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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 straightforward 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 restrict 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 around networks.

1. Introduction

Group-living is one of the six major evolutionary transitions (Maynard Smith & Szathmáry 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 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 that 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

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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; 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 & Cowlishaw 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 upregulation 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

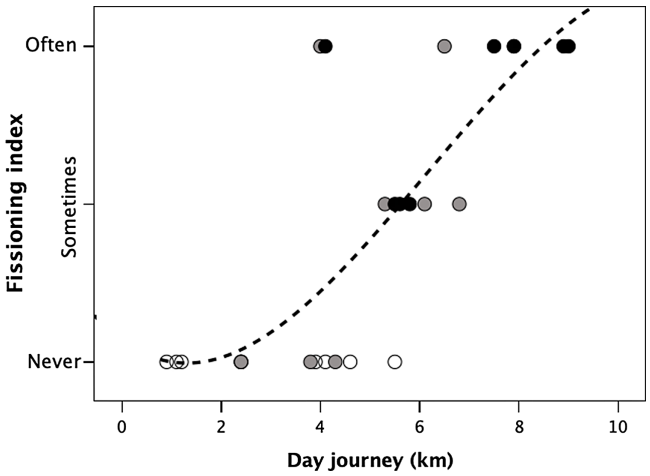


Figure 1. Fissioning index for 24 baboon (*Papio*) populations plotted against study group size. Unfilled symbols: group size <35; grey symbols: groups 35-75; filled symbols: groups >75. Fission index: 0 = never (compact groups that always travel together); 1 = sometimes (groups become dispersed during foraging but always sleep together); 2 = often (groups fragment during foraging and sometimes sleep apart). Source of data: Dunbar & Shultz (2023).

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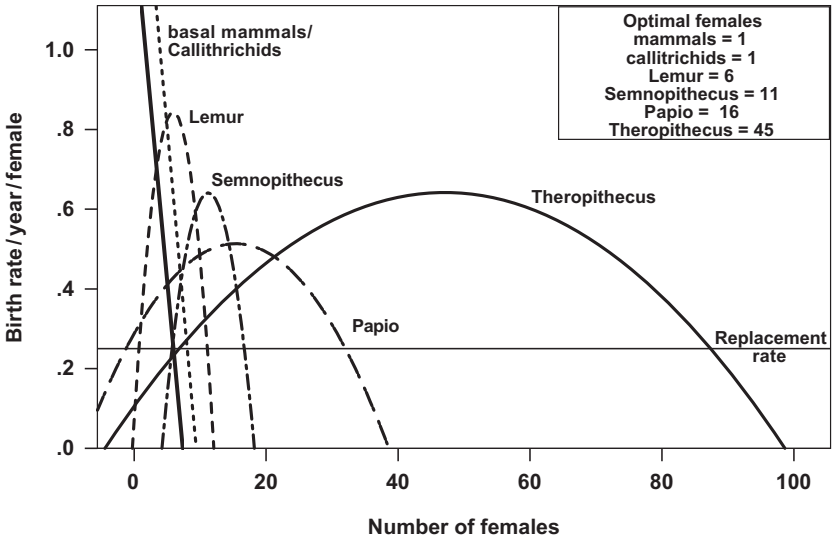


Figure 2. The infertility trap results in declining fertility in mammals as a direct result of stress created by low-level conflict between reproductive females. In basal mammals, birth rate per adult female per year (adjusted for litter size) declines linearly with the number of females in the group, 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 ∩-shaped fertility curves created by females using 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).

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, 2001a; Son et al. 2012; Iwasa et al. 2017). This has been confirmed experimentally using naloxone (an endorphin antagonist that counteracts the uptake 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 ∩-shaped function of group size (Dunbar & Shultz 2021a). These ∩-shaped distributions turn out to be trade-off 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 ∩-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 ∩-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

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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 unless the group is at least 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 right-hand side of the ∩-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 2011; 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 (SBH) (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,

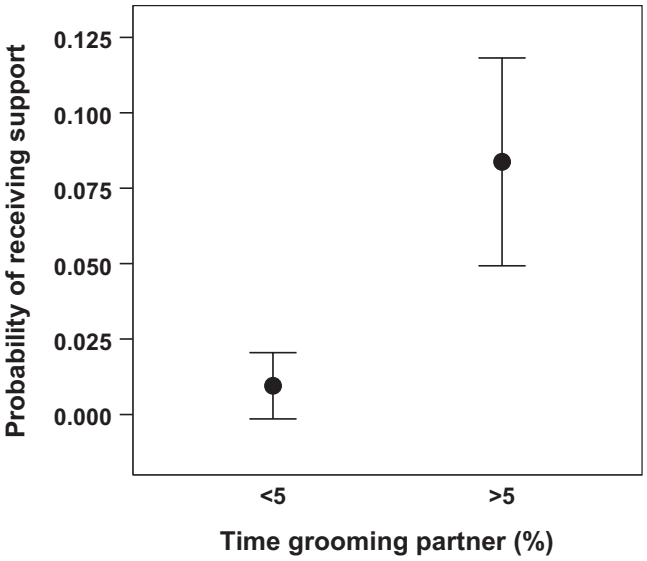


Figure 3. Grooming relationships build defensive coalitions. Mean (±se) probability that an individual gelada female will come to the support of another female from her harem if the latter is threatened by members of a neighbouring harem, as a function of whether the pair devote more or less than 5% of their available social time to grooming each other. Redawn from Dunbar (2018b).

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, they have 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).

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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 (Brodman Areas BA10), a brain region found *only* in anthropoid primates (Passingham & Wise 2012). These form the underlying basis for the 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, 2012). 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 of fracture lines 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

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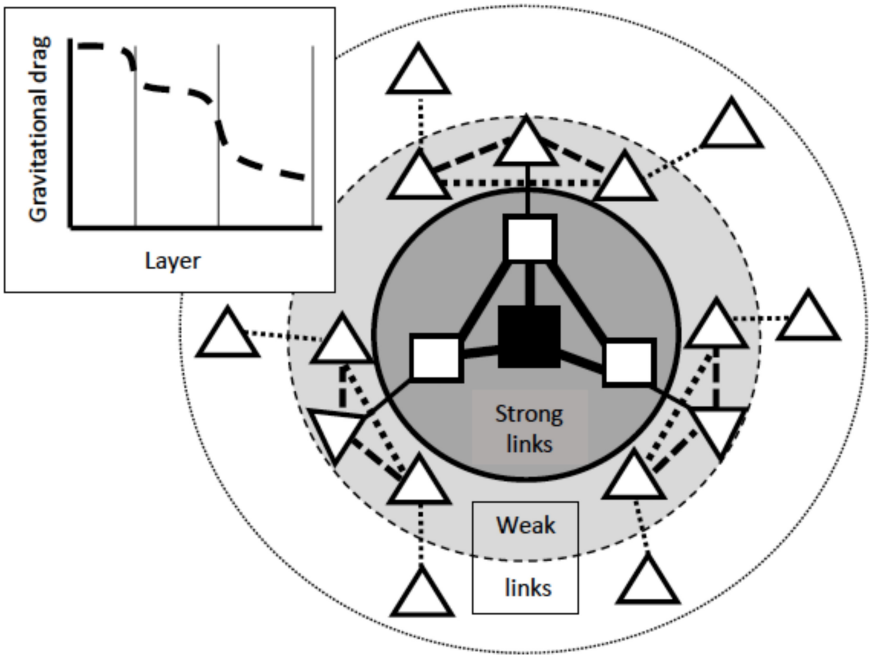


Figure 4. A schematic representation of the layered structure of primate and human egocentric social networks, as seen from the perspective of an individual ego (central black square). Unfilled squares: individuals that form strong links to Ego (direct grooming connections); unfilled triangles: individuals that form weak links to Ego (indirect grooming connections, or "friends-of-friends"). Width of lines connecting triangles indicates 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).

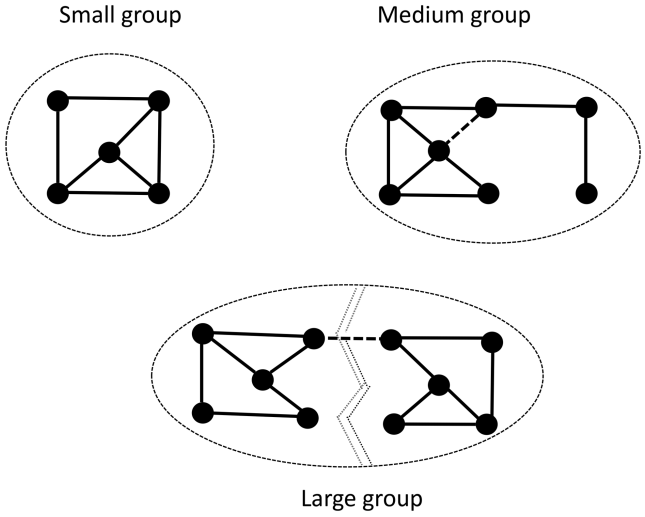


Figure 5. Schematic representation of the impact of increasing group size on network integrity (and hence group-level social cohesion) when individuals are limited in the number of others they can groom with (their degree). When animals can only groom with 2-3 other individuals, small groups of 4-5 individuals 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).

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 the 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 overheating, 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.

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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 up to additional grooming rather than, say, resting (Altmann & Muruthi 1988; Bourgeaud et al. 2021). In one experimental manipulation, for example, free-living animals in a food-rich environment fed for 5-15% less time than 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 (*Piliocolobus*) 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 a relationship, the stronger it will be. However, 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 monoamine oxidase-A gene (the so-called "warrior gene" linked with antisocial behaviour) and positively associated with the volume of specific brain regions (Moffitt et al. 2001; Carlisi et al. 2020). A number of long-term human studies have shown that the capacity for self-control during early childhood is a very strong predictor of adult social competencies, relationship stability, and antisocial behaviour (Tremblay et al. 1994; Moffitt et al. 2001; Bari & Robbins 2013; 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

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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 & 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, 2012), 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 from the conventional analysis for the SBH, 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 2023).

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. 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 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 fission 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 belong 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

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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, 1985), *Pan* (Rawlings et al. 2023), and *Gorilla* (Harcourt & Stewart 2007).

Group size is uncontroversial for most primate species, but open to misinterpretation in those species that have fission-fusion social systems (Dunbar & Shultz 2021b, 2023). 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 temporal discounting 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 2023). 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 2025).

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 the same analysis has been run 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 ordinary least squares regression analyses to radically underestimate the slope (Dunbar & Shultz 2021b, 2023).

Data for both individual groups 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 used 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±5.24 SD (with 5.6±1.96 adult females, N=13 genera; species-level mean = 13.9 ±5.3 with 7.6 females) for the lower grade and 36.0±5.39 (with 13.4±1.25 females, N=7 genera; species mean = 36.7±11.4 with 14.3 females) for the upper grade, with a natural breakpoint between the two grades at a group size of ~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. 2000; Dunbar 2020; Dunbar & Shultz 2021b; Escribano 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*, *Piliocolobus*, *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 subsection, 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

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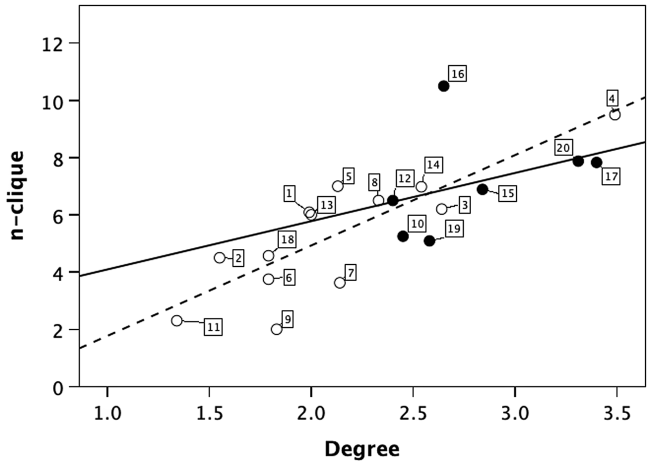


Figure 6. Mean n-clique size plotted against mean degree for individual genera, differentiating genera with mean group size <25 (unfilled symbols, dashed regression) versus >25 (filled symbols, solid regression). Numbers beside symbols indicate genus: 1, *Lemur*; 2, *Eulemur*; 3, *Callithrix*; 4, *Cebus*; 5, *Sapajus*; 6, *Saimiri*; 7, *Alouatta*; 8, *Ateles*; 9, *Trachypithecus*; 10, *Semnopithecus*; 11, *Colobus*; 12, *Piliocolobus*; 13, *Nasalis*; 14, *Cercopithecus*; 15, *Chlorocebus*; 16, *Erythrocebus*; 17, *Macaca*; 18, *Theropithecus*; 19, *Papio*; 20, *Pan*. Data are given in SI Dataset-1.

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 (β=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 (β=0.558, r^2=0.311, p=0.151) than in those with small social groups (β=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 ~9.7 at a degree size of ~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±2.0 versus 13.4±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±2.1 versus 7.1±1.9; t_{18}=1.93, p=0.070), although they do differ significantly in degree (means of 2.12±0.72 versus 2.80±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±0.72: t[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[ratio=1.0] = 4.92, df=8, p=0.001), and approximates 2 (mean 1.96±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 predictions: 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

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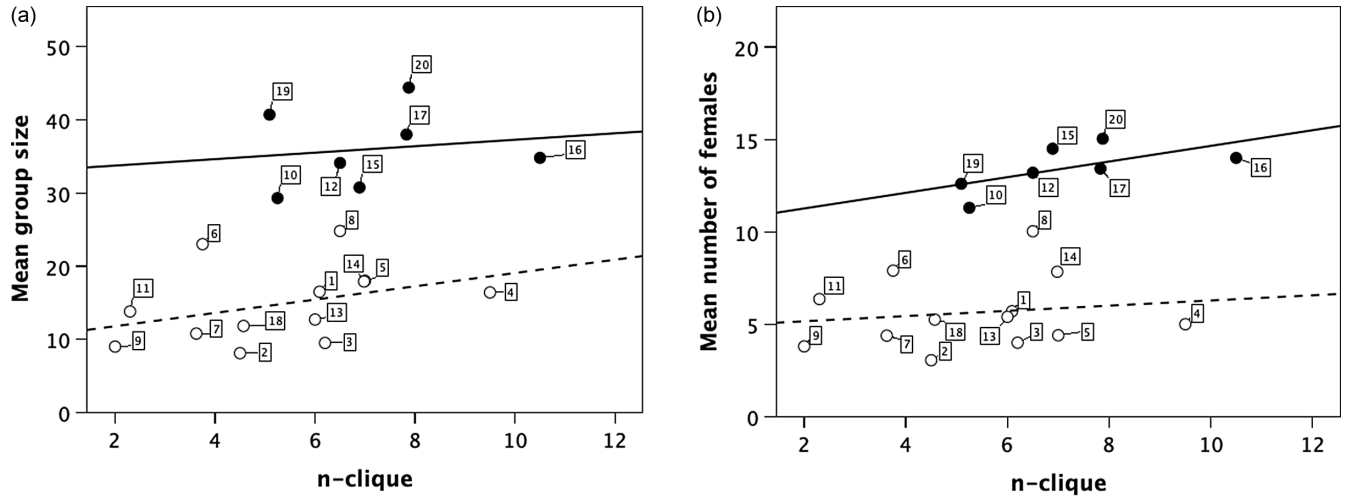


Figure 7. (a) Mean number of adult females per group and (b) mean group size for individual genera plotted against mean n-clique size, differentiating genera with mean group size <25 (unfilled symbols, dashed regression) versus >25 (filled symbols, solid regression). The social unit for Theropithecus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

Table 1. Summary of predictions and results

Prediction		Trait correlates within*: Small groups	Trait correlates within*: Large groups	Small<large§
Structural solution				
1a	Degree ∝ *n*-clique	+	0	<
1b	n-chains ∝ group size	0	0	=
1c	n-chain includes all adult females	+	-	>
1d	Fragmentation risk limits group size	–	+	<
Behavioural solution				
2a	Groom time ∝ group size	0	+	<
2b	Degree ∝ group size	0	0	<
2c	Groom/degree ∝ group size	0	+	<
2d	Groom time ∝ with %leaf	0	-	<
Cognitive solution				
3a	Neocortex size ∝ group size	+	+	<
3b	Executive cognition ∝ group size	+	+	<
3c	Self-control ∝ group size	0	+	<
3d	Mentalising ∝ group size§	0	0	<

*0 = no relationship; +/- = significant positive/negative correlation. A pattern displayed as "0 . . . +" in the two columns implies an exponential relationship: the dependent variable is initially unrelated to group size, but increases exponentially after a threshold group size (e.g. 2a, 2b, 3c).
§Larger groups score significantly higher (>) or lower (<) on trait than small groups, or do not differ (=)

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

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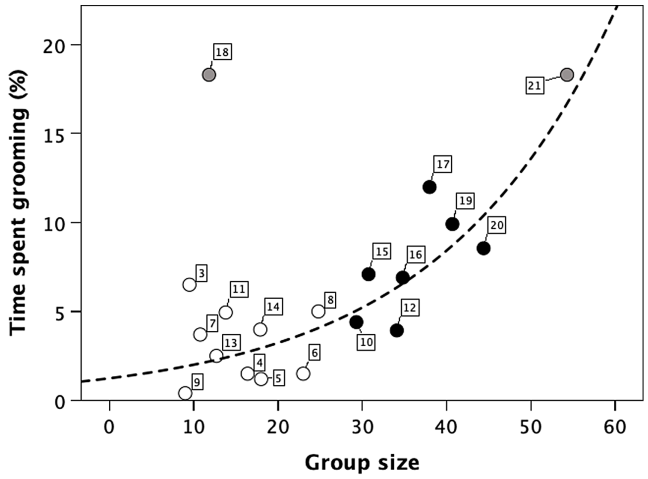


Figure 8. Mean time devoted to grooming for individual genera plotted against mean group size, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). *Theropithecus* (grey symbols) is shown for two different definitions of group size: 18, harem size; 21, clan size (typically 3-4 harems). The regression line is the exponential fit to the data excluding gelada. The upturn on the left-hand 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.

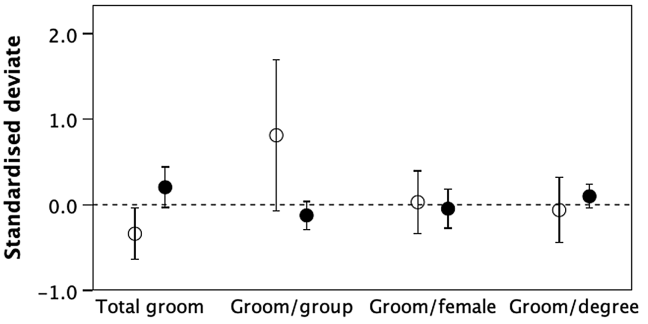


Figure 9. Mean (±1se) standard deviations for grooming variables, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). The social unit for *Theropithecus* is identified with the harem reproductive unit. Total groom is the mean percent of the day devoted for 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).

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

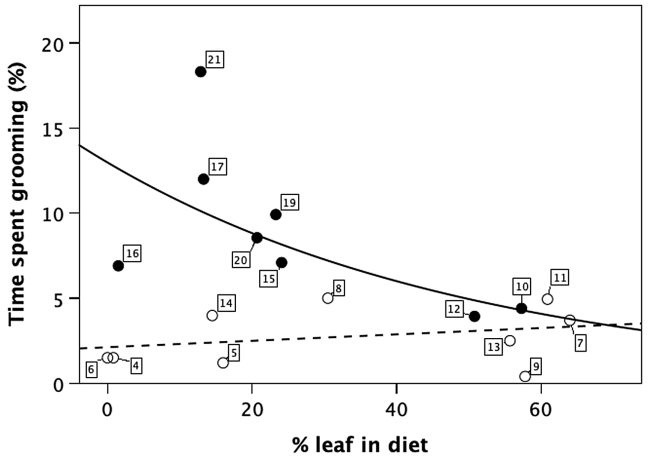


Figure 10. Mean time spent in social grooming (percent of 12-hour day) for individual genera as a function of the percentage of the diet composed of leafage for upper grade (filled symbols) and lower grade (unfilled symbols) taxa. Numbers beside symbols indicate genus, as defined in Fig. 6. Data are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

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 up 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, Grabowskia 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 up 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

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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 showing 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, 2010a).

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 χ^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, ΔBIC_{2vs3}=−39.1 vs -46.1 = 7.0; inhibition: $F_{2,6}$=49.3, p=0.0002, ΔBIC_{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 Bayesian Information Criterion value comparing a partition into 2 versus 3 grades being the more significant, where ΔBIC=2 indicative of a significant difference at p≈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.

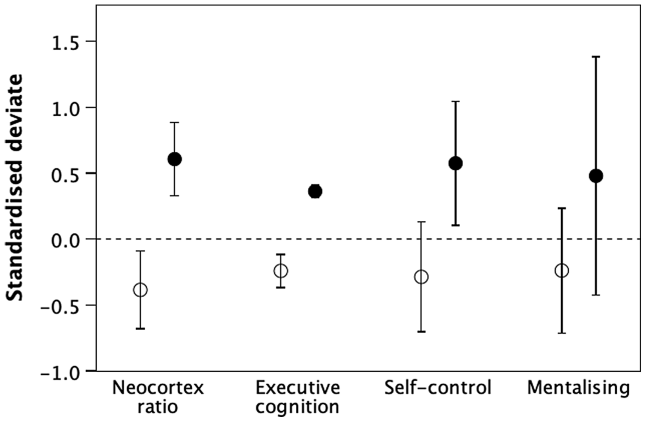


Figure 11. Mean (±1se) standard deviations for four cognition variables, differentiating genera with mean group size <25 (unfilled symbols) versus >25 (filled symbols). A score of 0 indicates the overall mean value for the sampled genera. Neocortex ratio data are from Dunbar & Shultz (2021b); executive 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 and assigned to the relevant grade.

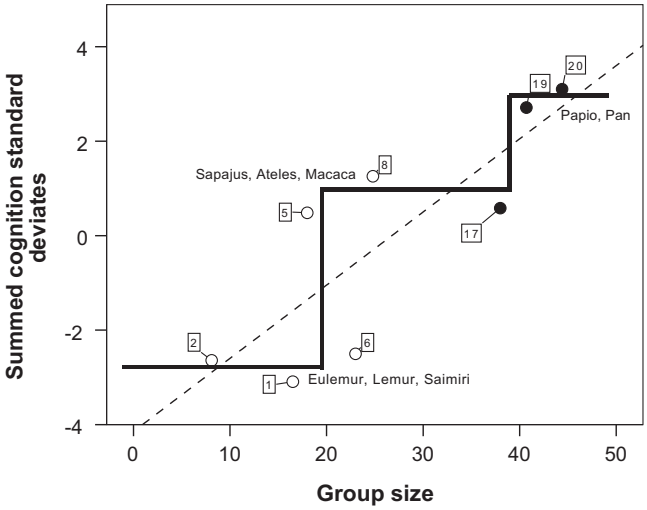


Figure 12. Summed cognition index (sum of standard deviation score on three cognition indices, excluding mentalising) plotted against mean group size for individual genera. Dashed line is the linear regression through the data. The stepped thick line indicates what appears to be successive phase shifts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

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 (λ=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

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et al., this also yields a single factor with equally high loadings: λ=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 deviations 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 at 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 ~6 and ~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 upper limits on group size of ~18 and ~37 (Fig. 7a), close to the previously identified mean values for group size at ~16 and ~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 right-hand 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 and 25) rely on structural solutions to hold the group together. Once group size exceeds ~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 ~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,

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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 has 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 trade-off 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

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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 arbitrarily 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). 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 up time for additional grooming and to fuel the evolution of a larger brain. This reinforces the evidence from all previous analyses of the SBH (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 2023) that a change in diet and foraging strategy was a necessary prerequisite (not the selection factor) for fuelling 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 psycho-physiological 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).

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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), just as it does in primates.

In addition, many birds that live in stable groups outside the breeding season engage in conspicuous forms of vocal chorusing or "flock-talk" (examples include babblers, Guinea fowl, and starlings). This form of "undirected" vocalisation has recently been shown to upregulate the endorphin system 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 sounds have been shown to trigger an endorphin response through a class of afferent C-tactile spiral ganglion neuron receptors attached to the cochlea (Dunbar et al. 2021b).

How far the abilities of any 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 2025). 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 have 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. 2020), 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, 2012; MacLean et al., 2014; Dunbar & Shultz 2025) and mentalising (Devaine et al. 2017; Dunbar & Shultz 2023) 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 competencies 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 et al. 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. 2016; Dunbar 2022b), singing (Pearce et al. 2015, 2016, 2017b), dancing (Tarr et al. 2015, 2016, 2017), feasting (Dunbar, 2017; 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), story-telling 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

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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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Open Peer Commentary

What human trust networks reveal about cognitive mechanisms of group cohesion in primates

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Abstract

Drawing on our previous work on human trust networks, we provide further evidence of how group structure can foster group cohesion. But this work also raises doubts about two central tenets of the target paper: (1) the role assigned to cognitive abilities in group cohesion and stabilization; and (2) the emphasis on group size as the critical variable.

In previous work carried out in multi-ethnic regions of Northern Ghana and Mexican Yucatan (Acedo-Carmona & Gomila, 2019, 2015a, 2015b, 2014), we have provided evidence of how the structure of trust networks determines levels of cooperation and cohesion. Our central result was that several social structures can be found, but that levels of cooperation with nonpersonally-trusted partners – a measure of social cohesion – are higher when the structure of the social network is scale-free, so that some individuals who are trusted by a clique, trust themselves. This result converges with Dunbar's "friends-of-a-friend" effect. However, against Dunbar's argument, this structure is based on basic cognitive and emotional capacities that make possible the structure in the first place, calling into question Dunbar's differentiation of mechanisms of group cohesion in terms of structural, behavioral, and cognitive strategies. And second, our work suggests that structure does not determine a maximal group size, also against one of Dunbar's central contentions. We discuss these two points in turn. As a conclusion, we suggest that primate cognition cannot be explained as an evolutionary solution to a social coordination problem.

