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### Structural and Cognitive Mechanisms of Group Cohesion in Primates

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### **Short Abstract**

Living in groups is more stressful and less straight forward than we usually assume. In order to live in large groups, mammals need to find solutions that allow these stresses to be defused. I show that, in primates, this has involved successively adding increasingly costly structural, behavioural and cognitive solutions that are dependent on the evolution of large brains. Primate social evolution consists of a series of glass ceilings on group size that restricted the habitats that species could occupy.

### **Long Abstract**

Group-living creates stresses that, all else equal, naturally lead to group fragmentation, and hence loss of the benefits that group-living provides. How species that live in large stable groups counteract these forces is not well understood. I use comparative data on grooming networks and cognitive abilities in primates to show that living in large, stable groups has involved a series of structural solutions designed to create chains of 'friendship' (friends-of-friends effects), increased investment in bonding behaviours (made possible by dietary adjustments) to ensure that coalitions work effectively, and neuronally expensive cognitive skills of the kind known to underpin social relationships in humans. The first ensures that individuals synchronise their activity cycles; the second allows the stresses created by group-living to be defused; and the third allows a large number of weak ties to be managed. Between them, these create a form of multilevel sociality based on strong versus weak ties similar to that found in human social networks. In primates, these strategies appear successively at quite specific group sizes, suggesting that they are solutions to 'glass ceilings' that would otherwise limit the range of group sizes that animals can live in (and hence the habitats they can occupy). This sequence maps closely onto the grades now known to underpin the Social Brain Hypothesis and the fractal pattern that is known to optimise information flow round networks.

**Key words:** social networks, grooming, social cognition, weak ties, multilevel sociality

## 1. Introduction

Group-living is one of the six major evolutionary transitions (Maynard Smith & Szathmary 1997). However, group-living is much more challenging than is usually assumed, for two very different reasons. One is that living in close proximity to others generates stresses that negatively impact on female fertility (in particular), creating a centrifugal force that, all else equal, naturally drives animals apart (Dunbar & Shultz 2021a). Among males, these stresses often lead to heightened levels of violence that can become disruptive as well as having lethal consequences (baboons: Wittig et al. 2008; chimpanzees: Wittig et al. 2014; humans: Dunbar 2022a). The second is a natural tendency for animals who are foraging together to drift apart as their activity schedules become desynchronised, resulting in the inevitable fragmentation of social groups (Sigg & Stolba 1981; King et al. 2009; Harel et al. 2021).

In less social species, this gives rise to unstable herds that convene and disperse as circumstances dictate. In contrast, species that live in stable social groups, as most primates do, face both problems simultaneously, and solutions that counteract these forces are necessary if they are to be able to live in large groups. Hamadryas baboons (*Papio hamadryas*) provide a particularly clear example of this. The modular structure of their groups allows very considerable dispersal of the constituent harems (distances of up to 1 km); without behaviours such as “notifying” that allow harem males to negotiate the general direction of travel during the day, and hence which midday waterholes and evening sleeping sites the units will converge on (Kummer 1968; Sigg & Stolba 1981), it would be impossible to maintain band coherence during foraging. In the absence of such solutions, stable social groups of more than a dozen animals could not exist (Dunbar & Shultz 2021a). Yet primates (including humans), together with a handful of other mammals, live in large stable groups.

I argue here that it was the need to manage these two problems that selected for many of the distinctive behavioural and cognitive features that are characteristic of primates and, by extension, underpin much of human sociality. To set the scene, I first review these stresses in more detail, and then

suggest three ways in which primates have dealt with them. The three strategies are not mutually exclusive alternatives; rather, they represent a suite of strategies that, I suggest, were adopted stepwise as the need to evolve ever-larger groups in response to environmental challenges in some lineages led to increasing levels of stress.

### *1.1. Why group-living is stressful*

Living in groups incurs costs that act as dispersive forces that drive individuals apart. Ecologists have always assumed that these costs are ecological, but in fact the costs of ecological competition are modest, and by far the least important. The substantive costs are entirely social. They come in two forms: animals drifting apart when their activities become desynchronised and the fact that group-living is highly stressful.

Over the course of a day, animals naturally drift apart simply because some individuals continue feeding while others go to rest (Ruckstuhl & Kokko 2002; Ruckstuhl & Neuhaus 2002; Calhim et al. 2006; Dunbar & Shi 2008). This is largely a consequence of differential rates of gut-fill in small and large bodied individuals (Ruckstuhl & Neuhaus 2002). However, when group size is large and/or day journeys are long, even primate groups are likely to become dispersed and, in the limit, fragment during the day's foraging (chimpanzees; Lehmann et al. 2007a; baboons: Dunbar & Dunbar 1975; Anderson 1981; Sigg & Stolba 1981; Dunbar 1992; King & Cowlishaw 2009; Castles et al. 2014; Harel et al. 2021). Fig. 1 illustrates this with data from baboon (*Papio*) populations.

One reason for this is that animals of different body size have different walking speeds (Harel et al. 2021). Although all cursorial mammals pace at approximately the same rate (strides per minute), larger bodied animals have longer legs, and therefore cover more ground per stride (Alexander & Jayes 1983; Schmidt-Nielsen 1984). As a result, when travelling long distances, longer legged individuals quickly outdistance the shorter-legged members of their group. This is compounded by the fact that

smaller bodied individuals have smaller stomachs that fill more quickly, obliging them to go to rest when larger bodied animals want to continue foraging. This is a particular problem for ruminants and other foregut fermenters (e.g. howler monkeys and Old World colobine monkeys): because the microbiota that are responsible for fermentation are highly sensitive to heat, fermentation can only occur when the animal is at complete rest (van Soest 1994). If a group of animals is to remain together, some mechanism is needed to ensure that individuals are motivated to synchronise their activity cycles so as to overcome the centrifugal forces that would naturally result in group fragmentation. In effect, they have to suppress the temptation to continue foraging when others want to rest (or continue resting when others want to forage). Failure to do this results in the dispersal of groups, as can readily be observed in many herd-forming ungulates and flock-forming birds.

The second problem is a consequence of the fact that mammalian menstrual endocrinology is extremely sensitive to social stress: even modest levels of stress result in lowered fertility as group size increases across a wide range of mammal taxa (sciurid rodents: Hoogland 1981; Armitage 1991; Geraghty et al. 2015; ungulates: von Borell et al. 2007; Einarsson et al. 2008; primates: Rowell 1970; Bowman et al. 1978; Abbott 1984; Abbott et al. 1984; humans: Zacur et al. 1976; Schenker et al. 1992; Sanders et al. 1997; Sheiner et al. 2003; An et al. 2013; Pettay et al. 2016; Schliep et al. 2015). In some cases, conflict between females can even cause the complete suppression of puberty (callitrichid primates: Abbott et al. 1981; most canids: Moehlman & Hofer 1997; suricates: Young et al. 2006; Clutton-Brock et al. 2010; mole rats: Bennett 1994; Faulkes et al. 1990). This effect is essentially a by-product of the mechanism that manages postpartum amenorrhoea so as to prevent female mammals becoming pregnant while lactating or under reproductively adverse circumstances (Prior 2022). Just how sensitive the system is to stress is demonstrated by the fact that simply removing a subordinate female from her social group will, within a matter of weeks, trigger puberty and initiate menstrual cycling in

callitrichids (Abbott et al. 1981; Saltzman et al. 1997). This physiological response to stress imposes strict limits on group size (the 'infertility trap': Dunbar & Shultz 2021a).

This infertility effect is completely independent of access to food, as has been demonstrated in both wild (chimpanzees: Pusey & Schroepfer-Walker 2013; Dunbar 2019; baboons: Dunbar 1980; Hill et al. 2000; Huchard & Cowlshaw 2011) and captive (baboons: Garcia et al. 2006) populations. This is a well-studied problem in domestic stock: crowding has an insidious effect on fertility even when forage is unlimited (Dobson & Smith 2000; Dobson et al. 2012; Pierce et al. 2008). In fact, food intake only seems to influence fertility adversely under conditions of near-starvation (i.e. when loss of body mass is >15%) (ungulates: Clutton-Brock et al. 1983; Albon et al. 1983; mongoose: Creel et al. 2013; primates: Williams et al. 2007; Gesquiere et al. 2018; humans: Dean 1949; Stein & Susser 1975; Arends et al. 2012).

The mechanism that causes this infertility effect is now well understood. Endorphin up-regulation is triggered by any social or physical stress as part of the organism's natural adaptation to physical or psychological pain (the main function of the endorphin system). However, as with most biological processes, chronic overactivation has deleterious consequences (Amir et al. 1980). One of these is that it inhibits the production of gonadotropin-releasing hormone (GnRH) in the hypothalamus, thereby blocking the luteinising hormone (LH) surge that precipitates ovulation (Ferin 1984; Howlett & Rees 1986; Laatikainen 1991; Kalra & Kalra 1996; Ziegler et al. 1990; Seifer & Collins 1990; Gordon et al. 1992; McNeilly et al. 1994; McNeilly 2001; Son et al. 2012; Iwasa et al. 2017). This has been confirmed experimentally using naloxone (an endorphin antagonist that counteracts the production of endorphins) or by disengaging the hypothalamus, thereby re-engaging the ovulatory hormonal cascade (Li et al. 2010; Geraghty et al. 2015). In some species (e.g. rats), this system is so sensitive that even the stress induced by being physically handled for short periods can be sufficient to block the cyclic release of gonadotrophins necessary for ovulation (Euker & Reigle 1973).

These two processes act in tandem. Fragmentation during foraging is an unavoidable natural process (an outcome of random foraging decisions), but it is exacerbated by the infertility trap – and any other factor (e.g. direct conflict) that causes animals to move apart from each other. Herd-living species like many large-bodied ungulates solve the infertility trap but ignore the fragmentation problem (the cheap solution), but group-living species like primates have to be able to solve both at the same time if they are to maintain group coordination (the expensive solution).

### *1.2. How mammals defuse the stresses of group-living*

In mammal species that have simpler social arrangements (e.g. some rodents and carnivores, as well as many artiodactyl ungulates that live in small, unstructured, usually unstable groups), the infertility trap is so insidious that it limits the number of adult females that can live together as a group to about five – and then only when environmental conditions make it worth the females' while bearing the cost of declining fertility. In these species, fertility declines linearly and steeply with the number of females in the group (Fig. 2, thin linear "basal mammal" line on the left side of the graph). This is also true of some primates (e.g. callitrichids: dotted linear line immediately adjacent to basal mammal line). In these species, females actually do best to live on their own (i.e. not with other females), but if environmental circumstances make group-living preferable, they can do so – but only up to a point, and at an increasing cost in terms of fertility.

In primates, with their multi-generational groups, a group of five females equates to a total group size of 15-20 individuals (Dunbar et al. 2018a). Many primates live in stable groups of this size. However, a significant number of primates live in much larger groups, and their fertility is a  $\cap$ -shaped function of group size (Dunbar & Shultz 2021a). These  $\cap$ -shaped distributions turn out to be tradeoff between the infertility cost (driven by female-female interactions) and the benefits provided by group-living (driven by group size as a whole, principally reflecting protection from predators, but in some cases



also by the presence of males) (see Dunbar et al. 2018b; Dunbar & MacCarron 2019; Dunbar 2019; Dunbar & Shultz 2021a). These  $\cap$ -shaped distributions cluster into four distinct groupings (Dunbar & Shultz 2021a). Fig. 2 illustrates these four clusters with a representative genus in each case (*Lemur*, *Semnopithecus*, *Papio* and *Theropithecus*, respectively). For these  $\cap$ -shaped distributions, fertility is maximised, respectively, at 6, 11, 16 and 45 adult females (equivalent to total group sizes of approximately 15, 35, 50 and 135). The first three turn out to be the mean values for the different group/brain size grades in the primate Social Brain relationship (Dunbar et al. 2018a; Dunbar & Shultz 2021b). The fourth (largest) cluster is characteristic of a small number of herd-forming species such as *Papio hamadryas* and *Theropithecus gelada* (both of which have a modular form of fission-fusion sociality).

Those mammals that live in larger groups typically adopt one of two strategies to deal with the infertility trap. The great majority do so by forming unstable herds that convene as and when necessary (e.g. the appearance of a predator or the appearance of a temporarily rich resource patch) and then disperse once proximity to others is no longer necessary (Sutcliffe et al. 2016). These herd-forming species (mostly large-bodied ungulates and mysticete cetaceans) avoid the infertility trap by allowing individuals to join and leave on a daily or even hourly basis; in this way, they can defuse the stresses without necessarily sacrificing the benefits of being able to form large groups when they need to do so. In these species, individuals are effectively anonymous, with personalised relationships beyond mother and young-at-heel being rare. Conflicts are typically managed on an *ad hoc* basis using directly observable dyadic power differentials, often based on simple visual cues. The cognitive demands are minimal beyond those required for the more conventional functions of foraging.

The problem faced by herding species, however, is that they run the risk that individuals might be caught by a predator after they have left a herd and are alone. Most animals foraging on their own or in small groups devote a lot more time to monitoring the environment (both for predators and for

hostile conspecifics) (Lazarus 1978; Bertram 1980; Underwood 1982; Shi et al. 2010; Beauchamp et al. 2021), as indeed do humans (Dunbar et al. 2002). In contrast, primates (and a small number of other largely species-poor intensely social taxa, including equids, tylopods [camelids], some sciurids and suricates, elephants and delphinids: Shultz & Dunbar 2010a; Dunbar & Shultz 2021a) have opted to form stable social groups: doing so means that individuals minimise the risk of being caught on their own when a predator happens to appear. The cost they bear is that groups can only downsize by undergoing fission, and, if predation risk is to be reduced to acceptable levels, fission cannot happen until the group is twice the habitat-imposed minimum size (Dunbar et al. 2009). The effect is to force the animals into the region of the infertility trap as reflected in the righthand side of the  $\cap$ -shaped fertility curve. To do so, they need to evolve strategies to move the infertility trap as far to the right as possible.

In most cases, the stability of larger bonded groups is underpinned by female-female (but sometimes female-male) coalitions that buffer individuals against the pressures created by the close proximity of too many other individuals. These species, both primate and non-primate alike, are characterised by relationships that involve repeated, often exclusive affiliative interactions and are often lifelong (Dunbar & Shultz 2010). In contrast to herding species, where vigilance is directed out of the group to the environment, vigilance behaviour in bonded species is mainly directed inside the group, with a strong focus on social partners (and especially so in pair-living species) (Dunbar 1983; Dunbar & Shultz 2010). These coalitions allow females to defer the impact of the infertility trap, thereby enabling them to live in (somewhat) larger groups without incurring a fertility penalty.

### *1.3. The mechanisms of social bonding*

In primates, bonded relationships ('friendships': Silk 2002; Dunbar & Shultz 2010; Massen et al. 2010; Brent et al. 2014) are established and maintained by a dual process mechanism that involves two distinct neural channels that work independently, but in tandem with each other. One involves the

brain's endorphin system and is underpinned by social grooming; it operates below the consciousness 'horizon' in that it involves emotional 'raw feels' (Kirk 1994). In effect, this provides the pharmacological 'glue' that creates an emotional bond that draws two individuals towards each other (Depue & Morrone-Strupinsky 2005; Dunbar 2010a, 2018a; Machin & Dunbar 2010; Loseth et al. 2014). The other is more explicitly cognitive and involves the evaluation of relationship quality, and gives rise to the Social Brain Hypothesis (Dunbar & Shultz 2017, 2021b).

The bonding function of grooming is a consequence of the fact that grooming ('soft touch') triggers the release of endorphins in both primates (Fabre-Nys et al. 1982; Keverne et al. 1989) and humans (Nummenmaa et al. 2016; Fidanza et al. 2021). The sweeping hand actions involved in grooming trigger the central endorphin system via a highly specialised peripheral nerve system, the afferent c-tactile (CT) nerves (Björnsdotter et al. 2009; Olausson et al. 2010; Jackson et al. 2021). The receptors for these nerves in the skin respond *only* to light, slow stroking at exactly 3 cm/sec (Croy et al. 2016), approximately the speed of hand movements during grooming. In humans, light stroking on the torso has been shown, using positron emission tomography neuroimaging, to upregulate the central endorphin system (Nummenmaa et al. 2016). Aside from the fact that the sense of bonding created by the endorphin system ensures that social partners stay near each other, the frequency of social interaction has been shown to predict willingness to provide coalitionary support in primates (Fig. 3) (Seyfarth & Cheney 1984; Dunbar 1980, 2018b), as well as altruistic aid in humans (Sutcliffe et al. 2012; Burton-Chellew & Dunbar 2015).

Although much has been made of oxytocin as a social hormone, in fact its role is much more limited than that of the endorphin-dopamine system (which acts in tandem in a push-pull arrangement) (Pearce et al. 2017a, 2018). In humans, oxytocin plays an important role in facilitating dyadic (mainly romantic) relationships, but it plays little or no role in social predispositions or in managing larger scale effects relating to social networks (Pearce et al. 2017a, 2018). Even so, many of the effects it produces in

the context of dyadic relationships may actually be due to the fact that the circumstances that elicit an oxytocin response also elicit endorphins (Pearce et al. 2017a). More importantly, endorphins have two major benefits over oxytocin as a bonding agent. First, it has a much longer half-life. Oxytocin has a half-life measured in minutes, whereas endorphins have a half-life measured in hours, and so remain functional in the system for much longer (Dunbar 2021a). Second, oxytocin works by influencing only *your* personal behaviour: it is something you either have or don't have, depending on the particular genetic alleles you possess for its receptors (Pearce et al. 2017a). In contrast, you can influence *someone else's* endorphin response by, for example, grooming them. For more details, see Dunbar (2021a).

The social relationships created by this bonding mechanism turn out to have direct fitness consequences. Longitudinal field studies have yielded considerable evidence that, at least in species that live in large groups, socially well-embedded females recover faster from injuries, have lower stress responses to disruptive events, live longer, give birth to more offspring and have more surviving offspring than socially less successful females (chimpanzees: Wittig et al. 2016; baboons: Silk et al. 2003, 2009, 2010; Wittig et al. 2008; Archie et al. 2012; Cheney et al. 2016; macaques: McFarland & Majolo 2013; Lehmann et al. 2016; Brent et al. 2017; wild horses: Linklater et al. 1999; Cameron et al. 2009; Nuñez et al. 2015; dolphins: Frère et al. 2010). The evidence for humans is even greater, and in many cases based on extremely large prospective samples: the number and quality of close friendships is the single best predictor of mental health and wellbeing, physical health and wellbeing and even future longevity (see, for example, Holt-Lunstad et al. 2010; Rosenquist et al. 2011; Cruwys et al. 2013; Yang et al. 2016; Kim et al. 2016; Cundiff & Matthews 2018; Santini et al. 2021). One reason for the direct health benefits of sociality is that the endorphin system upregulates natural killer (NK) cells in the white blood cell system and hence, in effect, tunes the immune system (Mandler et al. 1986; Puente et al. 1992; Sarkar et al. 2012).

The second component of the dual process mechanism involves a suite of high order cognitive skills that include causal reasoning, analogical reasoning, one-trial learning, the

comparison of alternative strategic outcomes (so as to be able to choose the best), self-control (inhibition) and mentalising (understanding others' intentions). These are all associated, in particular, with the brain's frontal pole (Brodmann Areas BA9/10), a brain region found *only* in anthropoid primates (Passingham & Wise 2011). These form the underlying basis for the Social Brain Hypothesis (SBH), and are a reminder that the SBH is *not* simply a matter of memory capacity and associative learning. In anthropoid (but apparently not strepsirrhine) primates, these forms of meta-cognition allow relationships to be managed in a more nuanced, fast tracked way (Dunbar 1998, 2018a; Brent et al. 2014) by allowing individuals to make rapid, reliable inferences about others' intentions, as well as allowing them to evaluate whom they have coalitions with, how powerful those allies are, and how likely they are to come to their ally's aid (Datta 1983). In large part, this is made possible by the capacity, unique to anthropoid primates, to engage in one-trial learning (i.e. the ability to infer a generalisation from a single observation), in contrast to the more laborious process of associative learning on which all other mammals and birds have to rely (Passingham & Wise 2011). The cognitive processes that underpin the SBH are computationally (Dávid-Barrett & Dunbar 2013) and neurophysiologically (Lewis et al. 2017) very expensive.

## **2. Primate solutions to the fragmentation problem**

While coalitions might solve the problem of the infertility trap, they do not *per se* solve the problem of how to maintain group coordination. When groups become larger, they will inevitably disperse and fragment, thus setting an upper limit to their size. In the limit, groups will simply fragment into their constituent coalitions. To ensure that the group as a whole remains coordinated and stays together (and hence provides the benefits that accrue from group-living), those species that need to live in large groups must find some mechanism that enables group cohesion to be maintained. There are, in principle, three possible ways to solve this problem. They focus on structural, behavioural and cognitive

solutions. These strategies are not necessarily alternatives, but rather are additive in that they may be solutions to successive glass ceilings on group size. Essentially, they differ in terms of the costs that the animals have to incur in terms of investment in time-costly activities like grooming or energy-expensive brain tissue to support sophisticated cognition.

### *2.1. Structural solutions (Hypothesis H1)*

The simplest option for maintaining group cohesion is to use network structure to solve the coordination problem. When seen from the perspective of the individual, social networks naturally partition into two distinct components: grooming cliques (in network terminology, their degree, defined as the number of grooming partners an individual has) and grooming chains ( $n$ -cliques, defined as the set of individuals linked together by a chain of such ties, even though they do not all individually groom each other) (Kudo & Dunbar 2001; Lehmann & Dunbar 2008; Escribano et al. 2022). To some extent, the distinction reflects that drawn by Granovetter (1973) between 'strong' and 'weak' ties in human social networks.

Fig. 4 illustrates the difference when seen from the perspective of one individual (the black square at the centre). The strong ties consist of those in the inner circle with whom the individual has direct grooming connections (white squares), making up its degree; the weak ties are those in the outer circles with whom Ego has only indirect ties (triangles) (making up its  $n$ -clique when added to its degree). If we map the personal chains of every group member on top of each other, we have a highly interconnected web-like structure with pairs of individuals often connected via several different intermediaries (a feature characteristic of robust networks). Well-connected networks have a spider's web structure, and are less likely to fragment than hub-and-spoke networks where the links that hold the clique together are only those between Ego and its individual partners, with no ties between the partners themselves.

