



Social structure as a strategy to mitigate the costs of group living: a comparison of gelada and guereza monkeys

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ARTICLE INFO

Article history:

Received 8 May 2017

Initial acceptance 5 July 2017

Final acceptance 6 November 2017

MS. number: 17-00390R

Keywords:

fertility
grooming
group size
social networks
stress

In mammals, and especially primates, group size and social complexity are typically correlated. However, we have no general explanation why this is so. I suggest that the answer may lie in one of the costs of group living: mammalian reproductive endocrinology is extremely sensitive to stress, and forms one of the hidden costs of living in groups. Fertility declines with group size widely across the social mammals, including primates, and will ultimately place a constraint on group size. However, some species seem to have been able to mitigate this cost by forming bonded relationships that reduce the impact of experienced aggression, even if rates of aggression remain high. The downside is that they reduce network connectivity and hence risk fragmenting the group by providing fracture lines for group fission. To explore this, I compare network indices and fertility patterns across the same range of group sizes for two species of Old World monkeys, *Colobus guereza* and *Theropithecus gelada*: the former relatively unsocial, the latter intensely social with frequent use of grooming-based alliances. Compared to those of the guereza, gelada social networks lose density more slowly, maintain connectedness more effectively and are less likely to fragment as they increase in size. Although fertility declines with group size in both species, in gelada the impact of this effect is deferred to larger group sizes. The differences in fertility and network structure both predict the very different maximum group sizes typical of these two species, as well as the typical sizes at which their groups undergo fission. This finding may explain aspects of wider mammalian sociality.

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A key innovation in some of the more intensely social mammals, including anthropoid primates, elephants, equids and delphinids, is the capacity to form intense, typically lifelong, bonded relationships (sensu Silk, 2002; see also Curley & Keverne, 2005; Dunbar, 2017; Dunbar & Shultz, 2010; Massen, Sterck, & de Vos, 2010; Silk, Altmann, & Alberts, 2006; Silk et al., 2010a,b; Smuts, 1985). In primates, these relationships are invariably based on regular mutual grooming. Besides creating structure within social groups (primates: Kudo & Dunbar 2001; Lehmann & Dunbar, 2009; elephants: Wittemyer, Douglas-Hamilton, & Getz, 2005; orcas: Hill, Bentley, & Dunbar, 2008), these relationships commonly provide the basis for recruiting support against third party aggression and harassment (Dunbar, 2012; Dunbar & Shultz, 2007, 2017; Harcourt, 1992), but they also create stress lines where fission will occur (baboons: King, Douglas, Huchard, Isaac, & Cowlshaw, 2008;

elephants: Archie, Moss, & Alberts, 2006). Harcourt (1992) pointed out that primate coalitions are unique in that they are established long before they are needed; in contrast, the kinds of coalitions found in most other birds and mammals are typically 'of the moment' (i.e. due to a momentary convergence of interests), short lived and less likely to involve risky altercations. In fact, it is likely that the same claim can be made for alliances in some of the more intensely social nonprimate mammals (elephants: Archie et al., 2006; dolphins: Ford, Ellis, & Balcomb, 2000; Lusseau et al., 2003; bats: Kerth, Perony, & Schweitzer, 2011; see also Shultz & Dunbar, 2010a). As a result, the distinction is now often drawn between coalitions (casual support offered during specific altercations) and alliances (long-term relationships that form the basis of regular coalitionary support).

Long-lasting social relationships of the kind found in primates and some other mammals have demonstrable fitness implications for females: grooming partners are more likely to respond to each other's distress and alarm calls (primates: Seyfarth & Cheney, 1984; Micheletta et al., 2012), and individuals who are socially well

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embedded and/or have more grooming partners are harassed less often, have lower cortisol levels in response to stressful events, and greater longevity and reproductive success (primates: Archie, Tung, Clark, Altmann, & Alberts, 2014; Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Dunbar, 1984; Engh et al., 2006; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010a,b; Wittig et al., 2008; equids: Cameron, Setsaas, & Linklater, 2009; dolphins: Frère et al., 2010).