The role that cognitive abilities play in group cohesion and stabilization

Dunbar's argument is that mammals that live in stable social groups use two strategies to keep and reproduce the group, besides group structure itself: grooming, as a form of affiliative interaction, and a suite of higher-order cognitive skills. This dichotomy overlooks the role of "mid-level" mechanisms that combine emotional and cognitive components, such as trust itself or empathy (Pérez-

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Manrique & Gomila, 2022, 2018), among other forms of social bonding and affiliation.

Importantly, and in contrast with cognitive abilities, these emotional dispositions involve a motivational component that is evolutionarily more effective to keep cooperative commitments and avoiding free-riding than cognition itself (Jablonski, 2021; Frank, 1993). In other words, it is wrong to assume that higher cognition is the only way to make cooperation and social coordination possible in bigger groups. As a matter of fact, the paper is full of examples of species that achieve group stability and cohesion without going cognitive. Therefore, the contention that the evolution of cognition in primates is driven by social pressures is not warranted.

For instance, as suggested by the paper itself, instances of group synchronization and entrainment, based on the "do as your neighbor" rule, may turn out to be a very effective solution to group coordination, a solution that does not require higher cognitive abilities. It is found in different species (Bates & Byrne, 2010), including primates, whose capacity for observation and learning by imitation is well-established (Whiten, 2000; Whiten & van de Waal, 2017), and that imitation induces affiliation (Dignath et al., 2021; Dignath et al., 2018).

Another example can be observed in species such as termites, bees, and ants, which secrete chemicals that serve to drive their coordinated actions and cohesion when required by the environment, without needing for cognitive complexity (Barbero, Mannino, & Casacci, 2023; Mizumoto et al., 2021; Pernal, 2021). In primates, this chemical mechanism, present with the secretion of endorphins, is related to the cognitive mechanism because it is linked to social contact (Dunbar, 2025). However, there are studies showing that primates' more complex cognitive abilities can be more difficult to coordinate collective action within a group than the chemical mechanism of ants (Dreyer et al., 2025).

Second, acknowledging these emotional-cum-basic cognitive abilities also entails that the differentiation of structural, behavioral, and cognitive strategies of group coordination is misleading. Just as different kinds of social structures can be distinguished at the same time in humans, as our work on trust networks shows the same point can be made for social mammals, where different structures can be distinguished depending on the kind of link chosen: status, patterns of residence, and affiliation but grooming, but also by empathy.

Likewise, large groups may exist with very weak cohesion. The structural mechanisms that enable the maintenance of relatively stable large groups, are compatible with such groups being comprised of smaller ones that coexist to a certain extent, due to the cognitive limitations of managing an excessively large number of relationships (Operario & Fiske, 1999), resulting in larger groups maintaining relatively weak internal cohesion (Alvarez-Rodriguez et al., 2021). This weakness of the large group may occur when individuals spend more time cultivating their closest relationships, perhaps to secure their ties against other cliques competing for resources, which causes greater distancing between coalitions (Chae, 2022; Morris-Drake, 2022). Similarly, in humans, our work shows that a large group may be composed of multiple cliques without much contact among them (Acedo-Carmona & Gomila, 2019, 2013a, 2013b).

Third, the cognitive strategy may be suboptimal when the environment is unstable. For example, we found evidence that the cognitive mechanism of trust creates obstacles for individuals to adapt to rapidly changing environments in the short and medium term (Acedo-Carmona, Munar, & Gomila, 2018). Furthermore, trust is also easily susceptible to adversely affect relationships when it is negatively stimulated or when negative experiences are experienced (Davidson & Satta, 2021; Weiss et al., 2021).

Social structure and group size

In the target paper, Dunbar insists on his well-known argument for an intimate link between group coordination and group size, so that group size is thought to be dependent on the structural, behavioral, or cognitive strategies evolved to achieve group coordination. The assumption is that the bigger the group, the better, and that bigger groups require more cognitive abilities.

While it is true that social structure itself has a limited scope that depends on group size (La Macchia et al., 2016; Sato, 1988), it is also true that this limit can be overcome as long as such structures are extended through imitation (Bhoopchand et al., 2023). On the other hand, group size is sensitive to ecological conditions, not only to the strategy available for group coordination. Of course, some habitats may not impose any pressure on group size, but in our work in Northern Ghana, we found that cooperation among different ethnic groups was promoted precisely for the scarcity of resources available. The moral is that group cohesion may turn out to be as high as required by the environment, not a consequence of the suite of cognitive abilities developed.

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What makes social abilities sophisticated? Not recursive mentalising

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Abstract

To explain human social sophistication, and proximal phylogenetic steps leading to it, Dunbar claims that mentalising expands to increasingly high levels of recursion. However, the evidential basis for this claim is weak, exposing both a limitation in Dunbar's account and in the field's current understanding of social sophistication.

One pillar of Dunbar's account is that increasing social sophistication depends upon the ability to reason about mental states with increasingly high levels of recursion. Relevant evidence of such recursive mentalising comes from two sources: tests that explicitly require recursive mentalising and tests where recursive mentalising is one available interpretation of behaviour on strategic games. Neither source of evidence suggests that levels of recursive ability vary in the ways required to support Dunbar's claims.

Explicit tests of adults' recursive mentalising build on classic tests of children's reasoning about 1st order false beliefs and 2nd order beliefs about false beliefs (e.g., Wimmer & Perner, 1983; Perner & Wimmer, 1985). Dunbar and colleagues (Oesch & Dunbar, 2017; see also Kinderman, Dunbar, & Bentall, 1998; O'Grady et al., 2015; Stiller & Dunbar, 2007) developed social narratives and asked participants about the validity of statements such as:

> "*Frank realised that Betty wanted Brian to think that Frank believed that Betty knew Frank was worried that Brian knew Frank was confused with respect to Betty's desire that Frank buy free range or organic produce for a cooked breakfast with bacon and eggs for Betty and a lunch salad with lettuce and tomatoes for Brian.*" [correct answer = False; underlined verbs indicate putative recursive steps].

This question is designed to test 9 levels of recursive mentalising, and participants typically answer questions from level 1 to level 9. As described in the target article, most adults appear to manage 4 or 5 levels, with some appearing to manage 6-8, and an extensive programme of studies finds correlations between individual differences in levels of success and many socially relevant factors including cooperativeness (Paal & Bereczkei, 2007), social network size (Stiller & Dunbar, 2007), grey matter volume in regions of the "social brain" (Lewis et al., 2011; Powell et al., 2010), and (negative correlations) with psychopathic traits (Vonk et al., 2015).

A weakness in this otherwise impressive evidence base is its exclusive reliance on questions structured in the same way as the example above, because any problem with this method endangers the conclusions based upon it. Wilson et al. (2023) identified a critical problem by demonstrating that these questions are prone to high levels of false positives. In the above example, the correct answer "false" would be given by someone who reasoned at 9 levels of recursion, but also by someone who reasoned at any level above level 1. Wilson et al. compared performance on examples of the original stimuli with new narratives and questions that greatly reduced the potential for false positives. On the original stimuli, adults performed at the high levels previously reported, but much more poorly on the new narratives, even when participants were strongly incentivised and given unlimited time to respond. With the normal incentives in place, above-chance performance was only observed for level-5 reasoning in one out of four cases, and

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even then only 9/33 participants gave the correct answer. Presumably, many adults are capable of higher levels of recursive mentalising given external support from pen, paper, or spreadsheet. However, without such support many showed little evidence of reasoning above level-2, as observed in many 7-year-old humans. This revised estimate of adult humans' recursive reasoning performance leaves little room for variance that could explain differences between individuals or species, as required by Dunbar's account.

Evidence from strategic behaviour is also relevant and is both cited and analysed in Dunbar's target article. However, it is no more supportive of high levels of recursive mentalising. Such studies have participants play simple strategic games such as hide-and-seek over multiple trials against artificial opponents that implement strategies of varying sophistication. For example, a simple "level-0" opponent "hider" might adapt their hiding to avoid the location where a participant had looked more frequently on previous trials. A "level-1" participant seeker who took account of this strategy (and so biased their search away from their previous search pattern) would find the level-0 hider more frequently. A "level-2" hider would model such a dependency of the seeker's behaviour on the hider's past behaviour. They would again be beaten by a "level-3" participant seeker who took account of this strategy to bias their search behaviour.

Such studies are elegant demonstrations of strategic behaviour at varying levels of sophistication (e.g., Charpentier & O'Doherty, 2018; Devaine et al., 2014; Lee & Seo, 2016; Yoshida, Dolan, & Friston, 2008; Yoshida et al., 2010). However, these studies seldom provide evidence that human adults reason beyond "level 2," a result that converges strikingly with evidence of strategic reasoning from behavioural economics (e.g., Camerer, 2003), and the findings from explicit recursive mentalising described above. Although evidence of higher levels of recursive sophistication has been reported (e.g., Yoshida et al., 2008), success reflects learning over many trials. This affords bootstrapping of performance whereby an increasingly sophisticated response strategy may develop over time even though the level of recursion on a given trial remains low (Wilson et al., 2023). Finally, no such study includes a control condition that allows recursive mentalising to be distinguished reliably from recursive reasoning about behaviour. Indeed, one of the first papers to adopt these methods states "we are not suggesting that players actually compute their optimal strategy explicitly or indeed are aware of any implicit inference on the opponent's policy" (Yoshida et al., 2008, p. 12).

In sum, evidence from studies of strategic behaviour suggests that levels of recursion are generally low, that sophisticated behaviour is the product of learning not one-shot reasoning, and such studies do not clearly resolve the question about whether mentalising is involved at all.

Altogether, Dunbar's hypothesis about cognitive solutions to the pressures of group living is left without a candidate social-cognitive process to underwrite it. This poses a challenge for the target article. It also exposes a critical weakness in current research on mentalising in adults, which provides clear grounds for believing that mentalising abilities vary over and above general cognitive abilities, but no satisfactory account of why (Yeung, Apperly & Devine, 2024).

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Why not reduce reactive aggression too?

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Abstract

Grooming is one strong mechanism allowing primate groups to grow larger and more cohesive, but a reduction in reactive aggression responses can be expected to have contributed to this trend too. There is indeed a partial overlap between the neurobiology of grooming and the neurobiology of reactive aggression.

In his target paper, Dunbar provides a compelling account (and a comprehensive testing) of the structural, behavioral, and cognitive mechanisms that make possible the creation and maintenance of large animal groups (with a focus on primates). According to his view, these mechanisms allow to circumvent the two main problems resulting from group life: stress and dispersion. Dunbar's view is that stress can be attenuated through the potentiation of the endorphin system via direct grooming or grooming-like activities, like vocal chorusing (or, in the case of humans, a panoply of language-related activities). Furthermore, the development of advanced social cognition skills would allow to maintain weak ties with individuals one cannot groom with.

Since stress management is a crucial component of Dunbar's model, other mechanisms contributing to reduce socially induced stress can be expected to have favored the creation and maintenance of larger primate groups. In this commentary, I wish to argue that Dunbar's model would benefit from the consideration of the evolutionary strategies aimed, specifically, at reducing reactive aggression responses. The activation of the endorphin system that results from grooming and grooming-like activities can be seen as a reward mechanism that compensates for social stress. By contrast, the attenuation of reactive aggression responses could be seen as a desensitization mechanism that reduces the impact of social stressors. This latter mechanism entails the hypoactivation of the hypothalamic-pituitary-adrenal axis, which is typically observed in many domesticated animals (e.g., Ericsson et al., 2014), but also in humans (Chrousos et al., 1982), who have been claimed to have gone through a self-domestication process (Hare, 2017). Because lower levels of reactive aggression favor closer and more frequent contacts between individuals (this in turn facilitating the creation of larger groups that are less prone to fragmentation), this mechanism could be seen as part of the "behavioral solution" advocated for by Dunbar. Nonetheless, it can be also regarded as part of his "cognitive solution". One main reason is that, neurobiologically, the attenuation of reactive aggression responses is achieved by increasing the control of selected cortical areas, particularly the prefrontal cortex, over the subcortical components of the circuit of aggression, including the striatum (Lischinsky & Lin, 2020). This mechanism thus partially overlaps with the brain circuits supporting advanced social cognitions, since, as noted by Dunbar, the prefrontal cortex is important for mentalizing abilities as well, which are a key aspect of our social brain. Interestingly, the mechanism controlling reactive aggression also partially overlaps with the circuits that regulate abilities that are relevant for bonding, like vocalization or language. This is because the striatum also contributes to such (see Murphy, Hoshi, & Benítez-Burraco, 2022 for a detailed discussion). A piece of evidence supporting this view is that domesticated animals, in which stress signalling in the striatum is attenuated, exhibit more variable vocalizations than their wild conspecifics (O'Rourke et al., 2021). Likewise, moving now to the human self-domestication hypothesis, it has been proposed that selected changes in the brain circuits highlighted above might account for our sophisticated syntactic abilities, and more generally, for our cross-modal thinking, which are both at the core of our advanced linguistic, pragmatic, and narrative capacities (see Benítez-Burraco & Progovac, 2021; Benítez-Burraco, Ferretti, & Progovac, 2021 for details). The consideration of human cognitive disorders in particular, conditions impacting on our social brain, provides additional support to the view above. In autism spectrum disorders (ASD), high reactive aggression co-occurs with high stress levels, but also with reduced socialization abilities, specifically, an impairment of some of the high order cognitive skills highlighted by Dunbar as part of his Social Brain Hypothesis, most notably the ability to understand others' intentions (mentalizing), but also linguistic and communicative capacities (see Benítez-Burraco, Lattanzi, & Murphy, 2016 for an overview).

To finish, I wish to argue that the dopamine system could serve as a potential linker of the two mechanisms contributing to increase group cohesion in primates, namely, the grooming-dependent mechanism and the reactive aggression-dependent mechanism. Accordingly, as noted by Dunbar, the endorphin system acts in tandem with the dopamine system. But it also happens that attenuated stress responses, as found in species showing low levels of reactive aggression, also impact on dopamine signaling (through glutamatergic activity), further promoting some of the behavioral and cognitive modifications highlighted above, particularly, more variable vocalizations (see O'Rourke et al., 2021 for details). Compared to other primates, humans show, specifically, increased dopaminergic innervation of fronto-striatal circuits involved in episodic memory retrieval (Clos, Bunzeck, & Sommer, 2019), and speech and language learning (Raghanti et al., 2016). These dopamine-dependent changes can be thus related to our advanced mental travel abilities and our linguistic capabilities, respectively, and should be of interest to Dunbar's model, in view of the fact that storytelling is one key grooming-like activity promoting group complexity.

In conclusion, Dunbar's model certainly captures and explains in sound and novel ways how larger and more cohesive primate groups are formed and maintained, but it could be improved with the consideration of other mechanisms also promoting cohesion, specifically, the reduction in reactive aggression responses, considering the links and overlaps that exist between the neurobiology of grooming and the neurobiology of aggression.

Author contributions. ABB conceived the paper, reviewed the available literature, and wrote the paper.

Antonio Benítez-Burraco: conceptualization, methodology, writing, and supervision.

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A fishy perspective on the social brain hypothesis

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Abstract

Ectotherms, particularly fish, challenge traditional brain evolution theories by exhibiting advanced cognitive abilities despite their smaller brains. While the social brain hypothesis may apply within clades, sensory-motor systems likely explain the brain size differences between average-brained ectotherms and endotherms. Evolved complex sensory-motor systems suggest that brain evolution models should expand to include sensory and motor systems, beyond cognitive processes alone.

Dunbar (2025) offers novel analyses of the mechanisms underlying the social brain hypothesis, presenting new evidence that brain size variation in primates is driven by group size and the associated cognitive demands. The analyses oppose environmental explanations that propose complex foraging strategies – such as tool use, hunting, or food caching – require enhanced problem-solving abilities, lead to larger brains (DeCasien, Williams, & Higham, 2017; González-Forero & Gardner, 2018; Schaik et al., 2023). While we do not dispute Dunbar's findings, our aim is to place them within a broader context of vertebrate brain size and cognitive evolution. The social brain hypothesis has also been successfully applied to other clades, despite their smaller brain-to-body size compared to primates. For instance, the hypothesis can apply to fish, not only across species but also within the same species, thanks to the exceptional neural plasticity observed in fish (Bijl et al., 2018; Emery, Pessina, & Bshary, 2025; Alejandro, Svante, & Niclas, 2009; Pollen et al., 2007; Triki et al., 2024). Thus, the social brain hypothesis primarily explains some variation within taxa rather than the broader differences in brain size across taxa. Despite the sophistication of Dunbar's analyses, they account for only a small fraction of the variation observed in brain size, leaving a significant portion of this variation unexplained. This remaining gap in understanding warrants further attention and investigation.

Fish cognition challenges existing hypotheses on brain and cognitive evolution (Triki, Van Schaik, & Bshary, 2025). Despite having brains roughly ten times smaller than those of similarly sized endotherms (Jerison, 1973), many fish exhibit remarkable cognitive abilities, suggesting they possess cognitive toolkits comparable to those of average- and even large-brained endotherm species (Brown, 2015, 2012; Bshary, Wickler, & Fricke, 2002; Bshary and Brown, 2014; Kohda et al., 2023, 2019). Research on fish cognition has revealed that they excel in various tasks once thought to be exclusive to endotherms, particularly primates. Fish have demonstrated abilities such as social learning (Brown, 2023), cognitive flexibility (Warren, 1960), inhibitory control (Lucon-Xiccato, Gatto, & Bisazza, 2017), numerical reasoning (Agrillo, Piffer, & Bisazza, 2010; Triki and Bshary, 2018), spatial memory (Aronson, 1951), transitive inference (Hotta et al., 2020), object permanence (Triki et al., 2023), generalization (Wismer, Grutter, & Bshary, 2016), cooperative hunting (Bshary et al., 2006) and even self-recognition in the mirror test (Kohda et al., 2019, 2023). Importantly for one of Dunbar's arguments, fish show clear evidence of one-trial learning (Blank et al., 2009; Triki and Bshary, 2019). These findings challenge the notion that certain cognitive processes, including those for social behavior, require large brains. Instead, they suggest that many complex cognitive abilities can be supported by relatively small brains. This raises a key question: what similarities and differences between ectotherms and endotherms could account for this tenfold disparity in brain size?

Current brain evolution hypotheses do not account for the evolution of sensory and motor systems or their integration (Barrett, Henzi, & Barton, 2021; Triki, Van Schaik, & Bshary, 2025). A thorough examination of current knowledge and evidence suggests that, on a broader scale, the most significant differences likely lie in the sensory and motor systems and their integration (Triki, Van Schaik, & Bshary, 2025), particularly in relation to the transition from water to land (MacIver & Finlay, 2021). In fact, the sensory-motor skills of fish are less sophisticated than those of mammals and birds, where terrestrial and aerial life generally demand more advanced sensory-motor integration compared to aquatic life (MacIver & Finlay, 2021). Importantly, some species stand as exceptions to this trend, such as elephant fish. These weakly electric fishes rely on complex electromagnetic sensing to navigate and forage in murky waters – a perceptual system that is highly demanding in terms of neural resources. This characteristic

likely explains why their brain-body allometry falls within the range recorded for mammals (Nilsson, 1996).

The emphasis on sensory-motor systems in vertebrate brain size evolution raises two questions. The first relates to how we define animal cognition. While the classic definition by Shettleworth (2010) primarily focused on cognitive processes and perception, we have recently expanded the definition to provide a broader perspective and emphasize the role of sensory-motor systems: "*Animal cognition is the array of skills animals utilize to gather information via their sensory systems, process that information through cognitive mechanisms, store it, make decisions, and execute goal-relevant behaviors through motor skills facilitated by sensory-motor integration*" (Triki, Van Schaik, & Bshary, 2025). The second question is whether the sensory-motor systems primarily evolved for social or environmental demands – and how we define "social" interactions. For instance, a gazelle's ability to run swiftly over uneven terrain likely evolved as an adaptation to predation risk, yet predator-prey interactions can still be considered social (Oliveira & Bshary, 2021). Regarding more sophisticated sensory-motor systems, dexterity or anatomical features associated with dexterity – such as beak size in birds – accounts for a significant proportion of the variance in the data (Heldstab et al., 2016; Song et al., 2024). In favor of selection on environmental intelligence, many intelligent species (e.g., primates, corvids, and dolphins) integrate visual, tactile, and motor systems to manipulate objects. Tool use, in particular, relies on the interaction between sensory feedback and motor planning (Merel, Botvinick, _& Wayne, 2019). On the other hand, many vertebrates engage in multimodal communication (e.g., visual, auditory, and chemical signaling), which requires the integration of multiple sensory inputs to generate appropriate motor responses. For example, in songbirds, the ability to mimic and learn songs depends on auditory feedback and precise motor control of vocal muscles (Adam et al., 2021). In relation to the target article, groomer-groomee interactions in primates likely rely on key sensory-motor system involvement and the integration of sensory feedback, highlighting the role of these systems in social behaviors.

In conclusion, brain evolution hypotheses, including the social brain hypothesis, should expand their scope to incorporate the role of sensory-motor systems in decision-making in order to capture the full range of vertebrate brain evolution.

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Group-mindedness as evolved solution to deal with group-living

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Abstract

Challenges of group-living include foundational problems of cooperation and coordination that extend beyond anthropoid primates and may potentially be managed through evolved group-mindedness rather than expanded neocortical size and enhanced capacities for executive functions.

Dunbar persuasively argues that a central problem that mammals confront is how to manage the challenges that arise from living in large, stable groups. Some of the stresses identified can be succinctly summarized as having to do with two kinds of problems that permeate group-living – problems of cooperation, and problems of coordination (De Dreu, Gross, & Romano, 2024). While Dunbar mainly refers to the latter in terms of staying together despite different needs, cooperation and coordination extends far beyond group cohesion and is important for many species in terms of territory defense, food acquisition and rearing of offspring. The problem of cooperation is that when paying some cost resulting in safety and prosperity individuals can hardly achieve alone, individuals are better off when others cooperate and they themselves do not. Cooperation is exploitable by free-riding, and this requires the individual to spend effort on detecting whom to cooperate with, and whom to avoid. The problem of coordination is that collective action requires individuals to adapt their actions to those of others, with failure to do so leading to costly outcomes for individuals and their group. The problem of coordination requires individuals to spend effort in detecting what others do or will do, and to adjust oneself accordingly.

Often, group-living requires dealing simultaneously with problems of cooperation and coordination. Cooperative hunting, for example, requires individuals to take personal risks and to contribute effort to align their actions within the coalition. Dunbar's analysis suggests that primates successively exploited different kinds of strategies to solve these intricate problems of group-living, including enhanced cognitive capacities involving energetically costly forms of executive functions and mentalising.

While capacities for executive function are critical for solving problems of cooperation and coordination, Dunbar's analysis overlooks that evolved capacities for enhanced cognitive skills are necessarily in-group bounded and 'parochial.' There is good evidence that humans solve problems of cooperation and coordination first and foremost in terms of what could be termed "group-mindedness" – a tendency to perceive and treat 'in-group' members more favourably than strangers and 'out-group' members (Brewer, 1999; Brooks & Yamamoto, 2022; Romano et al., 2021). Group-mindedness, and related concepts such as social identification (Brewer, 1999) and group entitativity (Lickel et al., 2000), involves a sense of belonging to the in-group, which can explain the increased willingness to work together towards common objectives (Brooks & Yamamoto, 2022; Ellemers, Spears, & Doosje, 1997; Tomasello et al., 2012), to aggressively defend the in-group against outside enemies, and to join coalitionary raids on neighbouring groups and communities (De Dreu & Triki, 2022; De Dreu et al., 2016; Lemoine et al., 2022).

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Unlike the cognitive solutions postulated by Dunbar, group-mindedness is organized at the group level and not reliant on tracking dyadic interactions. Furthermore, whereas the cognitive solutions offered in Dunbar's analysis reside in the primate's neocortex, group-mindedness likely involves the evolutionary ancient and structurally and functionally preserved social decision-making network in the vertebrate brain (O'Connell & Hoffman, 2011; Rilling & Young, 2014). This network includes various brain nuclei known for their crucial roles in regulating social recognition, affiliation and parental behaviour, responses to social stressors, and aggression (Goodson, 2005; Rilling & Young, 2014; De Moura Oliveira et al., 2021) and is critically dependent on neurohormonal modulations in the oxytocinergic circuitry (De Dreu & Kret, 2016; Samuni et al., 2017; Triki, Daughters, & De Dreu, 2022). Group-mindedness involves neural structures and functions seen across a range of species. It may have evolved as well in other animal species than anthropoid primates.

As an explanatory mechanism, group-mindedness has several advantages compared to the analysis offered by Dunbar. First, Dunbar's analysis largely rests on the anatomical volume of the primate's neocortex, but brain size is a rather removed proxy of the number and interconnectivity of cortical neurons that make up brain functionality (Roth & Dicke, 2005). Group-mindedness as an explanatory mechanism more directly relies on the functionality of the vertebrate's social decision network, that can be independent of anatomical volume and structure. Second, group-mindedness as a solution to the problems of group-living can extend beyond primate species to social vertebrates more general. Indeed, not only primates but various other mammalian species live in stable groups, breed cooperatively, hunt together (Ausband & Mitchel, 2021; MacNulty et al., 2014; Range & Marschall-Pescini, 2022) and engage in intergroup contest and conflicts (Cassidy et al., 2015; De Dreu & Triki, 2022; Smith et al., 2012). Third, group-mindedness provides the animal a simple heuristic to quickly decide whether, how much and when to cooperate with others, and whether and how to adapt behavioral actions to those of others, independent of dyadic interaction histories. This makes group-mindedness cognitively less effortful and expensive than cognitive processes involved in perspective taking and inhibition. Fourth, group-mindedness can explain cooperation and coordination beyond the dyadic level, which is important for many species engaging in territory defense or cooperative hunting where success depends on numbers (Lemoine et al., 2020). Finally, and in contrast to executive function principles, group-mindedness captures that most if not all group-living species are inherently in-group bounded and parochial, with cognitive and behavioural investments spend on those the individual relies on for survival and reproduction – those that are familiar rather than not, physically close rather than distant, and phenotypically similar rather than dissimilar.

