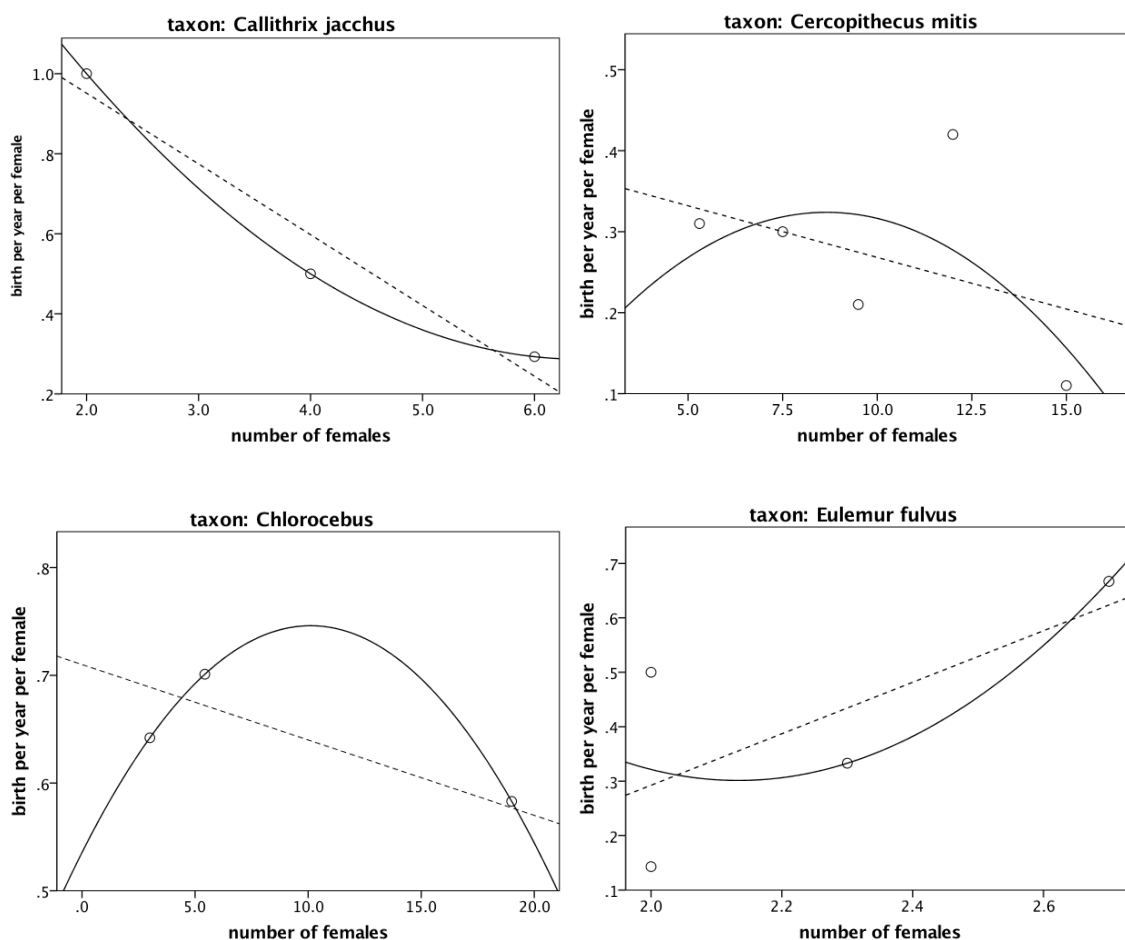
Mean birth rate as a function the number of females in each group for individual primate genera.

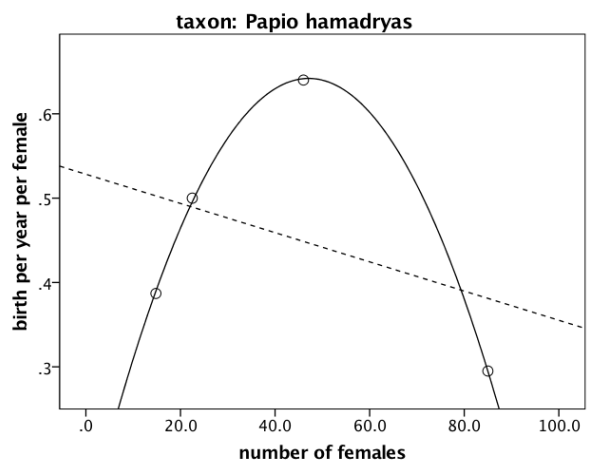
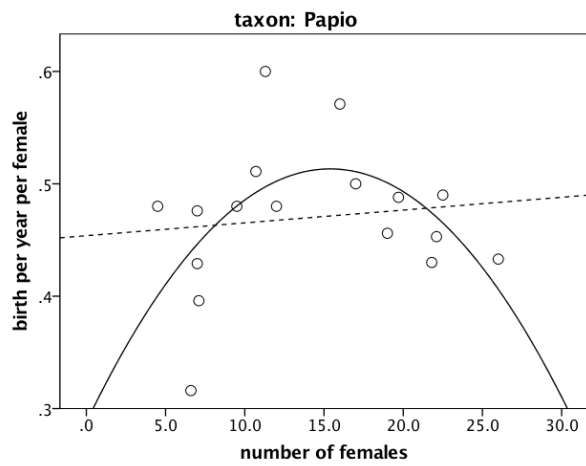
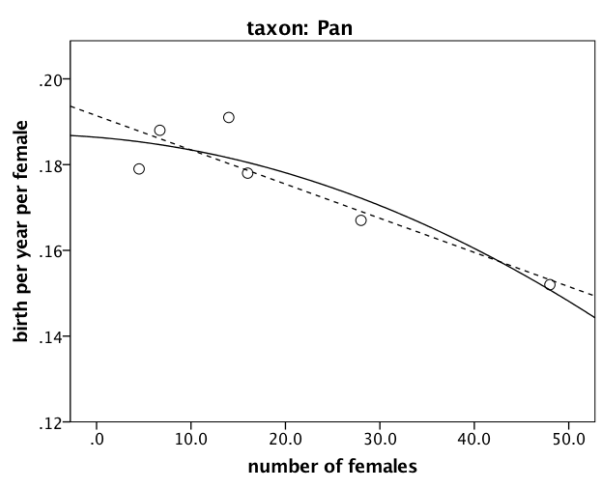
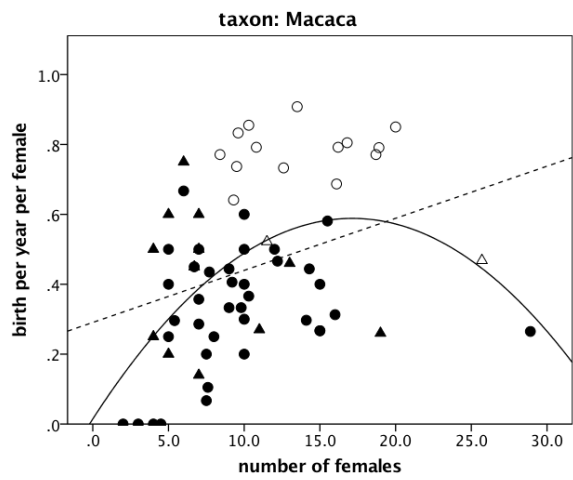
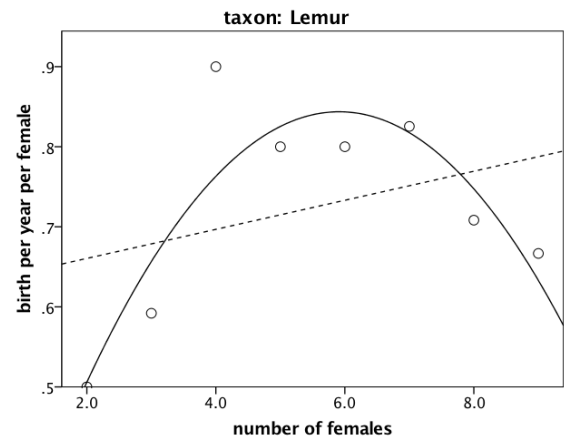
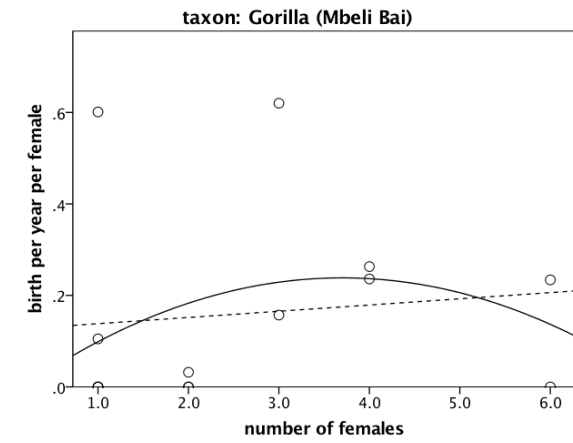
Except for *Lemur*, each datapoint is the average for one study group.