When an individual cannot afford the time to groom every member of its group, the extended chains of indirect relationships formed by  $n$ -cliques allow groups to maintain coordination during travel even when groups become moderately dispersed (Castles et al. 2014). Each individual simply has to monitor its principal partner(s), and a ‘friends-of-a-friend’ effect will keep the group together as an extended chain. This is essentially the mechanism bird flocks and fish schools use to maintain coordination: the rule “do whatever your neighbour does” is about as complicated as it needs to get (Ballerini et al. 2008; Sumpter 2010; Vicsek & Zafeiris 2012). This solution allows an animal to focus its attention on a very small number of individuals and then, in effect, get the other relationships for free through a form of gravitational drag. However, because the gravitational ‘force’ created by the bonding will decline with each successive step removed from the individual (Fig. 4, inset), its ‘reach’ (in respect of the size of group it can integrate) will inevitably set a limit on group size because fracture lines appearing between subnetworks (Fig. 5). As a strategy, however, it has the obvious advantage that it requires minimum investment in either additional grooming time or high order cognitive abilities.

If primates solve their coordination problem solely by structural means, four predictions follow: (H1a) degree size and (H1b) the size of grooming chains should both increase proportionately to group size as individuals try to maintain relationships with as many group members as possible within the limits of the time they have available. Furthermore, (H1c) grooming chains should encompass most (if not all) of the adults in a group so as to hold them in a structural web, but (H1d) there is likely to be a limit beyond which effective coordination is difficult to maintain. The main issue is what the limiting group size is if only this mechanism is available.

## *2.2. Behavioural solutions (Hypothesis H2)*

In primates (and humans), the functionality of a bonded relationship (as indexed by willingness to provide a service) depends directly on the time invested in it (Fig. 3; see also Madsen et al. 2007;

Sutcliffe et al. 2012; Roberts & Dunbar 2015; Dunbar 2018a; Dunbar et al. 2021a). In addition, the fact that, so far as we know, endorphin upregulation only occurs in the recipient of grooming, not the groomer, means that bond strength depends on grooming being reciprocated: grooming pairs have to take it in turns to groom each other. The obvious solution is to increase the time devoted to social grooming. However, there are two issues. One is whether animals have sufficient spare capacity in their time budgets to devote more time to grooming. The other issue is whether it is better to groom with more individuals (increase their degree) or devote more time to existing grooming partners in order to maximise relationship quality so as to guarantee their willingness to provide coalitionary support.

The time budgeting issue is more serious than many might suppose. Grooming has to compete with other pressing ecological demands (foraging, travel, rest, etc). Unlike ungulates and many other mammals, anthropoid primates have an active day limited to 12 hours (they are either nocturnal or diurnal, but never both). As a result, most species' time budgets are close to their limit with little genuinely free time to play with (Pollard & Blumstein 2008; Dunbar et al. 2009). Spare capacity becomes available only when animals can reduce the demand for other activities.

Although all species rest at some point during the day and this might seem like free time, much of it is actually forced on the animals by the twin demands of digestion and thermoregulation, and so is not available for other activities (Dunbar et al. 2009; Korstjens et al. 2010). The brain is extremely sensitive to over-heating, and all tropical mammals are obliged to rest during the middle of the day when high ambient temperatures exceed the very narrow thermal tolerance of brain tissue (Mount 1979; Roberts & Dunbar 1991). Korstjens et al. (2010) showed that 'enforced rest' (as opposed to idle time) was mainly determined by ambient temperature (see also Dàvid-Barrett & Dunbar 2016). Even humans are not exempt from this in the tropics (the well known siesta phenomenon: Yetish et al. 2015). Indeed, Monsivias et al. (2017). Showed that the latitudinal variation in the length of the siesta in southern Europe correlates with ambient temperature. In addition, the thermal costs of digestion are a particular



problem for folivores, because the bacteria responsible for fermentation in the foregut are very sensitive to heat and, since any activity necessarily generates endogenous heat, fermentation will automatically shut down if animals are active (van Soest 1994). Nor is time sharing by grooming while resting an option: grooming itself generates significant quantities of internal heat (Giorgi et al. 2001).

Travel time offers some scope for adjustment: in poor quality habitats where longer day journeys are required, for example, *Papio* baboons travel up to four times faster than they do in rich habitats so as to reduce the time they need to devote to moving between food patches without having to sacrifice foraging time (Dunbar 1992). The scope for adjusting time in this way is, however, limited: walking faster is energetically expensive and this then has to be made up either by increased foraging or by reducing day journey length. Since all cursorial mammals walk at the same pace (strides per minute), the only way of increasing travel speed without incurring an energetic cost is to increase leg length (Alexander & Jayes 1983; Schmidt-Nielsen 1984), a solution adopted by some open country primates (e.g. patas monkeys) but more specifically by early *Homo*. However, the savings appear to be modest and limited to cursorial rather than arboreal species.

Realistically, the only activity category that can easily be adjusted to free up significant quantities of time is feeding, and the only viable way of doing this is to switch to a diet that offers higher nutrient extraction rates. That usually means a more frugivorous diet since fruits are nutrient-dense compared to leaves (whose nutrients are locked up within indigestible cellulose cell walls: van Soest 1994). When feeding time demand is experimentally reduced by providing access to high quality food sources, monkeys typically devote the time freed off to additional grooming rather than, say, resting (Altmann & Muruthi 1988; Bourgeaud et al. 2021). In one experimental manipulation, for example, freeliving animals in a food-rich environment fed for 5-15% less time than when in a food-poor environment, and invested that extra time in social interaction (Bourgeaud et al. 2021). The biggest benefits come for folivores, however: in colobines, it is possible to switch between the small groups characteristic of the folivorous

species (*Colobus*) and the much larger groups characteristic of frugivorous species (*Ptilocolobus*) simply by switching feeding time equations between the models for the two genera (Korstjens & Dunbar 2007).

How this extra grooming time is used, however, will depend on how time invested impacts on relationship quality. Broadly speaking, in both primates (Dunbar 1980) and humans (Sutcliffe et al. 2012; Burton-Chellew & Dunbar 2015), the more time devoted to relationship, the stronger it will be. However, the exact form of this relationship could take one of two forms. If the relationship between grooming time and relationship strength is asymptotic (i.e. there is an upper limit beyond which relationship quality does not improve even if more time is invested in it), then the best use of extra social time would be to invest in creating additional allies. On the other hand, if the effect is essentially linear (i.e. the more time spent grooming a partner, the stronger the relationship, with no upper limit), then the best strategy would be to continue investing more heavily in existing grooming partners so as to maximise bond strength.

This option, then, would predict that (H2a) as group size increases, animals will increase the amount of time devoted to social grooming. If tie quality is an asymptotic function of investment, (H2b) degree will be unrelated to group size (and might even decrease if core allies become more important as group size increases: Dunbar & Shultz 2007a), but (H2c) grooming time per degree will increase with group size (more time is invested in existing allies). However, if tie strength is an increasing linear function of investment, the opposite predictions will hold: (H2b\*) degree will correlate with group size, but (H2c\*) average time devoted to individual grooming partners should be unrelated to group size. A final prediction is (H2d) that, given the resting (fermentation) demand imposed by folivory, there will be a trade off between time devoted to social grooming and the species' degree of dietary folivory.

### 2.3. Cognitive solutions (Hypothesis H3)

If the combined structural and behavioural options are insufficient to allow large groups to form, a third possibility is that animals could resort to more sophisticated cognitive mechanisms that allow them to manage relationships with those individuals with whom they do not themselves groom (weak ties). There are two potential ways this might increase the stability of large groups. One is by allowing animals to synchronise their activities rather than pursuing their own immediate interests by continuing to feed and move when others want to rest, as we observe in ungulate herds. As the famous Stanford marshmallow experiments (Mischel & Ebbesen 1970) demonstrated, inhibiting desired behaviour does not come easily, even in humans. The second is more subtle and involves being able to manage relationships with individuals with whom one does not interact regularly (i.e. those beyond the immediate circle of direct grooming relationships). Minimising the risk of triggering or escalating unnecessary conflict with these individuals becomes crucial if the aim is to avoid driving them out of the group. This requires the ability to understand intentions (mentalising) as well as inhibit behaviour.

A number of studies have rather naively used inhibition as an index of foraging skill (among many others, see MacLean et al. 2014; Stevens 2014; Isaksson et al. 2018; Johnson-Ullrich & Holekamp 2020). In fact, self-control plays a much more important role in social contexts: it allows us to decide whether to escalate a conflict or walk away from it, and is central to the capacity to maintain behavioural synchrony with other group members (i.e. being willing to go to rest when the others want to rest, rather than continuing to feed) (Dunbar & Shultz 2023b). In humans, this capacity has been shown to be negatively associated both with the MAOA gene (the so-called “warrior gene”, linked with anti-social behaviour) and positively associated with the volume of specific brain regions (Moffitt et al. 2001; Carlisi et al. 2020). A number of longterm human studies have shown that the capacity for self-control during early childhood is a very strong predictor of adult social competences, relationship stability and antisocial behaviour (Tremblay et al. 1994; Moffitt et al. 2001; Bari & Robbins 2012; Pearce et al. 2018, 2019).

On its own, however, inhibition is not sufficient to manage relationships. Being able to read others' behavioural cues correctly, especially when both signal repertoire and group size are very large, is an essential requirement. Knowing how to finetune one's responses to others' threats or entreaties, or knowing whom to avoid conflict with because they have more allies (third party knowledge), allows animals to minimise the risk of triggering group fragmentation unintentionally by escalating conflict.

In humans, individual differences in mentalising competences correlate with differences in the volume of the default mode neural network – the single largest integrated connectome in the brain that links together, via massive white matter connections, processing (grey matter) units in the prefrontal cortex, the temporo-parietal junction and the temporal lobe with important extensions down into the limbic system and the cerebellum (Andrews-Hanna et al. 2010; Mars et al. 2012; Li et al. 2014). In humans, the volume of the default mode network correlates with mentalising competences and other indices of social skill (Carrington & Bailey 2009; van Overwalle, 2009; Andrews-Hanna et al., 2010; Powell et al. 2010, 2012, 2014; Lewis et al. 2011; Kiesow et al. 2020; Bzdok 2020; Bzdok & Dunbar 2020, 2022; Smallwood et al. 2021). Analogous findings have also been reported for macaques (Hayashi et al. 2020; Roumazeilles et al. 2021). Individual differences in the volume of the default mode network, but especially its grey matter processing units, also correlate with the size of individuals' personal social networks in both monkeys (macaques: Sallet et al. 2011; Testard et al. 2022; baboons: Meguerditchian et al. 2020) and humans (Lewis et al. 2011; Powell et al. 2012; Kanai et al. 2012; Kwak et al. 2018; Noonan et al. 2018). Powell et al. (2012) used path analysis to show that, in humans at least, the causal structure is: prefrontal cortex volume determines mentalising ability, which in turn determines personal social network size.

The default mode network exhibits significant enlargement in anthropoid primates compared to *Lemur catta* (the most social of the strepsirrhines) in ways that correlate with their much more sophisticated social relationships (Roumazeilles et al. 2022). Similarly, semi-solitary nocturnal

strepsirrhines like *Galago* lack the diversified temporal lobe connections characteristic of the more intensely social Old World monkeys and apes (Braunsdorff *et al.* 2021). Unusually for anthropoids, callitrichids lack a frontal pole (Passingham & Wise 2011), which may account for the fact that their groups are more role-based than relationship-based as in all other anthropoids (Dunbar 1995a,b; Lukas & Clutton-Brock 2018; Dunbar & Shultz 2021b; Shultz & Dunbar 2022). In primates, the default mode neural network, with its substantial white matter connections and grey matter processing units, makes up a very large proportion of the non-visual cortex, thereby contributing significantly to the disproportionately large brains characteristic of anthropoid primates (Finlay *et al.* 2001; Yeo *et al.* 2011). At some level, this even applies in birds: controlling for body mass, phylogeny and relevant ecological variables, species that have lifelong pairbonds (which are inevitably demanding in terms of behavioural coordination and trust) have significantly larger brains than either annual pairbonders or those species that mate promiscuously (Shultz & Dunbar 2010c).

This option predicts that species with larger groups will (H3a) have disproportionately larger neocortices, (H3b) score higher on executive function skills, (H3c) exhibit greater capacity for self-control and (H3d) have greater mentalising skills than those that habitually live in smaller groups. Note that hypothesis H3a differs the conventional analysis for the Social Brain Hypothesis, which normally plots group size against brain size. Here, we are asking whether differences in group size predict differences in neocortex size, and this will not necessarily yield the same result (see Dunbar & Shultz 2023a).

### **3. Testing the hypotheses**

It is important to be clear about the analytical strategy I adopt here. We are not comparing between mutually exclusive explanations here. Rather, we are trying to establish whether primates adopted any or all of the three solutions, and if so whether they were adopted at specific group sizes. Hence, I do not test *between* the hypotheses; rather, I test the *efficacy* of each hypothesis in turn by

asking whether there are limits on the size of group each could bond. Note also that we are here only interested in the *constraints* on evolving large groups, and not the reasons why large groups evolve. Consequently, I make no assumptions about why animals should want to live together in groups. Any plausible explanation will do. Instead, my question is: if animals want to live in large groups, how do they maintain group cohesion against the powerful internal (Infertility Trap, ecological competition) and external (activity scheduling, vegetation density) forces that cause groups to disperse.

### 3.1. Data and analyses

More detailed discussion of the data, indices and analyses is provided in the *Supplementary Information (SI)*. I summarise here only the main points that bear directly on the analyses that follow.

Although many studies have combined data on grooming and proximity for constructing social networks, I consider only networks based on grooming because my focus is specifically on how animals create bonded relationships. Spatial proximity is a *consequence* of having a relationship, not the mechanism used to create it. More importantly, proximity and grooming networks often correlate poorly (Castles et al. 2014; Smith-Aguilar et al. 2019; Collier et al. 2022), suggesting that they have different underlying motivations.

Data on the distribution of dyadic grooming frequencies were obtained for 92 social groups (953 adults) from 36 species (mean = 2.4, range 1-13, groups/species) belonging to 20 genera (mean = 1.8, range 1-7, species/genus). Only data for post-puberty individuals are included in the analyses (for present purposes, termed adults), since immatures always side with their mothers during group fissions and are not themselves party to decisions to stay or go. To avoid the common problem of network matrix saturation (i.e. everyone grooms with everyone else), I follow conventional practice and consider only strong ties, using the mean number of grooming bouts per available dyad (i.e. total grooming

divided by total number of dyads) as a criterion for differentiating between strong and weak ties (for technical justification, see Fig. S1).

The strong tie grooming matrix for each group was used to calculate two structural indices: the number of adult grooming partners for each individual (its degree) and the number of individuals connected to each other directly through a grooming relationship or indirectly through a chain of such relationships (an  $n$ -clique, indexed as all the individuals linked together by an unbroken chain of strong ties). Each individual in the group has a degree value between 0 and  $N-1$  (where  $N$  is the total number of adults in the group). In contrast,  $n$ -cliques are a characteristic of a group, not an individual; they can vary between 1 (every individual is in a separate  $n$ -clique) and  $N$  (all group members to a single  $n$ -clique), but the total number of individuals in all the  $n$ -cliques of a group must sum to total group size. In Fig. 4, the individual identified by the black square has a degree of 3, but belongs to an  $n$ -clique of 19 (every symbol in the graph can be reached from every other symbol via a chain of direct grooming relationships). Each of these indices was averaged first for each group, then for each species, and finally for each genus.

I include both males and females in the data. I do so for two reasons. First, while some primate species (e.g. *Papio*, *Cercopithecus*) are female-philopatric (females provide the stable core to the group), others (e.g. *Ateles*, *Pan*) are male-philopatric. Both face the same cohesion problem, despite engineering group cohesion in very different ways. Second, even in female-bonded species, females who lack female grooming/coalition partners sometimes use the group's male(s) as substitutes, treating the male in much the same way as they would a female grooming partner. Examples include *Theropithecus* (Dunbar 1984), *Papio* (Smuts 1988), *Pan* (Rawlings et al. 2023) and *Gorilla* (Harcourt & Stewart 2007).

Group size is uncontroversial for most primate species, but open to misinterpretation for those that have fission-fusion social systems (Dunbar & Shultz 2021b, 2023a). I use community size for species that have an atomistic fission-fusion social system (i.e. live in communities that disperse into small foraging parties during the day: *Ateles* and *Pan*) and the reproductive unit (harem) for species with a

modular fission-fusion system (*Theropithecus*). However, it is important to be mindful, in the latter case, that some functions may be subserved by higher grouping levels (e.g. the clan of 3-5 harems that regularly associate together). Where group size is potentially an issue (mainly grooming), I run separate analyses for both group types. For further details, see *SI*.

Although data are available for a much wider range of taxa on some behavioural ecology variables, in order to maintain sample homogeneity I consider only taxa that are included in the network analyses. As an index of inhibition (self-control), I combine data on two tasks: the A-not-B task from MacLean et al. (2014) and the Go/No-Go task from Stevens (2014). To combine these, I converted the original data for each task to standard deviations and then averaged the two scores (see Dunbar & Shultz 2023a). Note that I did not include the data on the cylinder task of MacLean et al. (2014) because, although it has been mistakenly used as an inhibition task in many studies, it is in fact a causal reasoning task (Dunbar & Shultz 2023b).

For the reasons given in more detail in the *Supplementary Information*, the analyses are not corrected for phylogenetic autocorrelation for three reasons. First, there is no phylogenetic signal for group size or any other behavioural ecology variables in primates (Kamilar & Cooper 2013; Dunbar & Shultz 2021a, 2023a). Phylogenetic methods assume that traits are genetically inherited. The social traits considered herein are not genetically inherited as such in primates; they are primarily a response to environmental and demographic factors, hence their often remarkable variability across populations of the same species (Strier et al. 2014). Second, in no analysis of primate data has any result ever differed when analyses have been run both with and without phylogenetic correction (Shultz & Dunbar 2022). Third, and of more importance, the data are clearly characterised by grades. Current phylogenetic methods do not allow grades in datasets to be differentiated, unless they are strictly taxonomic. If there are natural grades in a dataset, we risk falling foul of the Simpson-Yule Paradox (a version of the



Ecological Fallacy): this causes conventional OLS regression analyses to radically underestimate the slope (Dunbar & Shultz 2021b, 2023a).

Data for both individual group and genus averages are given in online *SI Dataset-1* and *Dataset-2*, respectively. All statistical tests are 2-tailed. Where directional hypotheses are being tested, I use a 1-tailed test and indicate so. For graphical clarity, all analyses are shown at genus level; the equivalent results for all group- and species-level analyses are given in the *SI*.

### 3.2. Results

I first use statistical clustering methods to determine whether distinct grades can be discerned in the distribution of group sizes in the sample of taxa included in the present analysis (for details, see *SI*). We have used these methods to identify natural partitions in demographic datasets in a wide range of species and contexts (see *SI*). These methods essentially search for natural breaks in the cumulative distribution of data. The two methods I use here both agree that the sampled species can be differentiated into two distinct clusters (grades) in respect of group size (Fig. S2). Mean genus level group sizes for the two grades are  $14.8 \pm 5.24$  SD (with  $5.6 \pm 1.96$  adult females,  $N=13$  genera; species level mean =  $13.9 \pm 5.3$  with 7.6 females) for the lower grade and  $36.0 \pm 5.39$  (with  $13.4 \pm 1.25$  females,  $N=7$  genera; species mean =  $36.7 \pm 11.4$  with 14.3 females) for the upper grade, with a natural breakpoint between the two grades at a group size of  $\sim 25$  (see *SI*, Fig. S2).

The basis of the analyses that follow, then, is how species manage to get from one adaptive state (small groups) to another (large groups). This question is not trivial: West et al. (2020, 2023) have shown that the fractal structure in both the distribution of primate group sizes (Dunbar et al. 2018a) and the internal structures of their groups (Hill et al. 2009; Dunbar 2020; Dunbar & Shultz 2021b; Escibano et al. 2022) are criticalities (points at which information flow round a social network is optimised). Network efficiency is maximised at the fractal values 5, 15, 50, 150, 500, and drops off significantly between them.

In the valleys between the peaks, groups become less coherent. This makes it difficult to transit across the valleys between two optima. Instead, a phase transition is required in which novel traits need to be evolved to bridge the gap and allow a rapid transition to the next level. Needless to say, the implication is that the selection pressure must have been very considerable to make this necessary.

Note that, although the two strepsirrhine species (both highly social lemurs) and the New World platyrrhine monkeys are included in the lower grade, and the only ape (*Pan*) is in the upper grade, Old World monkeys appear in both grades, cutting across taxonomic families. This indicates a functional division rather than a phyletic one (as is also the case with the social brain data: Dunbar & Shultz 2021b). In all three analyses, *Semnopithecus*, *Ptilocolobus*, *Chlorocebus*, *Erythrocebus*, *Macaca*, *Papio* and *Pan* are assigned to the upper grade, and *Lemur*, *Eulemur*, *Callithrix*, *Cebus*, *Sapajus*, *Saimiri*, *Alouatta*, *Ateles*, *Trachypithecus*, *Nasalis*, *Colobus*, *Cercopithecus* and *Theropithecus* (based on harem size) to the lower grade.

In the subsections that follow, I test the predictions for the three successive strategies as listed in section 2, distinguishing between these group size grades.

### 3.2.1. Structural solutions (Hypothesis H1)

In this sub-section, I ask whether there is an upper limit on the size of group that can be bonded by a simple structural solution based on a friends-of-friends chain structure. I first plot  $n$ -clique size against mean degree in order to determine whether the number of individuals an animal can groom with directly (its degree) sets a limit on the reach of its grooming chain. I then plot group size (and, separately, the number of females in a group) against  $n$ -clique size to determine whether groups are structurally integrated through a grooming chain or have structural weaknesses (disconnections between  $n$ -cliques) where groups are likely to fragment while foraging. The key issues here are: (1) whether primate social groups consist of a single  $n$ -clique (group: $n$ -clique ratio =1 – i.e. all adults are bound together in a single

chain) or several unconnected  $n$ -cliques (group: $n$ -clique ratio >1), and (2) at what group size the transition between these two occurs. In each case, I compare small and large clusters in order to determine whether they differ in their metrics.