Evidence for group mindedness in group-living animals other than humans is presently indirect, and research is needed to specify whether and how group-mindedness evolved for group-living. As a mechanism, however, group mindedness might better explain how social vertebrates – primates included – solve recurrent problems of cooperation and coordination through in-group bounded and parochial *integration* (e.g., cohesiveness, conformity) and *synchrony* (e.g., coordinated movement, mimicry, neural coupling) than metabolically expensive forms of cognitive skills. In anthropoid primates, including humans, capacities for enhanced cognitive abilities may be built atop more foundational capacities for group-mindedness that may have evolved in other group-forming species as well. Whether capacities for complex cognition are at all needed to deal with the recurrent stresses of group-living remains an open issue to be addressed.

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What problem does a fractal social network solve?

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Abstract

Dunbar's framework highlights the challenge of maintaining large, stable social networks given cognitive constraints. Expanding on this, I propose that fractal social networks function as lossy compression algorithms, efficiently reducing the complexity of social storage and retrieval. Rather than tracking all relationships explicitly, individuals rely on hierarchical abstractions and transitive inference, shifting storage complexity from $O(N^2)$ to $O(N \log N)$. This insight suggests broader implications for cognitive evolution, institutional organization, and artificial intelligence.

In this insightful paper, Dunbar raises a fundamental question: How do social species maintain stable, large-scale networks given cognitive and temporal constraints? Here, expanding on this theme I offer a brief complementary perspective from computational complexity and suggest that fractal social networks function formally as lossy compression algorithms, solving a specific class of problems related to information storage, retrieval, and coordination in large groups.

Why does social complexity need compression?

First, we define a social network $G(N, E)$, where N is group size and E is the number of edges. In a fully connected bidirectional network, the connectivity increases with group size as $E = N(N-1) = O(N^2)$. In small groups where the number of individuals remains relatively low, each member can explicitly track all relationships. The storage and retrieval costs at this scale remain modest, making social navigation relatively straightforward. However, as group size increases, the all-to-all tracking strategy becomes infeasible due to both memory constraints and retrieval efficiency. The cognitive cost of storing relationships grows quadratically with the number of individuals, making explicit tracking computationally intractable. The number of all possible pathways among the group grows even worse at $N!$. Furthermore, social decision-making requires quick access to relevant ties, but a flat social network structure lacks efficiency in lookup and recall.

Fractal networks as a computationally efficient solution

As shown by Dunbar and others, the solution that appears consistently across primate species, including human societies, is the fractal organization of social organization (Hamilton et al., 2007; Hamilton et al., 2020; Zhou et al., 2005; Dunbar, Carron, & Shultz, 2018; Hill, Bentley, & Dunbar, 2008; Sandeford, 2018). As we will see, this hierarchical, self-similar structure effectively reduces both cognitive and behavioral overhead. Instead of tracking all individual relationships, primates encode higher-order summaries that organize social connections into nested level, $k \in \Omega$, where Ω is the depth of the network. And so, let N_K be the group size at the kth level.

Using Dunbar's numbers, at the most intimate level, individuals maintain strong ties with a small core group, consisting of approximately five members, $N_1 = 5$, with whom they have frequent, high-bandwidth interactions; $E_1 = 20$. Beyond this core, a secondary group of trusted allies, generally around fifteen individuals, $N_2 = 15$, is maintained with bidirectional and strong connections; $E_2 = 210$. Expanding further, an extended network of approximately fifty individuals, $N_3 = 50$, where $E_3 = 2,450$ relationships are inferred rather than explicitly tracked, often using transitive closure principles, meaning that "friend-of-a-friend" logic helps individuals navigate these indirect ties. Beyond this, individuals belong to a wider community of approximately 150 members, $N_3 = 150$, where relationships are stored as categorical groups rather than explicitly maintained as individual ties, where $E_4 = 22,350$. Out of interest, the total number of all possible paths between 150 individuals is about 5.71×10^{262}, far greater than the number of atoms in the observable universe.

Mathematically, instead of maintaining a fully connected graph, social cognition compresses networks using a fractal scaling law:

$$E_k \approx CN_k^{\beta}, 0 < \beta < 1$$

and so, summing across all k hierarchical levels we have $E_\Omega \approx CN_\Omega^{\beta}$,

where C is the cognitive load of an individual, and β controls the efficiency of compression. This scaling law is ultimately derived from the fact $N_k \approx B^k$, where B is the branching ratio, often between 3 and 4 empirically in all kinds of social networks. A value of β closer to 1 implies minimal compression, while a value closer to 0 implies maximal compression. Note that in Dunbar's paper, the network degree of group sizes—a reasonable estimate of $E_k \sim N^{\beta}$—he reports is $\beta \approx 0.6 - 0.8$. It can then be shown that the total storage and retrieval complexity of this system then shifts from the brute-force quadratic growth of N^2 to a dramatically more efficient

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$N \log N$. This hierarchical compression model ensures that instead of every individual requiring explicit memory of every relationship, they rely on group-based abstractions and inferred social ties, substantially reducing the computational load while maintaining network cohesion. In other words, the cost of keeping track of the connectivity of an individual reduces from N to $\log N$.

Fractal networks as efficient coordination systems

The advantages of a hierarchical, fractal network extend beyond the reduction in memory requirements. Such network structures have the small-world properties, where local clustering is high, yet the presence of long-range weak ties ensures efficient connectivity across the broader network (Hamilton, 2022). This then vastly improves navigability, as weak ties function as shortcuts, reducing the search cost in large social groups.

Additionally, fractal networks enhance error tolerance, as the redundancy in layers ensures that if some social ties are lost or broken, the structure remains resilient and retains overall integrity. Furthermore, as groups grow beyond Dunbar's number, $N_k > 150$, the same fractal organization extends into formal institutions, where social roles and organizational structures take over cognitive limitations, enabling large-scale human societies to function effectively.

Social cognition as an evolved compression algorithm

If we accept that one of the key selective gradients to which the brain evolved in response to was optimizing social computation, then a fractal social network architecture is a natural collective solution. The human brain does not brute-force social coordination by storing all relationships explicitly. Instead, it organizes relationships hierarchically to reduce memory overhead. It uses heuristics to index them—kinship norms or friend-of-a-friend rules—to infer indirect ties, which minimizes retrieval costs and ensures that even individuals without direct interactions can be socially navigated through intermediaries. This balance between redundancy and efficiency provides resilience under social stress and environmental changes, allowing groups to adapt without overwhelming cognitive load.

The core question for future research

If fractality solves the problem of exploding complexity in social networks, a fundamental question remains: Are there universal scaling laws governing social cohesion and information compression across species and societies? To investigate this, researchers could apply information-theoretic measures of network compression to different social species and institutional structures. Additionally, simulations of scaling thresholds in social systems may provide insights into phase transitions in coordination, shedding light on why certain social structures persist while others collapse. Comparisons with artificial intelligence models, particularly how machine learning architectures handle large-scale social inference, could reveal parallels between biological social cognition and digital network optimization. It is intriguing to note scaling laws abound throughout the biological and social sciences (West, 2017; Bettencourt, 2021; Barenblatt & Isaakovich, 1996) though the explicit link to lossy compression has yet to be made, as far as I am aware.

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Flexible branches in the primate family tree?

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Abstract

Primate species deploy a suite of behavioural and cognitive adaptations to offset the costs of group-living. Dunbar uses species-level comparisons to posit a series of cumulative steps that describe large-scale phylogenetic patterns in the evolution of sociality. Here, we highlight the value of population-level variation within species for empirically testing the predicted socio-ecological correlations that underpin Dunbar's hypothesis.

In a new articulation of the Social Brain Hypothesis, Dunbar argues that increasing investment in the connectivity and alignment of a species' social relationships—made possible by dietary shifts—underpinned the evolution of "neuronally expensive" socio-

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cognitive skills that, in turn, favoured step-changes in primate sociality. For example, Dunbar calls attention to two species, *Theropithecus gelada* and *Papio hamadryas,* to argue, tacitly, for evolutionary convergence toward "super" group sizes on the basis of exceptional levels of social grooming and smaller-than-expected brain sizes. Such reasoning is rooted in the comparative method in biology, and it is undeniably compelling.

But there is a problem. The approach relies on summary values of a given trait, such as mean social group size, to identify commonalities between living species—the tips of phylogenetic branches—and infer processes that operated in the past. Dunbar uses it to impute selection on the primate lineages that gave rise to the variable expression of social brains today. Testing this hypothesis is difficult given the spotty nature of the fossil record, but there is a potential path forward: we could reorient our attention toward species-level plasticity, the "noise" that is more typically treated as an inconvenience.

The present version of the Social Brain Hypothesis is closely aligned with the evolutionary concept known as *Behavioural Drive* (Lister, 2014; Fannin et al., 2025). It holds that behavioural shifts must precede the evolution of corresponding morphological adaptations, such as expensive neuronal tissue. An essential precondition of behavioural drive is a high level of behavioural variability in the ancestral lineage, a "flexible stem" (Antón & Kuzawa, 2017). It follows that flexible stems—with exceptional levels of behavioural plasticity—predated the origin of every exemplary social brain, the final step-change in Dunbar's model. Such a view inevitably raises questions concerning the causes of such plasticity and the amount that matters, topics best assessed with modern species. Mounting evidence of extraordinary variation *within* primate species—between individuals, groups, populations—could offer an unrecognised opportunity to detect the socio-ecological mechanisms underpinning Dunbar's hypothesis.

Many primate species are highly social and long-lived. Describing their activity budgets and social relationships takes years of careful observation, often in challenging field conditions. As a result, a few well-studied populations have shaped our



Figure 1 (Hobaiter and Dominy). Patas monkeys (*Erythrocebus patas*) negotiating steep cliffs in the Ennedi Natural and Cultural Reserve, Chad. Photo credit: John Hall.

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understanding of species-typical behaviours (e.g., Kappeler & Watts, 2012). But this perspective has shifted in recent years; indeed, the behavioural plasticity of some populations has blurred even definitive species differences. For example, recent observations of wild chimpanzees (Giuliano et al., 2022; Koops et al., 2024) highlight the biases of our textbooks toward seminal studies of Tanzanian populations, in which groups of ~60 individuals live in high-degree fission-fusion societies (Nishida, 1968; van Lawick-Goodall, 1968). Yet, chimpanzee group sizes can vary from 10 to 200 individuals, with individual encounters between some community members occurring daily, monthly, or only yearly (Lehmann & Boesch, 2004; Wilson et al., 2014).

Such plasticity is conducive to testing the putative causal mechanisms underpinning Dunbar's hypothesis. If a given community is 2x larger than the species mean, then it predicts: i) greater investment in grooming time and longer grooming chains; ii) greater group stability in high-quality territories that minimise travel time between foraging patches; and iii) greater investment in cognitive solutions. These predictions invite systematic testing, but there is some tantalising support: the Ngogo super-community fractured along lines of increasingly entrenched, spatially-separated social "cliques" (Sandel & Watts, 2021), disrupting Dunbar's suggested web of grooming chains, argued to foster adult unity. In contrast, the Waibira super-community appears stable—but employs a rotating core-periphery social structure in which independent males cycle through socio-spatial associations (Badihi et al., 2022) and show greater investment in social signalling than smaller groups (Safryghin, 2024).

Understudied species (or unstudied populations outside of well-studied habitats) offer further opportunities. We recently completed preliminary fieldwork in the Ennedi massif, a remote corner of north-eastern Chad with a relict population of patas monkeys (*Erythrocebus patas*) in an extraordinarily arid rocky Saharan habitat (Figure 1). Encounters during the day reflected "species typical" group sizes of 20-30 individuals (Hall, 1966). In contrast, evening encounters at sparse water-holes could surpass 60-80 individuals—most likely the result of multiple groups converging on an essential resource during a limited daily access window. Some populations of other primate species, including baboons (Loftus et al., 2024) and bonobos (Samuni & Surbeck, 2023), form short-term (hours or days) "super-aggregations" across otherwise clearly separated group boundaries. Where populations show additional dynamic plasticity in social association, Dunbar's hypothesis predicts that the costs of doing so should be offset by matching population-specific fluctuation in other behaviours. For example, where competition for limited resources is offset through the increased use of mechanisms for social bonding—such as grooming or vocal exchanges—social "rules" about whether these activities only occur within, rather than across, group boundaries, may fluctuate depending on local resource availability.

Within-species behavioural plasticity not only provided the fuel for behavioural drive across primate evolution, but—where species retain plasticity—should continue to drive morphological differences. Where that plasticity relates to their capacity to form sophisticated social relationships, behavioural drive predicts a faster rate of change in the evolution of neurophysiologically expensive neocortical tissues, and increasing divergence/spread across the tips of the primate family tree. Crucially—while behavioural plasticity may be expressed as dynamic patterns of (super)grouping—concomitant impacts on expensive brain tissues would be stable. If populations, like the relict patas monkey population of the Ennedi plateau, habitually experience intermittent super-sociality as a behavioural response to an unusual local ecological niche—there should be observable differences in both their social behaviour and the underlying cognitive tissues that support it.

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Mental abstraction aids group cohesion in large social networks

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Abstract

Human social networks are far larger than those of nonhuman primates. Maintaining cohesion in large networks requires a robust mechanism that can accommodate the dense webs of connections within communities. A parsimonious account of how humans achieve social cohesion is *mental abstraction*, which enables individuals to construct fuzzy network representations that facilitate information flow tracking and mitigate conflict.

Maintaining a large social group is challenging. Dunbar proposes three solutions that help buffer against group fragmentation: (1) structural: maintain coordination by following one's neighbors, (2) behavioral: increase social grooming time, and (3) cognitive: leverage self-control and mentalizing to avoid conflict. While these solutions may be sufficient for maintaining smaller (nonhuman primate) groups around 50 members in size (Dunbar, 1992, 2024; Dunbar, Mac Carron, & Shultz, 2018; Pasquaretta et al., 2014), they are inadequate for explaining how humans establish and maintain cohesive social networks that are far larger. The sheer size of human social networks – which are typically three times as large as the largest social networks seen in primates (Hill & Dunbar, 2003) – requires a solution that is robust to coordination and fragmentation problems at larger scales. We suggest that mental abstraction is the fundamental mechanism driving humans' ability to maintain cohesion in large groups. Abstraction allows people to build efficient and useful representations of how individuals in their community are connected (Basyouni & Parkinson, 2022; Park et al., 2020; Son, Bhandari, & FeldmanHall, 2023). Relying on abstraction to construct a mental representation of one's social network provides the advantage of stripping away the granular details of individual ties, distilling complex relational patterns into a higher-order map of the broader network structure (Basyouni & Parkinson, 2022; Son et al., 2023; Xia et al., 2025). Abstraction thus enables humans to carve their networks on the major infrastructure scaffolding the community, a prerequisite to solving the unique challenge of maintaining group cohesion in larger networks.

While Dunbar's structural solution of simply following your neighbors might be sufficient for smaller networks where individuals have limited local connections, this approach would become brittle if scaled up, as the number of neighbors would increase exponentially. This problem is made even more complex when we consider human networks. Unlike those of primates, human networks contain numerous weak ties (Granovetter, 1973) that rapidly multiply as the network grows, making it nearly impossible to track all neighboring relationships. These weak ties also create structural holes where information is unlikely to flow between more distant contacts (Burt, 2014), further undermining group cohesion. To address these challenges, humans can leverage abstract knowledge of the broader structures within a social network. This enables individuals to more easily discern distinct communities and, critically, to detect bottlenecks or gaps where information might flow (or fail to flow) effectively. By identifying structural holes, humans can strategically fill the gap by becoming a bridge between two otherwise weakly connected communities to facilitate cohesion (and in the process, gain access to valuable social resources; Burt, 2014; Nan et al., 2008). Unlike primates, who align their behavior primarily with immediate neighbors, humans use these abstract network representations to maintain group cohesion by actively addressing structural inefficiencies (Teoh et al., 2025). Such intentional bridging behaviors help humans form a sparser, yet more resilient and cohesive, network structure than primate networks (Pasquaretta et al., 2014).

Similar logic applies to the behavioral solution. While primates maintain social ties through increased grooming, this strategy has an upper limit, especially in larger networks. Given the vast number of social connections humans must navigate, humans instead rely on verbal communication – such as gossiping – as a behavioral solution (Dunbar, 1998). Transmission of information does not follow the same properties as physical acts (Acemoglu, Ozdaglar, & ParandehGheibi, 2010; Chen, Castillo, & Lakshmanan, 2014; Daley & Kendall, 1964), since gossip, for example, can simultaneously reach many people within the network, thus making verbal communication qualitatively distinct from (and more efficient than) grooming. For gossip to strengthen social bonds rather than damage reputations, humans must gossip strategically. Abstract maps of a social network support adaptive decisions about whom to share information with and whom to avoid gossiping with Xia et al., 2025). For instance, in a scenario where it may be critical for information to only reach specific parts of the network but not others, an abstract representation of the network would facilitate predictions about the likelihood of gossip spreading along chains of connections stemming from the source, enabling more strategic social navigation.

And the cognitive solution? While better self-control and mentalization help prevent conflicts in groups, the highly dynamic nature of large social networks calls for a cognitive approach that goes beyond immediate, in-the-moment problems. Humans living in large groups must plan ahead and predict future social dynamics to preemptively prevent group conflicts that could have devastating consequences on social cohesion. Equipped with an abstract representation of one's community, humans can predict the formation (or dissolution) of future social connections (i.e., link prediction), as well as the consequences of those changes in social ties on the overall group dynamics and cohesion. This capacity for future-oriented thinking is particularly useful for mitigating group conflicts caused by negative ties (e.g., enemies), which naturally threaten group cohesion but are nonetheless part and parcel of human life (Offer, 2021). For instance, abstract network representations can help humans foresee a united group splitting into polarized factions, even when only a single negative relationship initially exists within the network. This foresight

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enables humans to identify potential fragmentation in advance and take preventive measures to maintain group stability (Ackermann, 2003; Axelrod, Daymude, & Forrest, 2021; Sherif, 1988). The absence of such cognitive foresight can have catastrophic consequences – as history has taught us. A striking example is the betrayal of Caesar by Brutus, in which an unanticipated rupture of a central tie ultimately led to Caesar's assassination and the collapse of the Roman Republic (Tempest, 2017).

Mental abstraction offers a comprehensive but parsimonious account for how humans address the challenge of cohesion in large groups and serves as an overarching framework that encompasses the three solutions proposed by Dunbar. While recent empirical research illustrates that humans build abstract mental representations for social networks (Hu et al., 2025; Jolly et al., 2023; Parkinson, Kleinbaum, & Wheatley, 2017; Son, Bhandari, & FeldmanHall, 2021, 2023, 2024; Teoh et al., 2025; Xia et al., 2025), little is known about whether nonhuman primates also do so. A key "to-be-tested" hypothesis that falls out of the abstraction solution is that the ability to create increasingly abstract representations of one's social network should directly scale with the size of their network. While research shows that humans with greater knowledge of abstract social structures move into more influential positions in their social network (Aslarus et al., 2025), highlighting the benefits of abstraction for navigating larger groups, future studies should examine whether greater mental abstraction capacity is directly linked to larger network size across species. The reverse relationship should also be examined: the larger the network, the greater the demand and utility for building abstract representations of that network.

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Cognitive perception of social stress as a critical mechanistic control of mood and mood-related brain signals

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Abstract

The paper of Dunbar (2025) on social stress is a strong demonstration that stress in itself can have a purely cognitive origin. The paper shows that the cognitive system can have profound impacts on the hypothalamus. As detailed in my commentary, this opens up new avenues of how to interpret psychiatric conditions, placebo, and other associations between perceptions and vegetative functions in the brain.

For neuroscientists dedicated to explain brain function and motivation as mechanistically emergent effects, this paper provides support for a potentially revolving insight: a strictly cognitive process, the individual's notion of the state of their social environment, can cause such profound stress that it can induce temporary infertility among females. The disruption of the reproductive function depends on the hypothalamus, implying that cognitive perception of social stress is a critical factor for hypothalamic function and therefore mood (Bao & Swaab, 2019). Dunbar (2025) also shows evidence that the social cognitive processes among primates can drive the individual to adopt almost any behavior to be able to defuse perceived social stress. The resulting behavioral strategies and the emergent "glass ceilings" that limit the maximum group sizes apparently depend on the cognitive limits of the species to find behavioral strategies to defuse the social stress, which scales with the social group size.

From a neurophysiological and psychiatric perspective, the paper presents an important opportunity to formulate new perspectives on how the internal brain signaling of stress and release from stress, potentially a powerful reward signal in itself, is organized. The physiological and evolutionary origin of stress is the need of the brain to regulate the activity distribution across our body and inner organs in relation to what actions we currently engage in, ultimately mediated via the autonomic nervous system (ANS). For example, when perceiving stressful situations such as the presence of a predator, it is important to prepare by redirecting more blood to the muscles rather than the gut. There are tremendous numbers of sensors across all inner organs (Wang & Chang, 2024), the skin, and the entire musculoskeletal body, which are dedicated to directly signal potential harm such as tissue damage, fatigue, or physiological/homeostatic imbalances, which the brain uses to redirect activity focus across our body (Mårtensson et al., 2025). In contrast, the notion of social wear and tear has no ground truth sensor signals. Our estimates of potential social imbalances instead must originate from our perceptual and reasoning capabilities in the cortex.

Hence, the findings of Dunbar (2025) demonstrate that the cognitive analyses of the social conditions can be the origin of stressful states internally in our minds. These internal states will be reflected in the activity of the brain circuitry, in the examples given by Dunbar (2025), even to the extent that hypothalamic function is impacted. In analogy with the ANS, these internal brain states continually lead to a rebalancing of activity across the brain for it to cope with the most acute contextual aspects, and the mediators of this rebalancing (Breton-Provencher et al., 2022) therefore can be viewed as increasing or decreasing their activity merely as a secondary, consequential effect. This would have revolving implications for psychiatry, which otherwise widely rely on what may be referred to as some form of "biochemical" pushbutton hypothesis, i.e., that our mood disorders are caused by imbalances in some specific brain-internal mediator (such as endorphin, oxytocin, dopamine, serotonin, histamine, noradrenaline, and acetylcholine). But it is widely known among practicing psychiatrists that the biochemical pushbutton hypothesis does not rhyme well with effects observed in reality, and other than pain relief, over the last few years, spectacular retrospective analyses demonstrated its inefficacy over placebo (Leichsenring et al., 2022; Moncrieff et al., 2023).

An important overlooked fact is that none of these mediator systems has any proven intrinsic mechanism to judge whether we are in a stressful or a beneficial situation. Current hypotheses that these mediators are primary causes of stress have instead implicitly assumed a *deus ex machina* function in them, such that they somehow magically "know" what a reward or a stressful situation would look like and regulate their signals based on that. But the only brain system that has a sufficiently rich intrinsic working memory (Goldman-Rakic, 1995; Kristensen et al., 2024) to evaluate whether a complex, abstract, and temporally evolving phenomenon like social network state is potentially harmful or beneficial is the cortical network. The cortex exerts its influences widely across the central nervous system (CNS), including on the limbic system and hypothalamus, and can concertedly control the release of the mediators listed above to balance the brain activity distribution depending on the perception of contextual state (Stratmann et al., 2018). Hence, there is a mechanistic infrastructure in the brain through which the cognitive perception of social stress can control what we traditionally think of as mood-related brain signals – but the mood may depend on the cortex itself.

That social interactions are stressful naturally depends on that we cannot control other individuals, and the social interaction is therefore inherently unpredictable. But then, why are social networks formed at all? What is the factor that can defuse the stress of the first social interaction we would ever have and thus allowing our cognitive systems to learn that social interactions can be beneficial? At least in mammals and marsupials, there is a greater stress that the first social interaction can defuse: nutritional needs, signaled by the hypothalamus. These needs can be relieved by breastfeeding or by providing for nutrient intake by other means. In animals, the process of suckling would hence lead to an early foundation in the cognitive system that social interactions have an element of major potential goodness (release from stress). This could, in turn, lead to a natural cognitive drive later in life to explore social interactions as a means of defusing other stress factors. Indeed, the nutritional stress (or gain) is indeed a key factor across different species of primates that drives the social network

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cohesiveness and the specific strategies adopted by the social group – and depending on the size of their cortex, these social networks can take on different levels of complexity (Dunbar, 2025). Indeed, whales can also exhibit highly differentiated social behaviors, where the feeding behavior and strategy tend to be unique for each social group (Jourdain et al., 2024). A related question is at what lower limit of cortex size can we begin to speak of true social behavior rather than herd-formation (Dunbar, 2025)?

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What holds groups together? How interdependence shapes group-living

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Abstract

Dunbar's emphasis on dyadic relationships in group formation overlooks the roles of interdependence and joint commitment in social cohesion. We challenge his premise by highlighting the importance of group-level processes, particularly where top-down group pressures like cooperative breeding and out-group threat can induce joint commitment as an alternate means to sustain group cohesion.

We greatly value Dunbar's emphasis on comparative research into the causes and consequences of variation in group size and structure, and also present several critical challenges to his approach and conclusions.

Dunbar's analysis of group cohesion in primates highlights two core challenges of group-living: the desynchronisation of activity cycles and the stress associated with close social proximity, both of which are expected to intensify as group size grows. These centrifugal forces, he suggests, are mitigated by evolved structural, behavioural, and cognitive mechanisms. However, this analysis lacks attention to the socioecological variations in the costs and benefits of group-living, focusing only on what he implies are universal costs of increased group size and explicitly denying attention to potential social benefits. Dunbar portrays groups solely as networks built up from dyadic social relationships, placing excessive emphasis on cognitive processes while neglecting the crucial roles of group-level dynamics and external forces, which can shape sociality and cohesion independently of higher cognition.