Wherever possible, all data come from the same study population, but some (notably *Pan*, *Papio* and *Theropithecus*) are for single groups from different populations. Environmental effects on fertility are known to be independent of demographic effects in these three taxa. Data are shown separately for four species of *Macaca* (unfilled circles: *M. cyclopis*; filled circles: two *M. fuscata* sites; unfilled triangle: *M. fascicularis*; filled triangles: *M. silenus*) and two study sites of *Semnopithecus*. A single regression is set through the data in each case, but each dataset separately yields a quadratic regression that is a better fit than a linear regression.

Dashed line: linear regression; Solid line: quadratic regression.

Regression statistics for linear and quadratic fits are given below in Table S2.





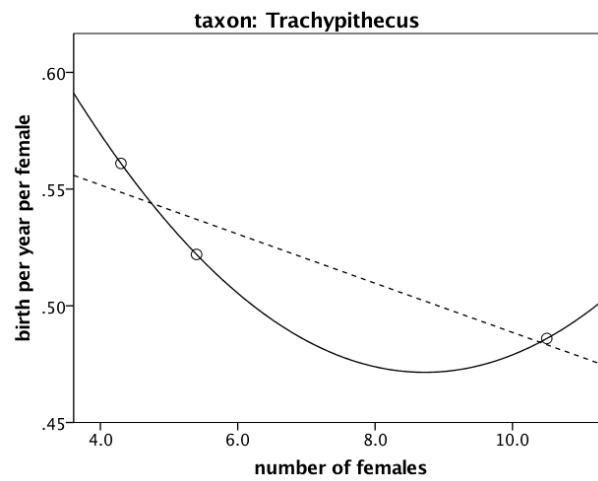
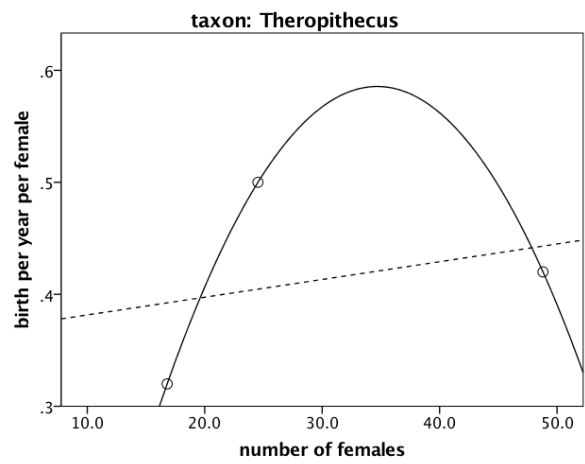
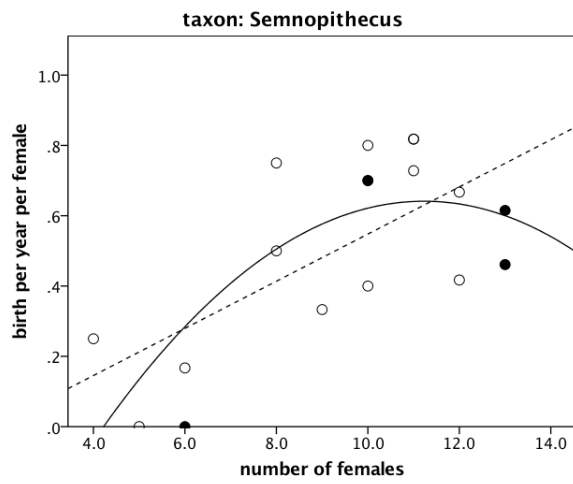


Table S2. Bivariate regression statistics. Dependent variable: Births per year per female. All significance levels are two-tailed.

(a) Regression against TOTAL GROUP SIZE

Dependent Variable:: birth per year per female

genusfert	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Callithrix	Linear	.983	56.236	1	1	.084	1.569	-.112	
	Quadratic	1.000	.000	2	0	.	.608	.167	-.018
Cercopithecus	Linear	.134	.464	1	3	.544	.429	-.008	
	Quadratic	.261	.354	2	2	.739	-.115	.055	-.002
Chlorocebus	Linear	.476	.908	1	1	.515	.738	-.004	
	Quadratic	1.000	.000	2	0	.	.170	.040	-.001
Eulemur	Linear	.814	8.746	1	2	.098	-.344	.103	
	Quadratic	.818	2.242	2	1	.427	-.716	.203	-.006
Gorilla	Linear	.000	.000	1	30	.989	.143	.000	
	Quadratic	.005	.070	2	29	.933	.190	-.014	.001
Macaca	Linear	.238	19.395	1	62	.000	.254	.006	
	Quadratic	.286	12.236	2	61	.000	.095	.017	.000
P.hamadryas	Linear	.013	.027	1	2	.885	.485	.000	
	Quadratic	.918	5.614	2	1	.286	-.160	.013	-4.838E-5
Pan	Linear	.799	15.920	1	4	.016	.192	.000	
	Quadratic	.812	6.481	2	3	.081	.188	.000	-8.611E-7
Papio	Linear	.032	.491	1	15	.494	.445	.001	
	Quadratic	.474	6.296	2	14	.011	.222	.011	.000
Semnopithecus	Linear	.541	18.880	1	16	.001	-.207	.033	
	Quadratic	.640	13.312	2	15	.000	-.999	.114	-.002
Theropithecus	Linear	.090	.099	1	1	.806	.365	.001	
	Quadratic	1.000	.000	2	0	.	-.384	.018	-8.516E-5
Trachypithecus	Linear	.998	449.313	1	1	.030	.619	-.005	
	Quadratic	1.000	.000	2	0	.	.638	-.007	5.918E-5

(b) Regression against NUMBER OF MALES IN GROUP

Dependent Variable:: birth per year per female

genusfert	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Callithrix	Linear	.054	.057	1	1	.850	.793	-.073	
	Quadratic	.054	.057	1	1	.850	.695	.000	-.012
Cercopithecus	Linear	.083	.272	1	3	.638	.660	-.375	
	Quadratic	.083	.272	1	3	.638	.660	-.375	.000
Chlorocebus	Linear	.324	.480	1	1	.614	.703	-.010	
	Quadratic	1.000	.000	2	0	.	.457	.083	-.007
Eulemur	Linear	.579	2.751	1	2	.239	-.153	.170	
	Quadratic	.639	.886	2	1	.601	.734	-.362	.074
Gorilla	Linear	.075	2.448	1	30	.128	.228	-.041	
	Quadratic	.100	1.608	2	29	.218	.338	-.158	.025
Macaca	Linear	.009	.361	1	39	.551	.546	-.005	
	Quadratic	.128	2.789	2	38	.074	.404	.047	-.003
P.hamadryas	Linear	.120	.272	1	2	.654	.538	-.003	
	Quadratic	.747	1.475	2	1	.503	.003	.045	-.001
Pan	Linear	.516	4.269	1	4	.108	.187	-.001	
	Quadratic	.594	2.196	2	3	.259	.180	.001	-7.276E-5
Papio	Linear	.076	1.230	1	15	.285	.441	.005	
	Quadratic	.155	1.285	2	14	.307	.393	.022	-.001
Semnopithecus	Linear	.056	.950	1	16	.344	.658	-.136	
	Quadratic	.056	.950	1	16	.344	.658	-.136	.000
Theropithecus	Linear	.193	.239	1	1	.711	.314	.010	
	Quadratic	1.000	.	2	0	.	-.622	.221	-.011
Trachypithecus	Linear	.001	.001	1	1	.985	.524	-.001	
	Quadratic	.001	.001	1	1	.985	.524	-.001	.000