Fig. 6 plots mean  $n$ -clique size against mean degree for the different genera as a function of the two group size clusters (see Fig. S3 for species- and group-level results). Overall, there is a significant linear regression ( $\beta=0.774$ ,  $r^2=0.599$ ,  $t_{18}=5.33$ ,  $p<0.0001$ ). However, the data clearly form two distinct grades: the slope (and the goodness-of-fit) is lower in genera with large social groups ( $\beta=0.558$ ,  $r^2=0.311$ ,  $p=0.151$ ) than in those with small social groups ( $\beta=0.827$ ,  $r^2=0.685$ ,  $p<0.001$ ), suggesting that the overall relationship may actually be asymptotic in the range of the upper grade.

An asymptotic relationship would suggest a maximum  $n$ -clique size of  $\sim 9.7$  at a degree size of  $\sim 2.5$ , with further increases in degree not yielding a significant increase in  $n$ -clique size. The asymptotic relationship suggests that, in larger groups, individuals are making extra effort to groom personally with disproportionately more of their  $n$ -clique members. This suggests that, at this point, there is a switch in emphasis, with more emphasis being placed on strong ties than on weak ties. Fig. S7 gives the results of a contrasts analysis for the data in Fig. 6, just to confirm that the grades are not taxonomic in origin: in fact, the grades seem to represent mosaic adaptation within closely related taxa, not phase shifts between distantly related ones.

Fig. 7 plots the mean total group size and the mean number of adult females, respectively, against mean  $n$ -clique for each genus, differentiated by group size cluster. (Species and group-level plots are given in Figs. S4 and S5.) It is evident that the data form two parallel grades that differ in their number of reproductive females ( $5.6\pm 2.0$  versus  $13.4\pm 1.3$ ;  $t_{18}=9.48$ ,  $p<0.0001$ ). The mean ratio between the two grades is 2.4 for both the number of females and total group size. The grades do not differ significantly in  $n$ -clique size (means of  $5.3\pm 2.1$  versus  $7.1\pm 1.9$ ;  $t_{18}=1.93$ ,  $p=0.070$ ), although they do differ significantly in degree (means of  $2.12\pm 0.72$  versus  $2.80\pm 0.40$ , respectively;  $t_{18}=2.88$ ,  $p=0.010$ ).

The female:*n*-clique ratios are of particular significance. A ratio of ~1.0 would indicate that the number of females in the group is linearly determined by the size of the grooming chain (all the females in the group belong to a single *n*-clique); a ratio >1.0 indicates that each chain typically includes only a proportion of the females (implying that there are structural holes, or fracture lines, in the group's grooming network that are fission risk points). In the lower grade, the female:*n*-clique ratios are not significantly different from unity (mean  $1.29 \pm 0.72$ :  $t[\text{ratio}=1.0] = 1.27$ ,  $df=11$ ,  $p=0.247$ ) indicating that most of the group's females are included within a single grooming chain,. In contrast, in the upper grade genera, the ratio differs significantly from unity ( $t[\text{ratio}=1.0] = 4.92$ ,  $df=8$ ,  $p=0.001$ ), and approximates 2 (mean  $1.96 \pm 0.36$ ), indicating that the females are typically divided between two (occasionally more) such chains. This implies that, in the upper grade genera, there are natural fracture points where the group is partitioned into two or more disconnected subnetworks.

These results are summarised in the upper section of Table 1. They indicate that, although degree increases linearly with group size (albeit with some suggestion of an asymptotic relationship), the size of grooming chains (*n*-cliques) does not correlate with the number of individuals who need to be bonded together in large groups. While small groups typically consist of a single *n*-clique, structural constraints mean that large groups become subdivided into disconnected cliques, and hence are more at risk of fragmentation. It is striking that, as group size increases, upper grade genera attempt to increase the number of the *n*-clique members they groom with in order to reinforce their ties (something that presages the behavioural solutions that we will examine in more detail in the next subsection).

These results suggest that simple structural adjustments to networks indices offer an effective solution for maintaining the cohesion and stability of small groups – but only up to group sizes of ~25. Hence, this option cannot account for the structural stability of large groups. Some other mechanism is, therefore, needed if group coherence is to be maintained in these cases. The next subsection considers the extent to which a behavioural solution (principally, changes in grooming time) could achieve this.

### 3.2.2. Behavioural solutions (Hypothesis H2)

The behavioural option proposes that larger groups could be bonded by increasing grooming time, and devoting the extra time available either to strengthening existing relationships or to increasing the number of grooming partners (in effect, increasing the size of the grooming chain). I test three specific hypotheses. First, whether total time devoted to grooming increases with group size (and whether this differs between group size grades), whether the two group size grades differ in key grooming time indices (grooming time per group member, per adult female, and per degree) and, finally, whether the additional grooming time is created by shifting to a more frugivorous diet. Between them, these allow us to determine the extent to which animals are able to increase grooming time, and, if they can, how they choose to invest the extra grooming time gained. The latter depends on the functional relationship between the time invested in a relationship and its resulting strength, and the implication this has for how time can best be used.

Fig. 8 plots time devoted to grooming against group size. Note that the gelada (*Theropithecus*) is plotted in two positions (grey symbols): according to its harem size (datapoint 18) and according to its clan size (datapoint 21). Time spent grooming increases exponentially with group size (excluding gelada: linear:  $r^2=0.504$ ,  $F_{1,15}=15.2$ ,  $p=0.001$ ; exponential:  $r^2=0.402$ ,  $F_{1,15}=10.1$ ,  $p=0.006$ ; concave quadratic:  $r^2=0.588$ ,  $F_{2,14}=7.1$ ,  $p=0.002$ ). The datapoint for gelada clan size clearly fits this overall distribution much more closely than that for gelada harem size, and with a greatly improved fit for the overall distribution (including gelada: exponential:  $r^2=0.497$ ,  $F_{1,16}=15.8$ ,  $p=0.001$ ; concave quadratic:  $r^2=0.795$ ,  $F_{2,15}=29.0$ ,  $p<0.0001$ ). The fact that a nonlinear (quadratic) regression gives a better fit than a linear one indicates that time devoted to grooming increases disproportionately as group size increases compared to what we would expect if they were simply grooming additional individuals at a constant rate. This suggests that the animals are investing increasingly more heavily in bonding as group size increases.

If more time is available for grooming, it can be used in one of two ways: by grooming more individuals (increased degree) or devoting more time to the same number of primary allies (stronger bonding). To determine which strategy upper grade taxa prefer, I compare values for total grooming time as well as grooming time per group member, per adult female and per degree for the two grades in Fig. 9. In order to plot these on the same graph, all scores were converted to standard deviates from the respective overall mean for each index. Given the results in Fig. 8, *Theropithecus* is included with clan size in the upper grade for Fig. 9. The difference between the two grades is significant for total grooming ( $t_{16}=3.55$ ,  $p=0.001$ ) and grooming time per degree ( $t_{16}=2.20$ ,  $p=0.021$ ), but not for grooming time per group member ( $t_{16}=0.06$ ,  $p=0.476$ ) or per adult female ( $t_{16}=0.223$ ,  $p=0.409$ ) (1-tailed tests in each case as a directional prediction is specified). This suggests that upper grade genera (including *Theropithecus*) devote more time to social grooming than the lower grade genera, and that they invest the additional time disproportionately in their existing core grooming partners – at the same time as slightly increasing the size of their grooming circle (i.e. degree: Fig. 6).

Animals' time budgets are not infinitely flexible, and in most cases they have little spare capacity to devote to additional grooming (Pollard & Blumstein 2008; Dunbar et al. 2009). The easiest way of solving this problem is to switch to a more frugivorous diet since fruits require less processing time than leaves (which have high digestion costs) or insects (which have high search time costs). Fig. 10 plots the mean percent of time that individual genera devote to social grooming against the mean percentage of leaf in their diet. The pattern is very different for lower and upper grade taxa (which includes *Theropithecus*). For lower grade taxa, there is no relationship between grooming time and diet (linear regression:  $r^2=0.085$ ,  $p=0.445$ ), but for upper grade taxa there is a significant negative relationship ( $r^2=0.530$ ,  $p=0.041$ ) that asymptotes at the same level as the lower grade taxa. It seems that a switch to an increasingly fruit-based diet frees off significant additional time from the foraging and resting time budgets to allow more time to be devoted to grooming.

In a comparative analysis of brain size in primates, Grabowska et al. (2023) found that, in primates, the switch from polygynandry-with-frugivory to polygynandry-with-folivory was invariably accompanied by a reduction in brain size – of a magnitude sufficient to result in a 50% reduction in brain size for folivores over the time span of the phylogeny. Not only do folivores not have sufficient spare capacity in their time budgets to provide for extra grooming, but it seems that they also have smaller brains as a result of the constraint on nutrient throughput – which means less neural tissue to support smart cognition.

The results for these tests are summarised in the middle section of Table 1. None of the grooming indices correlates with group size in the lower grade, but two (total grooming time and grooming time per degree) do so in the upper grade, giving rise to an exponential overall relationship between group size and total grooming time. In addition, it seems that only upper grade genera resort to a trade off between grooming time and diet; hence, it is only in these taxa who can opt for a behavioural solution for maintaining cohesion in large groups.

Overall, these results suggest that, once group size exceeds ~25, animals seek to strengthen their core alliances by investing more heavily in grooming with allies, and that to be able to do so they have to alter their diet so as to free off extra time. However, there is a limit to which time budgets can be adjusted to allow extra grooming time to be created. More importantly, it is clear from the structural analyses in Figure 7 that the increase in grooming time is mainly used to allow individuals to reinforce bonds with their  $n$ -clique members, not with the group as a whole. We are still left with the problem of how they prevent the other  $n$ -clique(s) in their group from drifting away during foraging once groups get large enough to consist of several disconnected subgroups. In the next subsection, I explore the possibility that they use “smart (social) cognition” to manage relationships with the weak tie members of their group.

### 3.2.3. Cognitive solutions (Hypothesis H3)

In this subsection, I test the hypothesis that the upper grade genera use ‘smart social cognition’ to manage weak ties with individuals that they do not interact with directly on a regular basis. Testing this by examining the way cognition is used to manage relationships is challenging for two reasons. First, demonstrating that individual differences in specific cognitive skills correlate with relationship management would require data at a level of detail that would be extremely difficult to collect, never mind study experimentally. Second, our current understanding of how specialised forms of social cognition are used is extremely limited, even in humans (the best studied species). For example, there is considerable experimental and neuroimaging evidence for humans that individual differences in mentalising correlate with social network size (Dunbar 2018a), but in reality we have no idea how these skills are actually used to do this. I will, instead, test this hypothesis indirectly by asking whether, in general, upper grade genera have better social cognitive capacities than lower grade genera. To do this, I compare the two group size clusters for performance on four relevant cognitive indices (neocortex ratio, executive cognition, self-control and mentalising). We know from the human literature that the latter two indices are directly involved in managing social relationships; the first two provide the neural and cognitive underpinnings that make these skills possible (Deaner et al. 2007; Shultz & Dunbar 2010).

Fig. 11 plots the data for the four cognitive indices, with scores again transformed to standard deviations of the respective means. There are no data for *Theropithecus* for any of these indices. I consider only genera that are included in the sample of network data. However, in the case of the mentalising index, data are available for only three such genera; I therefore included all seven genera studied by Devaine et al. (2017) and assigned these to the lower and upper grades as appropriate for the mean group size for their genus. For all four indices, upper grade genera score at higher levels than lower grade genera. Although the differences are individually significant only for neocortex ratio and executive cognition (neocortex:  $t_{16}=2.29$ ,  $p=0.018$ ; executive cognition:  $t_8=3.74$ ,  $p=0.003$ ; self-control:  $t_7=1.26$ ,



$p=0.124$ ; mentalising:  $t_4=0.80$ ,  $p=0.118$ ; 1-tailed tests in each case as the hypotheses being tested are directional), the results are all in the same direction. Using all the taxa available for executive function from Shultz & Dunbar (2010c) yields the same result for a significantly larger sample ( $t_{18}=2.10$ ,  $p=0.003$ ). Combining the four tests using Fisher's meta-analysis for small independent samples (Sokal & Rolf 1995) yields  $\chi^2=28.10$  ( $df=2*4=8$ ,  $p=0.0005$ ), indicating that, overall, the results are consistently more positive than would be expected by chance if there was no underlying trend.

Although all three cognitive indices increase with group size, they are in fact better described as forming a set of three grades similar to those observed with neocortex ratio (see Dunbar & Shultz 2021a) (executive cognition:  $F_{2,7}=34.16$ ,  $p=0.0002$ ,  $\Delta BIC_{2vs3}=-39.1$  vs  $-46.1 = 7.0$ ; inhibition:  $F_{2,6}=49.3$ ,  $p=0.0002$ ,  $\Delta BIC_{2vs3}=55.2$  vs  $46.1 = 9.1$ ; mentalising:  $F_{2,3}=41.7$ ,  $p=0.006$ ,  $\Delta BIC_{2 vs 3}=32.7$  vs  $25.1 = 7.6$ ; with the smaller BIC value comparing a partition into 2 versus 3 grades being the more significant and  $\Delta BIC=2$  indicative of a significant difference at  $p\approx 0.05$ ). This suggests that these cognitive indices change in a stepwise rather than a continuous fashion, just as neocortex ratio does, signalling the presence of grades in the data.

A principal components analysis of the three indices with the largest common sample (neocortex ratio, executive cognition and inhibition) indicates that these are best explained by a single dimension with high individual factor loadings ( $\lambda=0.853$ ,  $0.933$  and  $0.860$ , respectively, explaining 78.0% of the variance). (If we include mentalising with values for the other genera estimated from total brain size using the regression equation from Devaine et al., this also yields a single factor with equally high loadings:  $\lambda=0.962$ ,  $0.998$ ,  $0.998$  and  $0.896$ , respectively, explaining 93.0% of the variance.)

Given this, I created a single index by summing the standard deviates for the three indices (neocortex ratio, executive cognition and self-control), and plotted this generalised cognitive index against mean taxon group size (Fig. 12). Overall, there is a significant linear relationship (dashed line:  $F_{1,6}=12.48$ ,  $p=0.012$ ). However, there is a clear suggestion of a series of phase shifts (or grades) with

successive uplifts to new stable levels at group sizes of 15-20 and ~40 (indicated by the stepwise solid line). The species in the lowest grouping in Fig. 12 are those from the lowest grade (I) in the social brain relationship (see Dunbar & Shultz 2021b); those in the middle grouping from grade II; and those in the upper grouping from grade III.

The results from these tests are summarised in the bottom section of Table 1. As predicted, genera that live in large groups perform better on high order socio-cognitive functions than those that live in small groups. Although cognitive skills evolve piecemeal as group sizes increase across the primates, Fig. 12 suggests that they only reach their fullest development as a third phase of evolution when groups exceed about 40 in size. This suggests that there may be a series of glass ceilings that, when they are successfully breached, act to lift species onto successively higher socio-cognitive planes in such a way as to extend the range of group sizes that can be supported.

#### **4. Patterns in primate social evolution**

Overall, the results suggest that, in terms of network structure, this sample of primates divides into two distinct social grades: (1) genera that have small groups with fewer females and grooming chains ( $n$ -cliques) that include all the adult females in the group versus (2) genera that have large groups with more adult females and significant substructuring (more than one  $n$ -clique per group). Female: $n$ -clique ratios approximating unity (as in the lower grade) suggest that the reach of direct and indirect grooming imposes a limit on the number of females that can live together without resulting in substructuring. In contrast, the scaling ratio of ~2 for the upper grade genera suggests that larger groups arise by postponing fission that, in the lower grade genera, would inevitably have occurred at the size of the  $n$ -clique (and, under conditions of low predation risk, does in fact occur even in upper grade genera: Dunbar et al. 2018b; Dunbar & MacCarron 2019). The distribution of genera in these two grades is

essentially the same as those that appear in grades I/II and III in the social brain graph of Dunbar & Shultz (2021b).

In both grades, the size of the female cohort and total group size are an asymptotic function of extended grooming subnetwork ( $n$ -clique) size, suggesting that there are structural limits to the size of group that can be maintained as a coherent entity through personalised relationships. To increase group size beyond this limit, additional behavioural and cognitive mechanisms are needed in order to maintain cohesion. This suggests that only certain group sizes are possible, a finding confirmed both by the fractal distribution of primate group sizes (Dunbar et al. 2018a; Dunbar & Shultz 2021b) and by the fact that these numbers appear to act as attractors in terms of the efficiency of information flow through the system (West et al. 2020, 2023). Fig. 7b suggests that the limits on the number of females in the two grades are  $\sim 6$  and  $\sim 14$ , respectively. This is in close agreement with the finding that, in primates, fertility is optimised at female cohort sizes of 6.9 and 13.6 respectively (Dunbar & Shultz 2021a) in the two grades that correspond to those in Fig. 7b. These equate to limits on group size of  $\sim 18$  and  $\sim 37$  (Fig. 7a), close to the previously identified mean values for group size at  $\sim 16$  and  $\sim 31$  (Dunbar et al. 2018a).

Table 1 indicates whether each of the predictions was confirmed separately for genera with either small or large groups, and then, in the righthand column, whether genera with large groups performed at a higher level on the trait than those with smaller groups. Taken together, these results suggest that species with smaller group sizes (those between about 10-25) rely on structural solutions to hold the group together. Once group size exceeds  $\sim 25$ , novel behavioural and/or cognitive solutions are needed if a species is to maintain coherent groups. Both social grooming and social cognition provide ways of doing this, but do so by exploiting different processes at different costs. The first may necessitate a switch in diet to make more time available for grooming, whereas the second requires investing in energetically expensive brain tissue in order to upgrade cognitive abilities. Investing in grooming time allows animals to increase the number of individuals they maintain personalised

grooming relationships with (degree, and hence indirectly  $n$ -clique) and hence appears first. Cognitive solutions seem to be especially important once group size exceeds  $\sim 40$ , probably because they allow animals to manage weak ties beyond the number of individuals they can groom with.

Species are not, of course, obliged to pursue any of these options. At any given glass ceiling, they can: (a) stick with their current group sizes, and, as a result, remain in the habitats they have successfully occupied hitherto, (b) accept some degree of social disorganisation by living in less cohesive, more herd-like groupings in order to occupy a new riskier habitat without paying the cognitive cost required to change grade (but at some risk of being caught in a group of less than optimal size) or (c) opt to upgrade to one of the higher levels so as to be able to occupy new more risky habitats with more coherent groups.

That species do sometimes adopt the second option is evidenced by *Saimiri* (datapoint 6 in Fig. 12). In contrast to its sister-genus *Sapajus* (datapoint 5), *Saimiri* seems to have increased group size without a change in cognitive style. Despite being closely related, these two genera differ significantly in social style: *Sapajus* lives in cohesive, coherent social groups of modest size (mean sizes for four species = 16-21) whereas *Saimiri* groups are larger, notoriously chaotic and socially rather disorganised such that field workers have often had difficulty understanding their dynamics (mean sizes for three species = 18-54) (Dunbar et al. 2018a). *Saimiri* has much larger groups for its brain size than any of its sister genera, and sits on the least social grade of the primate Social Brain distribution that otherwise consists only of semi-solitary strepsirrhines (Dunbar & Shultz 2021b). The Old World monkey genus *Miopithecus* also has much larger (and much more disorganised) groups than its sister genus *Cercopithecus*, and also sits on this least social grade with *Saimiri* (Dunbar & Shultz 2021b). Further examples are discussed in Dunbar & Shultz (2021b).

The fact that advanced cognitive abilities may be necessary for the evolution of very large, stable groups might also explain the unusual modular fission-fusion social systems of *Theropithecus gelada* and

*Papio hamadryas* with their characteristic herd-like organisation. To date, there has been no convincing explanation as to why these two species have this unusual kind of social arrangement. The habitats they occupy (montane alpine grasslands and subdesert scrubland, respectively) are ecologically very different and the two species differ radically in their foraging patterns: one has very short day journeys with small harem-based groups that converge into large herds, while the other unusually long day journeys in which large groups disperse into small harem-based foraging parties. This suggests that foraging strategies are not the explanation. The one environmental feature that does unite them, however, is that both live in high predator risk habitats with very few large trees available as refuges. The need to be able to form very large groups when under threat from predators appears to be critical to their ability to occupy these habitats.

One possibility, then, is that their peculiar social systems are a consequence of the fact that they lack the social cognitive skills of their congeners (both species have somewhat smaller brains than other baboons). In both species, the intermediate clan unit of 3-5 harems (30-40 animals) is a much better fit for their brain size to the Social Brain relationship than either the small harems or the larger herd-like groupings (bands) in which they are often found. Hence, their solution has been to develop a flexible herd-like fission-fusion social system capable of responding to circumstances by forming temporary herds out of small stable groups (in both cases, clans substructured into harems) while using increased investment in grooming to reduce the stresses involved. Both species devote a great deal more time to social grooming than any other primate, including their congeners (18.3% and 17.2% of the day, respectively, compared to 5.7-12.2% for the three woodland *Papio* baboon species: Dunbar 1991). To maintain their largest natural groupings (bands that average 116.4 and 82.5, respectively, in size) as coherent stable groups would require an increase in cognitive skills and neocortex size that would place these two species midway between chimpanzees and modern humans. In effect, they seem to have been

forced by their environment to go far beyond the group size that they can comfortably maintain, and their only way of coping with this is a form of fission-fusion sociality that is cognitively less demanding.

Several other primate genera may exhibit adaptations of a similar kind. *Rhinopithecus* and *Nasalis*, for example, have stable harem-like groups that sometimes form larger unstable herds during foraging. Conversely, the Guinea baboon (*Papio papio*) and the two species of the terrestrial forest-living monkey *Mandrillus* (drills and mandrills) have groups that are (by conventional woodland baboon standards) unusually large (up to several hundred strong) and chaotic, but with hints of a weak harem-like structure (*P. papio*: Dunbar & Nathan 1972; Patzelt et al. 2011; *Mandrillus*: Hoshino 1985; Abernethy et al. 2002; Brockmeyer et al. 2015). It is notable that *P. papio*, at least, has rates of social grooming (18.9%: Dunbar 1991) comparable to those observed in the gelada and hamadryas, and much as would be predicted for the typical size of their groups.