Group processes reducible to the sum of dyads have been described as bottom-up, in contrast to top-down processes that inherently function at the group level (Brooks & Yamamoto, 2022). Dunbar's framework implicitly assumes that dyadic interactions simply scale up to account for group cohesion (i.e., bottom-up), but a more encompassing perspective requires acknowledging the essential role of top-down pressures in shaping group cohesion. While Dunbar states that "we are here only interested in the constraints on evolving large groups, and not the reasons why large groups evolve" (p. 22), these are not independent questions. Group-level solutions are shaped by the group-level problems they solve, which, in turn, define the capacities needed for their maintenance. They may incur some group-level costs, but these costs vary as a product of the species' socioecology, as opposed to being shaped solely by forces of desynchronization and stress that are implied by Dunbar to affect all species relatively equally. Therefore, to fully understand what keeps groups together, we must move beyond a perspective focused solely on dyadic interactions and focus on the causes and consequences of species' top-down group cooperation problems.

Dunbar's emphasis on relationship-tracking through large brains overlooks alternative routes to group stability, bonding, and cooperation. We suggest that the sense of commitment may be a fundamental driver of social cohesion in species facing top-down

group cooperation challenges. The sense of commitment has been conceptualised as a cognitive mechanism that arises when individuals rely on each other to achieve a shared goal, and as such, does not assume or depend on higher-order cognition (Michael, 2022). This raises the possibility that a sense of commitment may be at play in species where shared goals – such as territory defence, predator avoidance, cooperative breeding, or information transfer – generate interdependence. Interdependent goals, that is, goals where individuals depend on one another, may therefore generate commitment dynamics sustaining group cohesion in the absence of high-order cognition. Commitment, in this sense, serves as an alternative mechanism for group cohesion, challenging the assumption that strong social bonds enabled by rich cognitive capacities are the only solution to counter fragmentary forces, as Dunbar suggests. Group processes such as intergroup competition and cooperative breeding can create evolutionary conditions that foster a sense of commitment, reinforcing social cohesion without the need for sophisticated cognition (Silk, 2002; Silk, Kaldor, & Boyd, 2000).

Relatedly, Dubar's narrow focus on desynchronisation and stress-induced decreases in fertility is reductive and may misrepresent the broad range of collective costs that groups must overcome. As such, costs of group-living do not neatly track group size equally across species, but crucially depend on the species' socioecology. For example, among the largest reported non-human primate groups are the Angolan black-and-white colobus monkey (*Colobus angolensis*) and mandrill (*Mandrillus sphinx*), both living in groups that can reach more than 300 individuals, much larger than those of the big-brained great apes (Fimbel et al., 2001; Hongo, 2023). In such species, it may be a reduction to the costs of group-living, specifically in the absence of intense feeding competition among group members in these cases, that enables large groups to persist over time. When collective costs of sociality sufficiently decrease, large groups can emerge. This runs counter to the proposal of Dunbar that desynchronisation and reduced fertility are the main constraints on group size and can only be solved by large brains.

To guide future research on how the sense of commitment stabilises group cohesion and interacts with diverse collective costs of group-living in non-human primates, we propose to adapt a framework designed to spell out the minimal structure of situations which may give rise to a sense of commitment (Michael, Sebanz, & Knoblich, 2016) through a comparative approach across species inhabiting varied ecological niches. If indicators of a sense of commitment in this minimal sense vary across species in accordance with top-down group cooperation challenges (such as cooperative breeding), rather than group size and number of grooming partners, it would suggest that these capacities can provide an alternate pathway for group cohesion, while comparison of species according to their feeding competition within the same clade would help distinguish systems that accommodate costly group-living through cohesive forces from systems where group-living is simply less costly. We do not challenge the fact that rich cognitive abilities are crucial to life in large groups for some species, but our emphasis is that this narrow focus on an association between brain size and group size overlooks other social mechanisms of cohesion, mechanisms that are tuned to the group-level costs and benefits they address.

While large brains can indeed facilitate the tracking of numerous dyadic relationships, which are undeniably vital for many complex social phenomena, they are not necessarily what brings and keeps groups together. Instead, factors like group-level interdependence and the entailed commitment dynamics play crucial roles. Future research should work towards integrating these perspectives to better understand how and why species have evolved, and continue to maintain their distinctive group structures.

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Metacognition serves allostasis and co-evolves with the social brain

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Commentary on R.I.M. Dunbar "Structural and Cognitive Mechanisms of Group Cohesion in Primates"

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Abstract

In this commentary, I suggest a complementary view to the target paper's idea that primate social metacognition evolved as an adaptation to living in large groups. I present metacognition as a necessary step in the development of complex allostatic systems and suggest that intrinsic and social metacognition are dissociable, which can be studied in the mammalian default mode network.

In the target paper, Dunbar presents data supporting his Social Brain Hypothesis, where an increase in the size of primate groups is associated with structural, behavioral, and cognitive adaptations to social stress. He identifies endorphin-releasing social behaviors (primarily grooming) as the main stress-mitigating mechanism. The pressure of social stress is presented as the driving force behind the evolution of social and metacognitive capacities of the primate brain toward the ability for social mentalizing. This ability is considered crucial for living in large groups.

In this commentary, I want to draw attention to a complementary perspective on the evolution of metacognition. Mitigating stress by prosocial endorphin-releasing behaviors has its counterpart, which is stress tolerance via self-mentalizing. Self-mentalizing may play a role in mitigating social stress alongside with social mentalizing. Hence, metacognition can be seen as co-evolving with the social brain and not only as its emergent property. In this view, the primary function of metacognition is to (indirectly) regulate allostasis, with social mentalizing as an add-on in highly socialized species.

To make this case, I first frame metacognition as self-regulation or self-modeling, since to regulate an extrinsic process means to be its model according to the good regulator theorem (Conant & Ross Ashby, 1970). Thus, we can see the origin of metacognition in self-modelling, whose primitive forms may be considered as pro-metacognition. Pro-metacognition is already found in bacteria, the simplest biosystem. E. Coli can monitor its level of energy and membrane integrity and transduce this information to its effector protein which controls the bacterium's behavior (Alexandre, Greer-Phillips, & Zhulin, 2004). At a higher level of complexity, eucaryotic cells developed the system of Bcl-2 protein family that integrates information about the cumulative level of stress and growth factors to compute the cell's state of 'well-being' (Amaral et al., 2010). As domain-general models, pro-metacognitive systems are at the top of the information-processing hierarchy and contextualize the domain-specific information in order to model and track the 'state of the organism.'

The function of pro-metacognition is to keep the organism close to its homeostatic setpoints and to effect the allostatic transition to new setpoints to meet environmental demands. For example, when environmental conditions worsen, cells may go into the states of sporulation or dormancy (Lewis, 2000). This way, the organism can anticipate its future needs and take adaptive actions. An important notion here is the window of stress tolerance, where self-regulatory mechanisms can compensate for deviations from the setpoints without a state transition, such as the aforementioned sporulation or dormancy, so that the organism returns to the initial state of homeostasis. In this view, (brain) metacognition can be seen as serving the same function, that is, integrating/mentalizing domain-specific intero- and exteroceptive information to monitor and model the dynamics of the organism's well-being and to predict the necessary autonomic and external actions to either maintain its homeostasis or effect an allostatic transition. Social signals are one of those specific domains.

In the human brain, the default mode network (DMN) is often associated with both social and metacognition (Andrews-Hanna, Smallwood, & Spreng, 2014). Therefore, it seems plausible that DMN initially evolved as a higher-order domain-general network to model the organism's window of stress tolerance and thus regulate its stress response (analogous to the Bcl-2 protein network), and that in social species, it integrated social cognition. If so, we would expect a different connectivity in DMN-homologous networks of solitary vs social animals. A related hypothesis is that deficiencies in DMN (or DMN-homologs) connectivity with networks specializing in social cognition will leave DMN's socially-independent functions largely intact.

The hypothesis that the primary DMN's function is to integrate multimodal sensory information for anticipating and responding to environmental change was suggested a decade ago (Lu et al., 2012). It was spurred by the discovery of a DMN homolog in the rat brain. Rats, however, are social animals and may not be a good comparison model to tease DMN's social from intrinsic metacognitive functions. The primate DMN is functionally connected with such social cognition networks as the mirror neurons system (Molnar-Szakacs & Uddin, 2013) and the face processing circuitry (Schwiedrzik et al., 2015), and has an extensive intrinsic connectivity involved in theory of mind (Spreng & Andrews-Hanna, 2015). Comparative functional neuroimaging in other mammals may identify similar connectivity patterns in DMN homologs and provide an opportunity for comparison between social and solitary species from close taxa. Examples of such a comparison include rats vs hamsters, wolves vs foxes, chimpanzees vs orangutans, among others. Such studies can identify the 'minimal' DMN homolog concerned with only (or mostly) self-modeling metacognition.

Certain psychiatric conditions selectively affect social functioning. Perhaps, the most notable is autism spectrum disorder. There is ample evidence for functional, structural, and developmental abnormalities in the DMN of people with autism (Padmanabhan et al., 2017). Also, an aberrant functional connectivity between DMN and the salience network is found in social anxiety disorder (Lucherini Angeletti et al., 2021). Nevertheless, individuals with autism or social anxiety can be high-functioning and successful outside social settings.

To summarize, it appears that social and self-metacognition are to some extent dissociable, with self-metacognition likely being the primary higher-order mental capacity in the evolution of the mammalian brain. Further comparative studies can provide confirmation or disconfirmation of this notion.

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Dynamic unpredictability in grouping

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Abstract

Dunbar presents an intriguing analysis of variance in primate group sizes, and social glue's (grooming) relationship to cognitive evolution. This focus on primates with consistent and stable grouping excludes perspectives on the evolution of grouping beyond predation and competition. The analysis raises important questions about variation, dynamic sizes, and the conservation implications of variance for primate population extinction vulnerabilities.

Dunbar addresses three critical questions about grouping: what is a large vs a small group; what glues individuals together in groups; and what are the cognitive consequences of grouping. The vexed problem of "what is a group" is disregarded here since he limits his analysis to primates where groups can generally be defined and bounded, but addressing that question is still fundamentally important. As a non-primate, you don't need glue (grooming) if you school or herd; you also don't need complex recognition and inhibition mechanisms. However, fish (Kohda et al., 2019), birds (Emery et al., 2007), and possibly even gregarious wildebeest (Saltz, Palmer, & Beaudrot, 2023) do have decision capacities in the absence of "stable" groups. Excluding olfactory and vocal communication as glue mechanisms also excludes many non-primate but social species. So the question of groupingness (e.g. Moffett, 2024) remains to be debated and determined.

Perhaps what makes primates distinctive is the lack of much interesting variation in their groupings, since they follow clear fractal constraints. Dunbar notes the chaotic social and grouping dynamics of some primates; specifically squirrel monkeys, talapoins and mandrills. Could these species provide more insight into what makes groups evolutionarily interesting than the "boring" stable baboons and macaques, with their predictable rank and kin-determined cliques (Kappeler, 2019)? And if unpredictability underlies complex cognitive responses (Pellis, Pellis, & Himmler, 2014), then dynamic groupings should be particularly informative.

Thus, in order to understand the evolution of grouping, it might benefit us to focus on those very species that have dynamic structures; to try to make sense of the chaos in flexible groupings as evolved responses. What Dunbar calls the social infertility trap, the impact of social stress on female reproductive physiology, may be counterbalanced by shared infant care resulting in improved infant survival (Lee et al., 2016). The push away from gregariousness due to stress and competition is countered by the pull of greater reproductive success, beyond that of minimizing predation risk as proposed by Dunbar. Interestingly, primates use male infant care more than that from females, while shared female care may be more prevalent among carnivores, rodents and ungulates (Isler & van Schaik, 2012). Is this difference a function of cognitive capacity or of the energy costs of infant production, which are themselves linked since bigger brained babies cost mothers more in terms of both energy and time. A broader interspecific analysis may provide more answers to this question.

Species that have fission-fusion dynamics, where association and interaction decisions are made on a shifting temporal basis (Aureli et al., 2008), within a stable unit (e.g. chimpanzees, hyenas, lions) are amenable to fractal analysis; species with hypervariable and unpredictable grouping dynamics (dolphins, elephants and mandrills) may not be. Despite this constraint, social network analysis has provided clear insights into the complex structuring of sociality for some of these species (Sueur & Maire, 2014; Weiss et al., 2019), and these studies have emphasized the importance of feedback between maintaining relationships and physiological needs, affecting network stability. In addition, Strier, Lee, and Ives (2014) argued that inbreeding avoidance expressed through dispersal regimes underlies thresholds for fission-fusion dynamics compared with permanent group fissions, with fission-fusion more likely under female-biased dispersal with male philopatry and permanent splits more likely under male-biased dispersal with female philopatry. Limiting analyses of the drivers of association to competition and fertility suppression may obscure other important patterns determining grouping.

Another issue with the fractal analysis relates to the finding that the highest variance occurs at optimum group sizes; an instantaneous observation of a species' group size may or may not represent that species' characteristic group size or the historical demographic or social processes that resulted in that size in a population (Strier, 2017). Long-lived species such as primates are likely to experience

environmental and demographic dynamics over a lifetime that influence their group size and composition and the observed behavioural variation at any specific time, as well as producing differing responses to similar stimuli (Strier, 2017, p 8). These raise questions both about data quality from short versus long-term studies and more critically about shifting baselines – what was a historical group size, optimum or not, may never be known given anthropogenic alterations of primate habitats. Nor do the size metrics used here take into account the propensity for multi-species grouping seen in a number of primate and other species. However, ultimately the modelling of single species and multi-species networks should provide us with greater insights into what group sizes can or, under optimal conditions, should be, and Dunbar's analysis provides us with a way to explore these questions.

Dunbar's findings also have important implications for our understanding of primate population dynamics by providing a general framework against which we can assess how environmental processes impose group size deflections from a "norm". Deflections can include both long term climate change (e.g. aridification and tree loss for the Amboseli baboons: Altmann, Hausfater, & Altmann, 1985), immediate environmental catastrophes such hurricanes affecting *Macaca* populations (Testard et al., 2021), disease epidemics experienced by a variety of primate populations (Rouquet et al., 2005; Holzmann et al., 2010; Strier, 2021), or abrupt regime shifts in mortality as seen in *Brachyteles* (Strier & Ives, 2024). More generally, the findings imply, in terms of population resilience, that populations whose group sizes become synchronised by natural catastrophes at the low end of their distribution will be much more at risk of extinction than those with a wider range of group sizes simply because their fertility is so depressed. This is a testable hypothesis when the relative impact of fertility and mortality on group (and population) size can be assessed. Taking this association into account in our studies of primate populations could be of vital importance in assessing their ability for persistence in a changing world.

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Meta-cognition for music as a solution to the fragmentation problem

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Abstract

Meta-cognition enhances the social bonding hypothesis for musicality, integrating imagination, episodic simulation, causal inference, and inhibition. Music fosters group cohesion by engaging the endogenous opioid system, supporting intergroup understanding through vivid mental imagery, and facilitating socio-affective fiction. Additionally, causal inference enables contextual interpretation of music, while inhibition refines

musical coordination and executive function, reinforcing cognitive flexibility for cooperative social behavior.

The stressors of social life within large groups might have never been more apparent than in current society, but these stressors are not new. Dunbar argues that to maintain social cohesion despite these stressors, primates use social-structural, behavioral, and cognitive strategies, including vocalization, chorusing, and conversation. In this response, we spell out the links between Dunbar's insights on group cohesion and theories of the evolution and social functions of music.

Extending Dunbar's case leads to a reconceptualization of the social bonding hypothesis for the evolution of musicality, an account co-authored in BBS by one of us with other colleagues (Savage et al., 2021). The social bonding hypothesis posits that rhythm-based and pitch-based processes are design features of music that bring larger groups together. We had previously proposed that prediction and reward, as implemented by the dopaminergic reward and endogenous opioid systems (EOS), serve as the underlying mechanisms for this bonding. We now agree with Dunbar that meta-cognition encompasses an additional suite of cognitive mechanisms – including imagination, episodic simulation, causal inference, and inhibition – through which musicality brings large groups together.

Evidence for EOS-mediated musical effects on social bonding includes, but is not limited to, temporally synchronized processes. In addition to people moving together being more cooperative together (Cirelli, Einarson & Trainor, 2014; Hove & Risen, 2009; Rabinowitch & Meltzoff, 2017), sound elicits rhythmic movement in male more than female chimpanzees (Hattori & Tomonaga, 2020). Rhythmic swaying was sometimes accompanied by vocalization, reflecting a behavioral mechanism that allows music to trigger the EOS. Vocalizations of species like indris (*Indri indri*) and gelada baboons (*Theropithecus gelada*) constitute structured songs with distinct timing and pitch variations, suggesting a level of complexity that parallels aspects of human music (Gamba et al., 2016).

How meta-cognitive processes shaped the evolution of musicality is less clear in the animal world, but new work from music cognition shows that meta-cognition is entwined with musicality in humans. Trevor and Frühholz (2024) argue that music, beyond its effects on social bonding, evolved as a tool for socio-affective fiction (Trevor & Frühholz, 2024). According to this theory, music added a dimension of immersiveness to storytelling that enabled the elicitation of strong emotions, allowing listeners to practice the emotion regulation skills that promote harmonious living within large groups.

The vivid imaginings that music can elicit make it a powerful tool for intergroup understanding. Music elicits vivid episodes of scene construction in spontaneous thought, including autobiographical memories, future simulations, and fictional imaginings (Belfi et al., 2016; Margulis et al., 2022; Margulis & Jakubowski, 2024). These episodes engage the default mode network, including but not limited to the medial prefrontal cortex, which is also engaged during acts of musical creativity such as improvisation tasks (Belden et al., 2019; Vergara et al., 2021). Converging evidence from neuroimaging studies shows that regions of the default mode network also represent high-level musical event structure, thus providing a shared neural substrate for meta-cognition and socio-affective processing during music listening (Williams et al., 2022).

Part of meta-cognition entails causal inference, based on the available evidence for the perceptual system. In that regard, a recent review article argues that source sensitivity, defined as the capacity to infer the causal and contextual sources of music, plays an even stronger role in music appreciation than previously acknowledged (Thompson et al., 2023). Presented with musical sound, listeners automatically generate a representation of who created it, and the music's typical social contexts and functions. This ability emerges early in life, with five-month-olds responding preferentially to a melody previously sung in person by their caregiver in comparison to another highly similar melody (Mehr, Song, & Spelke, 2016). No such preference arose if the infant had previously encountered the melody on a screen or emitted by a toy. The contextual circumstances within which they were exposed to the melody shaped how they subsequently received it. Adults interpret music "as the sonic trace of social relationships between a group" (Aucouturier & Canonne, 2017) such that even when presented with novel musical excerpts, adults engage in mentalizing and infer their associational and contextual meaning, resulting in widespread intersubjectivity in the personal thoughts and imaginings the music evoked (Margulis et al., 2022; Wu et al., submitted). Individuals who report stronger musical skills (Müllensiefen et al., 2014) were also more accurate at categorizing Chinese and Western melodies by their cultural origin. This suggests that alongside more robust internal models of musical structure comes an enhanced capacity to infer social context.

Finally, inhibition is a fundamental meta-cognitive process in music-making, playing a crucial role in both individual and group coordination. Dunbar describes inhibition as a meta-cognitive skill for exerting self-control in social situations, and cases of inhibition are pervasive in musical behavior. Self-control is essential for learning to make music, as executive functions such as response inhibition enable musicians to synchronize their actions in ensemble settings, ensuring that they start, stop, and adjust their playing in unison. Multiple studies in music cognition have shown that children with musical training perform better on executive function tasks, especially response inhibition (Hennessy et al., 2019; Sachs et al., 2017; Zuk et al., 2014). Neurologically, inhibition is associated with the anterior cingulate cortex (ACC). This region is activated in musical tasks, for example, when singers adjust their vocal pitch in response to perturbed auditory feedback (Zarate, Wood, & Zatorre, 2010). This role of the ACC extends beyond human music-making – in primates, the same region governs explore/exploit behaviors, suppresses maladaptive responses, and encodes prediction errors as well as simulated reward signals (Hayden, Pearson, & Platt, 2009, 2011). The shared reliance on inhibitory control in both human and primate cognition suggests that musical engagement not only refines executive function but may also contribute to fostering social cohesion by reinforcing the cognitive flexibility necessary for cooperative behavior.

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It's not just about allies – The role of identity in stable ingroup memberships

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Abstract

Dunbar exclusively sees groups as arising through the aggregate relationships between individuals and thereby makes the serious omission of not considering the capacity of those individuals to categorize one another as ingroup versus outgroup members.

> How is it that, despite . . . apparent cognitive constraints on group size [in terms of the number of stable relationships individuals can maintain], modern human societies are nonetheless able to form super-large groups (e.g., nation states)?
>
> —Dunbar (1993, p. 692)

Dunbar's original (1993, p. 693) solution to this conundrum was that the "ability to categorise individuals into types clearly makes it possible to create very much larger groups than is possible by direct interaction." Apparently, he no longer thinks so, as he makes no mention of "types" (social specialization) in the current article. His focus has turned to the hypothesis that animals tailor their capacities to bond with allies to generate "stable social groups," including, in humans, exceptionally populous ones.

I quote Dunbar's above question in section 5 of my 2025 article for this journal, where I reach a different conclusion. The groups of interest to Dunbar (designated in Moffett [2025a] by the moniker

"societies," of which modern states represent an extreme) are products not of often malleable social relations but the constituent members' recognition of who belongs, and as such are ingroups, per social psychologists – in this instance, ones of an enduring sort.

Briefly: While societies foster social bonds, they aren't necessarily reducible to social networks even if you include their weak or indirect ties – and certainly not for many primates, humans among them (consider your foreign friend; or the misanthropic hermit who is still identifiably *American*): "Since societal borders needn't conform to the aggregated contacts between all its members . . . accurately describing a society requires going outside the logical universe of networks; similarly, portraying how networks relate to a society requires independently assessing who belongs where" (Moffett, 2025a). Nor are individuals necessarily aware of being part of a social network in the way society members perceive themselves as belonging together. For such reasons, the social connectedness (e.g., by grooming: Dunbar & Shultz, 2010) of individuals doesn't serve to effectively define, and distinguish, their memberships (which for humans include strangers who share an identity but lack even indirect ties). As Seyfarth & Cheney (2017, p. 83) conclude, "In the mind of a baboon . . . social categories exist independent of their members."

A category shift is required for an outsider to become integrated into a society. Upon joining a troop, a male vervet alters his call signaling he is an outsider to one indicating his initially low social rank (Seyfarth & Cheney, 1984). Robert Seyfarth (personal communication) tells me it's likely the troop members similarly adjust the calls they direct at the new arrival, even while some may continue their attacks on him.

I don't deny that social relations factor into group stability; we can expect that animals will evolve to categorize one another into groups of sizes and configurations that function effectively, perhaps including, e.g., Dunbar's "upper" and "lower grade" primate species (though his assertion in section 3.2 that there exist "distinct clusters," i.e., "grades," with "a natural breakpoint" between them, is baffling given the distribution of mean group sizes shown in Figure S2; note that internal cross-cutting groups could be a stabilizing factor for very large societies: Moffett, 2019, p. 134). Dunbar has insights regarding the social deterioration that can spread as a population grows, but I would argue that the resultant stresses lead to a category shift in who primates perceive as belonging to their group (Moffett, 2025b). In one carefully documented macaque troop, for example, the conflicts that led to a permanent severing shifted from fights between individual members of two recognizable factions to confrontations between the factions as a whole, as though the monkeys had ceased viewing one another as individuals and begun acting as collectives ("the two groups were becoming autonomous": Prud'Homme (1991, p. 14)). Goodall (2010, p. 239) wrote of the Kahama and Kasekela chimpanzee communities that had split off from each other at Gombe:

> [The chimpanzee] sense of group identity is strong and they clearly know who "belongs" and who does not. . . . And this is not simple "fear of strangers"—members of the Kahama community were familiar to the Kasekela aggressors, yet they were attacked brutally. . . . Moreover, some patterns of attack directed against non-group individuals have never been seen during fights between members of the same community—the twisting of limbs, the tearing off of strips of skin, the drinking of blood. The victims have thus been, to all intents and purposes, "dechimpized," since these are patterns usually seen when a chimpanzee is trying to kill an adult prey animal—an animal of another species.

While, as in other primate societies (e.g., Langergraber et al., (2014) for chimpanzee communities), breakdowns that result in permanent divisions appear to be inevitable in the long term, Moffett (2019, pp. 248-50) proposed that shared traits "marking" our ancestors' identities would help keep societies intact at sizes exceeding those of other primates despite the stressors that Dunbar describes. These generate such emotional connections that, as Brewer (1991, p. 475) states, "People die for the sake of group distinctions" – a preadaptation to the emergence of the nations which Dunbar puzzled over in the headlining quote, a topic with far-reaching implications (Moffett 2019, 2025a).

Other details: Dunbar brings up "a natural tendency for animals who are foraging together to drift apart as their activity schedules become desynchronized," but neglects how individual recognition keeps groups together. Many society-dwelling species stay connected at a distance via voice recognition and give a "lost call" to reconnect when out of contact (e.g., Todt et al., 2012). He sees the need to rest as taking time away from social grooming, which he claims is exhausting, even though the cited study (Giorgi et al., 2001) concerns bats stricken with tenacious mites. Might it be that all but the most sick or worn-out animal is free to groom (by what Dunbar calls "soft touch") or be groomed even as they thermoregulate or digest a meal (which ruminants absolutely can do while tending their allies: Daryl Codron, personal communication) The fact that Rose (1977) found that olive baboons spend thrice the time at rest that they do grooming one another argues against primates maximizing their efforts at building relationships.

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Spelling out the mechanism: functional support and modified stressor appraisal buffer a cost of increased group size

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Abstract

Dunbar suggests structural, behavioral, and cognitive mechanisms to mitigate the costs of living in large groups. While we generally concur with the notion of group size effects on female productivity, we call for a more explicit treatment of how functional support alleviates social costs and disagree with the outright dismissal of ecological drivers and phylogenetic inertia.

Living in stable cohesive groups comes with a number of costs, some of which increase over broad ranges of group size, including risk of infection and competition for access to resources, such as mates, safe spatial positions in the group geometry, food, and supportive partners (Krause & Ruxton, 2002). Dunbar provides a unique perspective on the problems faced by primates living in large groups. Here, we critically evaluate some of the premises of this framework in the light of the existing literature.