(c) Regression against NUMBER OF FEMALES IN GROUP

Dependent Variable: birth per year per female

genusfert	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Callithrix	Linear	.946	17.467	1	1	.150	1.305	-.177	
	Quadratic	1.000	.000	2	0	.	1.793	-.470	.037
Cercopithecus	Linear	.172	.625	1	3	.487	.396	-.013	
	Quadratic	.332	.496	2	2	.668	.012	.072	-.004
Chlorocebus	Linear	.619	1.626	1	1	.423	.691	-.005	
	Quadratic	1.000	.	2	0	.	.536	.042	-.002
Eulemur	Linear	.488	1.903	1	2	.302	-.653	.473	
	Quadratic	.579	.688	2	1	.649	5.480	-4.855	1.138
Gorilla	Linear	.024	.746	1	30	.395	.101	.014	
	Quadratic	.091	1.453	2	29	.250	-.034	.115	-.014
Lemur	Linear	.112	.754	1	6	.419	.624	.018	
	Quadratic	.772	8.480	2	5	.025	.072	.261	-.022
Macaca	Linear	.109	7.856	1	64	.007	.291	.015	
	Quadratic	.227	9.241	2	63	.000	.015	.067	-.002
P.hamadryas	Linear	.135	.311	1	2	.633	.528	-.002	
	Quadratic	1.000	1138.000	2	1	.021	.106	.023	.000
Pan	Linear	.804	16.445	1	4	.015	.191	-.001	
	Quadratic	.832	7.416	2	3	.069	.186	.000	-1.171E-5
Papio	Linear	.015	.227	1	15	.641	.454	.001	
	Quadratic	.292	2.890	2	14	.089	.288	.029	-.001
Semnopithecus	Linear	.448	13.005	1	16	.002	-.123	.067	
	Quadratic	.560	9.559	2	15	.002	-1.006	.293	-.013
Theropithecus	Linear	.086	.094	1	1	.811	.366	.002	
	Quadratic	1.000	.	2	0	.	-.414	.058	-.001
Trachypithecus	Linear	.863	6.281	1	1	.242	.594	-.011	
	Quadratic	1.000	.	2	0	.	.820	-.080	.005

We apply Fisher's meta-analysis to the 1-tailed directional significance levels in Table S2 to determine whether there are any consistent underlying trends. For all analyses, H_0 is a negative linear relationship or a quadratic that is \cap -shaped (i.e. positive-signed b and negative-signed b^2). The results are given in Table S3.

Table S3. Fisher's meta-analysis for individual predictor variables for birth rate

Predictor variable	Linear equation			Quadratic equation		
	χ^2	df	p	χ^2	df	p
Total group size	24.82	24	0.209	17.12	14	0.249
Number of males	23.52	24	0.264	14.92	20	0.781
Number of females	31.10	26	0.054	53.25	16	<0.0001

The results indicate that only the number of adult females is significantly more negative than would be expected by chance, with a quadratic being by far the better fit.

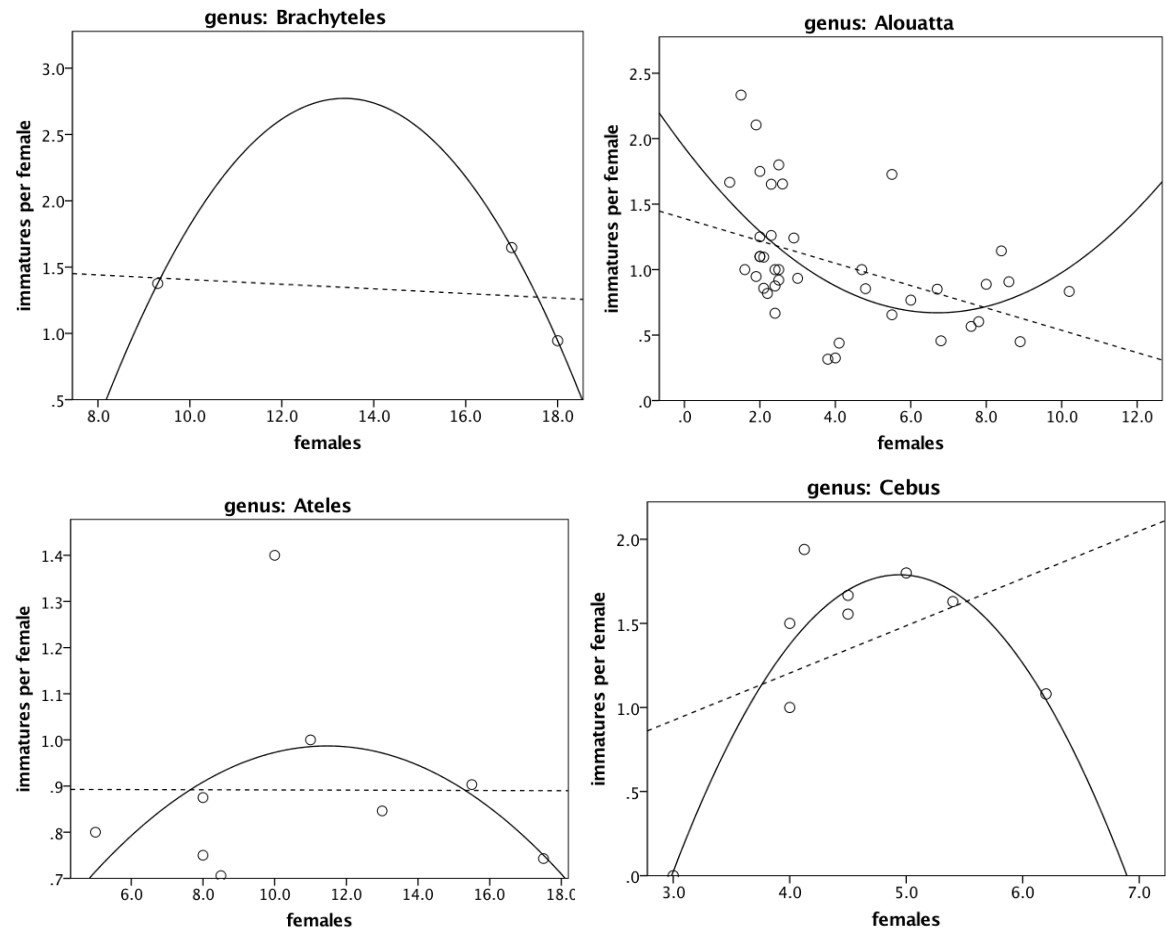
We then ran a similar analysis for the primate reproductive output data. The individual genus plots are given in Fig. S4, with the corresponding regression statistics in Table S4.