Humans may provide another example. In their “natural” state as hunter-gatherers, humans live in small relatively stable bands (camp groups) of 35-50 that coalesce locally into larger communities (or clans), and beyond that into tribes (Dunbar 1993; Zhou et al. 2005; Hamilton et al. 2007; Bird et al. 2019). Clans appear to provide protection against external threats (Lehmann et al. 2014), but would create insurmountable stresses (reflected in a linear relationship between camp group size and homicide rates: Dunbar 2022a) if they lived together. Instead, the stresses are defused by allowing the families of a clan to disperse between several bands, and then move between bands of the same clan when they feel the need. It seems that to lift group sizes from ~50 (as in chimpanzees) to ~150 and beyond (as in humans) required significant additional investment in cognition, as well as more efficient ways to increase grooming time via chorusing, dancing and conversation (Dunbar 2018a). Later, when there were significant pressures to live in very large permanent settlements, this had to be done not by further increases in cognitive abilities (brain size may actually be at its limit in modern humans), but by introducing a series of social institutions that allow the stresses to be defused (Dunbar 2022a). These

institutions were added stepwise as settlement sizes increased (Dunbar 2022a) in a manner similar to the demographic glass ceilings suggested for primates.

## 5. The tradeoff between bonding and cognition

Grooming provides the basis for coalition-formation in anthropoid primates (Dunbar 1980, 2018a; Seyfarth & Cheney 1984), and this clearly serves a crucial function in buffering females against the stresses created by living in close proximity to others (Dunbar & Shultz 2021a). However, while formal coalitions are characteristic of all the upper grade genera, they are rare (if not completely absent) among lower grade genera (Shultz & Dunbar 2022). Nonetheless, while coalitions might solve the stress problem, on their own they do not directly solve the associated coordination problem, and this becomes increasingly problematic in very large groups. In large groups, animals beyond the immediate grooming circle may not necessarily have direct personal knowledge of who has allies and who does not.

Managing peripheral relationships beyond one's own immediate grooming circle depends on the capacity to understand others' relationships, often on the basis of very limited knowledge. This rests on being able to make rapid judgments about the meaning of signals, to infer rules from single observations (one-trial learning) and to understand the nature of third party relationships so as to know when to escalate conflicts and when to avoid doing so (depending on whether or not the opponent has allies). Failure to be able to do this risks precipitating conflict, and ultimately group fission.

Understanding third party relationships has been reported for many of the upper grade genera (*Pan*: Wittig et al. 2014; Mielke et al. 2017; *Papio*: Kummer et al. 1974; Gore 1994; *Macaca*: Judge 1991; Sinha 1998; Kubenova et al. 2017; *Chlorocebus*: Cheney & Seyfarth 1986; *Cercocebus atys*: Mielke et al. 2017), but convincing evidence for such behaviour in any of the lower grade genera has not so far been reported. Similarly, many upper grade genera are able to evaluate the status of another individual on two or more dimensions simultaneously (e.g. kinship versus rank: chimpanzees: Mielke et al. 2017;

baboons: Bergman et al. 2003; macaques: Schino et al. 2006), whom an individual has alliances with (chimpanzees: Wittig et al. 2014; baboons: Kummer et al. 1974; Cheney & Seyfarth 1999; macaques: Datta 1983; Silk 1999) and, on the basis of observed reputation, how trustworthy an individual might be (chimpanzees: Russell et al. 2008). Again, with the exception of *Cebus* (and even then they prioritise rank over relationship quality: Kajokaite et al. 2019), similar competences have not, so far, been reported for any of the lower grade genera. Reconciliation (repairing relationships destabilised by conflict), a behaviour that depends on the ability to recognise that a relationship has been weakened (thus implying some minimal capacity to understand the social consequences of actions), has also been widely reported from upper grade genera but rarely (and usually with mixed results – and then only in the form of physical proximity without involving conciliatory signals or active grooming) in lower grade genera (Arnold et al. 2007).

These abilities are all dependent on executive function skills, and seem to play a crucial role in allowing primates in large groups to live together without destabilising the group either by misinterpreting others' intentions or by acting in ways that are disruptively aggressive or demanding. They may thus explain why, in primates, rates of conflict within female dyads are negatively correlated with species' group size (when controlling for neocortex size) (Cowl & Shultz 2017; see also Dunbar 2018b) when, all else equal, we might have expected aggression rates to increase with group size simply because, in large groups, there are more dyads that might fall out with each other, as well as the animals being under greater stress from crowding.

Being able to make rapid judgments about others' intentions depends on being able to read signals accurately and quickly (Roberts & Roberts 2020), and it is notable that, in primates, the complexity and size of both vocal and gestural communication repertoires are greater in species that live in larger groups and/or have bigger brains (McComb & Semple 2005; Dobson 2009, 2012; Dunbar 2012; Fichtel & Kappeler 2022). Damjanovic et al. (2022) found that chimpanzees that had larger social



networks (i.e.  $n$ -cliques) used a wider range of gestural signals, with these being supplemented by vocal signals when addressing the weaker ties beyond the immediate set of grooming partners.

The capacity to infer intentions from behavioural signals (mentalising) may play a particularly important role in maintaining group cohesion (Roberts & Roberts 2020). Some species, for example, have evolved signalling mechanisms explicitly designed to coordinate the timing and direction of travel. Examples include the ‘notifying’ rituals of hamadryas baboons and some macaque species that allow group members to negotiate the foraging route they will take during the day (Kummer 1968; Sigg & Stolba 1981; Sueur et al. 2011; Smith et al. 2022). Understanding the significance of these signals is only possible if others’ intentions can be correctly inferred (and generalised across circumstances).

The capacity to inhibit prepotent responses plays a particularly important direct role in managing conflict. However, for this to be socially effective it must be combined with the capacity to mentalise (which might explain why the two capacities seem to co-evolve). In hamadryas baboons, for example, it allows many males to live together without competing directly for each others’ females (the phenomenon of “triadic differentiation” or “pairbond respect”: Kummer et al. 1974). A somewhat analogous form of behaviour is exhibited by gelada: young adult males trying to enter a harem as a follower (secondary male) typically identify and target a peripheral female who has only weak bonds with the harem male (Dunbar 1984). If the male can persuade a peripheral female to groom with him, he will quickly become integrated into the social fabric of the harem because the harem male is rarely concerned enough to bother with him so long as he remains submissive – despite being very quick to detect when males are intent on taking over the whole harem (Dunbar 1984).

In both species, triadic differentiation depends on an ability to infer something about other individuals’ relationships and intentions on the basis of very limited information. Kummer et al.’s (1974) experiments on hamadryas baboons established that as little as 15 mins spent observing a pair interacting is sufficient for an observer male to infer whether or not the female is bonded to (or

interested in) the male with whom she has been paired. If she appears to show little interest in her male, the observer male will make a concerted bid to wrest her from the male. Something similar occurs in humans: being seen to be attached to a male reduces the risk of harassment for women (Mesnick's 'bodyguard' hypothesis: Mesnick 1997; see also Wilson & Mesnick 1997; Dunbar 2010b). These forms of behaviour make it possible for many adult males and females to coexist in large groups without constant conflict over females ("Deacon's Dilemma": Deacon 1997; Dunbar 2010b). This form of "triadic differentiation" in primates contrasts starkly with the situation in many colonially nesting birds where females are at constant risk of harassment as they leave and return to their nests if they are not accompanied by their mate (e.g. bee eaters: Emlen & Wrege 1986).

In summary, living in large groups imposes significant behavioural demands on animals if they are to be able to hold the group together for any length of time in the face of the pressures that will otherwise push the animals apart. Although we are inclined to take these behaviours for granted, the cognitive costs involved are far from trivial. They demand neurologically very expensive abilities that have to be paid for with energetically expensive neocortical investment (Dávid-Barrett & Dunbar 2013; Lewis et al. 2017). These findings thus provide a direct answer to the question raised by Healy & Rowe (2007) as to why larger brains should be necessary for more social species. Finding solutions to both the need for extra grooming time and the additional nutrient capacity to evolve a larger brain requires species to make adjustments to their diet – both to free off time for additional grooming and to fuel the evolution of a larger brain. This reinforces the evidence from all previous analyses of the Social Brain Hypothesis (including those by DeCasien et al [2017] and Powell et al. [2017]: for re-analysis of these studies' findings, see Shultz & Dunbar 2022; Dunbar & Shultz 2023a) that a change in diet and foraging strategy was a necessary prerequisite (not the selection factor) for fueling the additional energetic costs involved (Shultz & Dunbar 2022).

## 6. Wider Implications

I have argued that the central problem that all mammals have to deal with is how to manage the stresses that arise from living in large, stable groups when these are necessitated by the kinds of environments a species is attempting to occupy. These stresses are in part due to the psychophysiological pressures of living in close proximity (giving rise to the 'infertility trap'), but also in part to the fact that, as group size increases, it becomes increasingly difficult to maintain coordination and group cohesion during foraging. The two together create a strong centrifugal force that will cause large groups to fragment unless active steps are taken to mitigate these effects.

Primates face this problem especially intensely because of the kinds of bonded social groups they have evolved. I have suggested that, in order to manage this, primates successively exploited three different kinds of strategy: structural strategies that seek to exploit network characteristics, behavioural strategies based on creating more intense social bonds that protect females (in particular) from the destructive effects of the infertility trap, and novel cognitive capacities involving neurophysiologically expensive forms of meta-cognition (propositional thinking, one-trial learning, the capacity to compare outcomes from alternative options, inhibition and mentalising) that allow relationships to be managed more effectively with individuals who are beyond the immediate circle of grooming partners. These capacities seem to come onstream sequentially at quite specific group sizes, suggesting that they are associated with glass ceilings beyond which group size cannot be increased without introducing novel competences. These phase shifts do not follow taxonomic divisions (although there is a modest phyletic trend), but rather have a more mosaic form that reflects the ecological adaptations that individual species have needed to make when invading new habitats (see also Dunbar & Shultz 2021b).

Although primates are, as a group, the most social of all the mammals, they are by no means unique: other mammalian orders (notably equids, tylopods, elephants, delphinids, some herpestids and sciurids) have also evolved forms of bonded sociality (Shultz & Dunbar 2010a). It is, however, notable

that although most of these species do not (and, in some cases, cannot) groom as effectively as anthropoid primates, many engage in forms of physical contact (nuzzling, snuggling) that may be equally effective in triggering the endorphin system. Some of the more social birds (parrots and their allies, corvids; many pairbonded cooperative breeders) do a great deal of mutual preening (Kenny et al. 2017; Morales Piccard et al. 2020). In woodhoopoes, for example, the frequency of allo-preening increases with group size (Radford & Du Plessis 2006).

In addition, many birds that live in stable groups outside the breeding season engage in conspicuous forms of vocal chorusing (examples include babblers, Guinea fowl and starlings). This form of 'undirected' vocalisation has recently been shown to upregulate  $\beta$ -endorphins in birds (Riters et al. 2019), just as communal singing does in humans (Pearce et al. 2015, 2016, 2017b). Many pair-living bird species engage in tightly synchronised antiphonal calling, especially when they are foraging apart in dense bush (e.g. African boubou shrikes). As in primates, vocal complexity increases with flock size in species like the Carolina chickadee (Freeberg 2006). This might offer an alternative interpretation of the daily group chorusing (usually interpreted as having a territorial function) that is so characteristic of howler monkeys and gibbons. It may also be that whale song (usually interpreted as a contact call) in fact serves a similar bonding function, allowing a widely dispersed pod to 'groom' while travelling. In humans, low sound has been shown to trigger an endorphin response through CT-like SGN receptors attached to the cochlea (Dunbar et al. 2021b).

How far the abilities of any of non-primate taxa compare to those of primates is, however, far from clear. More detailed studies are required. If nothing else, however, the present results should at least remind us that not even all primates solve their social problems in the same way: all anthropoid primates live in bonded social groups and engage in social grooming, but differences in group size impose very different demands that require cognitively different solutions. Similarly, we know from the MacLean et al. (2014) studies that only anthropoid primates have the capacity for self-control (see

Dunbar & Shultz 2023b). It is also important to remember that few non-primates live in bonded social groups as large as those of anthropoid primates (Dunbar & Shultz 2021a); as a result, they will be much less prone to the coordination problem.

There is a need for more discerning studies of other mammals' social dynamics as well as their cognition to allow us to place them on a continuum with primates so as to evaluate the wider picture of cognitive evolution. So far, most such studies has tended to focus on rather low-key, food-finding abilities or cognitive capacities like short term memory that are so basic to life that all species have to have them (ManyPrimates et al. 2023), and hence are rather uninformative. Such evidence as there is suggests that, while other mammal orders might well exhibit their own novel cognitive adaptations (e.g. echolocation in delphinids, smell in canids), specialised forms of social cognition like self-control (Passingham & Wise 2011; MacLean et al. 2014; Dunbar & Shultz 2023b) and mentalising (Devaine et al. 2017; Dunbar & Shultz 2023a) appear to be unique to the anthropoid primates.

## **7. Implications for human evolution**

One final question is how these findings feed into human social and cognitive evolution. In most respects, human sociality, and the cognitive and neurobiological processes that underpin it, can be seen as being on the same trajectory as anthropoid primate sociality (section 4). Most of the specialised cognitive capacities that underpin anthropoid primate sociality are also crucial for the effective functioning of human relationships and social groups (Dunbar 2018a, 2021a,b). In some cases, human competences seem to be no better than those of great apes. The capacity to inhibit prepotent actions (self-control), for example, already seems to be close to ceiling in great apes, with full adult competence being achieved as early as six years of age in humans (Espy 1999). The same appears to be true of theory of mind (second order mentalising): though we share this with great apes, children achieve great ape level skills by about age five years (O'Connell & Dunbar 2002). Other competencies, however, are

significantly greater in humans than in any pongid. Adult human mentalising capacities, for example, extend for at least three more levels of intentionality beyond that achieved by great apes and young children (Kinderman et al. 1998; Stiller & Dunbar 2007; Henzi et al. 2007; Powell et al. 2012, 2014; Devaine et al. 2014; Dunbar 2014).

The same is true of social grooming and the role this plays in upregulating the brain's endorphin system. Although humans still make significant use of 'soft touch' as a social bonding mechanism (Suvilehto et al. 2015, 2019; Dunbar 2021a), there seems to be an upper limit on the size of groups that can be bonded by social grooming at ~50, mainly due to time constraints and the physical intimacy of touch (Dunbar 2022b). To circumvent this constraint, humans have found novel ways of triggering the endorphin system virtually (i.e. without involving direct physical contact), all of which scale up well to the size of contemporary human groups. These include laughter (Nummenmaa et al. 2015; Dunbar 2022b), singing (Pearce et al. 2015, 2016, 2017b), dancing (Tarr et al. 2015, 2016, 2017), feasting (Dunbar 2016; Tuulari et al. 2017), storytelling (Dunbar et al. 2016) and the rituals of religion (Charles et al. 2020) (see also Dunbar 2014). All these have been shown both to upregulate central endorphins and to elevate the sense of bonding (even with complete strangers) (Dunbar 2018a, 2021a).

It seems likely that these did not all appear together, but rather evolved in a stepwise fashion, first with archaic humans (*Homo ergaster/erectus*) around 2.4 Ma and later, around 600 ka, with the appearance of archaic humans (*H. heidelbergensis* and *H. neanderthalensis* and allies), leading into anatomically modern humans (Gowlett et al. 2012). The first step was relatively modest, and seems to have been solved mainly by finding a more efficient way of triggering the endorphin system (laughter as a form of chorusing, or 'grooming at a distance'), with only a very modest investment in novel cognition (Dunbar 2022b). The second required a combination of very substantial investment in cognition as well as the discovery of a suite other non-contact ways of triggering the endorphin system (Dunbar 2014).

Since conversational interactions (e.g. during feasting), storytelling and religion all depend on language, they are likely to have evolved late: although archaic humans (the Heidelberg and Neanderthal folk) certainly had the capacity to speak (and/or sing) (Dunbar 2009, 2023; Bannan et al. 2024), their mentalising capabilities appear to have been insufficient for them to have had language of the flexibility and complexity that we find in modern humans (Pearce et al. 2014; Dunbar 2014, 2023). Once fully modern language had evolved, however, it opened the way for much more sophisticated forms of bonding through shared cultural symbols in the form of the “Seven Pillars of Friendship” (Curry & Dunbar 2013; Dunbar 2018a, 2021b). Once again, we seem to see a series of discrete steps that reflect responses to phase shifts in group size, the first of which involved breaking through a glass ceiling imposed by limits on the reach of touch-based grooming as a bonding mechanism (Dunbar 2014, 2023).

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## References

- Abbott, D. H. (1984). Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. *American Journal of Primatology* 6: 169-186.
- Abbott, D. H., Keverne, E. B., Moore, G. F. & Yodyingyud, U. (1984). Social suppression of reproduction in subordinate talapoin monkeys, *Miopithecus talapoin*. *International Journal of Primatology* 5: 318-318.
- Abbott, D.H., McNeilly, A.S., Lunn, S.F., Hulme, M.J. & Burden, F.J. (1981). Inhibition of ovarian function in subordinate female marmoset monkeys (*Callithrix jacchus jacchus*). *Journal of Reproduction and Fertility* 63: 335-345.
- Abernethy, K. A., White, L. J. & Wickings, E. J. (2002). Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *Journal of Zoology* 258: 131-137.
- Albon, S.D., Mitchell, B. & Staines, B.W. (1983). Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology* 52: 969-980.
- Alexander, R. M. & Jayes, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *Journal of Zoology* 201: 135-152.
- Altmann, J. & Muruthi, P. (1988). Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology* 15: 213-221.
- An, Y., Sun, Z., Li, L., Zhang, Y., & Ji, H. (2013). Relationship between psychological stress and reproductive outcome in women undergoing in vitro fertilization treatment: Psychological and neurohormonal assessment. *Journal of Assisted Reproduction and Genetics* 30: 35-41.
- Anderson, C. M. (1981). Subtrooping in a chacma baboon (*Papio ursinus*) population. *Primates* 22: 445-458.
- Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R. & Buckner, R.L. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron* 65: 550-562.
- Amir, S., Brown, Z.W. & Amit, Z. (1980). The role of endorphins in stress: Evidence and speculations. *Neuroscience and Biobehavioral Reviews* 4: 77-86.
- Archie, E. A., Altmann, J. & Alberts, S. C. (2012). Social status predicts wound healing in wild baboons. *Proceedings of the National Academy of Sciences USA* 109: 9017-9022.
- Arends, J.C., Cheung, M.Y.C., Barrack, M.T. & Nattiv, A. (2012). Restoration of menses with nonpharmacologic therapy in college athletes with menstrual disturbances: a 5-year retrospective study. *International Journal of Sport Nutrition and Exercise Metabolism* 22: 98-108.
- Armitage, K. B. (1991). Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics* 22: 379-407.
- Arnold, K. & Aureli, F. (2007). Postconflict reconciliation. In: Campbell, C.J., Fuentes, A., MacKinnon, K., Bearder, S. & Stumpf, R. (ed.) *Primates in Perspective*, pp. 608-625. Oxford: Oxford University Press
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., Procaccini, A., et al. (2008). Interaction ruling animal collective behaviour depends on topological rather than metric distance: evidence from a field study. *Proceedings of the National Academy of Sciences USA* 105: 1232-1237.
- Bannan, N., Bamford, J. & Dunbar, R.I.M. (2024) The evolution of gender dimorphism in the human voice:



the role of octave equivalence. *Current Anthropology* (in press).

Bari, A. & Robbins, T. W. (2013). Inhibition and impulsivity: behavioral and neural basis of response control. *Progress in Neurobiology* 108: 44-79.

Beauchamp, G., Li, Z., Yu, C., Bednekoff, P. A. & Blumstein, D. T. (2021). A meta-analysis of the group-size effect on vigilance in mammals. *Behavioral Ecology* 32: 919-925.

Bennett, N.C. (1994). Reproductive suppression in social *Cryptomys damarensis* colonies e a lifetime of socially-induced sterility in males and females (Rodentia: Bathyergidae). *Journal of Zoology* 234: 25-39.

**Bergman, T.J., Beehner, J.C., Cheney, D.L. & Seyfarth, R.M. (2003).** Hierarchical classification by rank and kinship in baboons. *Science* 302: 1234-1236.

Bertram, B. C. (1980). Vigilance and group size in ostriches. *Animal Behaviour* 28: 278-286.

Bird, D. W., Bird, R. B., Codding, B. F. & Zeanah, D. W. (2019). Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. *Journal of Human Evolution* 131: 96-108.

Björnsdotter, M., Löken, L., Olausson, H., Vallbo, Å. & Wessberg, J. (2009). Somatotopic organization of gentle touch processing in the posterior insular cortex. *Journal of Neuroscience* 29: 9314-9320.

von Borell, E., Dobson, H. & Prunier, A. (2007). Stress, behaviour and reproductive performance in female cattle and pigs. *Hormones and Behavior* 52: 130-138.

Borgeaud, B., Jankowiak, B., Aellen, M., Dunbar, R.I.M. & Bshary, R. (2021). Vervet monkeys socialize more when time budget constraints are experimentally reduced. *Ethology* 127: 682-696.

Bowman, L. A., Dilley, S. R. & Keverne, E. B. (1978). Suppression of oestrogen-induced LH surges by social subordination in talapoin monkeys. *Nature* 275: 56-58.

Braunsdorf, M., Freches, G. B., Roumazeilles, L., Eichert, N., Schurz, M., Uithol, S. Bryant, K.L. & Mars, R.B. (2021). Does the temporal cortex make us human? A review of structural and functional diversity of the primate temporal lobe. *Neuroscience & Biobehavioral Reviews* 131: 400-410.

Brent, L. J., Chang, S. W., Gariépy, J. F. & Platt, M. L. (2014). The neuroethology of friendship. *Annals of the New York Academy of Sciences* 1316: 1-17.

