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To cite this article: R.I.M. Dunbar (2009) The social brain hypothesis and its implications for social evolution, *Annals of Human Biology*, 36:5, 562-572, DOI: [10.1080/03014460902960289](https://doi.org/10.1080/03014460902960289)

To link to this article: <https://doi.org/10.1080/03014460902960289>



Published online: 09 Sep 2009.



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ORIGINAL ARTICLE

The social brain hypothesis and its implications for social evolution

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(Received 23 March 2009; accepted 7 April 2009)

Abstract

The social brain hypothesis was proposed as an explanation for the fact that primates have unusually large brains for body size compared to all other vertebrates: Primates evolved large brains to manage their unusually complex social systems. Although this proposal has been generalized to all vertebrate taxa as an explanation for brain evolution, recent analyses suggest that the social brain hypothesis takes a very different form in other mammals and birds than it does in anthropoid primates. In primates, there is a quantitative relationship between brain size and social group size (group size is a monotonic function of brain size), presumably because the cognitive demands of sociality place a constraint on the number of individuals that can be maintained in a coherent group. In other mammals and birds, the relationship is a qualitative one: Large brains are associated with categorical differences in mating system, with species that have pairbonded mating systems having the largest brains. It seems that anthropoid primates may have generalized the bonding processes that characterize monogamous pairbonds to other non-reproductive relationships ('friendships'), thereby giving rise to the quantitative relationship between group size and brain size that we find in this taxon. This raises issues about why bonded relationships are cognitively so demanding (and, indeed, raises questions about what a bonded relationship actually is), and when and why primates undertook this change in social style.

Keywords: *Brain evolution, social brain hypothesis, primates, bonded relationships*

Introduction

Nearly 40 years ago, Jerison (1973) pointed out that primates have unusually large brains for body size compared to all other vertebrates. Although it was initially assumed that the evolution of large brains was driven by the demands of foraging and other aspects of survival, the broadly accepted consensus is now that primates evolved large brains to cope with their unusually complex social lives – an explanation now known as the social brain

hypothesis (Barton and Dunbar 1997). Although a number of alternative (mainly ecological) hypotheses have been offered for the evolution of large brains, most of these fail to distinguish between the causes and consequences of having a large brain (see Dunbar 2006, in press).

This is not the place to rehearse these arguments. However, exhaustive reviews of the alternative positions and the evidence to discriminate between them can be found elsewhere (Dunbar and Shultz 2007; Dunbar, in press). Dunbar and Shultz (2007), for example, used path analysis to resolve the issue, and showed that most of the alternative explanations for large brains are either constraints that have to be resolved in order to evolve a large brain or the opportunistic consequences of having done so. Currently, two versions of the social brain hypothesis exist. One focuses on the processes that underpin social cohesion and assumes that predation is the principal survival problem that animals have to contend with (Dunbar 1992; Dunbar and Shultz 2007); the other focuses on the social transmission of foraging skills, and assumes that food-finding is the factor that most limits survival (Reader and Laland 2002). The key issue here is which of these is the primary selection factor for big brains, and which the consequence (i.e. window of opportunity provided by having a large brain), since both almost certainly depend on the same cognitive competences. There is, however, considerable evidence to suggest that, in primates, group size is directly related to predation risk (see, for example, van Schaik 1983; Hill and Lee 1998; Hill and Dunbar 1998; Shultz et al. 2004). In contrast, there is little evidence to suggest that foraging skills alone (and especially socially acquired foraging skills) have a significant influence on individual fitness (see Altmann 2000).

The principal evidence adduced in favour of the social brain hypothesis has been a quantitative relationship between social group size and some measure of brain size (Dunbar 1992, 1998; Barton 1996; Barton and Dunbar 1997). In most cases, these analyses have focused on relative neocortex volume, on the grounds that it is the neocortex that has expanded out of all proportion to other brain units in primates (Finlay and Darlington 1995). In practice, the volumes of most brain regions correlate with each other (and hence with total brain size), so that many analyses have simply used total brain volume for convenience. On a large enough scale (i.e. a mouse-to-elephant scale), using total brain volume yields much the same results as a finer scale analysis of neocortex volume. However, mosaic evolution (Barton and Harvey 2000) in which, within this broad scale pattern, some areas have been emphasized at the expense of others can lead to anomalies in individual cases. One such example is the gorilla, which has a relatively small neocortex and a large cerebellum: Correlating group with total brain size yields an anomalous result in the gorilla's case, whereas correlating it with neocortex size results in a datapoint close to the regression line (Dunbar 2003b).