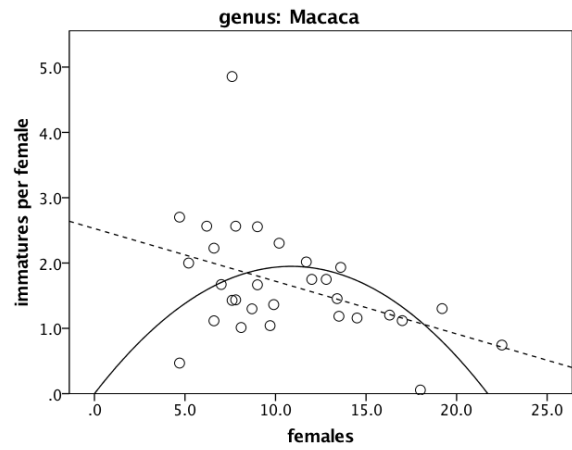
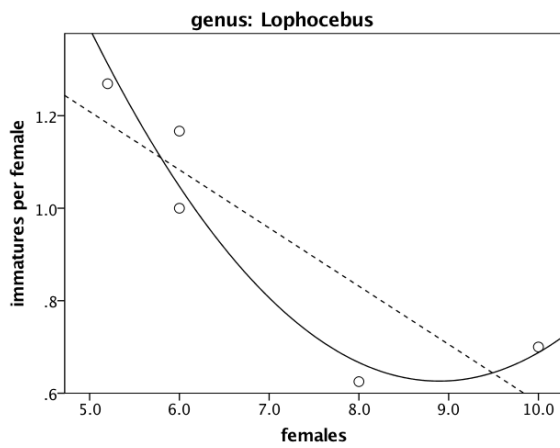
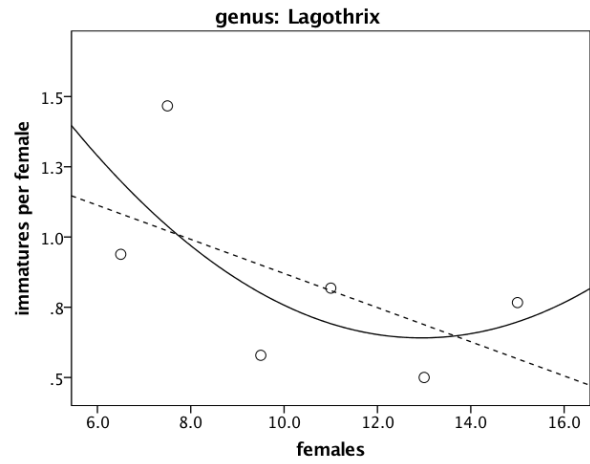
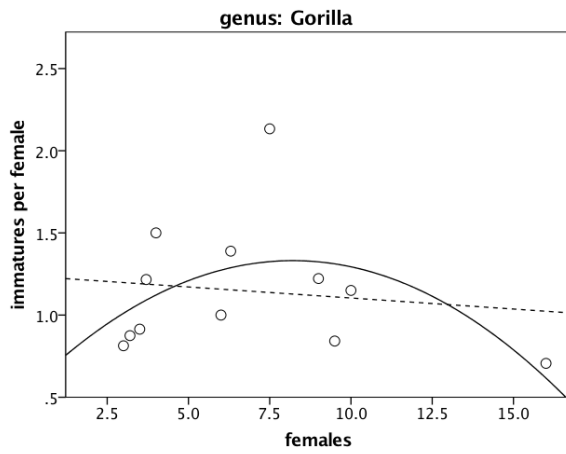
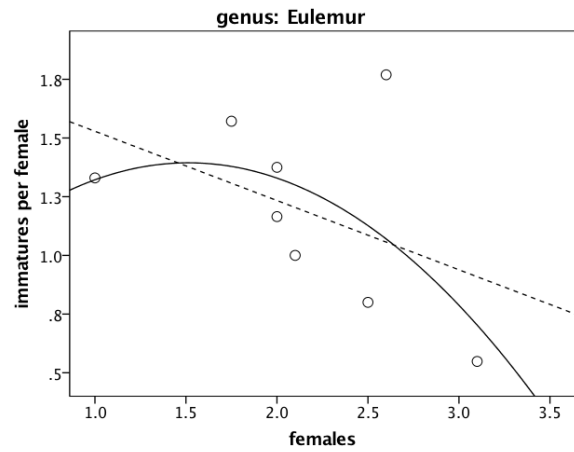
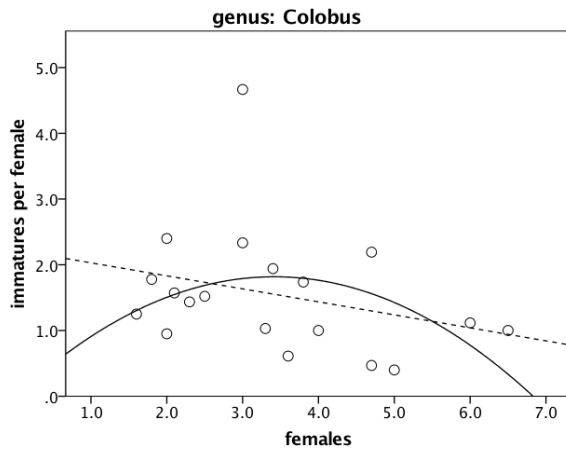
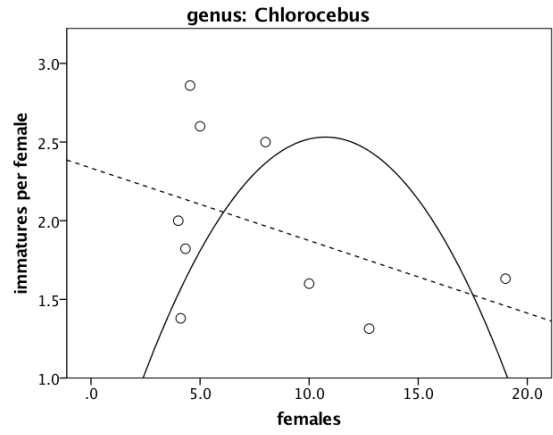
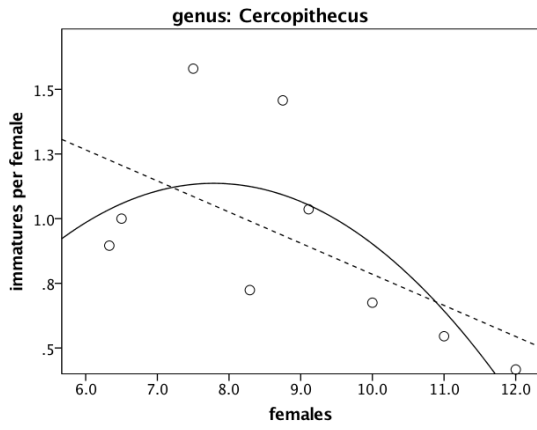
Figure S4
Mean reproductive output (immatures per female) plotted against mean number of females per group for different primate genera.

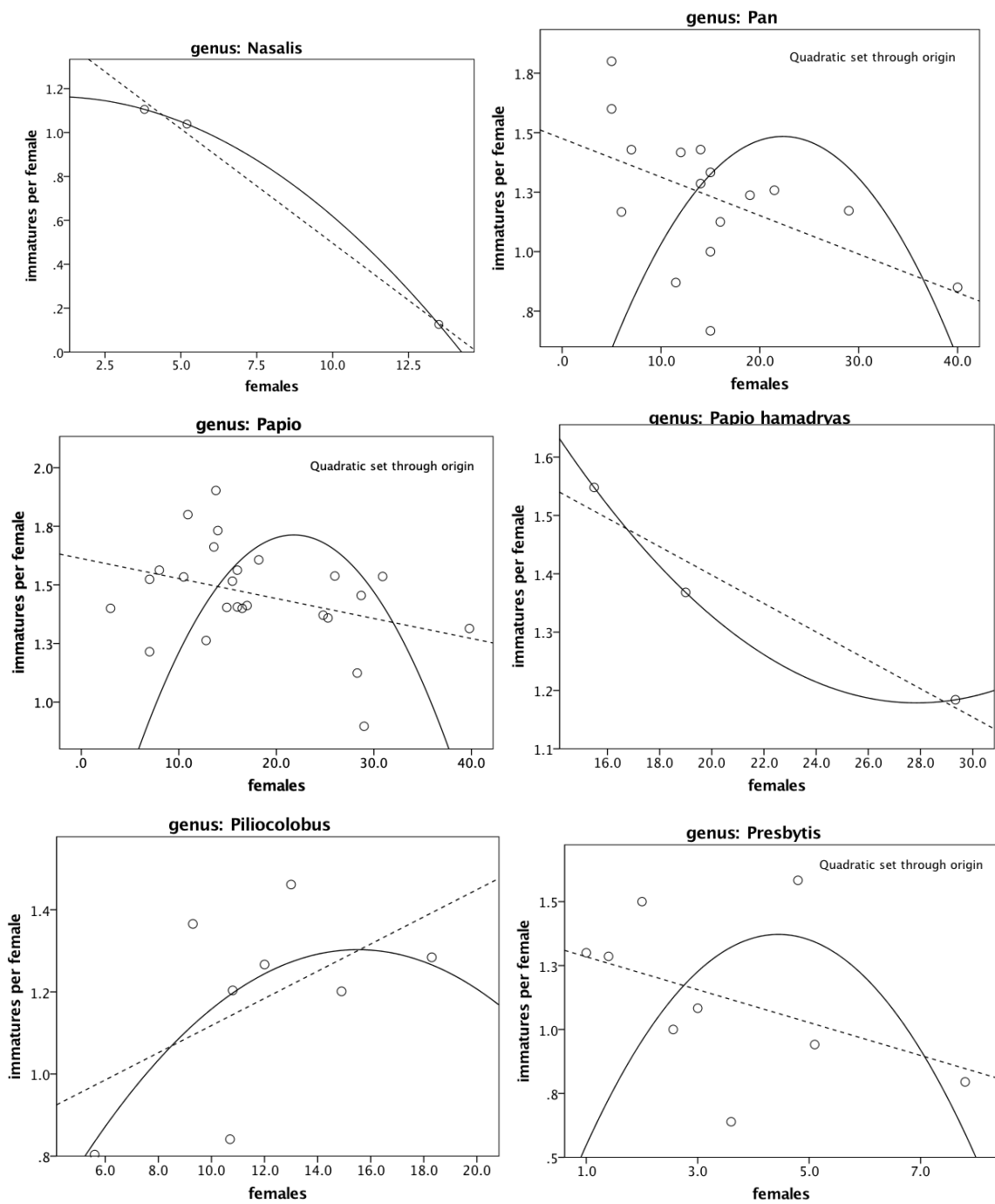
Each data point is the mean value for one study site, averaged across all censused groups. Most data points are the average of several groups, except *Pan* and *Papio* (where usually only one group is ever studied at a given site).

Dashed line: linear regression; Solid line: quadratic regression.

Regression statistics for linear and quadratic fits are given below in Table S4.