First, we propose scrutinizing the behavioral mechanisms suggested to alleviate the "stresses" associated with living in large groups, as the target article remains vague about the precise function of grooming and alliances. It is generally accepted that social strategies have evolved to mitigate the costs of group-living for at least some group members (Silk, 2007; Snyder-Mackler et al., 2020; Thompson, 2019). Importantly, different types of adversities arising from increasing group size are countered by distinct affiliative social strategies. For instance, casting a wide social net of tolerant, but not particularly strong affiliative relationships, may help maintain a safe central spatial position, whereas forming a few strong, lasting affiliative ties with equal and reliable partners provides access to monopolizable resources, if these partners serve as allies in outward aggressive conflicts (Ostner & Schülke, 2018). The two strategies are likely independent of each other. The strength of an individual's strong ties and the number of weak ties it forms (relative to the average strength) are not correlated across group members in 15 groups of five primate species (Schülke et al., 2022). In our reading, Dunbar argues that groups can grow larger if individuals invest more in the strength and number of strong affiliative relationships, because these relationships serve as alliances, but he does not explain how these function. Under Dunbar's central premise of purely social costs of group size we propose that alliances will provide two benefits. Strong affiliative relationships underlying alliances offer functional agonistic support when an individual is actually confronted aggressively, and consequently will also modify stressor appraisal. If an individual can count on a few reliable partners as allies, aggression is less likely to elicit a strong stress response, because escalation by the aggressor becomes less likely. Therefore, it is not (as proposed by Dunbar) the grooming received from a partner that buffers physiologically against within-group aggression, but the functional and perceived support provided by the strong relationships built and maintained by grooming and other affiliative behaviors.

Second, we question the proposal of an endorphin-driven infertility trap in larger groups driven solely by increased social stressors for several reasons. (i) The unified stress response originating in the hypothalamus in reaction to a diverse array of adversities produces CRH which is cleaved into ACTH triggering glucocorticoid release from the adrenal cortex and the precursor of beta-endorphin (Pilozzi, Carro, & Huang, 2021). Given the one-size-fits all nature of the stress response, the parallel endorphin and glucocorticoid release will not only be caused by heightened aggression in larger groups, but equally by increased feeding competition negatively affecting energy balance. Indeed, if primates are released from food scarcity by provisioning, group size often doubles as do reproductive rates which suggests ecological constraints overriding social stressors as the main predictor of fertility at least in these circumstances (Borries, Koenig, & Winkler, 2001; Takahata et al., 1998). Similarly, constrained access to food alone may explain very fine-grained diminishing returns with increasing group size particularly for capital breeders or relaxed income breeders that store energy for the upcoming reproductive event before they conceive (Brockman & van Schaik, 2005; Heesen et al., 2013; Jönsson, 1997; Koenig & Borries, 2001). Thus, we disagree with the dismissal of ecological influences on group size related decreases in productivity. (ii) The target article remains unclear why social stressors, i.e. aggression rate, increase with larger group sizes (independent of increased feeding competition) and why any increase in aggression – even aggression among third parties - should lead to a stress response. The stress response is an evolved response to restore disrupted homeostasis and not a reaction to something that has no fitness consequences (Beehner & Bergman, 2017; Brent et al., 2014; Ostner & Schülke, 2018). (iii) Related to the above, grooming itself seems an unlikely candidate to lift individuals out of an endorphin-caused "infertility trap" as grooming does not buffer, but instead enhances the endorphin response (Marchin & Dunbar, 2011; Pearce et al., 2017).

Third, we caution against dismissing the possibility of phylogenetic inertia as a factor explaining the observed distribution of group sizes and associated adaptations, as several of the traits discussed clearly cluster taxonomically. We provide three examples: (i) the soft touch of grooming cannot be a key mechanism across primates, because large platyrrhines do not use grooming as their main affiliative behavior (Aureli & Schaffner, 2007) and lemurs do not groom softly, but groom at high stroke frequencies using their specialized tooth comb and tongue instead of their hands which also puts an energetic limit to their total grooming time (Rosenberger & Strasser, 1985); (ii) changing diet to free time for grooming is not a flexible option for colobines. Foregut fermenters do not strive on diets rich in those fruits that Dunbar envisions (low in fiber and rich in carbohydrates), but suffer damage to their gut microbiome from associated changes in pH that may even hamper a return to a leafy diet (Goltenbolth, 1976). If colobines fall back on fruit when their preferred leaves are

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not available (Milich et al., 2014), these fruits are unripe, fibrous and lack juicy flesh (Davies, Oates, & Dasilva, 1999); (iii) females regularly engage in aggressive coalitions only in cercopithecines but not in lemurs, colobines, and most of the platyrrhines irrespective of group size which suggest phylogenetic constraints on the evolution of alliance formation for within-group conflict (Chapais, 1995; Nakamichi & Koyama, 1997). In summary, critical pieces of the pathway linking changes in grooming behavior to increased group size are not free to vary between species which calls for an analysis strategy closely tracking the shifts in different behaviors and in group size across the primate phylogeny.

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Play and laughter: overlooked pillars of social cohesion. Commentary proposal for structural and cognitive mechanisms of group cohesion in primates

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Abstract

While grooming and other forms of physical bonding are crucial for stress management, social play and laughter deserve equal recognition as tools for both stress relief and the reinforcement of social relationships. They play a pivotal role in the development of motor and social skills and serves as a foundational behavior in species that rely on cooperation and alliance-building.

We appreciate the insightful article on the role of grooming and social behaviors in stress management and bonding within social species. We would like to extend this discussion by highlighting the importance of social play and related facial expressions and vocalizations (e.g., laughter, play face, 50 KHz sounds) which, like grooming, are crucial for stress regulation, relationship maintenance, and the formation of social bonds—yet are largely overlooked in the target article.

As noted in the article, grooming triggers endorphin release, fostering bonding and reducing stress. We want to emphasize that social play and laughter similarly activate endorphin responses and play key roles in social cohesion (Palagi, de Waal, & Caruana, 2022; Burghardt et al., 2024). While laughter is briefly mentioned in relation to humans, social play is entirely omitted. We fear that the failure to address recent comparative data on these behaviors seriously undermines the target article and the evolutionary scalability of its model, depriving it of important empirical support. This is especially striking given the ubiquity and importance of play in humans, non-human primates, and indeed throughout the animal kingdom (Burghardt, 2005; Burghardt & Pellis 2019).

Social play activates the brain's reward system, reducing stress and promoting cognitive development in both humans and other animals and, here, we provide recent studies empirically demonstrating such effects (e.g., Wang & Aamodt 2012; Whitten et al., 2025). In societies with high tolerance and a need for cooperation, social play serves as a mechanism for assessing partners' willingness to invest in relationships while simultaneously allowing individuals to show vulnerability—key components of trust-building. Palagi (2023) provide evidence on primates and social carnivores that play may reduce group dispersal by fostering cooperation through these social cues.

In relation to grooming, social play may, in fact, be more important in social bonding, especially in young animals. Shimada and Sueur (2018) studied a habituated troop of wild Japanese macaques and recorded grooming and play bouts as well as social proximity and concluded that "the hypothesis that the biological function of social play among immature Japanese macaques is to strengthen their social bonds in the near future and develop their social life appears to be correct. For juvenile macaques, social play, rather than grooming, functions as an important social mechanism to strengthen affiliative relationships." They also showed the importance of social play in social bonding in wild chimpanzees (Shimada & Sueur 2014). Regarding laughter, this behavior is barely mentioned in the target article and only in relation to humans, despite the emerging literature on the social bonding function of laughter across species (Caruana, Palagi, & De Waal, 2022). This is quite remarkable considering that the author himself has provided substantial evidence over the years regarding the significance of this multimodal communicative mechanism as a replacement for grooming behavior, which is extensively discussed in the target article (Dunbar, 2012, 2022).

Social connection mediated by laughter and play faces becomes evident through the process of motor resonance, which is manifested neurally through mechanisms grounded in the Mirror Neuron System (Caruana et al., 2020; Billing, Cooper, & Scott, 2021; Del Vecchio et al., 2024) and behaviorally through the phenomenon of rapid facial mimicry (Davila-Ross and Palagi, 2022). Rapid facial mimicry has now been demonstrated in numerous species of social mammals, including humans (Hess & Fischer 2013), non-human primates (Demuru, Ferrari, & Palagi, 2015), carnivores (Nolfo, Casetta, & Palagi, 2021), ungulates (Maglieri et al. 2020), and cetaceans (Maglieri et al., 2024). Discussing the shared function of laughter and play faces in social bonding across species would strengthen the evolutionary scalability of the proposed model.

Finally, the connection between laughter and humor is worth mentioning. Humor is a complex cognitive faculty that alleviates tension and fosters social bonding through language—an ability with few counterparts in the animal kingdom, although teasing has been increasingly documented (Laumer et al., 2024). A recent theory suggests that humor primarily serves as a tool for social bonding via linguistic pragmatics, mirroring the role of play and laughter in social cohesion (Flamson & Barrett 2008). This insight adds an important piece to the puzzle, reinforcing the evolutionary continuity of these behaviors.

In short, while grooming and other forms of physical bonding may indeed be important for stress management and the formation of social bonds, social play and laughter deserve equal recognition as grooming and other physical bonding as tools for both stress relief and the reinforcement of social relationships. They play a pivotal role in the development of motor and social skills, serving as foundational behaviors in species that rely on cooperation and alliance-building. Furthermore, social play is perhaps one of the best avenues for studying social cognition and communication and its underlying evolution (Palagi et al., 2016).

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Removing the glass ceilings: diverse mechanisms for social cohesion

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Abstract

Dunbar suggests that social stressors set "glass ceilings" on the evolution of mammalian group size and cohesion. We argue that this glass ceiling narrative conceals three contentious anthropocentric assumptions. First, large stable groups would always be beneficial. Second, grooming is an indicator for maintaining group cohesion. Third, group size is primarily limited by cognitive or behavioral incapacity. We challenge all three assumptions.

Dunbar (2025) tells a story where primates with high brain-to-body ratios, like us, broke through the "glass ceilings" that limited our group size. He suggests that group size in primates is best explained by these cognitive limits, more than by other features like ecology. This ceiling-shattering narrative device may appropriately describe our evolutionary history. However, it also sets up a "tower" with humans at the top and all other animals somewhere below based on their more or less human-like socio-cognitive structure.

Applying this anthropocentric structure to other species implies that a more human-like social structure would benefit them. Dunbar (2025) does this when he renders social stressors as obstacles limiting stable group size and not adaptations. Dunbar notes, for example, that ungulates and some primates develop infertility in large groups, which they must overcome by having unstable groups. The same phenomenon can be described as an adaptation to prevent ecologically destructive large, stable groups.

This narrative positions cognitive and behavioral strategies as something that must develop to pass the obstacles, as opposed to imagining that obstacles arise to inhibit otherwise capable individuals. To conclude that we evolved large brains and grooming behavior to live in large, stable groups, we must rule out other explanations for the apparent lack of stability in large primate groups. In particular, we must set aside the possibility that large stable groups are sometimes less ecologically sustainable, and therefore less beneficial.

The first of Dunbar's (2025) two ceilings for primate groups limits many, typically leaf-eating, primates to "cliquey" small groups of 10 or fewer, which only temporarily congregate in larger "herd" like groups. He hypothesizes that their foraging does not allow sufficient grooming time to maintain large stable groups; primates whose diets allow more free time would maintain larger groups of 15–20 individuals through reciprocal grooming. Such a hypothesis runs contrary to an ecology-focused hypothesis that grazing or leaf-eating animals might benefit from smaller or more disparate groups, only forming large groups temporarily to prevent lasting ecological harm.

These ecological constraints can be removed by providing an overabundance of food. If the constraints on group size were cognitive, not ecological, we should expect that provisioning animals would not increase group size. And, if the grooming time was limited by foraging, we should expect provisioned animals to increase grooming time. However, provisioning the macaque population in Japan has led to a doubling of group size while maintaining the same social structures, every 7 years from 1952 to

1976, with populations reaching over 1000 members (Yamagiwa & Hill 1998). In laboratory studies, an overabundance of food (whole vs. chopped) did not mark a significant increase in grooming or self-grooming, with a reduced mean duration of grooming during the testing condition, but did mark increased time huddling in clusters and feeding (Sandri et al., 2017). In overabundance conditions in urban-dwelling macaques, there were no increases in grooming activities, but there were increases in behaviors that resembled play and leisure (Jayapali et al., 2023). Overabundance conditions likely change the underlying social dynamics that limit group size. These changes in ecological conditions likely lead to less strain on resource management and, therefore, relaxed social pressure. Their social maintenance strategies are not limited to grooming; they deployed various social maintenance strategies like increased play or huddling together while feeding.

Pluralistic social maintenance strategies other than grooming are widespread among animals, including those who live in "unstable and herd-like" social structures. For example, even vampire bats practice reciprocal food-sharing and live in large colonies (Wilkinson, 1984; Carter et al., 2020). There are also very low-effort ways to bond for primates and non-primates, including gentle touch (Monsó & Wrage, 2020; Jablonski, 2021), auditory signals (Teixeira da Cunha and Byrne, 2009; Xie et al., 2024), or merely being close while foraging or eating together. A pluralistic approach to social maintenance (Westra and Andrews, 2022) may reveal many behavior patterns that help group cohesion, leaving the grooming time constraint a permeable boundary, not a ceiling.

Dunbar's (2025) ceiling narrative ends with the claim that humans, when living as hunter-gatherers, often form large stable groups of about 40 individuals, which in turn form larger societies. He implies that there is something cognitively manageable and "natural" to this "grade" of group size. However, human hunter-gatherers are famously holders of ecological knowledge; they intentionally set social boundaries that spread out a population to conserve animal and plant populations (Hensen et al., 2021; Inksetter, 2018). Even human group size is interdependent with ecology.

3Early humans, and some of our closest great ape relatives, may have struggled to find the time and develop the skills needed to live in large, stable groups. We may have evolved large brains partly to overcome those obstacles. However, we risk problematic anthropocentrism if we insist that the social structures of other primates, or social animals more broadly, are limited by an incapacity for social maintenance of group cohesion. Instead, we might consider the mechanisms and stressors that limit their group size, like the infertility trap, as adaptations that evolved to prevent them from forming large stable groups with their existing social skills.

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Fairness expectations scaffolded the evolution of larger groups

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Abstract

We propose that the emergence of relationship-based social expectations and their evolution into fairness expectations played a key role in the size and cohesion of hominin societies. One of the central challenges of group living is the need to create and sustain stable and mutually beneficial patterns of cooperation. By

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regulating collaborative interactions, social expectations make group living less stressful.

Dunbar identifies cohesion as an important adaptive challenge for group living species and outlines structural, behavioral, and cognitive strategies for maintaining the stability of ever larger communities. Dunbar's discussion of cognitive strategies focuses on behavioral inhibition and mentalizing. While both capacities are undoubtedly crucial for group cohesion, this insightful analysis neglects a key stressor on group living: the need to regulate cooperative relationships within groups. From friendships to alliances, social bonds in primates serve not just to defang social tensions; they function as mutually beneficial collaborative relationships. Here, we argue that fairness functions as a crucial cognitive-emotional strategy for maintaining group cohesion. We describe how dyadic expectations that emerged in the context of nonhuman primate relationships evolved into humans' sense of fairness, allowing for larger and more cohesive groups in the process.

Dunbar is right to highlight friendship as a foundational mechanism underlying primate group cohesion. Friendships are dyadic cooperative relationships, which structure primate sociality. For example, chimpanzees trust their friends (Engelmann & Herrmann, 2016), help them more (Engelmann, Haux, & Herrmann, 2019), and console them more after conflict (Fraser, Stahl, & Aureli, 2008) relative to neutral partners. Friendship even predicts chimpanzees' willingness to join a territorial patrol—a high-risk behavior crucial for group cohesion (Samuni et al., 2018).

As Dunbar points out, building and maintaining friendships is a costly process, requiring both time spent grooming and a suite of cognitive and affective adaptations. For this investment to be worthwhile, the friendship needs to confer more benefits than the costs it incurs; staying attached to a free-rider will improve the fitness of no one. Stable friendships thus require regulatory mechanisms that ensure that both individuals remain satisfied with the relationship.

Primates expect certain manners of treatment from their collaborative partners and react with negative emotions when these expectations are violated (Engelmann et al., 2017; Ritov et al., 2024; Titchener et al., 2023). For example, chimpanzees express their dissatisfaction when a collaborative partner fails to live up to their expectations (Engelmann et al., 2017; Ritov et al., 2024). Such displays of negative emotion can act as a corrective force, influencing the partner to act as they expect them to and thereby stabilizing the relationship (Sell et al., 2017). In other words, social expectations can help individuals implement a strategy of "partner control" (Schino & Aureli, 2017). Chimpanzees' expectations are flexible, responding not just to outcomes but to their partners' intentions (Engelmann et al., 2022). This indicates that they rely on complex cognitive representations in addition to their strong affective component.

Nonhuman primates form these expectations based on prior interactions with the individual. Being the recipient of a cooperative act triggers a positive emotional response (e.g., gratitude); being the target of an uncooperative act triggers a negative emotional response (e.g., anger; Gervais & Fessler, 2017). These momentary emotional responses are linked to the identity of the actor causing them, updating an attitudinal representation of the actor and contributing to the formation (and dissolution) of an affective bond between both parties (Gervais & Fessler, 2017; Schino & Aureli, 2021). Hence, these expectations are relationship-specific in nature. Indeed, in a recent experiment, we compared food theft between friends and non-friends. Supporting this account, we recently found that friendship not only inhibited antisocial behavior but shaped chimpanzees' emotional reactions to it (Ritov et al., 2025).

Relationship-based social expectations can only scaffold cooperation with a limited number of partners. Given the high cost of close relationships, there are natural limits to the number of individuals one can form such bonds with. Therefore, even larger groups require a different type of mechanism to regulate collaborative relationships with distant group members (Dunbar's "weak ties").

The relationship-based expectations we see in other species evolved into fairness expectations in humans. In fairness, the protest is grounded not in an expectation for how a specific relationship-partner should treat us, but expectations for how *one* should be treated - i.e., how costs and benefits should be distributed between collaborative partners in general. While it has been argued that an aversion to unequal treatment is an ancestral trait, our recent meta-analysis has shown that this does not appear to be the case. Nonhuman animals respond to violations of social expectations, but they do not seem to care whether a conspecific is treated better than they are (Ritov et al., 2024). Fairness therefore appears to be a human-unique regulatory strategy.

The emergence of generalized fairness expectations allowed for the increase in group size and cohesion we see in humans. A sense of fairness guides how we treat others even when a prior relationship is lacking, allowing individuals with otherwise weak ties to coordinate their expectations. Furthermore, fairness expectations can manifest in a direct comparison of immediate costs and rewards, allowing even one-off interactions to be mutually beneficial—unlike relationship-based expectations, which depend on long periods spent grooming and in close proximity. As such, fairness expectations—and other normative standards—allow the sphere of people we collaborate with to be much larger than the number of people we are closely bonded with (Henrich et al., 2010).

To sum up, we propose that social expectations have played a central role in the size and cohesion of primate social groups. Nonhuman primates form social expectations within the context of close relationships, which allow for these relationships to be mutually beneficial and thus more stable over time. This relationship stability reduces the tensions inherent to group living. In humans, these expectations generalized to fairness expectations, which allow for mutually beneficial collaborations with a larger number of individuals. Dunbar's "cognitive solutions" can be thought of as a suite of adaptations enhancing group cohesion, within which social expectations deserve particular attention.

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Intentional communication reduces social stress by increasing the predictability of conspecifics' behaviour

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Abstract

Specialised forms of social cognition enable primates to manage the stresses of group living by allowing for flexible and intentional communication. This is used to increase the predictability of conspecifics' behaviour for both signallers and receivers. Intentional communication helps to overcome the stimulus-driven processing that may occur due to stress, enhancing attention allocation in receivers.

We agree with Dunbar that for primates: i) Living in large groups creates stresses arising from managing a larger set of differentiated social relationships; ii) Managing weak ties in groups in the upper grade cannot be achieved through direct or indirect grooming relationships and therefore requires more sophisticated cognitive mechanisms; iii) Communication plays a key role in managing these differentiated social relationships by helping primates read others' intentions (Section 5). A key question posed by Dunbar (Section 3.2.3) is how specialised forms of social cognition are actually used to manage social relationships. We argue that one key function of this specialised cognition is to allow for flexible and intentional communication which increases the predictability of conspecifics' behaviour, thereby reducing the physiological stresses associated with group living (Seyfarth & Cheney, 2018; Roberts et al., 2022). For signallers, communication is used to influence the receivers' behaviour and therefore make it more predictable, whilst for receivers, communication allows them to better predict the future behaviour of signallers, especially behaviour directed towards themselves (Seyfarth & Cheney, 2018). As an unpredictable social environment is a key factor in causing stress (Sapolsky, 2021; Seyfarth & Cheney, 2018, Roberts, Dunbar, & Roberts, 2022), any reduction in the uncertainty of conspecifics' behaviour associated with communication will be beneficial for both signallers and receivers.

Primates use a wide variety of communication to help meet the demands of living in complex social groups, including vocalisations, gestures and facial expressions (Seyfarth & Cheney, 2018). For both vocalisations (Fischer, 2017) and gestures (Roberts et al., 2012a), there is flexibility in both the production and usage according to the social context (Roberts, Vick, & Buchanan-Smith, 2012b). For example, across a number of primate species, a range of low-amplitude vocalisations (grunts) are used to signal affiliative intent when approaching another conspecific. This increases the predictability of behaviour between interacting dyads when they are in close proximity, which leads to vulnerability to potential aggression. In female chacma baboons (Silk, Seyfarth, & Cheney, 2016) and olive baboons (Silk et al., 2018), production of grunts on approach increased the likelihood of affiliative interaction and were used less frequently with strong bonds (mothers and daughters) and more frequently with weaker bonds (sisters and non-kin), where the risk of aggression is higher. This demonstrates the value of communication in increasing the predictability of behaviour of weak bonds for both signallers and receivers of communication.

In addition to vocal communication, gestural communication - voluntary movements of the arms, head, body postures and locomotory gaits – plays a particularly important role in managing weak ties and increasing the predictability of conspecifics' behaviour, as there is greater flexibility and intentionality in the use of gestures compared to vocalisations among the great apes (Tomasello & Call, 2019; Roberts & Roberts, 2020). Intentional gestural communication – communication that is targeted at a specific audience to produce a specific response – is a key feature of gestural communication

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(Roberts & Roberts, 2020; Tomasello & Call, 2019) that appears to play a central role in managing the demands of group living (Roberts & Roberts, 2020). By targeting communication to a specific individual through body posture, gaze and use of the appropriate modality, and persisting and elaborating in that communication until the desired response is achieved, for the signaller intentional gestural communication provides a way of increasing the probability of the desired response from the receiver (Tomasello & Call, 2019). For receivers of communication, intentional communication makes it clearer that the signal is directed specifically at them and is personally relevant to them, enabling them to detect and respond appropriately to the signal in a complex social environment with competing demands for their attention (Roberts & Roberts, 2020).

In larger social groups, using communication to increase the predictability of conspecifics behaviour becomes more important as there are more weak ties to manage, leading to a greater risk of misreading intentions and aggression (Section 4). Flexible use of communication with these weak ties can effectively signal both aggressive and affiliative intentions, facilitating group cohesion and avoiding physical aggression (Silk et al., 2016; Silk et al., 2018; Damjanovic, Roberts, & Roberts, 2022). In these larger groups, more complex communication repertoires - systems that contain a larger number of functionally distinct elements (Freeberg, Dunbar, & Ord, 2012) – enables a more nuanced understanding of conspecifics intentions. For example, combining signals across different modalities (Heesen et al., 2022), or using sequences of vocalisations (Leroux et al., 2023) or gestures (Roberts & Roberts, 2019), can increase the efficiency of the communication signal. Further, social stress can itself impair social bonding by disrupting attention allocation and conscious awareness, leading to stimulus-driven processing where individuals react primarily to the immediate stimulus features of the communication signal, rather than integrating wider contextual information (Roberts et al., 2022). Intentional communication directed at specific receivers (e.g. through eye gaze) mitigates these effects by enhancing attention allocation and conscious awareness, enabling the receiver to integrate broader contextual information (e.g. prior relationship, behavioural context, audience) to better interpret the signaller's intentions (Roberts et al., 2022).

This communication is underpinned by a suite of cognitive skills identified in Section 3.2.3, including inhibition and executive functioning. For signallers, these skills enable flexibility in signal production according to both the receiver and wider audience (e.g. selective production of copulation calls; Townsend, Deschner, & Zuberbühler, 2008), and adjusting the signal according to the visual attention of receivers (Tomasello & Call, 2019). For receivers, detecting whether communication is directly relevant to them, inferring the goal of signaller and deciding on an appropriate response also requires executive function skills (Roberts & Roberts, 2020). To conclude, a key selection pressure in the evolution of communicative complexity is the stresses arising from living in a large social group with many weak ties to manage (Seyfarth & Cheney, 2018; Roberts & Roberts, 2020). Intentional signals involving audience checking, response waiting, attention getting, turn-taking, communicative innovation and culture help overcome the stimulus-driven processing that can occur due to stress, enhancing attention allocation and enabling greater predictability of conspecifics' behaviour (Seyfarth & Cheney, 2018; Roberts & Roberts, 2020).

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Beyond the cortex–integrating hippocampal function into the Social Brain Hypothesis to explain advanced cognition

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Abstract

The Social Brain Hypothesis (SBH) connects primate brain size to social complexity but faces empirical limitations. We propose expanding the SBH by incorporating hippocampal functions across species, demonstrating how cognition emerges from both social and ecological pressures. This extended framework moves beyond cortical-centric models, providing a comprehensive understanding of brain evolution and the origins of human cognitive abilities, including language.