Although often presented as a simple quantitative relationship between group size and brain size, the social brain hypothesis is properly constituted in terms of social complexity, with the group size effect being an emergent property of how well animals handle complex relationships. Indeed, a number of analyses have demonstrated correlations between various indices of behavioural complexity and brain size. Pawlowski et al. (1998), for example showed that, in promiscuously mating primates, male mating strategies are a function of relative neocortex size. In this case, the correlation between male dominance rank and mating success was a negative function of neocortex ratio: In other words, in larger brained species, low-ranking males are able to subvert high-ranking males' abilities to monopolize matings, but in small-brained species they are not (presumably because they lack the cognitive abilities to exploit loopholes such as alliances and female choice). Similarly, Kudo and Dunbar (2001) found that grooming clique size (a proxy for alliances) correlated with

relative neocortex size (see also Dunbar and Shultz 2007), while Byrne and Corp (2004) reported that rates of deception (standardized by number of studies on the species) also correlated with neocortex size.

Despite this, the social brain hypothesis continues to be interpreted as a purely quantitative relationship between group size and brain size. There have, as a result, been a number of attempts to generalize this relationship to other higher vertebrates, usually with mixed success. Some have claimed (at best weak) relationships between group size and brain size (Dunbar and Bever 1998), others have found only qualitative (i.e. categorical) relationships (Pérez-Barbería and Gordon 2005; Shultz and Dunbar 2006), while yet others have argued that no such relationship exists and have instead sought alternative explanations in terms of, for example, sexual selection (Beauchamp & Fernandez-Juricic 2004; Garamszegi et al. 2005; Pitnick et al. 2006; Schillaci 2007).

In fact, it seems that we have all been trying to shoehorn what, at the emergent level of social system, is in reality a qualitative (i.e. categorical) relationship into a quantitative form. On more careful analysis, it turns out that this quantitative form of the social brain hypothesis is more or less unique to primates (and perhaps only anthropoid primates). Shultz and Dunbar (2007) found that, among mammals and birds in general, the social brain hypothesis takes a qualitative rather than a quantitative form: Social group size does not correlate with brain size in any of these taxa and, instead, it is species that live in pairbonded (i.e. monogamous) social systems that have the largest brains, when phylogeny and a range of life history and ecological variables are partialled out. By pairbonded, we usually refer to a lasting (sometimes, but not always, lifelong) relationship between a male and a female, normally for reproductive purposes. In most mammalian and avian orders, pairs of this kind typically live alone in separate territories, with both pairbond and territory often guarded against invasion by same-sex rivals.

One reason for emphasizing lifelong pairbonds is that the bird data show quite uncompromisingly that species with annual pairbonds have brains that are significantly smaller than those of species that have lifelong pairbonds (Shultz and Dunbar 2007), implying that there is a significant difference between these two categories of pairbonded social systems. In contrast, primates exhibit a very strong signal for social group size: No matter how the data are analysed, there is a significant relationship between mean species group size and relative neocortex size. This suggests that there was an important phase transition in the form of the social brain effect at some early stage during primate evolution. In some way, primates (and this may refer specifically to anthropoid primates) have altered the form of the social brain hypothesis by generalizing a pairbond relationship into a more general form of bonded relationship (something that we might think of, anthropomorphically, as friendships).

Despite this phase transition, it is perhaps worth noting that, hidden beneath the quantitative group size effect, one can still detect a weak signal from a monogamy effect even among the primates. If absolute neocortex volume is adjusted for mean social group size, and the data are plotted separately for the main socio-cognitive grades (prosimians, simians and apes), it is evident that monogamous species that live in long term pairs have larger neocortices than species that mate polygamously (Figure 1). Both taxon grouping and mating system have significant independent effects on residual neocortex size (overall model: $F_{8,29} = 3.81$, $p = 0.004$; taxon: $F_{3,29} = 4.71$, $p = 0.009$; mating system: $F_{3,29} = 3.51$, $p = 0.028$; interaction effect, NS). Note that, although callitrichids (marmosets and tamarins) have commonly been thought of as having a monogamous mating system, doubts have been raised in respect of the nature of monogamy in these taxa (Dunbar 1995; Fuentes 1998), and for this reason they are separated off in Figure 1. These doubts would seem to