These close 'friendships' (Silk 2002), mediated via social grooming, inevitably give rise to structured social networks (primates: Kudo & Dunbar, 2001; Lehmann & Dunbar, 2009; other mammals: Hill et al., 2008; Wittemyer et al., 2005) that resemble the layered networks found in humans (Arnaboldi, Passarella, Conti, & Dunbar, 2015; Dunbar, Arnaboldi, Conti, & Passarella, 2015; MacCarron, Kaski, & Dunbar, 2016; Sutcliffe, Dunbar, Binder, & Arrow, 2012). However, not all anthropoid primates exhibit this kind of structuring. While cercopithecine monkeys live in groups that typically consist of a number of small, self-contained cliques whose members mainly confine their interactions to themselves (Dunbar, 1983a; Kudo & Dunbar, 2001; Lehmann & Dunbar, 2009), other Old and New World monkeys such as colobines and many cebids typically have less highly differentiated relationships and typically exhibit less complex forms of social behaviour and communication (Byrne & Corp, 2004; Dobson, 2009, 2012; McComb & Semple, 2005).

Despite these benefits from sociality, living in groups incurs costs in a number of different respects, including competition for access to resources (van Schaik, 1989), additional travel and social time demands and disrupted time budgets (Dunbar, Korstjens, & Lehmann, 2009), all of which impose physiological stress on the animal. Irrespective of whether resources are involved or not, animals that live in groups also experience constant low to moderate levels of harassment from other group members. This can range from casual, even accidental, displacements during foraging, to direct theft of resources that an individual has just harvested, to outright attack (sometimes for no immediate reason, as when one individual persistently targets another). In addition, aggression involving third parties inevitably spills over to affect others, even though they may not be directly involved, thereby giving rise to psychological stress. Because of this, low-ranking animals often visually check the location of dominant individuals (Alberts, 1994; Caine & Marra, 1988; Hirsch, 2002).

The reproductive endocrinology of female mammals is extremely sensitive to stress. In primates, females subject to even modest levels of social stress experience reduced levels of fertility (rodents: Geraghty et al., 2015; ungulates: von Borell, Dobson, & Prunier, 2007; Einarsson, Brandt, Lundeheim, & Madej, 2008; primates: Abbott, 1984, 1987; Abbott, Keverne, Moore, & Yodyingyud, 1984, 1986; Bowman, Dilley, & Keverne, 1978; Rowell, 1970; humans: An, Sun, Li, Zhang, & Ji, 2013; Buck Louis et al., 2011; Caldwell, Immerwahr, & Ruzicka, 1982; Ji et al., 2013; Laatikainen, 1991; Pettay, Lahdenperä, Rotkirch, & Lummaa, 2016; Sanders & Bruce, 1997; Schenker, Meirou, & Schenker, 1992; Schliep et al., 2015; Seifer & Collins, 1990; Zacur, Chapanis, Lake, Ziegler, & Tyson, 1976), in some cases even complete reproductive suppression (callitrichid primates: Abbott, Hodges, & George, 1988; Abbott, McNeilly, Lunn, Hulme, & Burden, 1981; Abbott et al., 1984; many canids: Moehlman & Hofer, 1997; mole-rats: Bennett, 1994; Faulkes, Abbott, & Jarvis, 1990). In some species, stress is even known to cause pregnant females to abort (sheep: Howarth & Hawk, 1968). The mechanism is now well understood, and mainly involves the way prolactin and endorphins, triggered by social or physical stress, inhibit the production of gonadotrophin releasing hormone, thereby blocking the luteinizing hormone surge needed to precipitate ovulation (Abbott, 1988; Gordon, Hodgen, &

Richardson, 1992; Guidotti & Grandison, 1979; Margulis, Altmann, & Ober, 1993; McNeilly, 2001a,b; McNeilly, Forsyth, & McNeilly, 1994; Ziegler, Widowski, Larson, & Snowdon, 1990). 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 & Riegle, 1973).