In the target article, the author has provided a valuable framework for understanding the evolution of large brains (Dunbar, 2024). However, this framework exhibits significant limitations when evaluated in light of comparative evidence. First, the Social Brain Hypothesis (SBH) predominantly relies on a correlation between neocortex size and group size in primates, positing that larger brains evolved to facilitate the management of larger social groups and complex social interactions. Yet comparative studies challenge this relationship. Research on non-primate species – including insects, flocking birds, fish, and cetaceans – demonstrates that taxa with relatively small brains can exhibit sophisticated social behaviors and sustain large group sizes. For example, paper wasps (Polistes fuscatus) display individual facial recognition and maintain complex dominance hierarchies despite their minimal brain size (Tibbetts, 2002). Similarly, certain ant species, such as Oecophylla smaragdina, engage in advanced cooperative behaviors, including coordinated nest-building and territorial defense (Patel & Bhatt, 2020). Among birds, species like the cliff swallow (Petrochelidon pyrrhonota) form colonies comprising thousands of individuals, exhibiting intricate social dynamics such as communal nesting and collective information sharing (Brown & Brown, 1996). Starlings (Sturnus vulgaris), known for their highly coordinated murmurations and complex communication systems, achieve these feats with brains significantly smaller than those of primates (Ballerini et al., 2008; Hausberger et al., 1995). In fish, the cleaner wrasse (Labroides dimidiatus) demonstrates advanced social behaviors, including cooperation and conflict resolution (Pinto et al., 2011). Cetaceans, such as baleen whales, further challenge the SBH by displaying social learning and cultural transmission (Garland & Carroll, 2022), despite having small brains relative to their large bodies (Ridgway et al., 2017). Conversely, some primates with large brains, such as orangutans, exhibit predominantly solitary lifestyles, suggesting that brain size alone does not predict social complexity (Van Schaik & Van Hooff, 1996). Moreover, a large-scale analysis of 140 primate species revealed that brain size was predicted by diet, rather than social factors (DeCasien et al., 2017). Collectively, these findings indicate that the relationship between brain size and social group structure is not as straightforward as the SBH proposes.

Second, the author assumes that advanced cognitive abilities evolved to manage social relationships. However, many species exhibit rich cognitive repertoires that are not directly tied to social complexity or even exist in the absence of complex social structures. For instance, New Caledonian crows (Corvus moneduloides), which typically live in small family groups (Holzhaider et al., 2011), exhibit advanced tool-making and problem-solving skills, such as crafting hooked tools (Bayern et al., 2018; Gruber et al., 2019). Similarly, Clark's nutcrackers (Nucifraga columbiana), which live in small groups or pairs, display exceptional spatial memory and the ability to compare and optimize caching strategies – abilities linked to ecological demands rather than social complexity (Clary & Kelly, 2011). Even cephalopods, particularly octopuses, exhibit advanced learning and memory despite lacking complex social interactions (Amodio et al., 2019). These examples demonstrate that cognitive complexity can arise in response to ecological challenges, such as foraging demands or environmental unpredictability, rather than social pressures, underscoring the diverse evolutionary pathways to intelligence.

In this context, I propose that the SBH can be refined by shifting from a predominantly cortical-centered framework to one that integrates the functional contributions of subcortical structures, particularly the hippocampus – a phylogenetically conserved brain structure central to the episodic memory system. The episodic memory system not only underpins both ecological and social adaptive functions, such as recalling past interactions, alliances, and conflicts (Mettke-Hofmann, 2014; Rubin et al., 2014), but also reflects evolutionary adaptations, as the size and organization of the primate hippocampus evolve in line social pressures (Todorov et al., 2019). The hippocampus also supports what Dunbar (2024) called "expensive cognitive skills," such as one-trial learning (forming durable memories from single experiences; Squire, 1992), causal reasoning, analogical reasoning, simulating strategic future outcomes, and mentalizing (inferring others' intentions). By enabling one-trial learning and bridging past experiences with future goal-directed scenarios, the hippocampus underpins a core process vital for delaying gratification (e.g., "If I eat this now, I'll regret it later"). During this process, automatic behaviors are overridden, and self-control is exerted (Edelson & Hare, 2023). Furthermore, it integrates self-relevant and other-relevant information to facilitate mentalizing via self-projection (e.g., "What would I do in their situation?"; Buckner & Carroll, 2007). The hippocampus also offers valuable insights into the evolutionary trajectory of human cognition, such as language (Zhang & Shi, 2021). For example, hippocampal-dependent mental simulation and scene construction support mentalizing, critical for decoding communicative intent and the acquisition of complex syntactic structures (De Villiers & Pyers, 2002; Boeg Thomsen et al., 2021), while its one-trial learning capacity enables rapid word-referent mapping in vocabulary acquisition (Warren & Duff, 2014). Additionally, hippocampal-prefrontal interactions regulate linguistic self-control, suppressing irrelevant associations

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during communication and fostering the referential function of human language (Badre & Wagner, 2007; Eichenbaum, 2017). These functions demonstrate how the hippocampus anchors language in real-world referents (see also Shi, 2024 for related discussion). In summary, by broadening the SBH to incorporate the hippocampus and its contributions to language evolution, we can achieve a more comprehensive understanding of the diverse evolutionary pathways that have shaped cognition across species. This refined perspective not only resolves inconsistencies in the current framework but also highlights the interplay between social and ecological pressures in driving brain evolution.

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Beyond individual selection: adaptive networks and collective social niche construction

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Abstract

Dunbar explains primates group cohesion through cognitive and structural mechanisms like grooming and social cognition. We extend this by highlighting collective social niche construction, where emergent social properties arise from feedback loops, selection pressures, and self-organisation. Adaptive social networks evolve through multilevel selection, cultural transmission, and ontogenetic changes, shaping survival, cognition, and collective intelligence across species.

Dunbar explores how individual cognitive and structural mechanisms, such as grooming-based bonding and social cognition, enable primates to maintain group cohesion and overcome the constraints of living in large social groups. While Dunbar focuses on individual-level mechanisms, we propose that group cohesion and primate social networks should also be understood as emergent properties shaped by higher-level selection and self-organized processes driven by dynamic feedback loops and collective interactions.

Since the beginning of humanity, social relationships have been shaped by pressures affecting survival and interactions (Boyd & Richerson, 2004; Harari, 2014; Henrich, 2017). The COVID-19 pandemic exemplifies these dynamics, as social distancing mimics adaptive behaviours in the animal kingdom, where individuals modify social interactions to balance pathogen risk and resource access (Romano, MacIntosh, & Sueur, 2020). This feedback loop between individual decisions and emergent social structures influences group cohesion through modularity and division of social roles. Darwinian natural selection extends beyond individual traits, incorporating cultural transmission and population dynamics, demonstrating that genetic, epigenetic, and cultural evolution collectively shape these adaptive responses (Ashe, Colot, & Oldroyd, 2021; Birch & Heyes, 2021; Claidière et al., 2014; Henrich & McElreath, 2003; Jablonka & Lamb, 1998; Nowak, 2006).

A study on human social interactions (Almaatouq et al., 2020) showed that dynamic networks with high adaptation rates improved group performance in changing environments. High adaptation led to more centralised networks, while less adaptable networks maintained prolonged social learning, reducing errors in stable environments. Network plasticity, as a key adaptive mechanism, refines individual actions. Similarly, adaptive networks in animal societies evolve through multilevel selection, favouring behavioural phenotypes that enhance network efficiency (Cantor et al., 2021; Fisher & McAdam, 2017; Gross & Blasius, 2007; Sueur et al., 2019). Social network evolution including group cohesion and fission-fusion should be examined at multiple levels rather than solely at individual cognition (Fisher & McAdam, 2017; Nowak, 2006; Sueur, 2023).

The relationship between network properties and cognition supports the social brain and cultural intelligence hypotheses (Dunbar, 1998; Muthukrishna et al., 2018; van Schaik, Isler, & Burkart, 2012). Network efficiency in primates correlates with neocortex size, suggesting an evolutionary link between social learning and cognitive abilities (Pasquaretta et al., 2014). The ability of macaques to adjust social tolerance and group cohesion post-hurricane to optimise shade access for thermoregulation (Testard et al., 2024) illustrates behavioural modulation based on physiological needs. Network topology also predicts brain structure in rhesus macaques (Testard et al., 2022) and baboons (Meguerditchian et al., 2021), highlighting links between individual cognition and social structures (Sueur, 2023; Sueur et al., 2019).

Collective social niche construction extends niche construction theory to social networks, where individual interactions shape and are shaped by social structures. Genetic, cultural, and ontogenetic processes drive network topology shifts, enabling populations to adapt dynamically. Cultural evolution, driven by social learning and information transmission, rapidly alters network structures, impacting the adaptive landscape of populations. Genetic selection on personality traits and social behaviours can lead to network topologies enhancing group fitness. Social network evolution is influenced not only by genetic selection but also by ontogenetic development and cultural transmission. Social structures can shift through learning and experience-based adjustments, such as age-related behavioural changes or modifications based on environmental feedback. These evolving networks influence selection pressures, information flow, and resource distribution, affecting individual fitness.

Collective social niche construction integrates social evolution, highlighting the feedback loop between individual behaviours and emergent social organisation. Individual exchanges between populations can facilitate the selection of network topologies, much like phenotypic evolution in sticklebacks (Farine, Montiglio, & Spiegel, 2015), where social interactions drive covariance among individuals (Neumann & Bell, 2023). Multilevel selection favours phenotypic variation, leading to mutualistic benefits and specific network topologies (Costello et al., 2023; Farine et al., 2015). In similar ecological conditions, populations favouring modular network structures show higher survival rates during disease outbreaks (Romano et al., 2020). Modularity in networks can arise due to high interaction costs, while integrated networks may emerge when beneficial interactions are frequent (Marcoux & Lusseau, 2013; Romano et al., 2018, 2024; Sah, Mann, & Bansal, 2018). This adaptive structuring highlights the role of both genetic evolution and cultural evolution in shaping the network topology.

Beyond selection, adaptive networks in many species emerge through self-organisation. This principle, seen in complex collectives (Bonabeau et al., 1997; I. D. Couzin & Krause, 2003; Puga-Gonzales et al., 2017), underscores the role of local interactions in shaping global network structures. Integrating insights from theoretical morphology, network science, and biological architectures enhances our understanding of adaptive networks. The 'network morphospace' framework (Avena-Koenigsberger et al., 2015) categorises networks based on connectivity traits, aiding in the identification of generative rules and constraints. Network geometry (Boguñá et al., 2021), incorporating shortest paths and dynamic processes, reveals symmetries such as fractality and scale invariance, applicable to brain function and social topology. Biological systems exhibit multiscale architecture, where each level – from molecules to social groups – solves distinct problems through collective dynamics (Centola, 2022; I. Couzin, 2007; McMillen & Levin, 2024). This nested structure underscores how collective intelligence drives adaptive functionality across biological and social scales including group cohesion and fission-fusion dynamics as Dunbar proposes.

By integrating niche construction and social network evolution, collective social niche construction provides a comprehensive framework for understanding adaptive connectivity including group cohesion and fission-fusion dynamics in animal societies. This approach emphasises the role of the network topology in enhancing fitness and survival, offering valuable insights into the evolution of sociality. Adaptive networks adjusting group cohesion and group size arise through a combination of genetic selection, cultural transmission, ontogenetic development, and

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self-organisation, illustrating the complex interplay between individual behaviours and emergent social structures. Understanding these dynamics deepens our knowledge of social evolution and offers new perspectives on the interdependence of cognition, sociality, and environmental adaptation.

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Behavioral ecology shapes structural, behavioral, and cognitive solutions

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Abstract

Life history strategies adaptively calibrated to levels of environmental harshness and unpredictability shape not only the fundamental issue of fertility but also whether and to what extent people engage in the structural, behavioral, and cognitive solutions proposed by Dunbar. Considering behavioral ecology can, therefore, add nuance to Dunbar's novel and important theory.

Dunbar's arguments about how mammals, especially primates and humans, adapt to the challenges of living in groups are both novel and important for understanding human social structure, behavior, and cognition. Nuance to Dunbar's view can be added, however, by considering the implications of behavioral ecologic and life history theory. In brief, organisms, including humans, adapt to the challenges of their environment by making trade-offs to deal with limited resources, both temporal and energetic (Del Giudice & Belsky, 2011; Figueredo et al., 2007; Maranges et al., 2025). Challenges in the environment include harshness (i.e., sources of morbidity-mortality: threat, deprivation) and unpredictability (i.e., stochastic changes in harshness or environment structure). Both evolutionarily and ontogenetically, humans adapt to cues of harshness and unpredictability via suites of physiological, cognitive, and behavioral strategies that make the most of the environment for reproduction, parenting, and investing in one's group.

These strategies are generally described on a spectrum, from slow to fast. Slower, versus faster, life history strategies arise from more stable, more resource-deprived, less threatening childhood environments and feature later reproductive development and behaviors, fewer offspring, fewer sexual partners, and investing more in those familial and other social partners. On the other hand, those who experience more unpredictable and harsh childhood environments tend to evince faster life history strategies characterized by opposite patterns (Ellis et al., 2022; Figueredo et al., 2007).

Consider the fundamental issue of the infertility trap, which describes a curvilinear, upside-down-U relationship between group size and female fertility. This phenomenon itself cannot be understood separately from behavioral ecology. That is, fertility is also shaped by environmental harshness and unpredictability. Harshness as a lack of energetic resources is associated with delayed puberty/reproduction and fewer offspring. When faced with limited nutrition, energy, and survival resources, the adaptive response is to prioritize somatic maintenance and survival rather than reproduction (Ellis et al., 2009, 2022). In contrast, harshness as threat and unpredictability of resources or environmental structure are associated with earlier puberty and reproduction and more offspring (Belsky, Schlomer, & Ellis, 2012; Ellis et al., 2009, 2022). When faced with high levels of threat or unpredictability linked to one's morbidity/mortality, time and energy would be better allocated toward earlier and greater reproduction rather than one's future, which is at risk or uncertain. The former strategy entails more temporal and energetic investment in existing offspring, whereas the latter entails less investment in each, balancing energy to environmental demands, which has downstream implications for the proposed structural, behavioral, and cognitive solutions.

With respect to structural solutions, the very size and stability of the group based on grooming cliques and chains will be shaped by harshness and unpredictability. For example, harshness as resource deprivation is associated with being other-oriented (Maranges et al., 2021; Stephens, Markus, & Townsend, 2007), while harshness as threat is associated with more empathetic concern but fewer social connections (Ceballos & Watt, 2023; Maranges et al., 2021). The harsher (but more stable) the environment, the smaller but more stable the group should be. This facilitates sharing stable, limited resources across the group, and in humans, this is facilitated by more "grooming" (i.e., caring about and investing in close others) but having a smaller network. If there is certainty about resources, people will share their energy and time with their strong ties. However, unpredictable environments are associated with less empathetic concerns and low social support provisioning. Accordingly, unpredictable environments should give rise to more unstable groups, with less "grooming" behavior (i.e., caring about and investing in close others; Maranges et al., 2021). Indeed, faster, versus slower, life history strategies are characterized by a strategic withholding of investment in family and others in the community as well as fewer tight and loose social ties (Figueredo et al., 2007).

Dunbar also posits that behavioral investment in close social partners is made possible by eating densely nutritious foods, thereby freeing up time and energy for those investments. Harshness and unpredictability are paramount inputs into organisms' eating behaviors, which become dysregulated by high levels of these environmental challenges. That is, environmental harshness and unpredictability predict modern-day eating disorders, which cluster with fast life history strategies (Leyva & Hill, 2018; Lie et al., 2021; Luo, Niu, & Chen, 2020; Nettersheim et al., 2018; Ross & Gill, 2002). For example, harshness as threat predicts higher likelihood of engaging in binge/purging behaviors (Lie et al., 2021), which both use up food resources and waste the energy benefits. Thus, unpredictability and harshness interfere with a quintessential behavioral adaptation to group living according to Dunbar and must be taken into account.

Finally, behavioral ecology directly and strongly shapes the cognitive solutions (i.e., self-control, mentalizing, and executive

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function) facilitated by a larger neocortex (Maranges et al., 2022, 2025; McLaughlin, Sheridan, & Nelson, 2017; Sheridan et al., 2017). Harshness, as both deprivation and threat, and unpredictability undermine development of neocortical systems (McLaughlin et al., 2017; Sheridan et al., 2017), resulting in faster life history strategies characterized by poorer executive functioning and self-control (Davies et al., 2021; Fields et al., 2021; Maranges et al., 2022). Unpredictability selects for poorer mentalizing capacities, whereas harshness (as resource deprivation) often selects for and slow life history feature stronger mentalizing capacities (Ceballos & Watt, 2023; Figueredo et al., 2007; Maranges et al., 2022). Variation in these cognitive solutions then accounts for the link between environmental pressures and social decisions about protecting and helping others (Maranges et al., 2022). These patterns suggest that the cognitive solutions to group living are strongly affected by the ecology, which should be considered in concert with the inherent stressors of group living Dunbar outlines.

We argue for the importance of applying a behavioral, ecological, and life history theoretical framework to understand the problems and solutions to group fragmentation and the infertility trap. Applying this perspective both complements and extends Dunbar's work by providing novel hypotheses about solutions to group living. Whether particular solutions will be evinced and efficacious depends on the life history strategy of the group members, which depends on the ecology.

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Core affective mechanisms maintaining group cohesion

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Abstract

As the third solution to group dispersion, Dunbar proposes primates use several higher order cognitive skills to especially manage 'weak ties' in a nuanced and fast-tracked way, therewith avoiding unnecessary conflicts. We here argue that subconscious, automatic processes including attention allocation and behavioral or neurophysiological state matching can serve a similar function in maintaining group cohesion.

In the target article, Dunbar outlines three different primate solutions to negate the natural and social mechanisms that drive large groups apart: structural (grooming networks), behavioral (increasing grooming time), and cognitive (to manage 'weak links'). For the latter, Dunbar specifically suggests several forms of meta-cognition are crucial because they allow individuals to consciously manage their relationships: e.g., inhibition (self-control) in conjunction with reading other's behavioral cues through mentalizing can help to avoid unnecessary conflicts possibly leading to group fragmentation (target article, sect. 2.3). However, we argue that primates also subconsciously and automatically attune to each other in many different ways, both externally and internally. For example, synchronization or mimicry at the physiological and behavioral level might increase group cohesion by matching other's physiological states. Moreover, automatically turning attention to the emotional expressions of group members might help to readily detect their emotional state and act accordingly. In this commentary, we will discuss how these mechanisms are equally (if not more) important for maintaining group cohesion as the meta-cognitive abilities discussed by Dunbar.

Attention is a limited resource that greatly impacts what information from the environment is being processed. In primates, implicitly and automatically turning attention to emotional expressions of conspecifics favors processing of valuable social information. This gives the higher order cognitive processes that Dunbar discusses the necessary input for providing rapid social judgements and fast adequate responses. Socio-emotional attentional biases can be directly investigated in computerized tasks. Several studies using attention-capture or looking time paradigms have shown that orangutans, bonobos, chimpanzees and rhesus macaques show an attention bias toward socio-emotional versus neutral or other control scenes (e.g., Fumihiro & Tomonaga, 2010; Kret et al., 2016; Pritsch et al., 2017; van Berlo et al., 2024; Whitehouse et al., 2016). Results so far have been mixed (e.g., Kret, Muramatsu, & Matsuzawa, 2018), suggesting a selective bias toward negative socio-emotional stimuli and an influence of familiarity with the expressor (e.g., van Berlo, Bionda, & Kret, 2023). Future studies examining primate species with varying group sizes (such as baboons) could provide valuable insights into the role of socio-emotional attention bias.

Automatic mimicry has been observed on many different levels and in many different species (for a recent overview, see Diana & Kret, 2025). Evidence is especially widespread for motor mimicry (involving muscle movements), for example contagious yawning (orangutans, van Berlo et al., 2020; lemurs, Valente et al., 2022; pigs, Norscia et al., 2021; budgies, Miller et al., 2012), scratch contagion (spider monkeys, Valdivieso-Cortadella et al., 2023; Japanese Macaques, Nakayama, 2004; orangutans, Laméris et al., 2020), and mimicry of facial expressions (bonobos, Bertini et al., 2022; gelada baboons, Mancini, Ferrari, & Palagi, 2013; macaques, Scopa & Palagi, 2016; meerkats, Palagi et al., 2019). Evidence for autonomic mimicry, such as changes in heart rate, skin conductance, and pupil diameter, is largely limited to humans due to obvious ethical and practical constraints. In nonhuman species, research on mimicry has primarily focused on behavioral aspects, leaving autonomic mimicry largely unexplored (see Diana & Kret, 2025). However, one study using eye-tracking showed that chimpanzees mimic pupil size of conspecifics (Kret, Tomonaga, & Matsuzawa, 2014).

Automatic mimicry is widely assumed to have an affiliative function and to increase social bonding. By matching each other's affective state (or "emotional 'raw feels' "), it can therefore provide a social glue keeping primate groups together, a function similar to the one Dunbar proposes for endorphins (target article, sect. 1.3). However, it has recently been proposed to also serve a more general predictive function related to the environment, including the behavior of conspecifics (Diana & Kret, 2025). This implies that the effect of mimicry is not always positive, but that, by predicting the behavior of conspecifics, it tends to smoothen social interactions. Being able to reliably predict and act upon negative behaviors and expressions of conspecifics may be equally important for maintaining group cohesion by avoiding unnecessary escalations. In the target article, Dunbar also discusses how being able to predict behavior of group members, especially of 'weak ties', is crucial to avoid unnecessary conflicts that can drive groups apart. However, he stresses the importance of higher-order cognitive functions to explicitly evaluate and manage relationships with group members that are not in an individual's direct grooming clique. Taking a step down, we propose that automatic mimicry can serve the same function in providing nuanced and fast-tracked ways to predict the social environment and manage social relationships.

In summary, we propose that attention allocation and automatic mimicry are underlying mechanisms that facilitate Dunbar's cognitive solution to primate group fragmentation. They strengthen social bonds and ease communication, thereby ameliorating the social stresses of group living. The role of these implicit mechanisms should be taken into account when considering how primates deal with the challenges that come with living in large groups. They seem to be present across species and genera and could provide a crucial 'glue' between conspecifics living together in large groups. Further investigating these mechanisms behaviorally and experimentally by employing novel techniques in touchscreen and eye-tracking based tasks, can shed further light on how they increase group cohesion in primates.

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On the forces that bind us

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Abstract

Dunbar proposes strategies to solve the fragmentation problem experienced by group-living animals. We highlight that bondedness not only mitigates stress but also provides structural scaffolding for group stability. Furthermore, we posit tolerance as a complementary mechanism smoothing social interactions and argue that variation in cohesion-promoting traits reflects context-dependent socio-ecological pressures, challenging static models linking sociality to cognition. Finally, we propose two further mechanisms—cultural transmission and dominance dynamics—that can enhance social cohesion by aligning behaviour and reducing uncertainty.

One of the key challenges for animals living in large, stable groups is overcoming the inherent pressures that pull individuals apart – what Dunbar has termed centrifugal forces (Dunbar, 2025). Among these are the internal psycho-physiological costs of close proximity, such as chronic social stress that can lead to reproductive suppression in females, known as the "infertility trap." Dunbar proposes that in primates, this trap is overcome by the formation of enduring female–female coalitions, which buffer individuals from social stress and enhance reproductive success. These coalitions are built through selective, high-quality social bonds – primarily maintained through grooming – that function not only to mitigate stress but also to enhance predictability and trust within the social network.

Dunbar mainly phrases selective social bonding as a solution to the infertility trap. We conjecture that social bonds may go much further in addressing the broader problem of group fragmentation, which Dunbar solves by advancing structural, behavioral, and cognitive strategies (Dunbar, 2025). Strong, reliable bonds between individuals can actually serve as the scaffolding for structural cohesion within a group (Grueter et al., 2020; Silk, 2025). This ultimately increases resilience to socio-ecological disturbances and reduces the cognitive load associated with maintaining "weak ties." In this sense, bondedness acts as both a behavioral and structural solution (*sensu* Dunbar) to the problem of maintaining group cohesion at scale. This might be of particular importance in species that rely on personalized relationships rather than anonymous group membership, like primates.

Besides close bonds, another key factor in supporting cohesion may be social tolerance. In primatology, social tolerance is increasingly viewed as a behavioral trait rather than an emergent

phenomenon following from (unrelated) social patterning (DeTroy, Haun, & van Leeuwen, 2022). Tolerance involves allowing or condoning others to benefit when something is at stake (DeTroy et al., 2022), and thus facilitates behaviors such as cooperation and social learning (van Schaik, 2003; Harrison, van Leeuwen, & Whiten, 2021; van Leeuwen et al., 2021). Levels of tolerance also consistently differ from one another within groups and individuals of the same species (Cronin et al., 2014; Fichtel, Schnoell, & Kappeler, 2018; van Leeuwen et al., 2023). This pattern points to tolerance being an active rather than passive vector in the equation of social bonding, both at the dyadic and group level. Unlike strong bonds, which are selective and intensive, social tolerance operates as a low-cost, extensive mechanism, allowing for smoother interactions and reducing the risk of fission. Consequently, it may enable groups to scale up in size by reducing the need for cognitive tracking of relationships across the entire group.

The question then arises: what underlies stable interspecific and intraspecific variation in social tolerance? One possibility is that social tolerance is itself grounded in cognitive capacities – particularly inhibitory control (a cognitive solution sensu Dunbar (Dunbar, 2025)). The ability to inhibit impulsive or aggressive responses allows individuals to tolerate proximity with a wider range of group members. In this view, tolerance is not merely an emotional or temperamental trait, but a cognitive one. This would suggest that social tolerance, like bondedness, may ultimately be a cognitively mediated solution to group cohesion, albeit one that operates through generalized, low-intensity mechanisms rather than selective, emotionally rich ties. Indeed, this framework opens up a testable hypothesis: that species with greater inhibitory control should also exhibit higher baseline levels of social tolerance and greater group-level cohesion.