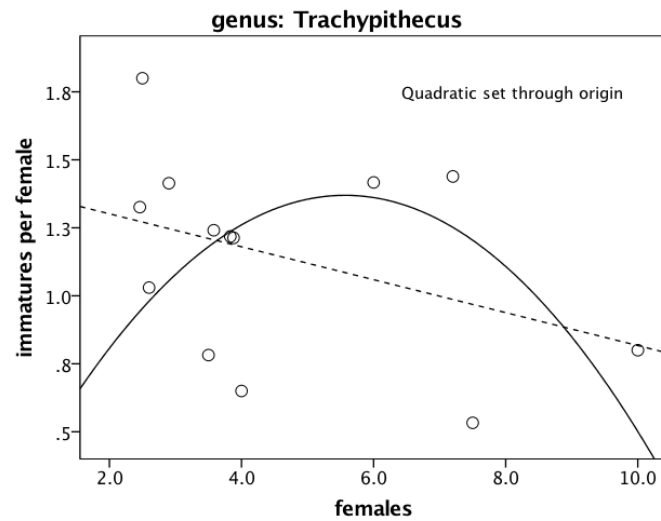
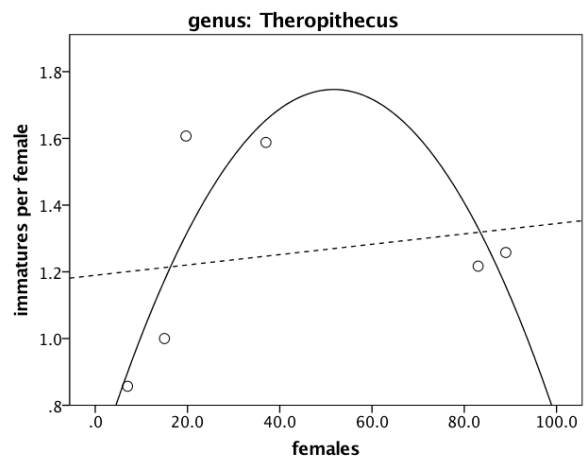
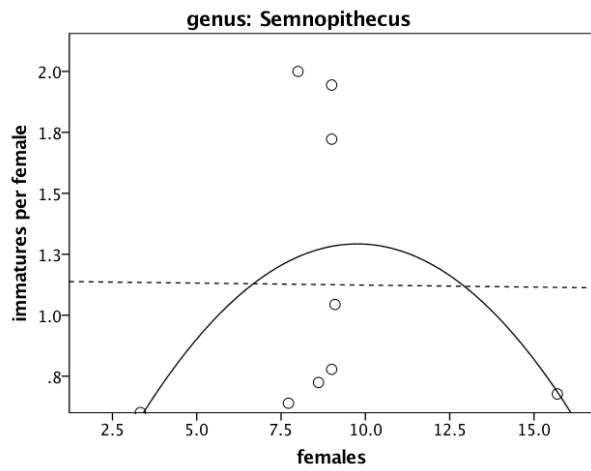
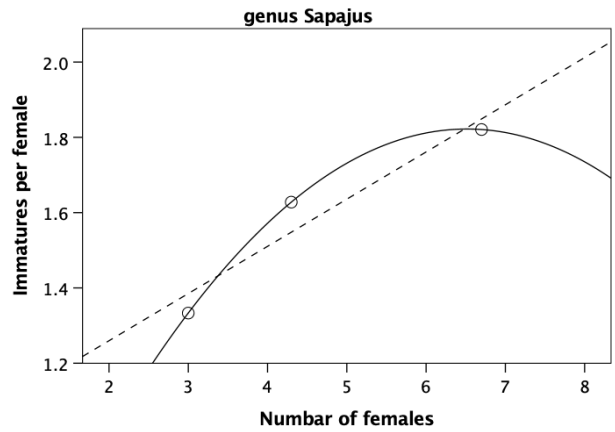
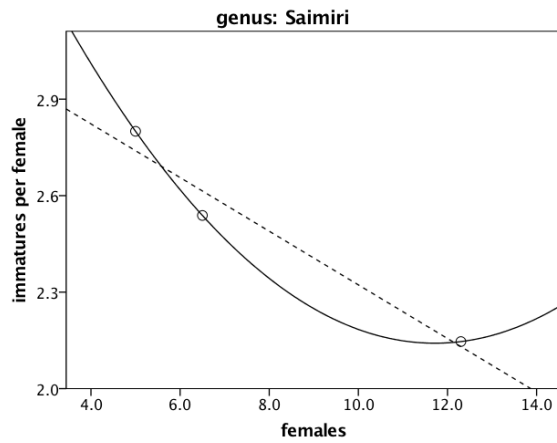


Table S4. Bivariate regression statistics. Dependent variable: reproductive output (immatures per female). All significance levels are two-tailed.

(a) Regression against TOTAL GROUP SIZE									
Dependent Variable:: immatures per female									
genus	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Alouatta	Linear	.073	2.994	1	38	.092	1.324	-.027	
	Quadratic	.167	3.722	2	37	.034	2.282	-.209	.007
Ateles	Linear	.016	.083	1	5	.785	.802	.003	
	Quadratic	.454	1.662	2	4	.298	-1.089	.149	-.002
Brachyteles	Linear	.165	.198	1	1	.734	1.782	-.010	
	Quadratic	1.000	.	2	0	.	-4.369	.286	-.003
Cebus	Linear	.689	15.542	1	7	.006	-.497	.128	
	Quadratic	.735	8.321	2	6	.019	-1.370	.320	-.009
Cercopithecus	Linear	.158	1.313	1	7	.289	.398	.027	
	Quadratic	.200	.751	2	6	.512	1.651	-.103	.003
Chlorocebus	Linear	.061	.455	1	7	.522	2.236	-.009	
	Quadratic	.125	.430	2	6	.669	1.562	.037	-.001
Colobus	Linear	.276	6.467	1	17	.021	.283	.124	
	Quadratic	.453	6.613	2	16	.008	3.289	-.477	.026
Eulemur	Linear	.004	.026	1	6	.877	1.128	.008	
	Quadratic	.034	.087	2	5	.918	1.477	-.082	.005
Gorilla	Linear	.000	.000	1	10	.997	1.148	-5.138E-5	
	Quadratic	.431	3.410	2	9	.079	-.215	.173	-.005
Lagothrix	Linear	.113	.511	1	4	.514	1.169	-.010	
	Quadratic	.571	1.997	2	3	.281	-3.016	.260	-.004
Lophocebus	Linear	.864	19.048	1	3	.022	2.531	-.093	
	Quadratic	.884	7.651	2	2	.116	6.322	-.530	.012
Macaca	Linear	.032	.928	1	28	.344	1.232	.013	
	Quadratic	.075	1.095	2	27	.349	-.101	.098	-.001
Nasalis	Linear	.902	9.157	1	1	.203	2.385	-.129	
	Quadratic	1.000	.000	2	0	.	-.858	.398	-.020
Pan	Linear	.116	1.836	1	14	.197	1.396	-.003	
	Quadratic	.117	.862	2	13	.445	1.435	-.005	1.206E-5
Papio	Linear	.048	1.150	1	23	.295	1.567	-.002	
	Quadratic	.079	.943	2	22	.405	1.387	.005	-6.283E-5
Papioham	Linear	.941	16.019	1	1	.156	2.025	-.010	
	Quadratic	1.000	.000	2	0	.	3.569	-.054	.000
Piliocolobus	Linear	.319	2.816	1	6	.144	.840	.011	
	Quadratic	.499	2.487	2	5	.178	.343	.046	-.001
Presbytis	Linear	.031	.222	1	7	.652	1.248	-.014	
	Quadratic	.132	.456	2	6	.654	1.926	-.180	.009
Propithecus	Linear	.013	.013	1	1	.927	.067	.079	
	Quadratic	.013	.013	1	1	.927	.067	.079	.000
Saimiri	Linear	.930	13.368	1	1	.170	3.379	-.030	
	Quadratic	1.000	.	2	0	.	6.496	-.239	.003
Sapajus	Linear	.854	5.858	1	1	.249	1.132	.027	
	Quadratic	1.000	.000	2	0	.	.374	.121	-.002
Semnopithecus	Linear	.546	8.421	1	7	.023	-.028	.052	
	Quadratic	.559	3.806	2	6	.086	.471	-.002	.001
Theropithecus	Linear	.046	.194	1	4	.683	1.176	.001	
	Quadratic	.611	2.351	2	3	.243	.658	.015	-5.594E-5
Trachypithecus	Linear	.005	.058	1	11	.814	1.206	-.005	
	Quadratic	.027	.141	2	10	.870	.669	.083	-.003