A decline in fertility with either rank (baboons: Altmann & Alberts, 2003; Dunbar, 1980; Garcia, Lee, & Rosetta, 2006; Smuts & Nicholson, 1989; chimpanzees: Pusey & Schroepfer-Walker, 2013) or group size (primates in general: Harcourt, 1987; van Schaik, 1983; baboons: Dunbar & Sharman, 1983; Hill, Lycett, & Dunbar, 2000; African and Asian colobines: Borries, Larney, Lu, Ossi, & Koenig, 2008; Dunbar, 1988; Srivastava & Dunbar, 1996) has been widely documented in primates, as well as other mammals (zebra: Pluháček, Bartoš, & Čulík, 2006; most canids: Moehlman & Hofer, 1997; hyaena: Holekamp et al., 1996; badgers: Woodroffe & MacDonald, 1995; marmots: Downhower & Armitage, 1971; mongoose: Creel, Creel, Wildt, & Monfort, 1992; meerkats: Young et al., 2006; rodents: Huck, Lisk, & McKay, 1988; Kinahan & Pillay, 2008; Wey, Burger, Ebensperger, & Heyes, 2013). Such effects have also been noted in humans, where female fertility is often lower in polygamous households than in either monogamous ones (Bean & Mineau, 1986; Muhsam, 1956; Smith & Kunz, 1976) or polygamous families in which the wives occupy separate households (Borgerhoff Mulder, 1989; Chojnacka, 1980).

Ecologists invariably assume that any within-group fertility differentials are due to differences in food intake arising from scramble competition (e.g. Koenig, 2000). In fact, starvation itself triggers the endorphin system (e.g. as a response to hunger pangs or the physiological stress that hunger causes), thereby precipitating infertility in mammals (sheep: Dobson, Fergani, Routly, & Smith, 2012; pigs: Clarke, 2014). While lack of food can certainly cause the reproductive system to shut down, this usually happens only in cases involving significant weight loss (>15%) or excessive exercise (e.g. athletes) (primates: Williams, Berga, & Cameron, 2007; humans: Boyar et al., 1974; Bullen et al., 1985; Dean, 1949; Ellison 1990; Frisch, 1987; Frisch & McArthur, 1974; Howlett et al., 1984; Kirchengast & Huber, 2001; McClure, 1968; Nattiv et al., 2007; Smith, 1947; Warren & Perloth, 2001). Even then, it is the hypothalamic pathway that regulates this, rather than nutrition per se (Kalra & Kalra, 1996; Schwartz & 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 can easily be mistaken for the other. So even though nutrient constraints will usually be the major factor influencing gestation and lactation, the loss of fertility under adverse ecological conditions could in fact be due to the stress rather than the shortage of nutrients per se.

Irrespective of whether social or ecological stress is the ultimate cause, the fact that fertility declines with group size has significant implications for female fitness for animals that live in social groups. There will be intense selection pressure on females that are doing poorly in terms of fertility to leave in order to join smaller groups (Dunbar et al., 2009; van Horn, Buchan, Altmann, & Alberts, 2007), with an inevitable downward pressure on average group size. In effect, fertility should act as a limit on the evolution of group size in mammals. If groups are to increase in size beyond this limit in response to environmental demands such as predation risk, some behavioural mechanism will be needed to buffer females against these stresses. Failure to find solutions that allow larger numbers of individuals to live together will inevitably prevent species from occupying high-risk terrestrial or open country habitats where large groups are necessary to provide a defence against predators (Bettridge & Dunbar, 2012; Bettridge, Lehmann, and Dunbar, 2010; Dunbar et al., 2009; van Schaik, 1983; Shultz, Noe, McGraw, & Dunbar, 2004).

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