Following from the documented group-level variation in primates' behavioral phenotypes (e.g., see (van Leeuwen, Cronin, & Haun, 2018; Kerjean, van de Waal, & Canteloup, 2024; Koops et al., 2024)), we posit that Dunbar's analysis falls short in acknowledging *variability*. Selective pressures on group size vary across environments (Siepielski et al., 2013), shaping social complexity in ways that static models may overlook. Factors such as predation, resource availability (Foster et al., 2012), and competition fluctuate across regions, meaning the benefits of group living are context-dependent. In areas with low predation and abundant resources, large groups offer little advantage, reducing the need for strong social cohesion. This challenges the idea that social group size alone drives cognitive evolution, as many cognitively advanced species – like orangutans or corvids – live in small groups or alone. A testable prediction from this view is that the link between sociality and cognitive demands is strongest where socio-ecological pressures make group coordination essential, such as in high-predation or inter-group competition environments (Radford, Majolo, & Aureli, 2016; Samuni et al., 2020).

Building on Dunbar's proposed solutions to the fragmentation problem, we propose two additional mechanisms that are essential for maintaining group cohesion in primates: cultural transmission and dominance dynamics. In humans, culture is a fundamental mechanism for social cohesion through creating a sense of belonging and group identity (Tomasello, 1999; Bell, Richerson, & McElreath, 2009; Chudek & Henrich, 2011). Cultural norms help regulate social behavior, reducing conflict, and promoting cooperation in societies of all sizes (Chudek & Henrich, 2011). Cultural behaviors in animals have the potential to enhance social cohesion in a similar way (Cantor & Whitehead, 2013). When individuals within a group learn and adopt specific behaviors from one another – such as vocalizations, foraging strategies, or customs such as handclasp grooming or social games (McGrew et al., 2001; Rendell & Whitehead, 2001; Perry, 2011, p. 2001) – these practices help define group membership (van de Waal, Borgeaud, & Whiten, 2013; Berdahl et al., 2018; O'Corry-Crowe et al., 2018). Furthermore, by aligning behavior within a group, culture may reduce social uncertainty, minimize conflicts, and foster cooperation. All of these contribute to greater group stability. As such, culture may function as a short-cut bonding principle, leveraged by relatively low-cost mechanisms of social learning (Hoppitt & Laland, 2008). In this sense, cultural transmission offers a complementary route to Dunbar's bonding mechanisms, allowing species to mitigate the fragmentation problem and sustain complex social structures.

Another way in which group cohesion can be secured is by dominance structures. Dominance dynamics can streamline groups by formalizing behavior and enabling dominant individuals to police others (Flack et al., 2006; Beisner et al., 2016). However, Dunbar does not elaborate this aspect of living in social groups. In many species, hierarchical social structures provide a framework for maintaining order and minimizing conflict as group size increases. Despotic systems, in which a clear dominance hierarchy regulates access to resources and mating opportunities, may allow species to sustain larger groups without requiring extensive cognitive investment in relationship management (Kaburu & Newton-Fisher, 2015; Bhattacharjee et al., 2023). In contrast, more egalitarian societies, where individuals must engage in frequent social negotiation to maintain group cohesion, may demand greater cognitive complexity (Aureli, Schaffner, & Schino, 2022; Rincon et al., 2023). This suggests that dominance style plays a key role in determining the maximum stable group size a species can maintain (Tibbetts, Pardo-Sanchez, & Weise, 2022). A possible testable prediction is that species with strict dominance hierarchies, such as baboons and macaques, should be able to sustain larger groups with lower social instability compared to more egalitarian species like bonobos, where group cohesion relies more heavily on intricate social negotiations.

Taken together, building on Dunbar's foundation (Dunbar, 2025), we propose that social tolerance, cultural transmission, and dominance dynamics offer additional, complementary mechanisms that help overcome the challenges of group living.

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Facial expression is a group cohesion solution

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Abstract

Facial expression has evolved as a solution to the primate group living problem. A growing body of empirical evidence suggests that the evolution of facial expression has been driven by the need to bond. Dunbar's theories of group cohesion are therefore key to understanding primate (including human) facial expression.

Facial expression has evolved as a solution to the primate group living problem. Involving both behavioural and cognitive processes, primate facial expression has diverged in complexity from those of mammalian relatives. We are only just starting to understand how facial expression functions in the form and maintenance of primate social relationships, but the evidence we have so far suggests that the evolution of facial expression has been driven by the need to bond (Schmidt & Cohn, 2001). Dunbar's theories of group cohesion are therefore key to understanding primate (including human) facial expression.

Dunbar proposes that primates need structural, behavioural, and cognitive solutions to avoid group fragmentation (strategies that are not mutually exclusive). Facial expression is a prime candidate solution, operating across these strategies in three ways. First, facial expressions act as cues to an individual's future behaviour (Waller, Whitehouse, & Micheletta, 2017). Whether this is underpinned by cognitive reading of intentions or simpler associative learning is an interesting question, but the function is the same. Knowing how others are likely to act next allows individuals to prepare an optimal response, synchronise behaviour, and (importantly) avoid conflict. Illustrating this, primates predict a peaceful outcome when they see others using any facial signals, including facial threats (Waller, Whitehouse, & Micheletta, 2016), presumably as the sharing of the potential willingness to engage in conflict allows all parties to act promptly to diffuse the aggression. Second, the facial expressions of others can be used to understand third parties and their relationships. There has been a historical focus on thinking of facial expressions as revealing information within a dyadic context (when directed towards 'you'), but their potential utility within third-party dynamics is in many ways much greater. Observing the nonverbal behaviour exchanged between others can be incredibly informative about the nature of their relationship (Bergman & Sheehan, 2013; Dunbar et al., 2022). Again, bystanders can then use this information to avoid potential ensuing conflict, take heed of blossoming alliances, identify the social centrality of other individuals, and manage their own relationships with those parties. In particular, this could be a powerful mechanism to keep track of the 'weak' ties in the social group (indirect social connections), which Dunbar suggests is important. Third, Dunbar argues that one-trial learning gives anthropoid primates the ability to generalise from single experiences, allowing a more nuanced management of social relationships. We agree, and within the facial expression domain, this is particularly important, as an isolated glance, baring of teeth, or eyebrow raise between parties can be significant and meaningful; it does not need to be repeated to be indicative of a relationship.

We argue that facial expression, via these processes, acts as a bonding mechanism. This function has been evidenced through analysis of individual differences, whereby individuals who use facial expression well (either as a producer or observer) leverage social advantages. Macaque groups led by facially expressive males have greater social cohesion, and expressive male macaques occupy more central positions in their social groups (and are thus recipients of social advantages) (Whitehouse et al., 2024). Similarly, facially expressive humans are more likeable and can be better at negotiating during conflict (Kavanagh, Whitehouse, & Waller, 2024). Dunbar points out that demonstrating how individual differences in specific skills correlate with relationship management is difficult, and we agree; but this body of evidence in relation to facial expression is building. Other forms of communication, such as vocalisation and gesture, could function similarly, but unlike facial expression, there is little data at present showing how individuals differ in their communicative capacity in these other domains and whether they leverage this to navigate their social worlds better.

Human and non-human primate facial expression has been of interest to scientists for decades, featuring heavily in Darwin's early comparisons of behaviour across species (Darwin, 1872). Why, then, are studies relating to its social cohesion function in relative infancy? We argue that the dominant emotional framework (Ekman, 1992) in which facial expression is commonly approached tends to distract from this approach. If facial expressions are seen only as 'expressions' of subjective feeling state (which is currently heavily debated: Barrett et al., 2019), it is hard to envisage (and test) how they operate as solutions to the group living problem. In contrast, if they are approached as predictive (Fridlund, 1994) and adaptive (Williams, 2002) signals, this better explains how they might help individuals avoid conflict, cooperate, and synchronise behaviour.

One outstanding question is whether human facial expression is different from that of other primates. Did humans leverage the primate facial expression mechanism to break a glass ceiling in group size? Humans produce approximately 100 facial movements per minute during conversational social interaction (Rollings et al., 2024), which is higher than other primates (e.g., 67 facial movements per minute in rhesus macaques during affiliation: Whitehouse et al., unpublished data), but there is no current evidence that absolute function differs. One possibility, however, is that the evolution of language has shifted the function of primate facial expression in humans, by entwining facial movement with language and creating a more multimodal, communicatively rich social interaction where intentions, goals, and predictive cues are shared accurately and rapidly (Jack & Schyns, 2015). The reality is that the discrete, basic universal expressions (happy, angry, sad, disgusted, surprised, fearful) are rarely used in spontaneous social interaction (with the exception of smiling which may not necessarily indicate actual happiness: Kavanagh et al., 2024) and instead facial movements pepper conversations allowing individuals to predict each other's responses (Emmendorfer & Holler, 2025). These real-world behaviours need to be studied within an evolutionary framework, with explicit comparison to those of other primates, if we are to understand whether this represents a step-change social bonding mechanism. Dunbar's theories about the mechanisms of group cohesion are therefore important to help generate and test predictions about human facial behaviour, particularly to understand the differences between humans and other primates, and not just the similarities.

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Primates' social cognitive bonding mechanisms are more complex than we thought, yet not quite human–lessons from great ape triadic social bonding

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Abstract

The current manuscript rightly points out that non-human primates evolved complex social cognitive skills to maintain weaker social ties. However, these capacities are likely more expansive than currently proposed: research shows that apes behave more socially to those with whom they experience similar things, suggesting that they possess some precursor of humans' capacity to bond through shared experiences.

The target article proposes that to form and maintain weak social ties, some primate species developed two specific social cognitive mechanisms, namely self-control and mentalizing, the latter of which primarily facilitates social bonding by allowing individuals to read others' intentions from their intentional (or even communicative) behavior. At the end of the article, the author rightly points out that humans have taken an extra big social cognitive step that catalyzes large-scale social bonding. Humans bond through conversation (Aron et al., 1997; Bosson et al., 2006), music and dance (Cirelli et al., 2017; Hove & Risen, 2009; Pearce et al., 2015; Weinstein et al., 2016), games (Artinger et al., 2006; Dabbish, 2008; Depping & Mandryk, 2017; Zheng et al., 2002), rituals (Charles et al., 2021; Singh et al., 2020), and even by simply watching something together with others (Wolf et al., 2015; Wolf & Tomasello, 2020b). In other words, humans seem to have a unique social cognitive capacity to bond through social activities centered around shared experiences (Wolf & Tomasello, 2023).

There is no doubt that humans are unique in how much time and energy they invest in creating such experiences. Yet the psychological differences between humans and other primates in this regard are smaller than one might expect. In recent research (Wolf & Tomasello, 2019), Chimpanzees and Bonobos watched a video of a playing juvenile conspecific while an experimenter either watched with them or not. The apes sought out subsequent interaction faster with the experimenter who watched with them than with the experimenter who did not. Similarly, pairs of Chimpanzees who watched a video on the same screen subsequently spent more time together than pairs of Chimpanzees who watched the video on separate screens (i.e., not being able to see their partners' screen).

This increase in social behavior would be hard to explain from the currently proposed social cognitive framework. During these procedures, apes were not in any way interdependent, nor explicitly communicating or signaling. More generally, if the apes used mentalizing to infer their partner's intentions, it seems unlikely that, in these specific study contexts, the act of (not) looking at the same screen taught them something about their partner's intentions that bore relevance to their social interaction or was otherwise relationally meaningful.

Instead, what these results seem to suggest is that the apes were not only making inferences about the intentions of others toward them, but that they were also, at some level, *comparing others' mental states about the world to their own*. As such, where social bonding in non-human primates has generally been assumed to be dyadic (i.e., behavior or communication is directly aimed at the individual), it seems like great apes also possess some triadic social bonding capabilities, by bonding with those who are reacting to the world in the same way they do.

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As the target article points out, humans do seem to be uniquely creative when it comes to finding ways to trigger their triadic social bonding systems. However, rather than this being a direct consequence of the acquisition of language or symbolic communication, there is a deeper underlying cognitive explanation: Humans' effective social bonding in these activities seems to be undergirded by a capacity to create more complex representations of the relationship between their minds and those of others (Shteynberg et al., 2023; Wolf & Tomasello, 2023). Specifically, humans are capable (and motivated) to create shared metacognitive representations: During social interactions, they infer mutual awareness about having mental states similar to others, which converge on the same part of reality. These inferences can be created through language, but also through triadic touch (i.e., touch in response to things happening in the world) or by engaging in communicative eye contact (Siposova et al., 2018): In a comparative study (Wolf & Tomasello, 2020a), children and apes were watching a video while an experimenter in front of them did so as well. However, in one condition, the experimenter turned around and made communicative eye contact in response to the video starting, whereas in the other condition, the experimenter simply turned to the video and started watching (eye contact was made later in the procedure, to keep this factor constant across conditions). Results showed that human children who made eye contact with the experimenter in response to what occurred on the screen (i.e., inferred mutual awareness of their experience being shared) sought out a subsequent interaction with the experimenter faster than children who were merely observing the experimenter going through a similar experience. The apes, however, did not seem to react to this attempt to create mutual awareness at all.

These results have two implications for the social cognitive dimension of forming and maintaining weaker social ties in primates. First, the final step that bridges the bonding gap toward human-like social bonding activities seems indeed related to a capacity to represent (multiple) mental states (perhaps recursively). However, its core psychological underpinnings seem more specific than a general capacity for high-level multilayered recursive mindreading or language, namely a specific capacity to create shared metacognitive representations or mutual awareness about the relationship between one's own mental states and those of others. This capacity not only forms the foundation for human language and other forms of symbolic communication, cultural norms, and social institutions that allow large scale social bonding (Clark & Brennan, 1991; Grice, 1957; Searle, 1992; Shteynberg et al., 2023; Tomasello, 2019) but, importantly, in itself also directly elicits social closeness.

Second, it seems that at least some non-human primates (i.e., great apes) are more similar to humans than many scholars have long thought. Chimpanzees and Bonobos behave more socially and seek out interactions more often with those with whom they undergo similar (vs different) experiences. This suggests that they, at some level, bond triadically by making inferences about the relationship between their others' mental states and their own, at least in a rudimentary way. How far this capacity extends within the primate phylogenetic tree remains, however, unknown and is thus a crucial endeavor for future research.

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Tolerance as a key mechanism for large-scale social cohesion

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Abstract

Grooming and cognition support primate group cohesion but are insufficient for maintaining stability in large groups. We propose tolerance, the capacity to accommodate social stress, as an additional mechanism. Tolerance fosters flexible social skills and cooperation beyond small cliques. Shaped by hormonal adaptation and development, tolerance plays a foundational role in overcoming group size limits by sustaining complex social networks.

Dunbar posits that grooming and social cognition are key mechanisms for maintaining group cohesion, particularly in primates. However, these mechanisms alone are insufficient to explain how stability is maintained in large groups where conflicts inevitably arise. Here, we highlight tolerance as an additional mechanism crucial for large-scale social cohesion. We argue that tolerance underpins flexible social skills and supports cooperative ties beyond close kin or small cliques, thus playing a foundational role in the evolution of complex primate societies, including our own.

Tolerance, defined as the ability to accommodate social stress and conflicts, strengthens cohesion by reducing social friction and enabling more stable and frequent coalitions. Without tolerance, even sophisticated cognitive skills, such as reasoning about others' mental states, would have limited utility in social interactions, as individuals would struggle to share the benefits of joint effort (Hare & Tomasello, 2005). For instance, chimpanzees can understand false beliefs and strategically manipulate others' visual access to maximize their own payoffs (Karg et al., 2015; Krupenye et al., 2016). Yet, their cooperation is often constrained by low tolerance, even when they recognize that they cannot solve a problem alone. When rewards for joint effort can be easily monopolized or when sharing becomes necessary, tensions rise and cooperation collapses (MacLean & Hare, 2013; Melis, Hare, & Tomasello, 2006). This limitation may help explain why chimpanzees, even in populations exhibiting relatively high levels of cooperation and ecological pressures favoring coordinated hunting, still tend to hunt in small parties of only three to four individuals (Boesch, 2002).

In contrast, bonobos, who share a common ancestor with chimpanzees dating back approximately 1.5 to 2.1 million years (Fontsere et al., 2022), exhibit significantly higher levels of social tolerance, particularly in feeding context, and collaborate more effectively (Hare et al., 2007; Jaeggi, Stevens, & Van Schaik, 2010; Nolte, Sterck, & Van Leeuwen, 2023). Associated with enhanced tolerance, bonobo foraging parties tend to be larger than those of chimpanzees, both in absolute size and as a proportion of their unit-group (Furuichi, 2009; Mulavwa et al., 2008; Surbeck & Hohmann, 2008). Moreover, when neighboring groups meet, bonobos frequently exhibit joint foraging behaviors and forms of intergroup cooperation (Cheng et al., 2022; Lucchesi et al., 2020; Samuni & Surbeck, 2023). They voluntarily share food even with unfamiliar individuals and display flexible cooperative-communicative skills based on their understanding of others' mental states (Tan & Hare, 2013; Townrow & Krupenye, 2025). Such extensions of sociality beyond immediate group boundaries underscore tolerance as a foundational element for larger-scale social comity.

While endorphin release may indirectly reduce aggression by promoting positive social experience, tolerance involves direct regulation of emotionally defensive responses. For instance, chimpanzees exhibit elevated testosterone reactivity in anticipation of social interactions, which prepares them for competition and lowers the potential for tolerance (Sobolewski, Brown, & Mitani, 2012; Wobber, Hare, et al., 2010). In contrast, bonobos show increased cortisol release in similar social contexts, indicating stress responses that facilitate passive coping strategies (Wobber, Hare, et al., 2010). These strategies include mitigating anxiety through sociosexual contact, which stimulates oxytocin release and is more effective than grooming alone (Clay & de Waal, 2015; Moscovice et al., 2019). The aggression-buffering effects of stress responses are not unique to bonobos. Macaques, for instance, experience heightened social stress when closely related individuals are in proximity during foraging, as indicated by increased rates of scratching, a behavior associated with elevated cortisol levels (Sekizawa & Kutsukake, 2025). However, following scratching, macaque interactions are less likely to escalate into aggression and more likely to become affiliative (Whitehouse, Micheletta, & Waller, 2017). Additionally, cooperative behaviors with socially close partners further reduce cortisol levels, reinforcing stress-alleviating mechanisms that preserve social bonds (Stocker et al., 2020).

These tolerant responses to social stress likely result from selection against aggression. In animals artificially selected for tolerance toward humans, increased serotonin levels in the brain are among the earliest physiological markers of reduced emotional reactivity (Agnvall et al., 2015; Popova et al., 1991; Wang et al., 2018). Correspondingly, compared to chimpanzees, bonobos have twice the density of serotonergic axons in the amygdala (Stimpson et al., 2016). In macaques, variation in serotonergic gene profiles is associated with sociality as well. Individuals carrying two copies of the long allele of the 5-HTTLPR gene, which encodes the serotonin transporter, show lower aggression and greater social engagement (Brent et al., 2013; Watson et al., 2015). More broadly, across primates, serotonin

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concentrations correlate with impulse control and play a central role in regulating vigilance, balancing the detection of social threats with affiliative behaviors (Higley & Linnoila, 1997; Mikheenko et al., 2015; Weinberg-Wolf & Chang, 2019; Westergaard et al., 2003). These patterns suggest that shifts in social cognition are closely linked to hormonal adaptations that facilitate tolerance.

Although Dunbar's framework gives limited attention to developmental processes, selection acting on an extended developmental window may also play a crucial role in shaping tolerance (Hare, 2017). Under pressures of social complexity, primates have evolved prolonged juvenile periods that allow for more opportunities for social learning, including the acquisition of aggression-regulating skills (Joffe, 1997; LaFreniere, 2011). This extended developmental phase may provide more affordance for sustained tolerance, as juveniles across primate species tend to be more tolerant than mature individuals (Pereira & Fairbanks, 2002). Delays in the maturation of adult-level inhibition over social responses may help sustain juvenile-like tolerance into later developmental stages, as observed in bonobos and Barbary macaques (Rosati & Santos, 2017; Wobber, Wrangham, & Hare, 2010). Humans exhibit the most pronounced form of this pattern. Our uniquely prolonged dependency, marked by early-developing cooperative-communicative capacities and an extended period for socialization, likely facilitates emotional and behavioral regulation essential for maintaining cohesion within large, diverse, and dynamic social groups (Hare, 2017; Hawkes, 2014; Vollhardt, Migacheva, & Tropp, 2009).

In summary, we broaden the discussion of primate social evolution by proposing tolerance as a crucial factor enabling species, including humans, to overcome the "glass ceilings" on group size by sustaining social cohesion. Moreover, since tolerance likely scaffolds advanced social skills, fostering affective regulation (e.g., through enriched rearing environments; Honess & Marin, 2006) rather than relying solely on cognitive solutions may be key to managing complex social networks.

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Author's Response
Unpacking social complexity

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Abstract

I first summarise the argument in the target article so as to make the main points clear. I then address a number of major misunderstandings (mainly in relation to the social brain hypothesis), consider some specific issues that require clarification, and finally identify points that would merit more detailed consideration. I conclude with a list of possible future projects.

I will respond to the commentaries under three broad headings: misunderstandings (mostly of the social brain hypothesis), specific points of detail that need to be clarified, and issues that have much wider implications and warrant more detailed consideration. I will finish by identifying a number of suggestions that would merit pursuing in future research. However, let me first begin by summarising the argument in the target article.

The article makes three key points: (1) in mammals, group-living is *much* more challenging (even for humans!) than we have been inclined to assume, creating a downward pressure favouring the smallest groups possible (in the limit, a solitary life); (2) when highly social species live in groups, it is because they do so for a reason, not simply because they can; and (3) in order to live in large groups (those >15), they have to be able to neutralise what are otherwise overwhelming costs. I identify two forces that create this downward pressure on group size: the infertility trap and group coordination (the synchrony problem). These automatically come into play whenever two or more mammals live in close spatial proximity.

I suggested that anthropoid primates have adopted a series of strategies that are additive in their capacity to neutralise these centrifugal forces; I argue that these were brought into play sequentially as species tried to overcome the challenges of evolving ever larger group sizes in order to cope with new environmental stresses or colonise new habitats. These were: network structure solutions (essentially creating an attention network), forming bonded cliques based on upregulating the endorphin system through social grooming, and evolving more sophisticated forms of social cognition that allow a wider network of virtual relationships to be inferred on the basis of observation alone (including, for example, the capacity to make third party comparisons: X's relationship to Y is like my relationship to Z). These three solutions differ in the maximum size of group they can support and in their cognitive and energetic costs.

Matters of factual detail

Several commentaries (**van Leeuwen & Roth**, **Krupnick**, **Shi**) allude to the fact that orangutans are solitary. They are not. They certainly forage on their own (in most, *but not all*, habitats), but in actual fact, they are very social. This is why they are usually housed in groups in zoos; on a number of behavioural markers, they are as social as gorillas (Dunbar, 2026). Orangs live in (dispersed) communities, just like chimpanzees do. This is because both species are living under ecologically challenging conditions on the limits of a much wider former biogeographic distribution – in the case of orangs, one that extended right up into mainland China. Orangs just take the enforced dispersal to its limit. Under further climate warming, both gorillas and chimpanzees will do the same (Korstjens, Lehmann, & Dunbar, 2010; Lehmann, Korstjens, & Dunbar, 2010). The community size for orangs, based on two reliable field studies, is in fact 14 (about what would be expected for their neocortex ratio, and very similar to gorillas). When we undertake comparative analyses, it is essential to compare like with like; we should not compare foraging group size in one species (orangs) with social group size in others (gorillas and chimpanzees).

Bshary & Triki and Shi imply that primate brain evolution may be better explained by the demands of foraging rather than sociality, citing DeCasien, Williams, and Higham (2017) as evidence. The apparent desperation to defend at all costs an exclusively foraging explanation for everything is beginning to read like a religious mantra, more especially given that, unlike the social brain hypothesis, the foraging hypothesis hasn't actually moved on conceptually at all since the 1980s. We still have no idea what is involved, how cognition influences food intake, or whether individual differences in foraging skills influence either survival *or* fertility; in contrast, there is very extensive evidence on all three points in respect of social skills, not just for primates but also for humans and for other large-brained group-living mammals (summarised in Dunbar, 2018b, 2025).

The real problem, however, is that the DeCasien et al. analysis (and that of Powell, Isler, and Barton [2017], who made a similar claim) is statistically flawed beyond possibility of redemption. They used ordinary least squares regression when the data do not meet the minimum standards required *and* ignored grades (thereby falling doubly foul of the Yule-Simpson paradox, a version of the ecological fallacy, which, in the limit, can cause the sign of a slope to reverse). In addition, by reversing the causality of the axes in order to run a multiple regression, they inadvertently tested a developmental hypothesis when they thought they were testing a selection hypothesis (thereby falling foul of Dobzhansky's Dictum) (see Dunbar & Shultz, 2021a, 2023; Shultz & Dunbar, 2022). Asking a different question will inevitably yield very different results, as Wartel, Lindenfors, and Lind (2019) pointed out. The only statistically correct way to test hypotheses of this complexity is by path analysis. Four independent path analyses of different primate datasets (including both the DeCasien et al. and Powell et al. datasets) make it quite clear that sociality is the correct answer (with foraging skills as a constraint, *not* a selection factor) (Shultz & Dunbar, 2022). Of ~35 tests of the social brain using different datasets and a variety of methods, these are the only two that commit these errors and the only two to obtain contrary results (Dunbar & Shultz, 2023). Both claim that their analyses are novel in several ways, but in fact they are not: they use the same data and the same statistical methods as everyone else – they just ask a different question. I need say no more.

Shi reminds us that many small-brained species (insects, birds) live in large, complex social groups. This misses the point: the social brain hypothesis is actually about animals' abilities to manage *relationships*, not about group size or organisation (Dunbar, 1998). Group size is not a trait that natural selection can act on: it is an emergent property of animals' social competencies (which natural selection can select for). For the record, we and others have shown, in many analyses, that the social brain hypothesis takes the form of a much simpler categorical relationship between large-brained monogamous species and small-brained promiscuous species in insectivores, carnivores, ruminant ungulates, bats, prosimians, and birds (with lifelong pairbonder species having bigger brains than annual pairbonders in the latter) (Shultz & Dunbar, 2007, 2010a,b; Pérez-Barbería, Shultz, & Dunbar, 2007; Dunbar & Shultz, 2025a). It seems that pairbonded relationships are hard cognitive work (as, I am sure, most of us will be only too painfully aware). Anthropoid primates, and a very small number of other mammal taxa, extend the same cognition to a wider set of individuals.