Brent, L. J. N., Ruiz-Lambides, A. & Platt, M. L. (2017). Family network size and survival across the lifespan of female macaques. *Proceedings of the Royal Society, London*, 284B: 20170515.

Brockmeyer, T., Kappeler, P. M., Willaume, E., Benoit, L., Mboumba, S., & Charpentier, M. J. (2015). Social organization and space use of a wild mandrill (*Mandrillus sphinx*) group. *American Journal of Primatology* 77: 1036-1048.

Burton-Chellew, M. & Dunbar, R.I.M. (2015). Hamilton's Rule predicts anticipated social support in humans. *Behavioral Ecology* 26: 130-137.

Bzdok, D. & Dunbar, R.I.M. (2020). The neurobiology of social distance. *Trends in Cognitive Sciences* 24: 717-734.

Bzdok, D. & Dunbar, R.I.M. (2022). Social isolation and the brain in the pandemic era. *Nature Human Behaviour* 6: 1333-1343.

Calhim, S., Shi, J. & Dunbar, R. I. M. (2006). Sexual segregation among feral goats: testing between alternative hypotheses. *Animal Behaviour* 72: 31-41.

- Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. (2009) Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences USA* 106: 13850-13853.
- Carlisi, C.O., Moffitt, T.E., Knodt, A.R., Harrington, H., Ireland, D., Melzer, T.R., Poulton, R., Ramrakha, S., Caspi, A., Hariri, A.R. & Viding, E. (2020). Associations between life-course-persistent antisocial behaviour and brain structure in a population-representative longitudinal birth cohort. *Lancet Psychiatry* 7: 245-253.
- Carrington, S.J. & Bailey, A.J. (2009). Are there theory of mind regions in the brain? A review of the neuroimaging literature. *Human Brain Mapping* 30: 2313-2335.
- Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E., Cowlshaw, G. & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour* 96: 59-67.
- Charles, S.J., Farias, M., van Mulukom, V., Saraswati, A., Dein, S., Watts, F. & Dunbar, R.I.M. (2020). Blocking mu-opioid receptors inhibits social bonding in rituals. *Biology Letters* 16: 20200485.
- Cheney, D. L., & Seyfarth, R. M. (1986). The recognition of social alliances by vervet monkeys. *Animal Behaviour* 34: 1722-1731.
- Cheney, D. L. & Seyfarth, R. M. (1999). Recognition of other individuals' social relationships by female baboons. *Animal Behaviour* 58: 67-75.
- Cheney, D. L., Silk, J. B. & Seyfarth, R. M. (2016). Network connections, dyadic bonds and fitness in wild female baboons. *Royal Society Open Science* 3: 160255.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1983). The costs of reproduction to red deer hinds. *Journal of Animal Ecology* 52: 367-384.
- Clutton-Brock, T. H., Hodge, S. J., Flower, T. P., Spong, G. F., & Young, A. J. (2010). Adaptive suppression of subordinate reproduction in cooperative mammals. *The American Naturalist*, 176(5), 664-673.
- Collier, M., Albery, G. F., McDonald, G. C. & Bansal, S. (2022). Pathogen transmission modes determine contact network structure, altering other pathogen characteristics. *Proceedings of the Royal Society, London*, 289B: 20221389.
- Cowl, V. B. & Shultz, S. (2017). Large brains and groups associated with high rates of agonism in primates. *Behavioral Ecology* 28: 803-810.
- Creel, S., Creel, N., Wildt, D.E. & Monfort, S.L. (1992). Behavioural and endocrine mechanisms of reproductive suppression in Serengeti dwarf mongooses. *Animal Behaviour* 43: 231-245.
- Creel, S., Dantzer, B., Goymann, W. & Rubenstein, D.R. (2013). The ecology of stress: effects of the social environment. *Functional Ecology* 27: 66-80.
- Croy, I., Luong, A., Tricoli, C., Hofmann, E., Olausson, H., & Sailer, U. (2016). Interpersonal stroking touch is targeted to C tactile afferent activation. *Behavioural Brain Research* 297: 37-40.
- Cruwys, T., Dingle, G. A., Haslam, C., Haslam, S. A., Jetten, J. & Morton, T. A. (2013). Social group memberships protect against future depression, alleviate depression symptoms and prevent depression relapse. *Social Science & Medicine* 98: 179-186.
- Cundiff, J. M. & Matthews, K. A. (2018). Friends with health benefits: the long-term benefits of early peer social integration for blood pressure and obesity in midlife. *Psychological Science* 29: 814-823.

- Curry, O. & Dunbar, R.I.M. (2013). Do birds of a feather flock together? The relationship between similarity and altruism in social networks. *Human Nature* 24: 336-347
- Damjanovic, L., Roberts, S. G. & Roberts, A. I. (2022). Language as a tool for social bonding: evidence from wild chimpanzee gestural, vocal and bimodal signals. *Philosophical Transactions of the Royal Society, London*, 377B: 20210311.
- Datta, S. (1983). Relative power and the acquisition of rank. In: R.A. Hinde (ed.) *Primate Social Relationships*, pp. 103-12. Oxford: Blackwell.
- Dávid-Barrett, T. & Dunbar, R. (2013). Processing power limits social group size: computational evidence for the cognitive costs of sociality. *Proceedings of the Royal Society, London*, 280B: 20131151.
- Dávid-Barrett, T. & Dunbar, R.I.M. (2016). Bipedality and hair loss in human evolution revisited: the impact of altitude and activity scheduling. *Journal of Human Evolution* 94: 72-82.
- Deacon, T. (1997). *The Symbolic Species: The co-evolution of Language and the Human Brain*. London: Allen Lane.
- Dean, R.F.A. (1949). Women war captives in Russia. *British Medical Journal* 1: 691-695.
- Deaner, R.O., Isler, K., Burkart, J. & van Schaik, C.P. (2007). Overall brain size, and not encephalisation quotient, best predicts cognitive ability across non-human primates. *Brain Behavior and Evolution* 70: 115-124.
- DeCasien, A.R., Williams, S.A. & Higham, J.P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution* 1: 0112.
- Depue, R.A. & Morrone-Strupinsky, J.V. (2005). A neurobehavioral model of affiliative bonding: implications for conceptualising a human trait of affiliation. *Behavioral & Brain Sciences* 28:313-395.
- Devaine, M., Hollard, G. & Daunizeau, J. (2014). The social Bayesian brain: does mentalizing make a difference when we learn? *PLoS Computational Biology* 10: e1003992.
- Devaine, M., San-Galli, A., Trapanese, C., Bardino, G., Hano, C., Saint Jalme, M., Bouret, S., Masi, S. & Daunizeau, J. (2017). Reading wild minds: a computational assay of theory of mind sophistication across seven primate species. *PLoS Computational Biology* 13: e1005833.
- Dobson, S. D. (2009). Socioecological correlates of facial mobility in nonhuman anthropoids. *American Journal of Physical Anthropology* 139: 413-420.
- Dobson, H. & Smith, R.F. (2000). What is stress, and how does it affect reproduction? *Animal Reproduction Science* 60: 743-752.
- Dobson, H., Fergani, C., Routly, J.E. & Smith, R.F. (2012). Effects of stress on reproduction in ewes. *Animal Reproduction Science* 130: 135-140.
- Dobson, S. D. (2012). Coevolution of facial expression and social tolerance in macaques. *American Journal of Primatology* 74: 229-235.
- Dunbar, R.I.M. (1980). Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioural Ecology and Sociobiology* 7: 253-265.
- Dunbar, R.I.M. (1983). Structure of gelada baboon reproductive units. IV. Organisation at group level. *Zeitschrift für Tierpsychologie* 63: 265-282.
- Dunbar, R.I.M. (1984). *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton NJ: Princeton University Press.

- Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia Primatologica* 57:121-131.
- Dunbar, R.I.M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioural Ecology and Sociobiology* 31: 35-49.
- Dunbar, R.I.M. (1993). Coevolution of neocortex size, group size and language in humans. *Behavioral and Brain Sciences* 16: 681-735.
- Dunbar, R.I.M. (1995a). The mating system of callitrichid primates. I. Conditions for the coevolution of pairbonding and twinning. *Animal Behaviour* 50: 1057-1070.
- Dunbar, R.I.M. (1995b). The mating system of callitrichid primates. II. The impact of helpers. *Animal Behaviour* 50: 1071-1089.
- Dunbar, R.I.M. (1998). The social brain hypothesis. *Evolutionary Anthropology* 6: 178-190.
- Dunbar, R.I.M. (2009). Why only humans have language. In: R. Botha & C. Knight (eds.) *The Prehistory of Language*, pp. 12-35. Oxford: Oxford university Press.
- Dunbar R.I.M. (2010a). The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews* 34: 260-268.
- Dunbar, R.I.M. (2010b). Deacon's dilemma: the problem of pairbonding in human evolution. In: R.I.M. Dunbar, C. Gamble & J.A.J. Gowlett (editors) *Social Brain, Distributed Mind*, pp. 159-179. Oxford: Oxford University Press.
- Dunbar, R.I.M. (2012). Bridging the bonding gap: the transition from primates to humans. *Philosophical Transactions of the Royal Society, London*, 367B: 1837-1846.
- Dunbar, R.I.M. (2014). *Human Evolution*. London: Pelican and New York: Oxford University Press.
- Dunbar, R.I.M. (2017). Breaking bread: the functions of social eating. *Adaptive Human Behavior and Physiology* 3: 198-211.
- Dunbar, R.I.M. (2018a). The anatomy of friendship. *Trends in Cognitive Sciences* 22: 32-51
- Dunbar, R.I.M. (2018b). Social structure as a strategy to mitigate the costs of group-living: a comparison of gelada and guereza monkeys. *Animal Behaviour* 136: 53-64.
- Dunbar, R.I.M. (2019). Fertility as a constraint on group size in African great apes. *Biological Journal of the Linnean Society* 129: 1-13.
- Dunbar, R.I.M. (2020). Structure and function in human and primate social networks: Implications for diffusion, network stability and health. *Proceedings of the Royal Society, London*, 476A: 20200446.
- Dunbar, R.I.M. (2021a). Virtual touch and the human social world. *Current Opinion in Behavioral Science* 43: 14-19.
- Dunbar, R.I.M. (2021b). *Friends: Understanding the Power of Our Most Important Relationships*. London: Little Brown
- Dunbar, R.I.M. (2022a). Managing the stresses of group-living in the transition to village life. *Evolutionary Human Sciences* 4: e40.
- Dunbar, R.I.M. (2022b). Laughter and its role in the evolution of human social bonding. *Philosophical Transactions of the Royal Society, London*, 289B: 20210176.

- Dunbar, R.I.M. (2023). The origins and function of musical performance. *Frontiers in Psychology* 14: 1257390.
- Dunbar, R.I.M. & Dunbar, P. (1975). *Social Dynamics of Gelada Baboons*. Basel: Karger.
- Dunbar, R.I.M. & Dunbar, P. (1976). Contrasts in social structure among black-and-white colobus monkeys. *Animal Behaviour* 24: 84-92.
- Dunbar, R.I.M. & MacCarron, P. (2019). Group size as a trade-off between fertility and predation risk: implications for social evolution. *Journal of Zoology* 308: 9-15.
- Dunbar, R.I.M. & Nathan, M. (1972). Social organisation of the Guinea baboon, *Papio papio*, in Senegal. *Folia Primatology* 17: 321-334.
- Dunbar, R.I.M. & Shi, J. (2008). Sex differences in feeding activity results in sexual segregation of feral goats. *Ethology* 114: 444-451.
- Dunbar, R.I.M. & Shultz, S. (2007a). Evolution in the social brain. *Science* 317: 1344-1347.
- Dunbar, R.I.M. & Shultz, S. (2007b). Understanding primate brain evolution. *Philosophical Transactions of the Royal Society, London* 362B: 649-658.
- Dunbar, R.I.M. & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147: 775-803.
- Dunbar, R.I.M. & Shultz, S. (2017). Why are there so many explanations for primate brain evolution? *Philosophical Transactions of the Royal Society, London* 372B: 201602244.
- Dunbar, R.I.M. & Shultz, S. (2021a). The infertility trap: the fertility costs of group-living in mammalian social evolution. *Frontiers in Ecology and Evolution* 9: 634664.
- Dunbar, R.I.M. & Shultz, S. (2021b). Social complexity and the fractal structure of social groups in primate social evolution. *Biological Reviews* 96: 1889-1906.
- Dunbar, R.I.M. & Shultz, S. (2023a). Four errors and a fallacy: pitfalls for the unwary in comparative brain analyses. *Biological Reviews* (in press).
- Dunbar, R.I.M. & Shultz, S. (2023b). The social role of inhibition in primates and other animals. *BioRxiv* doi.org/10.1101/2020.10.26.354852
- Dunbar, R.I.M., Korstjens, A.H. & Lehmann, J. (2009). Time as an ecological constraint. *Biological Reviews* 84: 413-429.
- Dunbar, R.I.M., MacCarron, P. & Shultz, S. (2018a). Primate social group sizes exhibit a regular scaling pattern with natural attractors. *Biology Letters* 14: 20170490.
- Dunbar, R.I.M., MacCarron, P. & Robertson, C. (2018b). Tradeoff between fertility and predation risk drives a geometric sequence in the pattern of group sizes in baboons. *Biology Letters* 14: 20170700.
- Dunbar, R.I.M., Cornah, L., Daly, F. & Bowyer, K. (2002). Vigilance in humans: a test of alternative hypotheses. *Behaviour* 139: 695-711.
- Dunbar, R.I.M., Teasdale, B., Thompson, J., Budelmann, F., Duncan, S., van Emde Boas, E. & Maguire, L. (2016). Emotional arousal when watching drama increases pain threshold and social bonding. *Royal Society Open Science* 3: 160288.
- Dunbar, R.I.M., Frangou, A., Grainger, F. & Pearce, E. (2021a). Laughter influences social bonding but not prosocial generosity to friends and strangers. *PLoS One* 16: e0256229.

- Dunbar, R.I.M., Pearce, E., Tarr, B., Makdani, A., Bamford, J., Smith, S. & McGlone, F. (2021b). Cochlear SGN neurons elevate pain thresholds in response to music. *Scientific Reports* 11: 14547.
- Emlen, S. T. & Wrege, P. H. (1986). Forced copulations and intra-specific parasitism: two costs of social living in the white-fronted bee-eater. *Ethology* 71: 2-29.
- Einarsson, S., Brandt, Y., Lundeheim, N. & Madej, A. (2008). Stress and its influence on reproduction in pigs: a review. *Acta Veterinaria Scandinavica*, 50: 48.
- Escribano, D., Doldán-Martelli, V., Cronin, K. A., Haun, D. B., van Leeuwen, E. J., Cuesta, J. A. & Sánchez, A. (2022). Chimpanzees organize their social relationships like humans. *Scientific Reports* 12: 16641.
- Espy, K. A., Kaufmann, P. M., McDiarmid, M. D., & Glisky, M. L. (1999). Executive functioning in preschool children: Performance on A-not-B and other delayed response format tasks. *Brain and Cognition* 41: 178-199.
- Euker, J.S. & Riegler, G.D. (1973). Effects of stress on pregnancy in the rat. *Journal of Reproduction and Fertility* 34: 343-346.
- Fabre-Nys, C., Meller, R.E. & Keverne, E.B. (1982). Opiate antagonists stimulate affiliative behaviour in monkeys. *Pharmacology, Biochemistry & Behavior* 16: 653-659.
- Faulkes, C. G., Abbott, D. H., & Jarvis, J. U. M. (1990). Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction and Fertility* 88: 559-568.
- Ferin, M. (1984). Endogenous opioid peptides and the menstrual cycle. *Trends in Neurosciences* 7: 194-196.
- Fichtel, C. & Kappeler, P. M. (2022). Coevolution of social and communicative complexity in lemurs. *Philosophical Transactions of the Royal Society, London*, 377B: 20210297.
- Fidanza, F., Polimeni, E., Pierangeli, V. & Martini, M. (2021). A better touch: C-tactile fibers related activity is associated to pain reduction during temporal summation of second pain. *Journal of Pain* 22: 567-576.
- Finlay, B.L., Darlington, R.B. & Nicastro, N. (2001). Developmental structure in brain evolution. *Behavioral and Brain Sciences* 24: 263-278.
- Freeberg, T.M. (2006). Social complexity can drive vocal complexity: group size influences vocal information in Carolina chickadees. *Psychological Science* 17: 557–561.
- Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences USA* 107: 19949-19954.
- Garcia, C., Lee, P.C. & Rosetta, L. (2006). Dominance and reproductive rates in captive female olive baboons, *Papio anubis*. *American Journal of Physical Anthropology* 131: 64-72.
- Geraghty, A.C., Muroy, S.E., Zhao, S., Bentley, G.E., Kriegsfeld, L.J. & Kaufer, D. (2015). Knockdown of hypothalamic RFRP3 prevents chronic stress-induced infertility and embryo resorption. *ELife* 4: e04316.
- Gesquiere, L.R., Altmann, J., Archie, E.A. & Alberts, S.C. (2018). Interbirth intervals in wild baboons: Environmental predictors and hormonal correlates. *American Journal of Physical Anthropology* 166: 107-126.



- Giorgi, M. S., Arlettaz, R., Christe, P. & Vogel, P. (2001). The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). *Proceedings of the Royal Society, London*, 268, 2071-2075.
- Gordon, K., Hodgen, G.D., & Richardson, D.W. (1992). Postpartum lactational anovulation in a nonhuman primate (*Macaca fascicularis*): endogenous opiate mediation of suckling-induced hyperprolactinemia. *Journal of Clinical Endocrinology & Metabolism* 75: 59-67.
- Gore, M. A. (1994). Dyadic and triadic aggression and assertiveness in adult female rhesus monkeys, *Macaca mulatta*, and hamadryas baboons, *Papio hamadryas*. *Animal Behaviour* 48: 385-392.
- Gowlett, J.A.J., Gamble, C. & Dunbar, R.I.M. (2012). Human evolution and the archaeology of the social brain. *Current Anthropology* 53: 693-722.
- Grabowska, M., Kopperud, B.T., Tsuboib, M., Hansen, M.T. (2023). Both diet and sociality affect primate brain-size evolution. *Systemic Biology* (in press).
- Granovetter, M. S. (1973). The strength of weak ties. *American Journal of Sociology* 78: 1360-1380.
- Harcourt, A. H. & Stewart, K. J. (2007). *Gorilla Society: Conflict, Compromise, and Cooperation Between the Sexes*. Chicago: University of Chicago Press.
- Hamilton, M.J., Milne, B.T., Walker, R.S., Burger, O. & Brown, J.H. (2007). The complex structure of hunter-gatherer social networks. *Proceedings of the Royal Society, London*, 274B: 2195-2203.
- Hayashi, T., Akikawa, R., Kawasaki, K., Egawa, J., Minamimoto, T., Kobayashi, K., ... & Hasegawa, I. (2020). Macaques exhibit implicit gaze bias anticipating others' false-belief-driven actions via medial prefrontal cortex. *Cell Reports* 30: 4433-4444.
- Healy, S.D. & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society, London*, 274B: 453-464.
- Henzi, S.P., de Sousa Pereira, L., Hawker-Bond, D., Stiller, J., Dunbar, R.I.M. & Barrett, L. (2007). Look who's talking: developmental trends in the size of conversational cliques. *Evolution and Human Behavior* 28: 66-74.
- Hill, R.A., Lycett, J. & Dunbar, R.I.M. (2000). Ecological determinants of birth intervals in baboons. *Behavioral Ecology* 11: 560-564.
- Holt-Lunstad, J., Smith, T. B. & Layton, J. B. (2010). Social relationships and mortality risk: a meta-analytic review. *PLoS Medicine* 7: e1000316.
- Hoogland, J. L. (1981). The evolution of coloniality in white-tailed and blacktailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62: 252-272.
- Hoshino, J. (1985). Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo animal reserve, Cameroon. *Primates* 26: 248-273.
- Howlett, T.A. & Rees, L.H. (1986). Endogenous opioid peptides and hypothalamo-pituitary function. *Annual Review of Physiology* 48:527-36
- Huchard, E. & Cowlshaw, G. (2011). Female-female aggression around mating: an extra cost of sociality in a multimale primate society. *Behavioral Ecology* 22: 1003-1011.
- Harel, R., Loftus, J. C. & Crofoot, M. C. (2021). Locomotor compromises maintain group cohesion in baboon troops on the move. *Proceedings of the Royal Society, London*, 288B: 20210839.

- Isaksson, E., Urhan, A. U., & Brodin, A. (2018). High level of self-control ability in a small passerine bird. *Behavioral Ecology and Sociobiology* 72: 1-7.
- Iwasa, T., Matsuzaki, T., Yano, K. & Irahara, M. (2017). Gonadotropin-inhibitory hormone plays roles in stress-induced reproductive dysfunction. *Frontiers in Endocrinology* 8: 62.
- Jackson, E. E., McGlone, F. P. & Haggarty, C. J. (2021). The social brain has a nerve: insights from attachment and autistic phenotypes. *Current Opinion in Behavioral Sciences* 45: 101114.
- Johnson-Ulrich, L. & Holekamp, K.E. (2020). Group size and social rank predict inhibitory control in spotted hyenas. *Animal Behaviour* 160: 157-168.
- Judge, P. G. (1991). Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). *American Journal of Primatology* 23: 225-237.
- Kajokaite, K., Whalen, A., Panchanathan, K. & Perry, S. (2019). White-faced capuchin monkeys use both rank and relationship quality to recruit allies. *Animal Behaviour* 154: 161- 169.
- Kalra, S.P. & Kalra, P.S. (1996). Nutritional infertility: the role of the interconnected hypothalamic neuropeptide Y–galanin–opioid network. *Frontiers in Neuro-endocrinology* 17: 371-401.
- Kamilar, J.M. & Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society, London*, 368B: 20120341.
- Kanai, R., Bahrami, B., Roylance, R. & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society, London*, 279B:1327-1334.
- Kenny, E., Birkhead, T. R. & Green, J. P. (2017). Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years. *Behavioral Ecology* 28: 1142-1148.
- Keverne, E.B., Martensz, N. & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14:155-161.
- Kiesow, H., Dunbar, R.I.M., Kable, J.W., Kalenscher, T., Vogeley, K., Schilbach, L., Marquand, A.F., Wiecki, T.V. & Bzdok, D. (2020). 10,000 social brains: Sex differentiation in human brain anatomy. *Science Advances* 6: eaaz1170.
- Kim, D. A., Benjamin, E. J., Fowler, J. H. & Christakis, N. A. (2016). Social connectedness is associated with fibrinogen level in a human social network. *Proceedings of the Royal Society, London*, 283B: 20160958.
- Kinderman, P., Dunbar, R.I.M. & Bentall, R.P. (1998). Theory-of-mind deficits and causal attributions. *British Journal of Psychology* 89: 191-204.
- King, A.J. & Cowlshaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour* 78: 1381-1387.
- Kirk, R. (1994). *Raw Feeling: A Philosophical Account of the Essence of Consciousness*. Oxford: Oxford University Press.
- Korstjens, A.H. & Dunbar, R.I.M. (2007). Time constraints limit group sizes and distribution in red and black-and-white colobus monkeys. *International Journal of Primatology* 28: 551-575.
- Korstjens, A., Lehmann, J. & Dunbar, R.I.M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour* 79: 361-374.
- Kubenova, B., Konecna, M., Majolo, B., Smilauer, P., Ostner, J. & Schülke, O. (2017). Triadic awareness predicts partner choice in male–infant–male interactions in Barbary macaques. *Animal Cognition*, 20: 221-232.