(b) Regression against NUMBER OF MALES

Dependent Variable: immatures per female

genus	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Alouatta	Linear	.294	15.822	1	38	.000	1.720	-.307	
	Quadratic	.498	18.348	2	37	.000	3.228	-1.751	.302
Ateles	Linear	.060	.449	1	7	.524	.688	.042	
	Quadratic	.084	.276	2	6	.768	.171	.258	-.021
Brachyteles	Linear	.842	5.345	1	1	.260	1.877	-.053	
	Quadratic	.848	5.558	1	1	.255	1.615	.000	-.002
Cebus	Linear	.000	.000	1	7	1.000	1.353	-4.147E-5	
	Quadratic	.241	.955	2	6	.437	2.627	-1.176	.215
Cercopithecus	Linear	.685	15.213	1	7	.006	-1.068	1.840	
	Quadratic	.737	8.426	2	6	.018	-7.830	13.211	-4.625
Chlorocebus	Linear	.076	.574	1	7	.473	2.218	-.058	
	Quadratic	.078	.252	2	6	.785	2.117	-.012	-.004
Colobus	Linear	.010	.164	1	17	.690	1.798	-.139	
	Quadratic	.095	.837	2	16	.451	-.793	2.733	-.702
Eulemur	Linear	.282	2.357	1	6	.176	1.718	-.166	
	Quadratic	.411	1.746	2	5	.266	1.126	.256	-.065
Gorilla	Linear	.061	.652	1	10	.438	1.286	-.052	
	Quadratic	.126	.646	2	9	.547	.984	.157	-.025
Lagothrix	Linear	.004	.014	1	4	.911	.887	-.007	
	Quadratic	.110	.186	2	3	.839	.186	.226	-.016
Lophocebus	Linear	.001	.003	1	3	.961	.960	-.002	
	Quadratic	.195	.242	2	2	.805	1.222	-.127	.007
Macaca	Linear	.035	1.006	1	28	.324	1.903	-.044	
	Quadratic	.057	.817	2	27	.452	1.583	.056	-.005
Nasalis	Linear	.801	4.023	1	1	.294	2.470	-1.224	
	Quadratic	1.000	.	2	0	.	-2.428	6.176	-2.643
Pan	Linear	.110	1.739	1	14	.208	1.382	-.017	
	Quadratic	.115	.842	2	13	.453	1.321	-.006	.000
Papio	Linear	.090	2.281	1	23	.145	1.584	-.014	
	Quadratic	.167	2.200	2	22	.135	1.421	.034	-.003
Papioham	Linear	.241	.318	1	1	.673	1.570	-.014	
	Quadratic	1.000	.000	2	0	.	.344	.183	-.007
Piliocolobus	Linear	.001	.005	1	6	.944	1.169	.002	
	Quadratic	.035	.091	2	5	.914	1.262	-.049	.005
Presbytis	Linear	.144	1.181	1	7	.313	.445	.606	
	Quadratic	.365	1.726	2	6	.256	7.117	-10.201	4.215
Propithecus	Linear	.407	.685	1	1	.560	1.374	-.391	
	Quadratic	1.000	.	2	0	.	10.685	-10.082	2.447
Saimiri	Linear	.013	.013	1	1	.927	2.669	-.065	
	Quadratic	.013	.013	1	1	.927	2.591	.000	-.013
Sapajus	Linear	.302	.432	1	1	.630	.957	.203	
	Quadratic	1.000	.	2	0	.	15.099	-8.396	1.269
Semnopithecus	Linear	.164	1.374	1	7	.279	.750	.189	
	Quadratic	.291	1.231	2	6	.357	1.716	-.701	.149
Theropithecus	Linear	.023	.094	1	4	.774	1.197	.005	
	Quadratic	.224	.432	2	3	.684	.868	.088	-.003
Trachypithecus	Linear	.320	5.184	1	11	.044	.530	.404	
	Quadratic	.350	2.695	2	10	.116	-.108	1.287	-.275

(c) Regression against NUMBER OF FEMALES

Dependent Variable: immatures per female

genus	Equation	R Square	Model Summary				Parameter Estimates		
			F	df1	df2	Sig.	Constant	b1	b2
Alouatta	Linear	.207	9.908	1	38	.003	1.390	-.085	
	Quadratic	.298	7.839	2	37	.001	1.933	-.377	.028
Ateles	Linear	.000	.000	1	7	.992	.894	.000	
	Quadratic	.210	.798	2	6	.493	.132	.149	-.007
Brachyteles	Linear	.055	.058	1	1	.849	1.581	-.017	
	Quadratic	1.000	.000	2	0	.	-12.358	2.265	-.085
Cebus	Linear	.192	1.667	1	7	.238	.080	.281	
	Quadratic	.859	18.271	2	6	.003	-9.644	4.628	-.468
Cercopithecus	Linear	.351	3.778	1	7	.093	1.988	-.120	
	Quadratic	.519	3.238	2	6	.111	-1.754	.743	-.048
Chlorocebus	Linear	.180	1.533	1	7	.256	2.335	-.046	
	Quadratic	.182	.668	2	6	.547	2.440	-.073	.001
Colobus	Linear	.086	1.606	1	17	.222	2.227	-.198	
	Quadratic	.102	.912	2	16	.422	1.465	.260	-.059
Eulemur	Linear	.211	1.607	1	6	.252	1.824	-.295	
	Quadratic	.317	1.158	2	5	.386	.766	.831	-.275
Gorilla	Linear	.017	.176	1	10	.684	1.238	-.013	
	Quadratic	.274	1.699	2	9	.237	.536	.194	-.012
Lagothrix	Linear	.329	1.957	1	4	.234	1.477	-.061	
	Quadratic	.425	1.110	2	3	.436	2.893	-.348	.013
Lophocebus	Linear	.755	9.245	1	3	.056	1.838	-.126	
	Quadratic	.937	14.812	2	2	.063	4.605	-.895	.050
Macaca	Linear	.177	6.029	1	28	.021	2.527	-.081	
	Quadratic	.187	3.097	2	27	.062	2.038	.011	-.004
Nasalis	Linear	.995	187.881	1	1	.046	1.537	-.104	
	Quadratic	1.000	.	2	0	.	1.160	.010	-.006
Pan	Linear	.261	4.935	1	14	.043	1.475	-.016	
	Quadratic	.302	2.810	2	13	.097	1.651	-.038	.001
Papio	Linear	.130	3.440	1	23	.076	1.613	-.009	
	Quadratic	.159	2.072	2	22	.150	1.484	.007	.000
Papioham	Linear	.928	12.952	1	1	.173	1.885	-.024	
	Quadratic	1.000	.	2	0	.	3.054	-.135	.002
Piliocolobus	Linear	.282	2.355	1	6	.176	.787	.033	
	Quadratic	.405	1.703	2	5	.273	.157	.148	-.005
Presbytis	Linear	.189	1.635	1	7	.242	1.349	-.064	
	Quadratic	.191	.706	2	6	.530	1.381	-.085	.002
Propithecus	Linear	.992	118.390	1	1	.058	2.921	-.963	
	Quadratic	1.000	.	2	0	.	6.771	-4.109	.638
Saimiri	Linear	.955	21.381	1	1	.136	3.157	-.083	
	Quadratic	1.000	.000	2	0	.	4.147	-.343	.015
Sapajus	Linear	.839	5.195	1	1	.263	1.040	.123	
	Quadratic	1.000	.	2	0	.	-.205	.683	-.057
Semnopithecus	Linear	.000	.001	1	7	.982	1.140	-.002	
	Quadratic	.227	.880	2	6	.462	-.348	.336	-.017
Theropithecus	Linear	.033	.138	1	4	.729	1.190	.002	
	Quadratic	.679	3.170	2	3	.182	.612	.044	.000
Trachypithecus	Linear	.151	1.961	1	11	.189	1.422	-.061	
	Quadratic	.154	.909	2	10	.434	1.526	-.104	.004

The independent variable is females.

Table S5 gives the Fisher meta-analysis for the reproductive rate regressions, again testing a 1-tailed prediction against a negative linear equation or an explicitly \cap -shaped quadratic, using the regression parameters given in Table S4.

Table S5. Fisher's meta-analysis for individual predictor variables for reproductive output

Predictor variable	Linear equation			Quadratic equation		
	χ^2	df	p	χ^2	df	p
Total group size	56.58	48	<0.0001	41.02	38	0.0037
Number of males	67.62	48	<0.0001	49.47	40	0.0003
Number of females	109.18	48	<0.0001	48.87	38	0.0003

In this case, there isn't a great deal to choose between linear and quadratic forms. Both yield significant overall relationships, indicating that there is a consistent underlying trend in the data for both forms. However, in all three cases, a quadratic regression does give a better fit to the data than a linear regression (2-tailed matched-pairs t-tests: group, mean = 0.294 ± 0.35 vs 0.465 ± 0.37 , $t_{23} = -3.84$, $p = 0.0008$; males, mean = 0.209 ± 0.253 vs 0.377 ± 0.352 , $t_{23} = -3.92$, $p = 0.0006$; females, mean = 0.325 ± 0.332 vs 0.518 ± 0.353 , $t_{23} = -3.58$, $p = 0.0016$). The r^2 for number of females is significantly higher than that for number of males (matched $t_{23} = 2.25$, $p = 0.034$); although r^2 for females is also larger than that for total group size, it is not significantly so ($t_{23} = 0.99$, $p = 0.332$).