A second common misperception (also repeated by Bshary & Triki) is that the social brain hypothesis is some kind of non-ecological alternative to the ecological hypotheses. The social brain *is* an ecological hypothesis (Dunbar & Shultz, 2017; Shultz & Dunbar, 2022). The issue is, and always has been, whether individuals solve their ecological and life history (**Timbs & Manages,** please note) problems *individually* by trial-and-error learning or *socially* as a group (in which case extra cognitive work is required to maintain group cohesion through time, given that this doesn't come for free). The cultural intelligence hypothesis (van Schaik & Burkart, 2011), for example, is a subversion of the social brain hypothesis (it requires animals to live in stable groups so as to allow information exchange), not an alternative to it. The main difference between the two positions is simply whether energy intake (which doesn't require group-living) or predation risk (which does) is the principal factor limiting an individual's fitness.

A couple of minor points. **Ostner & Schülke** emphasise the importance of using phylogenetic methods (though without offering any reasons why). Phylogenetic methods are intended to guard against the risk of type I errors (rejecting the null hypothesis when it is true) due to the fact that closely related species are likely to inherit the same traits (the pseudo-replication problem). However, good statistical practice reminds us that they should only be used when there is evidence for a phylogenetic signal, since introducing an additional variable into a multiple regression inevitably reduces the degrees of freedom, and hence statistical power, thereby increasing the risk of type II errors (accepting the null hypothesis when it should be rejected). (This being so, we could in fact solve the statistical problem more easily by simply reducing the degrees of freedom.) In reality, contrary to their statement, the phylogenetic signal for group size and most behavioural and cognitive indices in primates is very low (Kamilar & Cooper, 2013), and at genus level, non-existent (Dunbar & Shultz, 2021a,b). Unfortunately, it seems that phylogenetic methods have become something of a virtue-signalling emblem, and are hence applied *de rigeur* without any forethought, often resulting in a significant reduction in the power of the statistical test being used.

Mention was made of a role for oxytocin and serotonin (**Zhiou et al.**). Oxytocin certainly plays some role in sociality, but in fact it is limited to mother-infant bonding and romantic relationships (having been evolutionarily co-opted from its fish origins, where it manages homeostasis of water balance to manage lactation in mammals). Its main disadvantages are that it is *very* short-lived (its half-life in the venous system is on the scale of minutes because it is excreted very quickly) and that it affects only the actor (if you have the right gene, you act prosocially). Not only are endorphins much longer-lasting (with a half-life in the order of hours), but their real benefit is that, through social grooming, they allow you to make *other individuals* prosocial towards *you* (see Dunbar, 2018b, 2025; Bzdok & Dunbar, 2022). At least in humans, we did not find evidence for any involvement of oxytocin at any social level other than romantic pairbonds, and even then endorphins were important (Pearce et al., 2017a, 2018). Indeed, it seems that even the original vole pairbonding claim is better explained by endorphins (Resendez et al., 2012, 2016; Inoue, Burkett, & Young, 2013). Similarly, serotonin may do many things physiologically, but it has only a very limited social signature (Pearce et al., 2017a). The issue here is not whether different neurohormones play a role in regulating social interactions, but which one(s) are crucial for social bonding and network coherence.

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The answer seems to be only β-endorphin and its stable mate dopamine (the two seem to work in a push/pull tandem fashion: see also **Loui & Margulis**).

Shi noted that many birds and insects live in complex societies, with some insects using pheromonal mechanisms to regulate sociality. The latter might be seen as paralleling the role that endorphins play as a form of social "glue" in primates. However, what these produce in insects is a highly regulated and regimented society – as is, in fact, also the case in mammals like mole rats who have a similar olfactory-based caste system. This does not make these societies complex. What makes *some* mammal and bird societies complex is that the animals' behaviour is facultative and highly flexible in a way that allows them to adjust their behaviour and social arrangements to differing environmental and demographic conditions. They can form "friendships" with complete strangers, for example, or choose one family member in preference to another. No insect does that.

Papadopoulis, Michlich & Andrews are concerned that my argument is anthropomorphic in that it sets humans up as the ideal to which all species must aspire. Aside from being an oddly Lamarckian "Great Chain of Being" view (discredited as long ago as the 1860s: Dunbar 2019), at no point do I suggest that what humans do is "better." Humans are mentioned at all only to indicate that they fall within the same spectrum as the great apes and the very social monkeys. Herd formation (aggregations) and stable group formation (congregations) are alternative adaptive peaks that function best under different environmental and biological conditions, with the first being *far* more common in mammals as a whole (Sutcliffe, Dunbar, & Wang, 2016). Having personally carried out field work on the behaviour and ecology of seven primate species, six ungulate species, two species of birds and one insect (dragonflies) (but, *mea culpa*, no fish or reptiles), my views are not coloured by what humans do, or by armchair preconceptions about what animals are presumed to do; they are coloured simply by what animals *actually* do.

Issues of theory and alternative mechanisms

Several of the commentaries offer interesting alternatives to grooming as the basis for the formation of stable groups: **Wolf** emphasises joint attention, **van Heijst & Kret,** mimicry and attention, Zhiou et al. focus on oxytocin, **Pelagi et al.** highlight play, **Benítez-Burraco** prefers aggression, and van Leeuwen & Roth and Zhiou et al., tolerance, while van Leeuwen & Roth and Shi favour the complexity of dominance hierarchies. All of these surely play a role – although, to be honest, it is difficult to see how mimicry, for example, can, in and of itself, influence the strength of social bonds in primates, given that even in humans the evidence is equivocal (Rauchbauer et al., 2023). Dominance rankings have always been considered an important feature of social organisation, but I would argue that any species that resorts to dominance hierarchies is likely to be one that relies on brute force and ignorance to get its way on a take-it-or-leave-it basis, rather than one that uses more sophisticated social strategies to negotiate a more equitable division of the spoils. By the same token, attention is really an outcome of having a relationship, not the determinant of the relationship (Dunbar & Shultz, 2010). Attention might indicate a desire to have a relationship, but it doesn't create one: a stranger who stares constantly at you can make you nervous – in baboons as much as in humans. Important as all these behaviours are socially, we need to remember that they only describe the bricks and mortar of dyadic relationships; our concern should also be to understand the building (i.e. groups and networks) they are used to create, and the functions these are designed to subserve.

A number of commentators (Benítez-Burraco, van Leeuwen & Roth, Zhiou et al.) argue for the importance of tolerance in understanding social evolution. I agree: tolerance is one of the skills of diplomacy that makes group-living possible for both animals and humans. But, like attention, tolerance is a behavioural description, not an explanation. It must depend on some kind of brain activity, and the most plausible suggestion is inhibition (self-control). That aside, we have no idea what tolerance actually is, how it is distributed across species, or what brain processes it requires. In contrast, we know a great deal about inhibition: we can measure it reliably using suitable behavioural tests, we know it is only found in anthropoid primates, and we can show that it varies significantly across species in a way proportional to core brain regions (Shultz & Dunbar, 2010c). Integrating work on tolerance and inhibition would surely be helpful.

Kaufman, among others, seems to take the view that I argue for an exclusively dyadic view of relationships. I am not sure why. The whole emphasis of the target article is on how to build an *alliance* that consists of several individuals integrated into a network, not a single dyadic relationship. Networks are, by definition, full of third-party relationships that are part of the deal. I have been arguing (for the past 50 years!) that, if we really want to understand social evolution in species like primates where group-living has been the key to their evolutionary success, we need to take a group-level perspective and consider multilevel selection (see also **Sueur & Deneubourg**).

De Dreu et al., Loui & Margolis, Pelagi, **Caruana and Burghardt**, **Ritov and Jacob & Engelman** raise matters that relate specifically to humans. I thank them for drawing attention to this genuinely interesting species and placing it in its proper context as part of a continuum with the other primates. Humans were not part of my remit for this target article, though I did include brief mention of them in order to point to some of the many continuities between humans and other primates. I have published experimental studies on the role of laughter, singing, dancing, music-making, rituals, feasting, and storytelling as crucial mechanisms that humans use for social bonding, both at the dyadic and the group level, and on the way all of them trigger the endorphin system (confirmed in several cases by positron emission tomography brain imaging or chemical deactivation of the brain's endorphin system) (for a summary, see Dunbar, 2021). Many of these studies were cited in the target article.

It is true that I did not consider play (Pelagi et al.), but that was because play is an activity that, outside of humans, is generally found only in juveniles, where it plays a vital role in the learning processes whereby mentalising, inhibition, and other socially crucial cognitive skills are fine-tuned. For reasons that elude me, the social brain often seems to be viewed as implying that animals are born capable of sustaining groups of a certain size. The social brain provides only capabilities; considerable practice is needed to be able to use these skills effectively in social contexts (as I have made clear right from the earliest papers: see Dunbar, 1998). This practice *has* to be done in face-to-face social contexts (and not online . . . !). This is why, as we have shown, the length of the period of socialisation (i.e. weaning to puberty – but *not* the period of parental investment from conception to weaning!) correlates, across primate species, with the size of both the neocortex (*not* the whole brain!) and group size (Joffe, 1997). Without play, there would be no social brain, and hence no groups.

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Several commentators (Bshary & Triki, **Lee & Strier**, Ostner & Schülke, Timbs & Menanges) emphasise the primacy of environmental quality and ecological competition (with passing mention of life history and behavioural ecology more generally) as the principal determinant of variation in both fertility and group size. With respect to fertility, the evidence is clear: both environmental quality *and* the number of females in the group are determinants, but they act independently (Hill, Lycett, & Dunbar, 2000; Dunbar, MacCarron, & Shultz, 2018a; Dunbar, 2019b; Dunbar & Shultz, 2021a). Environmental effects are random, and hence, in and of themselves, unlikely to influence the course of evolution – although they may have significant demographic consequences (e.g. by driving groups or populations to extinction). More importantly, the evidence is clear that environmental effects only start to influence fertility when animals have lost >15% of their body mass (i.e. are on the verge of starvation); in contrast social stress can cause females to become infertile even when they are fat and have access to unlimited food (Dunbar & Shultz, 2021a). In any case, the real cost of reproduction to female mammals is lactation, when females can lose up to 10% of their body mass (Dunbar & Dunbar, 1988; Dunbar, Anderson, & Knight, 2025; Dunbar, 2026).

I should add that we have explored the environmental determinants of group size (and variability) in a series of genus-specific, population-level time budget models (based on a linear programming approach) that have explicitly studied this in all the major Old World primate genera. Individual models have been built for *Colobus, Piliocolobus, Cercopithecus, Chlorocebus, Theropithecus, Papio,* the hylobatids, *Pongo, Gorilla,* and *Pan* (with a model for *Macaca* in progress), as well as some platyrrhines (*Ateles*, someone else was having a go at *Alouatta*) and an ungulate (with another antelope genus in progress) (for an early overview, see Dunbar, Korstjens, & Lehmann, 2009). These models are more accurate in predicting species' biogeographical distributions than the climate envelope models currently used by conservation biologists. In addition, they tell us which aspect of a species' biology constrains its distribution, as well as how much ecological stress *individual* populations are under (neither of which conventional biogeographic models do). One thing that emerges from these models is that, except on the margins of their biogeographical distributions, all species typically live in significantly smaller groups than their ecologies would allow. That deficit can be attributed to the infertility trap, but it also provides a buffer for the group to expand into during the lead up to group fission (Dunbar et al., 2009; Dunbar, MacCarron, & Robertson, 2018b).

Shi suggests that the coordination problem may not be such a serious problem as I make out – after all, starling flocks produce the most spectacular aerobatic displays using a very simple rule (do what your immediate neighbour does). Primates certainly exploit the same mechanism, but this does not mean that there is nothing more to what primates do. Mathematical modelling has shown that a set of coupled oscillators (i.e. foraging animals) will inevitably drift out of behavioural synchrony during the course of foraging (hence leading to the group breaking up) unless there is some kind of gravitational force (or social "glue") to maintain synchrony (Schaposnik, Hsu, & Dunbar, 2025). We should note, by the way, that starling murmurations only occur just before nesting in the evening, in perfect visibility conditions when everyone is free to do the same action, and normally only in winter; they never occur during the day when the birds are foraging or travelling to and from feeding areas. In other words, monkeys *can* do something starlings cannot, namely, maintain group coordination in poor visibility conditions, while foraging, all year round. If you think primate foraging is just a less complex two-dimensional version of a starling murmuration, try spending a day with monkeys foraging in dense vegetation. You will end up on your own; they won't.

Several commentators (Ritov et al., De Dreu et al.) emphasised the importance of cooperation, as opposed to coordination. The evolution of cooperation has been a matter of longstanding interest in evolutionary biology, psychology, anthropology, and economics. It has proved difficult to find a general explanation for the evolution of such behaviour – yet humans, and some animals, clearly do it. One reason for this conundrum is that cooperation is actually much rarer in real life than we tend to imagine. More importantly, the substantive issue is that there is a general tendency, mainly due to economists, to assume that social life consists of collaborations with strangers. It does not – not even in humans. Almost all our collaborations (other than rather specialised economic and financial transactions) are with members of our personal social network of ~150 family and friends. Within this very limited circle, we collaborate freely, but once beyond it, our relationships become strictly transactional (I'll help you out, but only if . . . .[you pay me in some way]) (Dunbar, Clark, & Hurst, 1995; Madsen et al., 2007). Even in hunter-gatherer societies, cooperation and altruism are focused on members of the group of known individuals (the clan of 100–200) – often widely misinterpreted (as De Dreu et al. do) as cooperation with strangers, on the mistaken assumption that the band (an unstable ecological unit) is *the* social grouping. It is not.

In other words, maybe we have been looking down the wrong end of the telescope. What comes first is living in groups – a pure coordination problem that does not involve a public good dilemma because everyone pays the same price by virtue of living in the group. Cooperation then comes for free because these groups are based on trusted relationships, thanks to repeated interactions (Dávid-Barrett & Dunbar, 2012).

A more important question touched on by several commentators (Kaufman; Papadopoulos et al.; Shi; Sueur & Deneubourg) is how to define complex sociality. Sueur & Deneubourg argue that it is all about multilevel selection and the emergent properties of networks. My response is: welcome to the club, but where has everyone else been all this time? Nonetheless, we need to be a little more nuanced than they seem to assume. A top-down network analysis is not an explanation: it is a description. We still need a bottom-up approach to explain why the network has the form it does (i.e. the outcome of individual psychology). Similarly, multilevel selection is simply a description of how fitness is sourced; it is not an explanation as such. It becomes interesting in the context of multilevel social systems only when we can apportion different components of fitness to different social layers. This, by the way, was precisely what Hamilton [1964] was getting at with his neighbourhood-modulated fitnesses, though the point of his original analysis is invariably lost by the conventional focus on his simplified formula and his rephrasing of this in terms of "inclusive fitness."

Bshary & Triki remind us that if fish can do anything primates do, then, if we want to claim that primates are different, we need to think about exactly how they are different and why. The answer is precisely what the target article is all about. We must be careful not to be seduced by superficialities in two separate respects. First, much confusion has been sown in the literature by naïve assumptions about the cognitive abilities that different tests index (Dunbar & Shultz, 2025b). This much has become apparent in the rather overblown claims that birds (and even cuttlefish!) have the

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capacity for self-control. They don't: the tests that have been used to measure self-control actually measure causal understanding, not strategic self-control (Dunbar & Shultz, 2025b). Second, it is one thing to claim that fish have many, or even all, of the basic cognitive abilities of primates, but quite another thing to conclude from this that there are no differences between them when we haven't tested for any of the more advanced forms of meta-cognition. Most forms of basic cognition (memory, learning, etc) are necessary for life and everyone has them. Not everyone has those forms of cognition like one-trial learning, inhibition, and mentalising that, in anthropoid primates, are built up out of these elemental components – and are dependent on specific brain regions (Brodman Area BA10) that only anthropoid primates have (Passingham & Wise, 2012), and hence even other mammals and birds don't possess (Dunbar & Shultz, 2025b).

Apperley questions the multilevel nature of mentalising. Mentalising is, by its very nature, infinitely recursive without limit. The only question is the empirical one of whether (and where) the limit is in humans, or any other species. Developmental psychologists have never been interested in anything beyond second-order intentionality (formal theory of mind: *I believe that you think* . . . .) since this marks the first major transition in five-year-old children. Our data consistently show that the upper limit for normal adult humans is at about fifth-order intentionality (involving five mental states – four other people's plus your own). It seems that the mistake Apperley makes is to assume all normal adults can manage that. But an average means what it says, and that means some perform at lower and a few at higher levels (in fact, the range in normal adults is approximately 3–6 levels of intentionality, based on half a dozen studies). The value Apperly quotes for success on fifth-order intentionality tasks in his study is similar to that in our data, so his results don't actually "disprove" anything.

That said, I agree that most everyday interactions rarely require more than third-order intentionality (*I believe that you think that Susan intends* . . . .), which is why third-order adults function just fine in society. Nonetheless, it is demonstrably the case that fiction (Carney, Wlodarski & Dunbar, 2014), jokes (Dunbar, Launay & Curry, 2016), and cartoons (Dunbar & Stirling-Middleton, 2024) are all rated as more enjoyable when their content requires higher orders of mentalising (providing it doesn't exceed fifth-order intentionality). That said, however, third-order adults prefer third-order stories, whereas fifth-order adults prefer fifth-order stories – in both cases, stories that challenge but don't exceed their individual mentalising competencies (Carney et al., 2014), probably because individual differences in mentalising correlate significantly with individual differences in syntactic understanding (the ability to unpack clauses) (Oesch & Dunbar, 2017). In addition, fifth-order mentalising sets the limiting size on conversation groups in Shakespeare's plays and modern films (Stiller, Nettle, & Dunbar, 2003; Krems & Dunbar, 2013), as well as everyday conversations (Krems, Neuberg, & Dunbar, 2016). In half a dozen samples (including one with N>1400: Street et al., 2025), five is the consistent upper limit. Individual differences in this limit correlate with the size of core brain regions (Lewis et al., 2011, 2017; Powell et al., 2010, 2014), as well as the number of friends an individual has (Powell et al., 2012). So it seems that even if we don't have fifth-order intentionality, we apparently still need it.

It is important to bear in mind that, among the primates, only the three great apes have formal theory of mind (second-order intentionality). Monkeys in general, as Devaine et al. (2017) showed, operate at first order, as do most other mammals with large brains. What we do know is that social cognition becomes *exponentially* more demanding in terms of neural processing with successive intentionality levels compared to simple causal reasoning or memory (see Lewis et al., 2017). Indeed, in primates, species' mentalising competences (in so far as we can determine quantitative differences in performance between species) correlate with neocortex (and especially frontal lobe) volume (Dunbar, 2009, 2026; Devaine et al., 2017).

I have suggested that the costliness of social cognition stems from the need to create a mental model of the mindstates/intentions of the other individuals involved. **Hu, Xia & Feldman-Hall** make a similar point in suggesting that part of the computational demand of large groups stems from the need to create a mental model of the network. In fact, West et al. (2020, 2023) argue that primate and human social networks involve a dual mapping exercise in which the animal has to cross-map the network as it sees it with the network as it imagines it (based on past experience), without the two leaking into each other (with the latter requiring cognitive inhibition). Note that this is not a memory problem, but a computational demand problem (the amount of work the brain has to do evaluating relationships that can change dynamically by the week, while factoring in third-party relationships) (see Dávid-Barrett & Dunbar, 2013).

Promising directions

Hamilton mentions Lossy compression as a way humans might create mega-communities, and a similar suggestion is made by **Moffett** in respect of the ability to categorise. The capacity to classify people into categories (kin/non-kin, my tribe, types of roles, honest/dishonest, etc) is precisely what allows humans to create mega-communities from tribes to nation states (Forgas & Dunbar, 2026), with these subject to the same scaling law as friends and family (Dunbar, 2020; Sandeford, 2018; Hamilton et al., 2020). How far this capacity permeates down the taxonomic scale is an open question. There is, as I noted in the article, evidence that the upper grade genera (mainly cercopithecines and apes) can factor kinship as well as dominance into their social calculations. Primates probably cannot go much beyond the social group, but culture allows humans to use labels (dialect, clothing, and knowledge) to do so on a very large, anonymous scale (my tribe, my religion, my political party, and my football fan club) (Dunbar, 2020; Forgas & Dunbar, 2026).

Both **Waller et al.** and **Roberts & Roberts** remind us that gestural communication in its many forms (including vocal metacommunication: see Dunbar et al., 2022) plays an important role in signalling relationship quality, both within a dyad and to third-party onlookers. It is surely significant that, across primates, the size of both vocal and facial gesture repertoires correlate with group size and brain size (Dunbar, 2012), suggesting that communication channels become more complex in order to exploit redundancy so as to reduce risk of misunderstandings. All these are important to know about, and not well enough studied.

Hobaiter & Dominy and Lee & Strier make the cogent point that studying within-species variation provides a way of testing the hypotheses. In fact, the infertility trap analyses *are* based on within-taxon (species or genus) analyses. The data to test this for the structural strategies that form the centrepiece of the target article are available in online *Dataset-S1*: each genus is based, on average, on a sample of 4.3 groups (2.4 groups per species, range 1–13). However, it would be naïve to assume that the three strategic modes appear by magic at different group size thresholds *within* species: cognition is, after all, a species-specific characteristic. Nonetheless, we might expect network structure and the balance

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between the different strategic modes to change in subtle ways with group size. Comparisons of grooming networks across group sizes for individual, groups of *Papio hamadryas* (Kummer, 1968), *Theropithecus gelada* (Dunbar & Dunbar, 1975; Dunbar, 1984, Dunbar et al., 2015), *Macaca fuscata* (Kudo & Dunbar 2000), and *Colobus guereza* (Dunbar et al., 2015) have shown that network structure changes with group size within species, as well as pointing to marked differences between species.

Krupnick calls for more neuroimaging studies on solitary versus social species. I am not sure whether this would help with understanding primates, because there aren't any solitary primates (those that forage alone, which once caused them to be classified as solitary, turn out to nest together quite contentedly). That said, a number of recent neuroimaging studies have compared lemurs, macaques, and humans, revealing striking differences in the presence and size of core brain regions important for sociality (with qualitative differences in brain organisation between lemur and the two anthropoids, and quantitative differences between the two anthropoids) (Roumazeilles et al., 2022). More studies on a wider range of species are desperately needed, not least because our knowledge of comparative brain organisation outside the primates is still very poor.

Both **Jörntell** and Krupnick raise the possibility that my findings may be relevant to psychiatry, and I agree that this is very likely. The number and quality of close friends is the single best predictor of both psychological *and* physical health and wellbeing, as well as future longevity (Dunbar, 2025). Understanding individual differences in relationship management may well be relevant to understanding some psychiatric conditions, and perhaps even how they should be treated (see also Charles, Dunbar, & Farias, 2020).

Avenues for future research

A number of directions for future research emerge out of this discussion. These include, but are not limited to: (1) testing whether the structural and behavioural changes within the same species also occur at group level; (2) conducting brain imaging studies on a much wider range of primate and especially non-primate species to obtain data on brain structural organisation and, more importantly, connectivity; (3) obtaining better cognition data on a wider range of species using more trait-appropriate tasks; (4) getting a better handle on mentalising and its demands in humans (about which we actually know very little); (5) determining the extent to which the capacity to categorise individuals into explicitly (i.e. linguistically) defined types (own clan, own tribe, own religion, etc) reduces cognitive load in humans, and whether, in attenuated implicit (i.e. non-linguistic) form, this also applies to any primates; (6) determining the group sizes at which ecological competition actually becomes an issue for animals in terms of gross energy intake (not simply whether or not they displace each other); (7) examining the group coordination (behavioural synchrony) issue in more species to determine at what group sizes this becomes a problem; (8) investigating the role of chorusing in social bonding; and (9) analysing the distributions of group size in a wider taxonomic sample to determine who does, and who does not, exhibit a fractal pattern. Most of these will be obvious from the earlier discussion, but let me briefly comment on three.

We still don't know what kinship means to animals or how they judge it – although familiarity at some early sensitive period in life is likely, since this seems to be true of humans (Madsen et al., 2007). We know that, in humans at least, kin and friend relationships are processed in different parts of the brain (Wlodarski & Dunbar, 2016; Roseman, Dunbar, & Arzy, 2024).

Group chorusing occurs in many species of primates as well as in some canids (wolves) and cetaceans (humpback whales). We have shown that, in humans, group singing upregulates the endorphin system as well as creating a deep sense of community bonding (Weinstein et al., 2016; Pearce et al., 2017b). Since it has recently been shown that vocal chorusing ("flock talk") upregulates the endorphin system in birds in a way that suggests a group-bonding function (Riters, Kelm-Nelson, & Spool, 2019), this raises the question as to whether similar chorusing behaviour in primates (notably howler monkeys, some colobines, and gibbons) might actually be for group bonding rather than territorial advertising as has conventionally been assumed. The same might also be true of some forms of contact calling that have a similar chorusing component (e.g. gelada baboons).

Multilevel sociality has been the subject of considerable interest in recent years. However, species that have a multilevel form exhibit two very different forms of modularity: irregular, casual modularity, and fractal modularity (Dunbar, 2026). The first are really herds: they are unstable, irregular in size, require little in the way of sophisticated cognition, and may not even offer a relevant fitness payoff (e.g. when animals simply converge on rich feeding grounds). Examples include the occasional very large groups of *Colobus angolensis* and *Rhinopithecus* (snub-nosed monkeys), perhaps even the mixed species groups of tamarins and guenons (Korstjens, Lehmann, & Dunbar, 2018). In species that have fractal modularity (orcas, elephants, baboons, great apes, and humans), the distribution of group sizes has a highly regular pattern, with each grouping layer being two or three times the size of the layer immediately inside it (Dunbar, 2026). The two kinds of multilevel grouping should not be confused. In order to understand the taxonomic distribution of fractal modularity and how and why it exists, we need more careful analyses of the patterning in the distribution of group sizes for a much wider range of species.

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