- Kudo, H. & Dunbar, R.I.M. (2001). Neocortex size and social network size in primates. *Animal Behaviour* 62: 711-722.
- Kummer, H. (1968). *Social Organization of Hamadryas Baboons*. Basel: Karger.
- Kummer, H., Götz, W. & Angst, W. (1974). Triadic differentiation: an inhibitory process protecting pair bonds in baboons. *Behaviour* 49: 62-87.
- Kwak, S., Joo, W., Youm, Y. & Chey, J. (2018). Social brain volume is associated with in-degree social network size among older adults. *Proceedings of the Royal Society, London*, 285B: 20172708.
- Laatikainen, T.J. (1991). Corticotropin-releasing hormone and opioid peptides in reproduction and stress. *Annals of Medicine* 23: 489-496.
- Lazarus, J. (1978). Vigilance, flock size and domain of danger size in white-fronted goose. *Wildfowl* 29: 135-145.
- Lehmann, J. & Dunbar, R.I.M. (2008). Network cohesion, group size and neocortex size in female-bonded Old World primates. *Proceedings of the Royal Society, London*, 276B: 4417-4422.
- Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. (2007a). Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology* 21: 613-634.
- Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. (2007b). Group size, grooming and social cohesion in primates. *Animal Behaviour* 74:1617-1629.
- Lehmann, J., Lee, P.C. & Dunbar, R.I.M. (2014). Unravelling the evolutionary function of communities. In: R.I.M. Dunbar, C. Gamble & J.A.J. Gowlett (eds) *Lucy to Language: the Benchmark Papers*, pp. 245-276. Oxford: Oxford University Press.
- Lehmann, J., Majolo, B. & McFarland, R. (2016). The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behavioral Ecology* 27: 20-28.
- Lewis, P., Rezaie, R., Browne, R., Roberts, N. & Dunbar, R. (2011). Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage* 57: 1624-1629.
- Lewis, P., Birch, A., Hall, A. & Dunbar, R.I.M. (2017). Higher order intentionality tasks are cognitively more demanding. *Social, Cognitive and Affective Neuroscience* 12: 1063-1071.
- Li, W., Mai, X. & Liu, C. (2014). The default mode network and social understanding of others: what do brain connectivity studies tell us. *Frontiers in Human Neuroscience* 8: 74.
- Li, X.F., Knox, A.M.I. & O'Byrne, K.T. (2010). Corticotrophin-releasing factor and stress-induced inhibition of the gonadotrophin-releasing hormone pulse generator in the female. *Brain Research* 1364: 153-163.
- Linklater, W. L., Cameron, E. Z., Minot, E. O. & Stafford, K. J. (1999). Stallion harassment and the mating system of horses. *Animal Behaviour* 58: 295-306.
- Loeth, G.E., Ellingsen, D.M. & Leknes, S. (2014). State-dependent m-opioid modulation of social motivation – a model. *Frontiers of Behavioral Neuroscience* 8: 430.
- McComb, K. & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters* 1: 381-385
- McFarland, R. & Majolo, B. (2013). Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters* 9: 20130428.

- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, J. M., *et al.* (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences USA* 111: E2140–E2148.
- Madsen, E., Tunney, R., Fieldman, G., Plotkin, H., Dunbar, R.I.M., Richardson, J. & McFarland, D.J. (2007). Kinship and altruism: a cross-cultural experimental study. *British Journal of Psychology* 98: 339-359.
- Mandler, R. N., Biddison, W. E., Mandler, R. A. Y. A. & Serrate, S. A. (1986). beta-Endorphin augments the cytolytic activity and interferon production of natural killer cells. *Journal of Immunology* 136: 934-939.
- Mars, R. B., Neubert, F. X., Noonan, M. P., Sallet, J., Toni, I. & Rushworth, M. F. (2012). On the relationship between the “default mode network” and the “social brain”. *Frontiers in Human Neuroscience* 6: 189.
- Massen, J., Sterck, E. & de Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour* 147: 1379-1412.
- Maynard Smith, J. & Szathmáry, E. (1997). *The Major Transitions in Evolution*. Oxford: Oxford University Press.
- McNeilly, A.S. (2001a). Lactational control of reproduction. *Reproduction, Fertility and Development* 13: 583-590.
- McNeilly, A.S., Forsyth, I.A. & McNeilly, J. R. (1994). Regulation of post-partum fertility in lactating mammals. In: *Marshall's Physiology of Reproduction*, pp. 1037-1101. Berlin: Springer.
- ManyPrimates, Aguenounoun, G., Allritz, M., Altschul, D. M., Ballesta, S.B., and 74 others (2020). The evolution of primate short-term memory. *Animal Behavior and Cognition* 9: 428-516.
- Meguerditchian, A., Marie, D., Margiotoudi, K., Roth, M., Nazarian, B., Anton, J.-L. & Claidière, N. (2020). Baboons (*Papio anubis*) living in larger social groups have bigger brains. *Evolution and Human Behavior* 42: 30-34.
- Mesnick, S. L. (1997) Sexual alliances: evidence and evolutionary implications. In: P.A. Gowaty (editor) *Feminism and Evolutionary Biology*. London: Chapman & Hall.
- Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C. & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science* 4: 171296.
- Mischel, W. & Ebbesen, E.B. (1970). Attention in delay of gratification. *Journal of Personality and Social Psychology* 16: 329-337.
- Moehlman, P.D. & Hofer, H. (1997). Cooperative breeding, reproductive suppression, and body mass in canids. In N.G. Solomon, & J.A. French (Eds.), *Cooperative Breeding in Mammals*, pp. 76-128. Cambridge, U.K.: Cambridge University Press.
- Moffitt, T., Caspi, A., Rutter, M. & Silva, P. (2001). *Sex Differences in Antisocial Behaviour: Conduct Disorder, Delinquency, and Violence in the Dunedin Longitudinal Study*. Cambridge: Cambridge University Press.
- Monsivais, M., Bhattacharya, K., Ghosh, A., Dunbar, R.I.M. & Kaski, K. (2017). Seasonal and geographical impact on human resting periods. *Scientific Reports* 7: 10717.
- Morales Picard, A., Mundry, R., Auersperg, A. M., Boeving, E. R., Boucherie, P. H., Bugnyar, T., ... & Slocombe, K. E. (2020). Why preen others? Predictors of allopreening in parrots and corvids and comparisons to grooming in great apes. *Ethology* 126: 207-228.

Mount, L.E. (1979). *Adaptation to Thermal Environment: Man and his Productive Animals*. London: Edward Arnold.

Noonan, M., Mars, R., Sallet, J., Dunbar, R.I.M. & Fellows, L. (2018). The structural and functional brain networks that support human social networks. *Behavioural Brain Research* 355: 12-23.

Nummenmaa, L., Tuominen, L., Dunbar, R., Hirvonen, J., Manninen, S., Arponen, E., Machin, A., Hari, R., Jääskeläinen, I.P. & Sams, M. (2016). Reinforcing social bonds by touching modulates endogenous  $\mu$ -opioid system activity in humans. *NeuroImage* 138: 242–247.

Núñez, C. M. V., Adelman, J. S. & Rubenstein, D. I. (2015). Sociality increases juvenile survival after a catastrophic event in the feral horse (*Equus caballus*). *Behavioral Ecology* 26: 138-147.

O'Connell, S. & Dunbar, R.I.M. (2002). A test for comprehension of false belief in chimpanzees. *Evolution & Cognition* 9: 131-139.

Olausson, H., Wessberg, J., Morrison, I., McGlone, F. & Vallbo, A. (2010). The neurophysiology of unmyelinated tactile afferents. *Neuroscience & Biobehavioral Reviews* 34: 185-191.

van Overwalle, F. (2009). Social cognition and the brain: a metaanalysis. *Human Brain Mapping* 30: 829-858.

Passingham, R.E. (2021). *Understanding the Prefrontal Cortex: Selective Advantage, Connectivity, and Neural Operations*. Oxford: Oxford University Press.

Passingham, R.E. & Wise, S.P. (2012). *The Neurobiology of the Prefrontal Cortex: Anatomy, Evolution and the Origin of Insight*. Oxford: Oxford University Press.

Patzelt, A., Zinner, D., Fickenscher, G., Diedhiou, S., Camara, B., Stahl, D. & Fischer, J. (2011). Group composition of Guinea baboons (*Papio papio*) at a water place suggests a fluid social organization. *International Journal of Primatology* 32: 652-668.

Pearce, E., Launay, J. & Dunbar, R.I.M. (2015). The ice-breaker effect: singing mediates fast social bonding. *Royal Society Open Science* 2: 150221.

Pearce, E., Shuttleworth, A., Grove, M., & Layton, R. (2014). The costs of being a high latitude hominin. In: R.I.M. Dunbar, C. Gamble & J.A.J. Gowlett (eds.) *Lucy to Language: The Benchmark Papers*, pp. 356-379. Oxford: Oxford University Press.

Pearce, E., Launay, J., van Duijn, M., Rotkirch, A., David-Barrett, T. & Dunbar, R.I.M. (2016). Singing together or apart: The effect of competitive and cooperative singing on social bonding within and between sub-groups of a university fraternity. *Psychology of Music* 44: 1255-73.

Pearce, E., Wlodarski, R., Machin, A. & Dunbar, R.I.M. (2017a). Variation in the  $\beta$ -endorphin, oxytocin, and dopamine receptor genes is associated with different dimensions of human sociality. *Proceedings of the National Academy of Sciences USA* 114: 5300-5305.

Pearce, E., Launay, J., MacCarron, P. & Dunbar, R.I.M. (2017b). Tuning in to others: Exploring relational and collective bonding in singing and non-singing groups over time. *Psychology of Music* 45: 496-512.

Pearce, E., Wlodarski, R., Machin, A. & Dunbar, R.I.M. (2018). The influence of genetic variation on social disposition, romantic relationships and social networks: a replication study. *Adaptive Human Behavior and Physiology* 4: 400-422.

- Pearce, E., Wlodarski, R., Machin, A. & Dunbar, R.I.M. (2019). Exploring the links between dispositions, romantic relationships, support networks and community inclusion in men and women. *PLoS One* 14: e0216210.
- Pettay, J.E., Lahdenperä, M., Rotkirch, A. & Lummaa, V. (2016). Costly reproductive competition between co-resident females in humans. *Behavioural Ecology* 27: 1601-1608.
- Pierce, B.N., Hensworth, P.H., Rivalland, E.T.A., Wagenmaker, E.R., Morrissey, A.D., Papargiris, M.M., Clarke, I.J., Karsch, F.J., Turner, A.I. & Tilbrook, A.J. (2008). Psychosocial stress suppresses attractiveness, proceptivity and pulsatile LH in the ewe. *Hormones and Behavior* 54: 424-434.
- Pollard, K.A. & Blumstein, D.T. (2008). Time allocation and the evolution of group size. *Animal Behaviour* 76: 1683-1699.
- Powell, J., Lewis, P., Dunbar, R.I.M., García-Fiñana, M. & Roberts, N. (2010). Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia* 48: 3554-3562.
- Powell, J., Lewis, P.A., Roberts, N., García-Fiñana, M. & Dunbar, R.I.M. (2012). Orbital prefrontal cortex volume predicts social network size: an imaging study of individual differences in humans. *Proceedings of the Royal Society, London*, 279B: 2157-2162.
- Powell, J., Kemp, G., Dunbar, R., Roberts, N., Sluming, V. & García-Fiñana, M. (2014). Different association between intentionality competence and prefrontal volume in left- and right-handers. *Cortex* 54: 63-76.
- Powell, L.E., Isler, K. & Barton, R.A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society, London*, 284B: 20171765.
- Prior, J.C. (2022). Adaptive, reversible, hypothalamic reproductive suppression: More than functional hypothalamic amenorrhea. *Frontiers in Endocrinology* 13: 893889.
- Puente, J., Maturana, P., Miranda, D., Navarro, C., Wolf, M. E. & Mosnaim, A. D. (1992). Enhancement of human natural killer cell activity by opioid peptides: similar response to methionine-enkephalin and  $\beta$ -endorphin. *Brain, Behavior, and Immunity*: 32-39.
- Pusey, A. E., & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society, London*, 368B: 20130077.
- Radford, A. N., & Du Plessis, M. A. (2006). Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. *Behavioral Ecology and Sociobiology* 61: 221-230.
- Rawlings, B. S., van Leeuwen, E. J. & Davila-Ross, M. (2023). Chimpanzee communities differ in their inter- and intrasexual social relationships. *Learning & Behavior* 51: 48-58.
- Riters, L. V., Kelm-Nelson, C. A. & Spool, J. A. (2019). Why do birds flock? A role for opioids in the reinforcement of gregarious social interactions. *Frontiers in Physiology* 10: 421.
- Roberts, A. I. & Roberts, S.B.G. (2020). Communicative roots of complex sociality and cognition. *Biological Reviews* 95: 51-73.
- Roberts, S.C. & Dunbar, R.I.M. (1991). Climatic influences on the behavioural ecology of Chanler's mountain reedbuck in Kenya. *African Journal of Ecology* 29: 316-329.
- Roberts, S.B.G. & Dunbar, R.I.M. (2015). Managing relationship decay: network, gender, and contextual effects. *Human Nature* 26: 426-450.

- Rosenquist, J. N., Fowler, J. H. & Christakis, N. A. (2011). Social network determinants of depression. *Molecular Psychiatry* 16: 273.
- Roumazeilles, L., Schurz, M., Lojkiewicz, M., Verhagen, L., Schüffelgen, U., Marche, K., ... & Sallet, J. (2021). Social prediction modulates activity of macaque superior temporal cortex. *Science Advances* 7, eabh2392.
- Roumazeilles, L., Lange, F. J., Benn, R. A., Andersson, J. L., Bertelsen, M. F., Manger, P. R., ... & Mars, R. B. (2022). Cortical morphology and white matter tractography of three phylogenetically distant primates: Evidence for a simian elaboration. *Cerebral Cortex* 32: 1608-1624.
- Rowell, T.E. (1970). Baboon menstrual cycles affected by social environment. *Journal of Reproduction and Fertility* 21: 133-141.
- Ruckstuhl, K. E. & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour* 64: 909-914.
- Ruckstuhl, K. E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77: 77-96.
- Russell, Y., Call, J. & Dunbar, R.I.M. (2008). Image scoring in great apes. *Behavioral Processes* 78: 108-111.
- Sallet J., Mars, R.B., Noonan, M.P., Andersson, J.L., O'Reilly, J.X., Jbabdi, S., Croxson, P.L., Jenkinson, M., Miller, K.L. & Rushworth, M.F.S. (2011). Social network size affects neural circuits in macaques. *Science* 334: 697-700.
- Santini, Z., Jose, P., Koyanagi, A., Meilstrup, C., Nielsen, L., Madsen, K., Hinrichsen, C., Dunbar, R. I. M. & Koushede, V. (2021). The moderating role of social network size in the temporal association between formal social participation and mental health: a longitudinal analysis using two consecutive waves of the Survey of Health, Ageing and Retirement in Europe (SHARE). *Social Psychiatry and Psychiatric Epidemiology* 56: 417-428.
- Sarkar, D. K., Sengupta, A., Zhang, C., Boyadjieva, N. & Murugan, S. (2012). Opiate antagonist prevents  $\mu$ - and  $\delta$ -opiate receptor dimerization to facilitate ability of agonist to control ethanol-altered natural killer cell functions and mammary tumor growth. *Journal of Biological Chemistry* 287: 16734-16747.
- Schenker, J. G., Meirow, D. & Schenker, E. (1992). Stress and human reproduction. *European Journal of Obstetrics & Gynecology and Reproductive Biology* 45: 1-8.
- Schmidt-Nielsen, K. (1984). *Scaling: Why Is Animal Size So Important?* Cambridge: Cambridge University Press.
- Schino, G., Tiddi, B. & Polizzi di Sorrentino, E. (2006). Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour* 71: 1069-1074.
- Schliep, K.C., Mumford, S.L., Vladutiu, C.J., Ahrens, K.A., et al. (2015). Perceived stress, reproductive hormones, and ovulatory function: A prospective cohort study. *Epidemiology* 26: 177-184.
- Seifer, D.B. & Collins, R. L. (1990). Current concepts of b-endorphin physiology in female reproductive dysfunction. *Fertility and Sterility* 54: 757-771.
- Seyfarth, R. M. & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308: 541-543.
- Sheiner, E., Sheiner, E. K., Potashnik, G., Carel, R. & Shoham-Vardi, I. (2003). The relationship between occupational psychological stress and female fertility. *Occupational Medicine* 53: 265-269.



Shi, J., Dunbar, R.I.M. & Beauchamp, G. (2010). Group-size effect on vigilance and foraging in a predator-free population of feral goats (*Capra hircus*) on the Isle of Rum, NW Scotland. *Ethology* 116: 329-337.

Shultz, S. & Dunbar, R. I. M. (2010a). Encephalisation is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proceedings of the National Academy of Sciences, USA*, 107: **21582-21586**.

Shultz, S. & Dunbar, R.I.M. (2010b). Species differences in executive function correlate with hippocampus volume and neocortex ratio across non-human primates. *Journal of Comparative Psychology* 124: 252-260.

Shultz, S. & Dunbar, R.I.M. (2010c). Species differences in executive function correlate with hippocampus volume and neocortex ratio across non-human primates. *Journal of Comparative Psychology* 124: 252-260.

Shultz, S. & Dunbar, R.I.M. (2022). Socioecological complexity in primate groups and its cognitive correlates. *Philosophical Transactions of the Royal Society, London*, 377B: 20210296.

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

Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour* 58: 45-51.

Silk, J.B. (2002). Using the 'F'-word in primatology. *Behaviour* 139, 421–446.

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

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

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

Sinha, A. (1998). Knowledge acquired and decisions made: triadic interactions during allogrooming in wild bonnet macaques, *Macaca radiata*. *Philosophical Transactions of the Royal Society, London*, 353B:619-631.

Smallwood, J., Bernhardt, B. C., Leech, R., Bzdok, D., Jefferies, E., & Margulies, D. S. (2021). The default mode network in cognition: a topographical perspective. *Nature Reviews Neuroscience* 22: 503-513.

Smith, J.E., Fichtel, C., Holmes, R.K., Kappeler, P.M., van Vugt, M. & Jaeggi, A.V. (2022). Sex bias in intergroup conflict and collective movements among social mammals: male warriors and female guides. *Philosophical Transactions of the Royal Society, London*, 377B: 20210142.

Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C. & Ramos-Fernández, G. (2019). Using multiplex networks to capture the multidimensional nature of social structure. *Primates* 60: 277-295.

Smuts, B. B. (1985). *Sex and Friendship in Baboons*. London: Routledge.

van Soest, P. J. (1994). *Nutritional Ecology of the Ruminant*. Ithaca NY: Cornell University Press.

Sokal, R. & Rolf, F. (1995). *Biometry*. New York: WF Freeman

- Son, Y.L., Ubuka, T., Millar, R.P. & Kanasaki, H. (2012). Gonadotropin-inhibitory hormone inhibits GnRH-induced gonadotropin subunit gene transcriptions by inhibiting AC/cAMP/PKA-dependent ERK Pathway in L[beta]T2 cells. *Endocrinology* 153: 2332-2343.
- Stein, Z., & Susser, M. (1975). Fertility, fecundity, famine: food rations in the Dutch famine 1944/5 have a causal relation to fertility, and probably to fecundity. *Human Biology* 47: 131-154.
- Stevens, J.R. (2014). Evolutionary pressures on primate intertemporal choice. *Proceedings of the Royal Society, London*, 281B: 20140499.
- Stiller, J. & Dunbar, R.I.M. (2007). Perspective-taking and memory capacity predict social network size. *Social Networks* 29: 93-104.
- Strier, K. B., Lee, P. C. & Ives, A. R. (2014). Behavioral flexibility and the evolution of primate social states. *PloS One* 9: e114099.
- Sueur, C., Deneubourg, J.L. & Petit, O. (2011). From the first intention movement to the last joiner: macaques combine mimetic rules to optimize their collective decisions. *Proceedings of the Royal Society, London*, 278B: 1697-704.
- Sumpter, D.J.T. (2010). *Collective Animal Behavior*. Princeton NJ: Princeton University Press.
- Sutcliffe, A.G., Dunbar, R.I.M. & Wang, D. (2016). Modelling the evolution of social structure. *PLoS One* 11: e0158605.
- Sutcliffe, A.G., Dunbar, R.I.M., Binder, J. & Arrow, H. (2012). Relationships and the social brain: integrating psychological and evolutionary perspectives. *British Journal of Psychology* 103: 149-168.
- Suvilehto, J., Glerean, E., Dunbar, R.I.M., Hari, R. & Nummenmaa, L. (2015). Topography of social touching depends on emotional bonds between humans. *Proceedings of the National Academy of Sciences, USA*, 112: 13811-16.
- Suvilehto, J., Nummenmaa, L., Harada, T., Dunbar, R.I.M., Hari, R., Turner, R., Sadato, N. & Kitada, R. (2019). Cross-cultural similarity in relationship-specific social touching. *Proceedings of the Royal Society, London*, 286B: 20190467.
- Tarr, B., Launay, J., Cohen, E. & Dunbar, R.I.M. (2015). Synchrony and exertion during dance independently raise pain threshold and encourage social bonding. *Biology Letters* 11: 20150767.
- Tarr, B., Launay, J. & Dunbar, R.I.M. (2016). Silent disco: dancing in synchrony leads to elevated pain thresholds and social closeness. *Evolution and Human Behavior* 37: 343-349
- Tarr, B., Launay, J. & Dunbar, R.I.M. (2017). Naltrexone blocks endorphins released when dancing in synchrony. *Adaptive Human Behavior & Physiology* 3: 241-254.
- Testard, C., Brent, L. J., Andersson, J., Chiou, K. L., Negron-Del Valle, J. E., ... & Sallet, J. (2022). Social connections predict brain structure in a multidimensional free-ranging primate society. *Science Advances* 8: eabl5794.
- Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour* 79: 81-107.
- Tuulari, J. J., Tuominen, L., de Boer, F. E., Hirvonen, J., Helin, S., Nuutila, P. & Nummenmaa, L. (2017). Feeding releases endogenous opioids in humans. *Journal of Neuroscience* 37: 8284-8291.
- Tremblay, R. E., Pihl, R. O., Vitaro, F. & Dobkin, P. L. (1994). Predicting early onset of male antisocial behavior from preschool behavior. *Archives of General Psychiatry* 51: 732-739.
- Vicsek, T. & Zafeiris, A. (2012). Collective motion. *Physics Reports* 517: 71-140.