Taking the results for birth rate and reproductive rate together, we conclude that quadratic regressions in number of females provide better fits to the data as a whole. And we therefore present the summary results only for number of females in the main text. However, for detailed analysis, we examine individual distributions genus by genus, as shown in Figs. S3 and S4, to decide whether linear or quadratic regressions provide the better fit in individual cases.

(a) *Determining the optimal number of females that maximises fertility*
(Main text: Figures 6 and 8, Table 1)

The fact that many of the data have a \cap -shaped quadratic form implies that there is an optimal number of females at which fertility is maximised. The distributions in Figs 4 and 5 suggest that these optimal values are not randomly distributed across the state space, but rather cluster into a number of subsets of approximately equal value. To determine whether or not the fertility patterns partition into definable subsets, we first determined the optimal number of females that maximised fertility, and then ran a k -means cluster analysis on these values.

To identify the optimal size of group that maximises fertility, we determine first whether the relationship between fertility and number of females is linear. Where there was a linear fit with data points at or close to $N=1$ female, optimal female cohort size is taken to be $N=1$. *Callithrix*

provides an obvious example in Fig. S3, as do all the genera in Fig. 2. For genera where a quadratic relationship provides the better fit, the optimal number of females is obtained by double differentiating the quadratic equation and solving for $\delta y=0$. A clear example is provided by *Papio hamadryas* in Fig. S3, and by lion in Fig. 3b.

For those genera where the best fit is negative linear, but data are available only for large groups, extrapolating a linear regression would result in an impossibly high fertility at $N=1$. In most of these cases, a regression set through the origin usually produces a clear quadratic relationship. In these cases, we assume that the distribution would be quadratic if we had data for smaller group sizes, and we take the optimum number of females as the value corresponding to the highest observed fertility value as the most conservative estimate. *Pan* in Fig. S3 (see also Dunbar 2019) and *Lagothrix* in Fig. S4 provide examples.

Eulemur in Fig. S3 is more ambivalent. The data form a positive linear relationship, but the range of variation in female number is extremely small (2.0-2.7). In fact, the observed values would fit comfortably on the left hand side of the *Lemur* curve. Since the reproductive output data for *Eulemur* in Fig. S4 have a clearer fit to a quadratic, we take the optimal number of females to maximise birth rates to be the maximum observed value, since this is the most conservative estimate. For reproductive output (Fig. S4), the quadratic equation provides a clear fit for this genus.

(b) *Endogenous determinants of within-taxon variation in fertility*
(Main text: Figure 7)

In ecology, quadratic relationships usually signal the presence of a trade off between two variables that influence the dependent variable in opposite ways (one positively, the other negatively). Although there are a number of possibilities, we consider as a first step the three demographic variables.

To determine whether the quadratic relationships can be explained as the outcome of a trade off between the linear effects of the demographic variables, we ran a set of multivariate regressions for each genus separately with birth rate (or reproductive output, as appropriate) as the dependent variable, and group size, number of males and number of females as predictor variables.

The results are given in Table S6. Most of the regressions fit a clear pattern with a positive slope on group size and a negative slope on female number. Number of males is significantly negative in some cases, but generally this variable has minimal effect.

Overall goodness of fit is very high (mean $r^2=0.727\pm0.358$ for birth rate, $N=12$; mean $r^2=0.879\pm0.136$, $N=23$ for reproductive output). About half the regressions are individually significant, but small sample sizes make significance difficult to reach in some cases even in cases where goodness-of-fit is very high.

Table S6. Multivariate Linear Regression models

(a) Dependent variable: Birth rate per year per female

Genus	Parameters				r ²	F	df	p
	constant	group size	males	female				
<i>Callithrix</i>	1.500	-	-0.073	-0.177	1.000			
<i>Cercopithecus</i>	0.826	0.022	-0.546	-0.043	0.335	0.17	3,1	0.907
<i>Chlorocebus</i>	0.594	-	0.035	-0.019	1.000			
<i>Eulemur</i>	-0.540	0.274	-0.362	0.063	1.000			
<i>Gorilla</i>	0.344	-0.008	-0.111	0.014	0.117	0.71	3,10	0.565
<i>Macaca</i>	0.478	0.021	-0.040	-0.041	0.663	24.26	3,37	<0.001
<i>Pan</i>	0.193	- 0.001	0.002	0.002	0.935	9.59	3,2	0.096
<i>Papio</i>	0.437	0.002	0.006	-0.007	0.120	0.59	3,13	0.632
<i>Papio hamadryas</i> *	0.315	0.007	-0.003	-0.017	1.000			
<i>Semnopithecus</i>	-0.236	0.027	0.007	0.016	0.547	5.63	3,14	0.010
<i>Theropithecus</i>	-0.033	-	0.146	-0.031	1.000			
<i>Trachypithecus</i>	0.626	-	- 0.013	-0.012	1.000			

* *Papio hamadryas* is treated separately because it has a very different social system, with much larger groups, than other *Papio* baboons.

(b) Dependent variable: Reproductive output (immatures per female)

Genus	Parameters				r ²	F	df	p
	constant	group size	males	female				
<i>Alouatta</i>	1.263	0.200	-0.387	-0.356	0.691	26.8	3,36	<0.001
<i>Ateles</i>	0.621	0.090	-0.016	-0.199	0.459	0.8	3,3	0.552
<i>Brachyteles</i>	1.511	-	-0.070	0.037	1.000	-	2,0	
<i>Cebus</i>	0.203	0.203	-0.116	-0.246	0.777	5.8	3,5	0.044
<i>Cercopithecus</i>	0.114	0.009	1.385	-0.097	0.847	9.2	3,5	0.018
<i>Chlorocebus</i>	1.397	0.153	-0.022	-0.464	0.845	9.1	3,5	0.018
<i>Colobus</i>	1.368	0.293	-0.305	-0.655	0.956	109.7	3,15.	<0.001
<i>Eulemur</i>	1.584	0.074	-0.226	-0.143	0.527	1.5	3,4	0.346
<i>Gorilla</i>	1.036	0.059	-0.111	-0.213	0.229	0.8	3,8	0.532
<i>Lagothrix</i>	1.532	-0.004	0.089	-0.106	0.569	0.9	3,2	0.571
<i>Macaca</i>	1.308	0.098	-0.040	-0.041	0.988	26.6	3,1	0.141
<i>Nasalis</i>	1.309	-	0.262	-0.123	0.797	34.0	3,26	<0.001
<i>Pan</i>	1.408	0.018	0.008	-0.073	1.000	-		
<i>Papio</i>	1.456	0.024	-0.020	-0.062	0.530	4.5	3,12	0.024
<i>Papio hamadryas</i>	1.872	-	0.011	-0.031	0.502	7.0	3,21	0.002
<i>Piliocolobus</i>	1.050	0.090	-0.096	-0.186	0.930	17.8	3,4	0.009

<i>Presbytis</i>	1.740	0.329	-1.190	-0.610	0.802	6.7	3,5	0.033
<i>Propithecus</i>	3.377	-0.064	-	-0.982	1.000	-		
<i>Saimiri</i>	2.866	-	0.127	-0.090	1.000	-		
<i>Sapajus</i>	1.353	-	-0.189	0.183	1.000	-		
<i>Semnopithecus</i>	0.620	0.102	-0.117	-0.170	0.964	45.1	3,5	<0.001
<i>Theropithecus</i>	1.150	0.053	-0.213	-0.075	0.755	2.1	3,2	0.344
<i>Trachypithecus</i>	0.926	0.144	0.089	-0.349	0.801	12.1	3,9	0.002

(c) *Determining the optimal number of clusters*
(Main text: Figure 8, Tables 1 and 2)

In order to determine whether a set of data constitute a single distribution or a set of overlapping distributions whose means differ, we applied k -means cluster analysis across the range $2 \leq k \leq 6$ to the optimal female cohort size determined for the two datasets (given in Table 1). As with most data reduction algorithms, no formal methods exist to determine the optimal number of clusters in a dataset, but conventional good practice is to minimise the number of clusters for maximum gain in fit, while avoiding clusters that contain very small numbers of members (clusters with a single member are considered especially undesirable). A common solution is to plot the goodness-of-fit (indexed by the F -ratio) against cluster number and seek the cluster number where the rate of change changes markedly (identified either as a clear peak in F or where F begins to asymptote), sometimes known in ecology as the ‘broken stick’ model.

Figure S5 plots the goodness-of-fit generated by k -means clustering against cluster number for the two fertility indices. The optimal number of clusters for the dataset by this criterion is indicated by the dashed vertical line. For birth rate (Fig. 4a), F increases much more slowly after $k=4$; for reproductive output (Fig. 4b), F clearly peaks at $k=5$. However, a 5-cluster solution for the reproductive output dataset yields one cluster with a single member. Since clusters with one member are considered undesirable, we combine clusters 4 and 5 to give a single cluster (cluster IV) with $N=5$ data points. Hence, we take $k=4$ to be the optimal solution in both cases.