West, B., Massari, G.F., Culbreth, G., Failla, R., Bologna, M., Dunbar, R.I.M. & Grigolini, P. (2020). Relating size and functionality in human social networks through complexity. *Proceedings of the National Academy of Sciences, USA*, 117: 18355-18358.

West, B., Dunbar, R.I.M., Culbreth, G. & Grigolini, P. (2023). Fractal structure of human and primate social networks optimizes information flow. *BioRxiv* doi.org/10.1101/2023.02.23.529431

Williams, N.I., Caston-Balderrama, A.L., Helmreich, D.L., Parfitt, D.B., Nosbisch, C. & Cameron, J.L. (2001). Longitudinal changes in reproductive hormones and menstrual cyclicity in cynomolgus monkeys during strenuous exercise training: abrupt transition to exercise-induced amenorrhea. *Endocrinology* 142: 2381-2389.

Wilson, M. & Mesnick, S. L. (1997). An empirical test of the bodyguard hypothesis. In: P.A. Gowaty (editor) *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers*, pp. 505-511. London: Chapman & Hall.

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

Wittig, R. M., Crockford, C., Langergraber, K. E., & Zuberbühler, K. (2014). Triadic social interactions operate across time: a field experiment with wild chimpanzees. *Proceedings of the Royal Society, London*, 281B: 20133155.

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T. & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications* 7: 1-8.

Yang, Y.C., Boen, C., Gerken, K., Li, T., Schorpp, K. & Harris, K.M. (2016). Social relationships and physiological determinants of longevity across the human life span. *Proceedings of the National Academy of Sciences USA* 113: 578-583.

Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., ... & Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology* 106: 1125-1165.

Yetish, G., Kaplan, H., Gurven, M., Wood, B., Pontzer, H., Manger, P. R., ... & Siegel, J. M. (2015). Natural sleep and its seasonal variations in three pre-industrial societies. *Current Biology* 25: 2862-2868.

Young, A.J., Carlson, A.A., Monfort, S.L., Russell, A.F., Bennett, N.C. & Clutton-Brock, T.H. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences, USA*, 103: 12005-12010.

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

Ziegler, T.E., Widowski, T.M., Larson, M.L. & Snowdon, C.T. (1990). Nursing does affect the duration of the post-partum to ovulation interval in cottontop tamarins (*Saguinus oedipus*). *Journal of Reproduction and Fertility* 90: 563-570.

Zhou, W-X., Sornette, D., Hill, R.A. & Dunbar, R.I.M. (2005). Discrete hierarchical organization of social group sizes. *Proceedings of the Royal Society, London*, 272B: 439-444.



## Legends to Figures

- Fig. 1. Fissioning index for 24 baboon (*Papio*) populations plotted against study group size. Unfilled symbols: group size <35; gray symbols: groups 35-75; filled symbols: groups >75. Fission index: 0 = compact groups that always travel together; 1 = groups become dispersed during foraging but always sleep together; 2 = groups fragment during foraging and sometimes sleep apart. Source of data: Dunbar & Shultz (2023a)
- Fig. 2. The infertility trap results in declining fertility in mammals as a direct result of stress created by low level conflict between reproductive females. In basal mammals, birth rate per adult female per year (adjusted for litter size) declines linearly with the number of females in the group, thereby placing a severe limit on group size. In order to live in larger groups, primates (and some other more social mammals) use coalitions to buffer themselves against this effect, but are unable to prevent the infertility trap eventually imposing a limit on group size. Thin solid line: mean slope for 5 weakly social mammals (European badger, feral goats, babirousa, marmots and a Neotropical ctenomyid rodent); heavy dotted line: callitrichids; heavy dashed and solid lines: representative genera for four distinct grades of primates illustrating increasingly  $\cap$ -shaped fertility curves created by when females use coalitions to defuse the stresses of group-living. Horizontal line demarcates replacement rate (defined as the production of two surviving offspring at the end of a lifetime); any population that falls below this line will go extinct. For details and data: Dunbar & Shultz (2021a)
- Fig. 3. Grooming relationships build defensive coalitions. Mean ( $\pm$ se) probability that an individual gelada female will come to the support of another female from her harem if the latter is threatened by members of a neighbouring harem, as a function of whether the pair devote more or less than 5% of their available social time to grooming each other. Redrawn from Dunbar (2018b).
- Fig. 4. A schematic representation of the layered structure of primate and human egocentric social networks, as seen from the perspective of an individual ego (central black square). Unfilled squares: individuals that form strong links to Ego (direct grooming connections); unfilled triangles: individuals that form weak links to Ego (indirect grooming connections, or 'friends-of-friends'). Width of lines connecting triangles indicate strength of relationship; dashed ties indicate indirect connections. The layers of the network are indicated by the shaded circles. Inset: bond strength indicating gravitational drag on dyads willingness to disperse as a function of network layer (i.e. relationship strength).
- Fig. 5. Schematic representation of the impact of increasing group size on network integrity (and hence group-level social cohesion) when individuals are limited in the number of others they can groom with (their degree). When animals can only groom with 2-3 other individuals, small groups of 4-5 individuals are well integrated (most individuals can groom with each other, or with two friends of a third party); but as group size increases, network chains become elongated and less integrated, until finally in large groups individuals are forced to choose which subgroup to focus on (creating natural fracture lines between subgroups that are only weakly linked).
- Fig. 6. Mean n-clique size plotted against mean degree for individual genera, differentiating genera with mean group size <25 (unfilled symbols, dashed regression) versus >25 (filled symbols, solid

regression). Numbers beside symbols indicate genus: 1, *Lemur*; 2, *Eulemur*; 3, *Callicebus*; 4, *Cebus*; 5, *Sapajus*; 6, *Saimiri*; 7, *Alouatta*; 8, *Ateles*; 9, *Trachypithecus*; 10, *Semnopithecus*; 11, *Colobus*; 12, *Ptilinopus*; 13, *Nasalis*; 14, *Cercopithecus*; 15, *Chlorocebus*; 16, *Erythrocebus*; 17, *Macaca*; 18, *Theropithecus*; 19, *Papio*; 20, *Pan*. Data are given in *SI Dataset-1*.

Fig. 7. (a) Mean number of adult females per group and (b) mean group size for individual genera plotted against mean n-clique size, differentiating genera with mean group size <25 (unfilled symbols, dashed regression) versus >25 (filled symbols, solid regression). The social unit for *Theropithecus* is identified with the harem reproductive unit. Numbers beside symbols indicate genus, as defined in Fig. 6. Data are given in *SI Dataset-1*.

Fig. 8. Mean time devoted to grooming for individual genera plotted against mean group size, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). Gelada (grey symbols) are shown for two different definitions of group size: 17, harem size; 21, clan size (typically 3-4 harems). The regression line is the exponential fit to the data excluding gelada. The upturn on the righthand side is due mainly to callitrichids and might reflect the fact that they are pair-living. Numbers beside symbols indicate genus, as defined in Fig. 6. Data are given in *SI Dataset-2*.

Fig. 9. Mean ( $\pm 1se$ ) standard deviates for grooming variables, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). The social unit for *Theropithecus* is identified with the harem reproductive unit. Total groom is the mean percent of the day devoted for grooming by all sampled populations of the genus (from Dunbar 2022). Groom/group, groom/female and groom per degree defined as the mean total grooming time for species divided by mean group size (from Dunbar et al. 2018a), by mean number of adult females (from Dunbar et al. 2018a) and by mean network degree (this study), respectively. Grooming data from Lehmann et al. (2007b).

Fig. 10. Mean time spent in social grooming (percent of 12-hour day) for individual genera as a function of the percentage of the diet composed of leafage for upper grade (filled symbols) and lower grade (unfilled symbols) taxa. Numbers beside symbols indicate genus, as defined in Fig. 6. Data are given in *SI Dataset-2*.

Fig. 11. Mean ( $\pm 1se$ ) standard deviates for four cognition variables, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). A score of 0 indicates the mean value. Neocortex ratio data are from Dunbar & Shultz (2021b); executive cognition is the arcsin transform of the proportion of correct trials on 8 standard executive function tasks, not including inhibition tasks (from Shultz & Dunbar 2010b); self-control is performance on an A-not-B task (from Shultz & Dunbar 2010b); the mentalising data (excluding one orangutan datapoint for an individual deemed to have Down syndrome) are from Devaine et al. (2017). All data except those for mentalising are for the sampled genera only; since there only three of the sampled genera have mentalising index scores, all the genera sampled by Devaine et al. are included.

Fig. 12. Summed cognition index (sum of standard deviate score on three cognition indices, excluding mentalising) plotted against mean group size for individual genera. Dashed line is the linear regression through the data. The stepped thick line indicates what appears to be successive phase shifts in the data (see text).

Table 1. Summary of predictions and results.

Prediction	Trait correlates within*:			
	small groups	large groups	Small<large <sup>§</sup>	
<b>Structural solution</b>				
1a	degree $\propto$ <i>n</i> -clique	+	0	<
1b	<i>n</i> -chains $\propto$ group size	0	0	=
1c	<i>n</i> -chain includes all adult females	+	-	>
1d	fragmentation risk limits group size	-	+	<
<b>Behavioural solution</b>				
2a	groom time $\propto$ group size	0	+	<
2b	degree $\propto$ group size	0	0	<
2c	groom/degree $\propto$ group size	0	+	<
2d	groom time $\propto$ with %leaf	0	-	<
<b>Cognitive solution</b>				
3a	neocortex size $\propto$ group size	+	+	<
3b	executive cognition $\propto$ group size	+	+	<
3c	self-control $\propto$ group size	0	+	<
3d	mentalising $\propto$ group size <sup>§</sup>	0	0	<

\* 0 = no relationship; +/- = significant positive/negative correlation. A pattern displayed as "0 ... +" in the two columns implies an exponential relationship: the dependent variables is initially unrelated to group size, but increases exponentially after a threshold group size.

§ Larger groups score significantly higher (>) or lower (<) on trait than small groups, or do not differ (=)

Figure 1

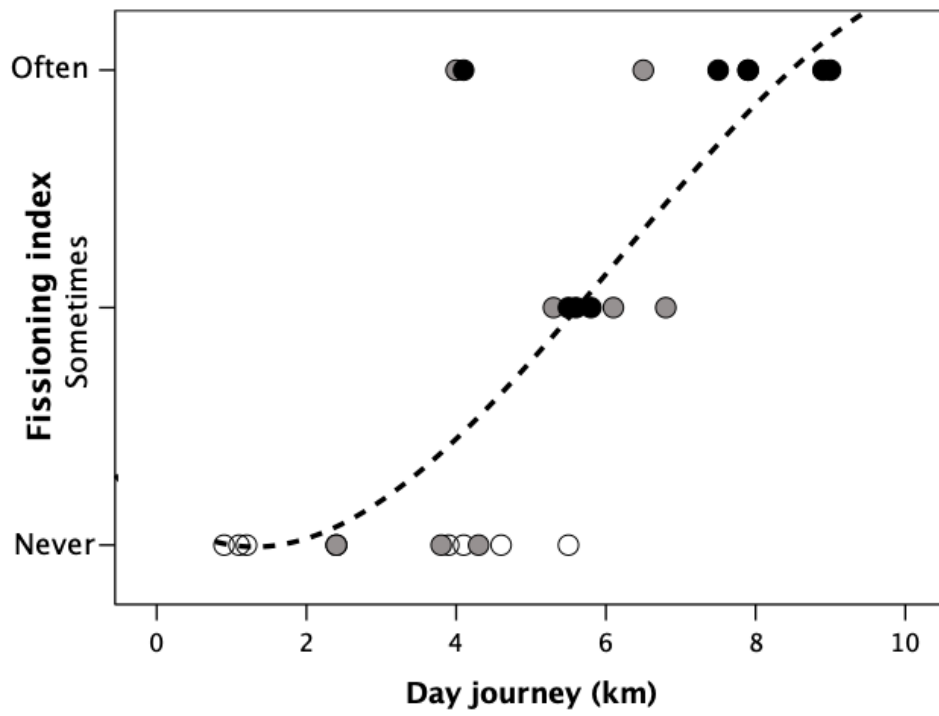


Figure 2

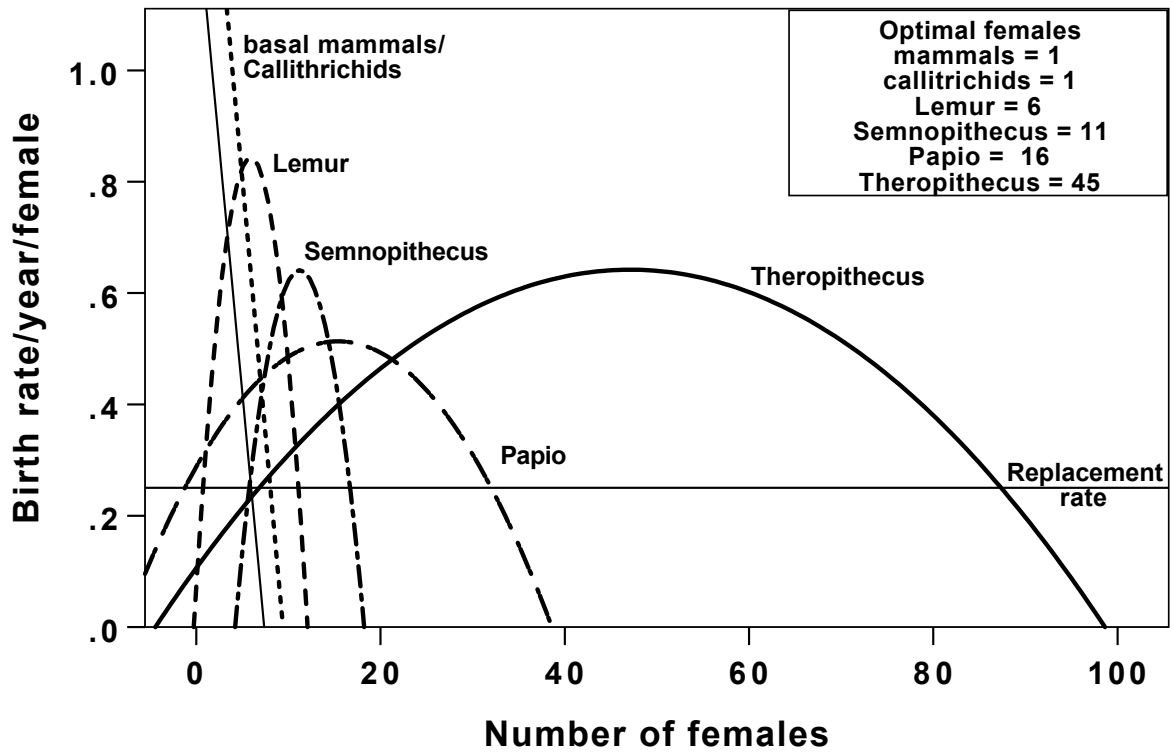


Figure 3

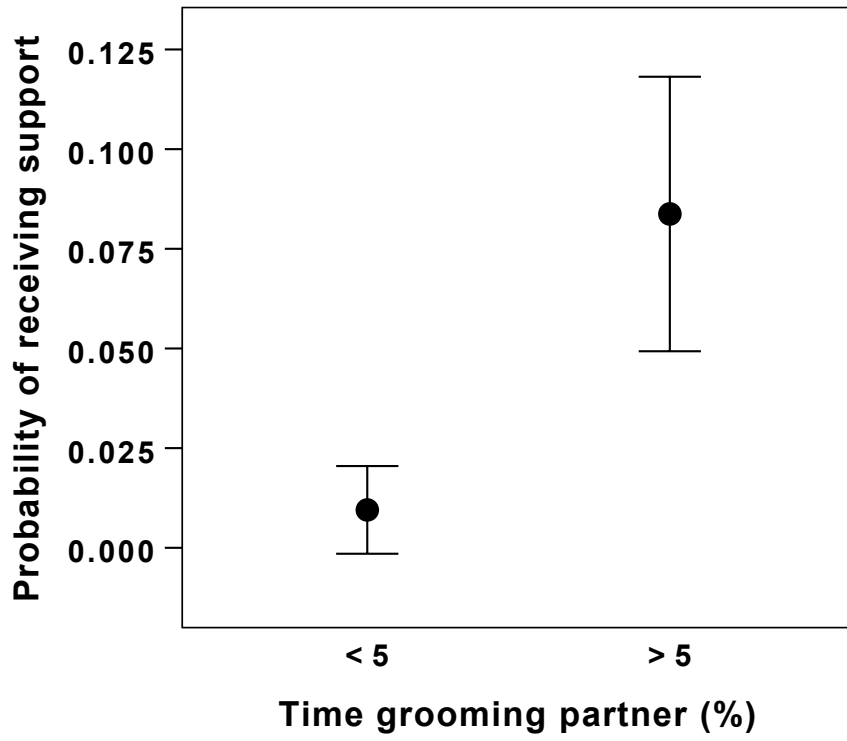


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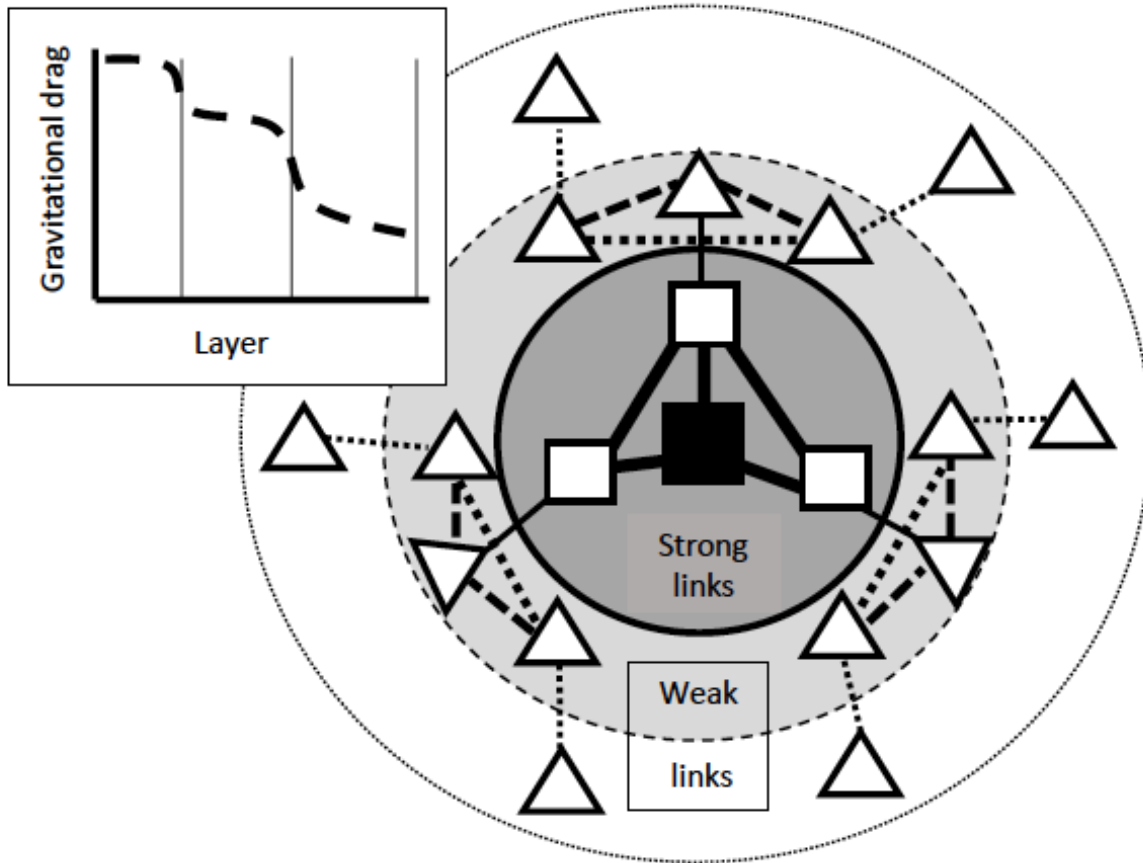
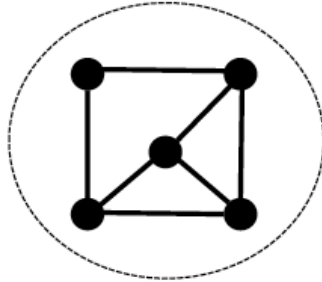
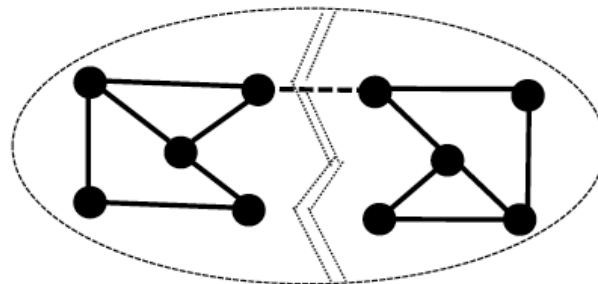
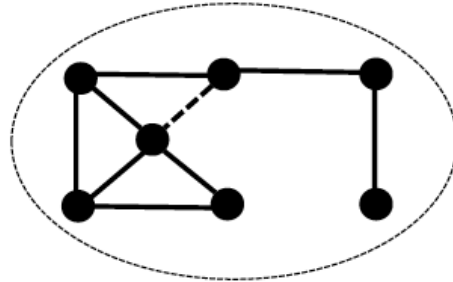