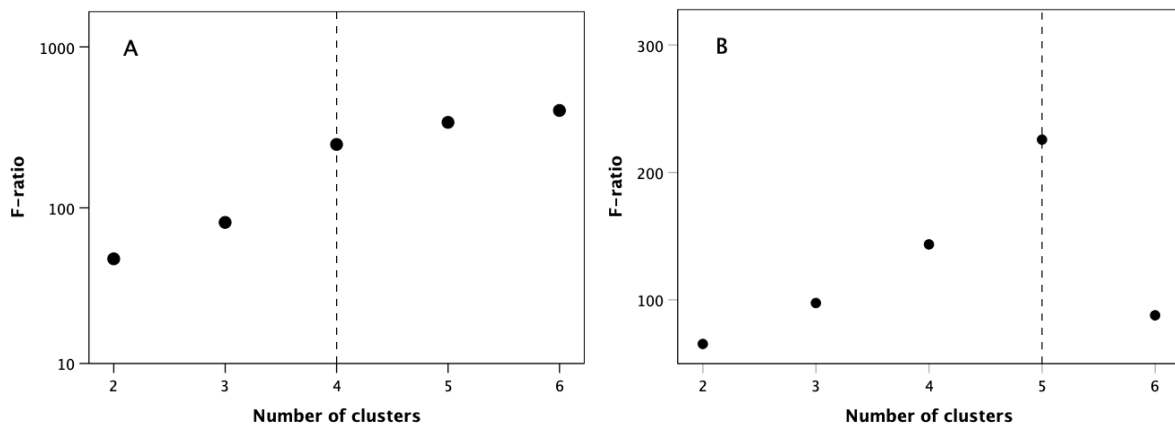


Figure S5

Goodness-of-fit (indexed as the F -ratio) for k -means cluster analysis of the adult female cohort size that maximises (a) birth rate and (b) reproductive output for individual genera. The vertical dashed line identifies the optimal number of clusters in each case. (a) includes both primates and other mammals; (b) includes only primates.

We compared the cluster assignments for the two primate fertility indices (Table 1) using Kendall’s correlation, since Kendall specifically recommended it for use when categorical data have an underlying continuum (as in this case) (see Maxwell 1961). Since the two cluster sets correlate (main text), we average them (rounding up) to yield a consensus cluster set (Table 2).

(d) *Exogenous determinants of within-taxon variation in fertility*
(Main text: Fig. 9)

We test two hypotheses that might explain the rising left hand side in those cases where fertility is a \cap -shaped function of female number. These hypotheses are essentially the functional explanations for living in large groups: protection against predation, and defence against conspecific competitor groups.

We use two indices of predation risk to test the first. One is observed predation rates, for which we use the data collated for different primate genera by Cheney & Wrangham (1987), averaging the values where there are estimates for several populations of the same genus. The other is the generalised predator risk of the habitats typically occupied by the taxon. Habitats vary in predation risk as a function of two key variables: the local density of predators and the availability of trees high enough to act as refuges (Cowlshaw 1994; Bettridge & Dunbar 2012). The principal predators of primates are large eagles (e.g. the South American harpy eagle [*Harpia harpyja*] and the African crowned hawk eagle [*Stephanoaetus coronatus*]), large felids (mainly leopard, lion, jaguar), hyaena and occasionally other primates (mainly chimpanzees, occasionally baboons). Following Hill & Lee (1998), we classified habitats into one of five categories on this basis (Table S5). Our criteria were that predation risk is lower in forest than in open habitats, and for arboreal compared to terrestrial species, as has been widely documented.

Table S5. Predator-risk classification of habitats occupied by primates

Risk index	Habitat	Comment
1	forest, arboreal, small bodied	more able to act cryptically
2	forest, arboreal, large bodied	easier for predators to spot
3	forest, terrestrial	greater exposure to cursorial predators
4	woodland, semi-terrestrial	
5	open country, terrestrial	no large trees as refuges

These two indices are not the same. Predation risk indexes the conjoint probability of encountering a predator while foraging and the likelihood that there will be a safe refuge nearby; predation rate is the residual risk that it has not been able to control by the species' anti-predator strategy (usually, living in large groups) (Hill & Dunbar 1998).

We test whether either of these indices correlate with consensus fertility cluster. If group size is a response to predator *risk*, then predation risk should increase across clusters. If group size is matched directly to predation risk, then predation *rate* should flatline across clusters, whereas if it correlates negatively, then increasing group size is actively reducing the animals'

exposure to predation risk; any other results imply that group size is not a functional response to predation risk.

We test the second possibility (that animals live in large groups as the result of an escalating war of attrition with neighbouring conspecific groups over access to resources) by asking whether the likelihood of an encounter with a neighbouring group increases across clusters. Conflicts with neighbouring certainly occur, and may result in the smaller group being driven off a resource (Markham et al. 2015). The substantive evolutionary issue is whether this happens with sufficient regularity to drive the evolution of group size across primates as a whole. We use Grueter's (2015) index of range overlap as a measure of the likelihood that neighbouring groups can expect to meet each other while foraging around their home ranges: when percentage overlap is high, animals are more likely to meet and have conflicts over resources. If range overlap increases across clusters, then it implies that animals live in increasingly large groups to reduce the risk of being defeated by a rival group; if there is no correlation, or the correlation is negative, then it is unlikely that animals live in groups for this reason.

We test all three predictions using Kendall's correlation statistic. The data for all the indices are given in *Online Dataset-5*.

(e) *Female slope parameter in multiple regression of fertility*

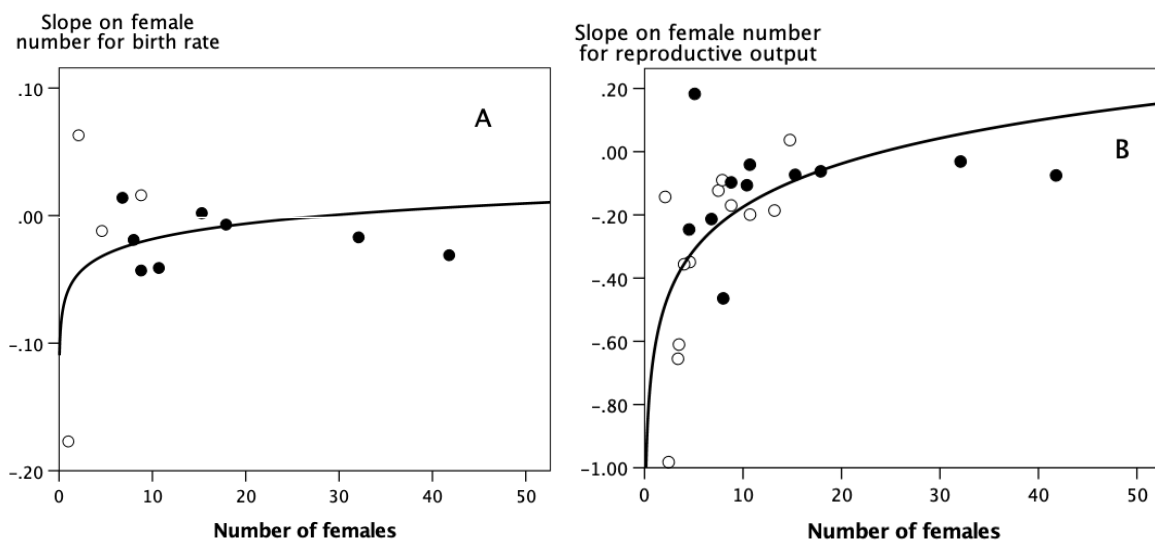


Figure S6

Slope parameter for number of females in multiple regression for (a) birth rate and (b) reproductive output. Filled symbols: genera with bonded groups; unfilled symbols: genera with unbonded groups. Regression lines are best fit logarithmic regressions. Fit for regressions are $r^2=0.321$ and $r^2=0.584$; ANOVAs, $F_{1,10}=1.15$, $p=0.309$ and $F_{1,21}=10.85$, $p=0.003$. Source: Table S6

Figure S6 tests the possibility that female fertility is a response to aggression within the immediate females with whom she associates, as opposed to the group as a whole. If this was true, then the slope on the regression of fertility against number of females should be flat, as it will be a function only of the first N females in the group. In fact, in both cases, the relationship is effectively a power curve rising to an asymptote approaching zero. More importantly, the

data points on the right hand side are predominantly genera that have bonded social groups, suggesting that bonded groups have arisen to reduce the magnitude of the effect of female numbers on fertility.

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