FIGURE 5

Small group



Medium group



Large group



Figure 6

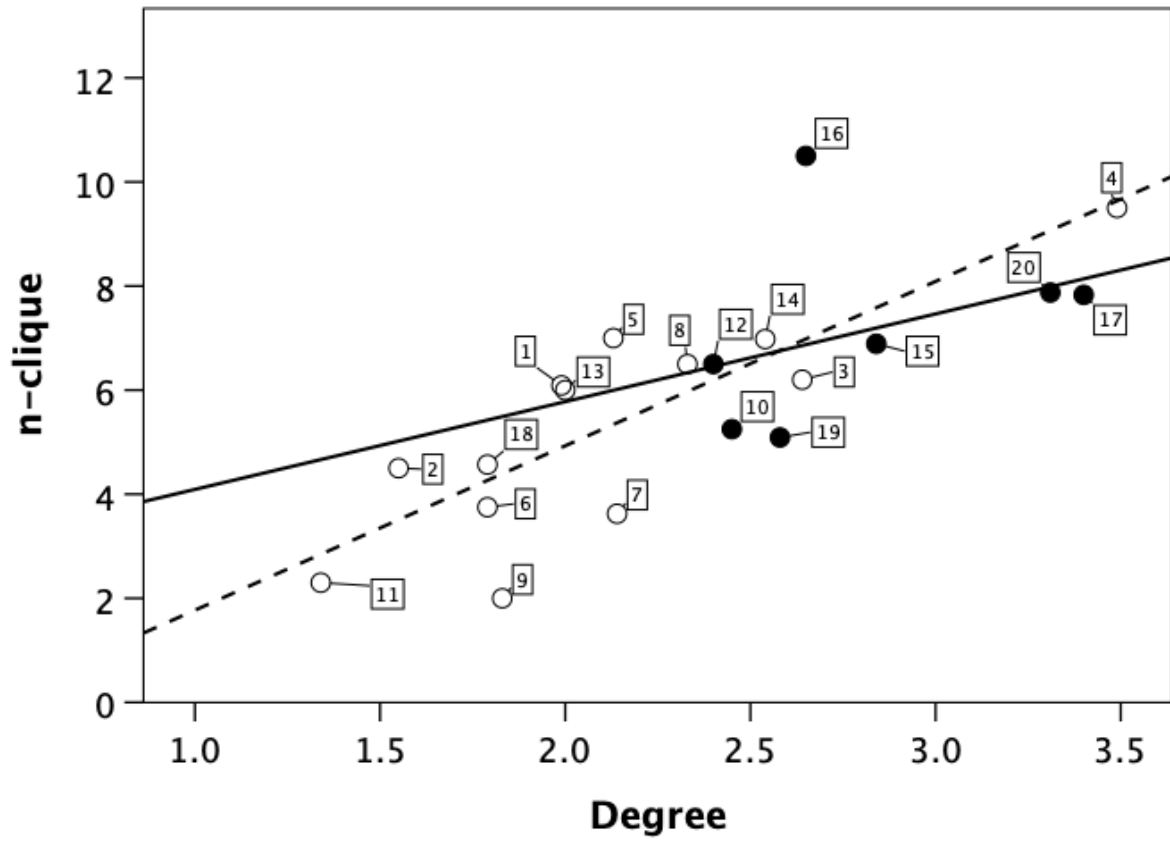
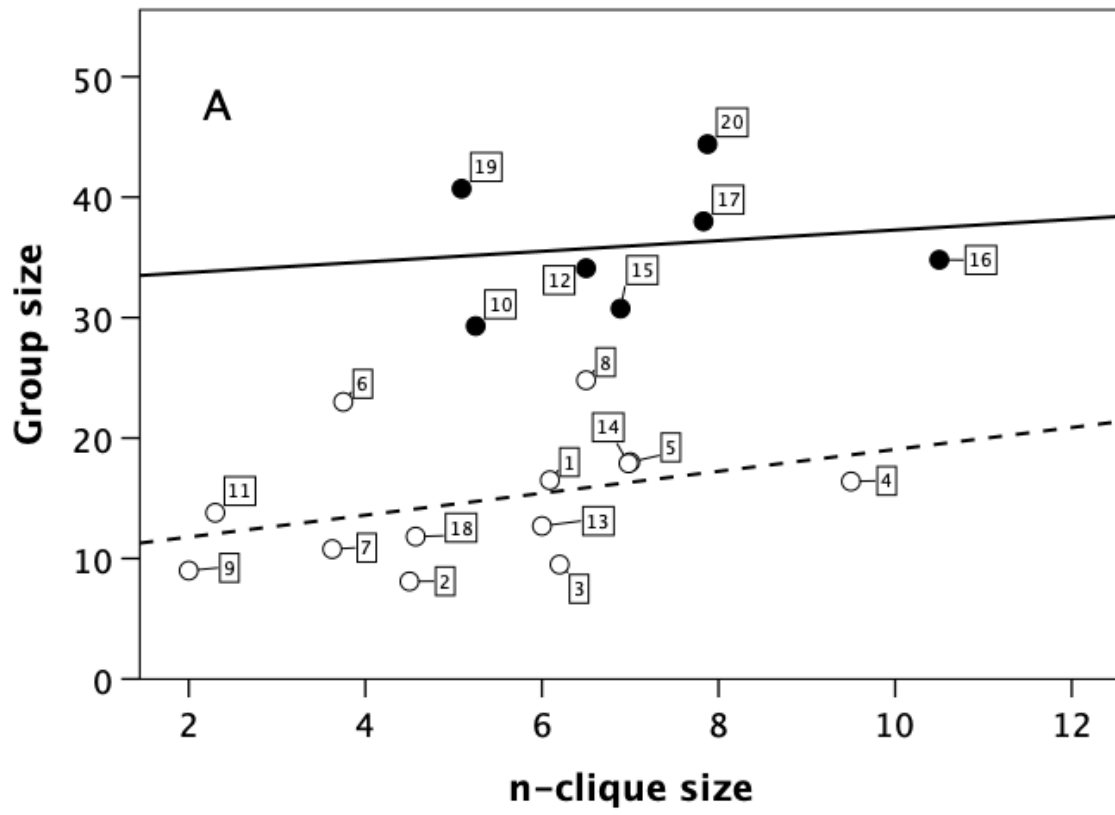


Figure 7



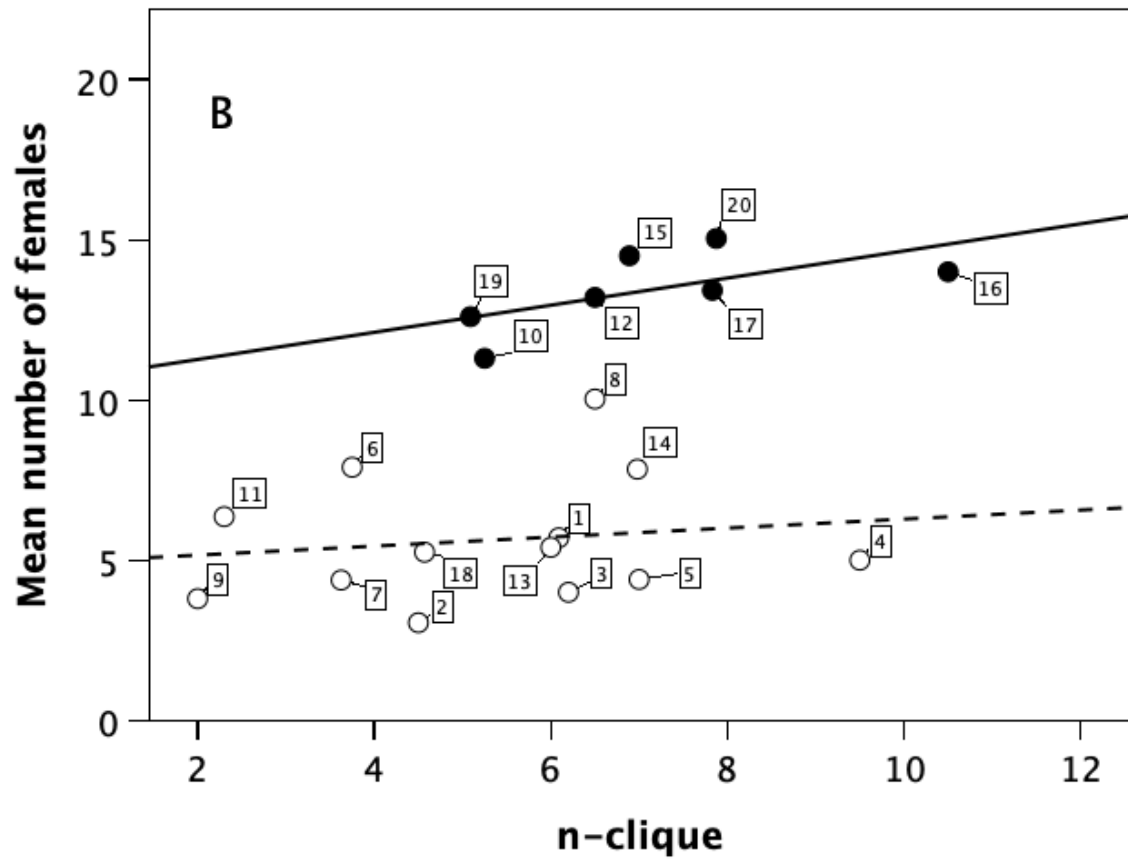


Figure 8

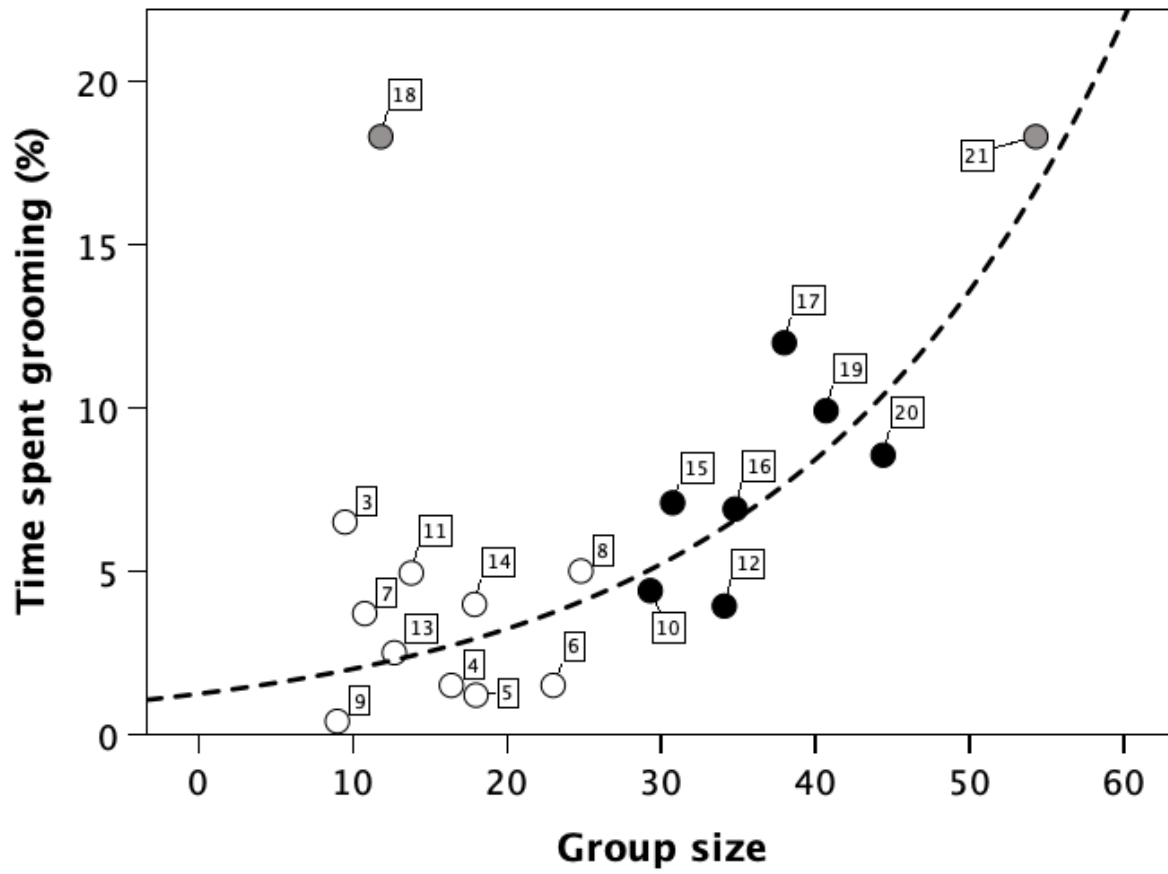


Figure 9

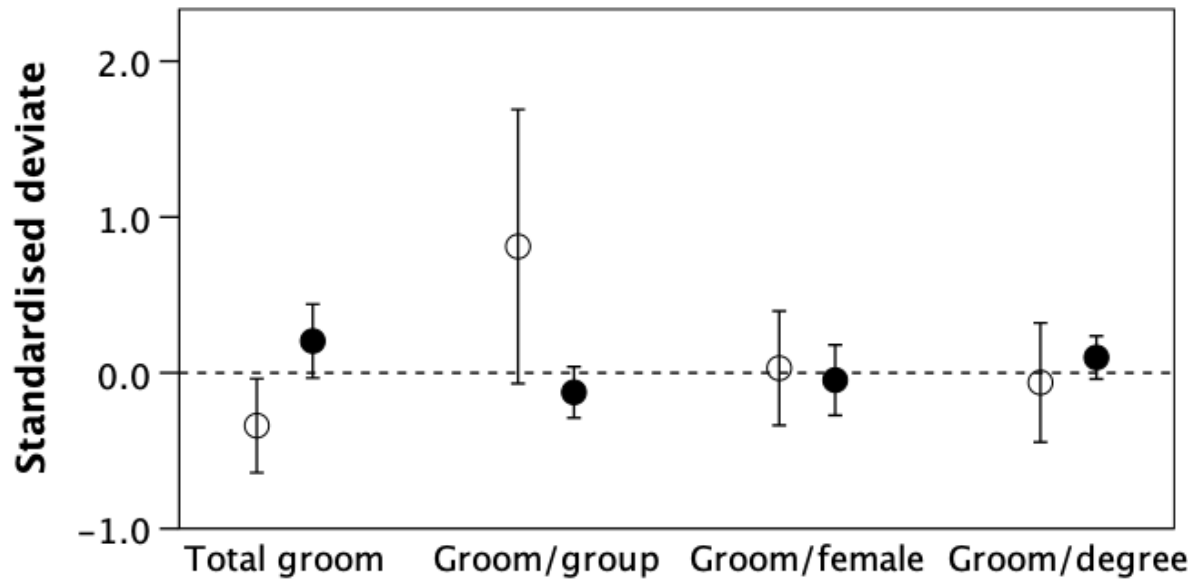


Figure 10

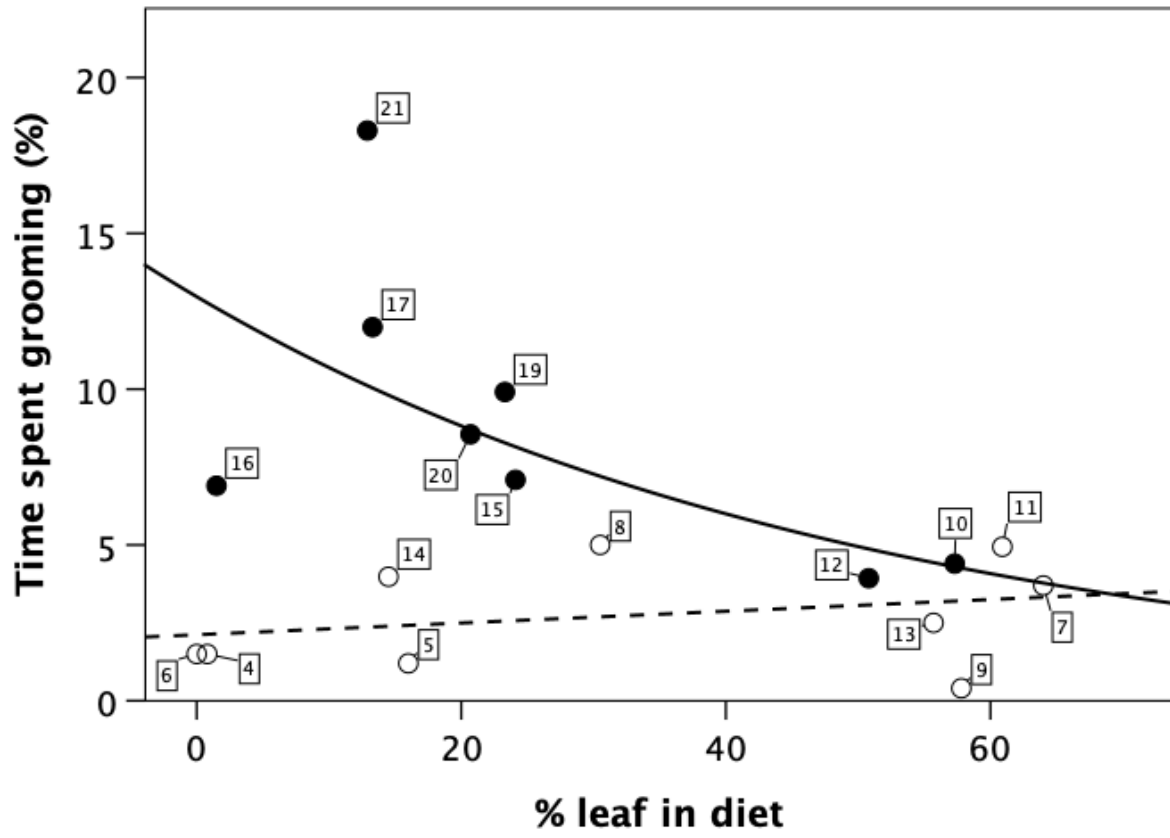


Figure 11

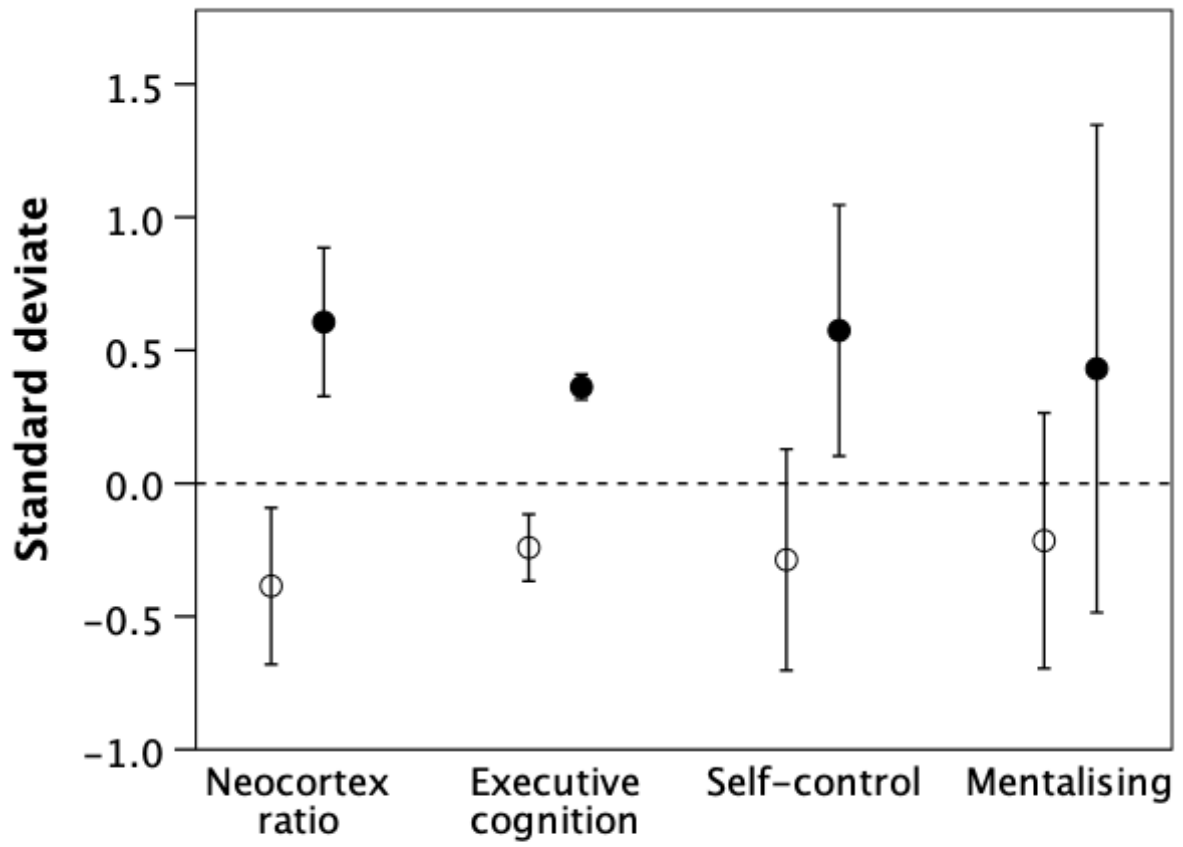


Figure 12