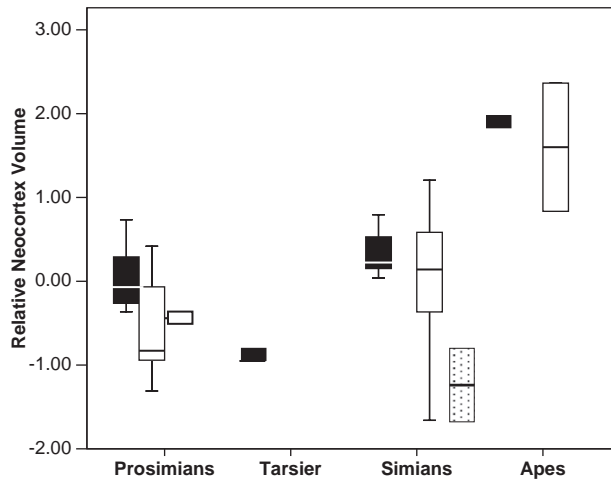


Figure 1. Median ($\pm 50\%$ and 95% ranges) for relative \log_e neocortex volume (adjusted for mean group size) for individual primate genera as a function of the mating system. Black bars: monogamous pairs; open bars: polygamous mating systems (left bar: semi-solitary; right bar: polygamous groups); hatched bars: callitrichids. The loris group (*Loris*, *Nycticebus*, *Perodictus*) has been excluded from the Prosimians because of uncertainty about their social system (and, hence, effective group size). The plotted value is the residual of observed \log_e neocortex volume relative to that predicted by the generic equation for neocortex volume regressed on group size for all primates: $\ln(\text{Neocortex volume}) = 1.008 + 7.728 \ln(\text{Group size})$ ($r^2 = 0.612$, $F_{1,40} = 63.2$, $p < 0.001$). I use absolute rather than relative neocortex volume here because, at least for primates, it turns out that it doesn't much matter what measure of brain size is used (see Dunbar 1992; Shultz and Dunbar, unpublished). Source: Neocortex volume data from Stephan et al. (1981); group size data from Smuts et al. (1987).

be vindicated by the fact that they have significantly smaller neocortices for group size than more conventionally monogamous monkeys. Callitrichids seem to have an unusually flexible social system that can vary over time within a single group between monogamy, polygyny, polygynandry and polyandry as a function of environmental and demographic conditions (Goldizen 1987; Dunbar 1995). In sum, while there is a weak signature due to pairbonding in primates, this effect is overwhelmed by the much stronger group size effect, and is only detectable if the group size effect is first partialled out.

It is important to appreciate that, even though the social brain may take a qualitative form among non-primate mammals (i.e. brain size is a function of categorical differences in mating system), the demands of sociality are still responsible for the evolution of brain size even in these taxa. Pérez-Barbería et al. (2007) showed that, among carnivores, ungulates and primates, there was a significant co-evolutionary effect in the phylogenetic transition from asociality to sociality (or, in the case of primates, smaller-than-average groups to larger-than-average groups) and from small to large brain volume. However, there is an important caveat on the generality of this overall relationship. Within the carnivores and ungulates (but *not* the primates), there were identifiable lag effects: Sometimes one variable changed without the other, or there were subsequent reversals after a change had occurred (i.e. following a transition from asocial/small-brain to social/large-brain, there might be a back-transition to asocial/large-brain or social/small-brain). Transitions of this kind occurred extremely rarely among primates, suggesting that the co-evolutionary linkage between brain size and sociality was much tighter in their case: One variable could never change without the other. As with the contrast between the qualitative and quantitative

forms of the social brain relationship, this likewise suggests that primate sociality may be qualitatively different from that of other mammalian taxa.

Two questions arise from these findings. First, why are bonded relationships of the kind we find in primates (and more generally in monogamously paired mammals and birds) so cognitively challenging that they require an unusually large brain? And, second, why are primates so different to other mammals and birds?

Why are relationships cognitively costly?

Given the finding that monogamous species have larger brains than species that mate polygamously or promiscuously, what is it that makes pairbonds cognitively so demanding? One problem here is that we as yet have no satisfactory definition of what a pairbond (or, more precisely, the process of being bonded) actually means. This is because we have conventionally defined pairbonds functionally (i.e. what pairbonds allow animals to do, usually in terms of cooperative reproduction or territorial behaviour), and there has been no real attempt to grapple with the question of just what a pairbond itself is. Consequently, we have no metric by which to compare the strength of (pair)bonds, either between individuals within a species or, worse still, between species. As a result, we cannot assess either the cognitive demands or the functional implications (in terms of fitness) of bonds of different quality. While this is clearly a major issue that needs dealing with, this is neither the time nor the place to do so. However, we can at least sketch out part of the framework of what needs to be addressed.

There would appear to be two main kinds of cognitive costs to pairbonding: Long term costs that derive from poor mate choice decisions and more immediate costs that arise through the demands of behavioural coordination. The long term costs reflect misjudgements in mate choice. If a mate turns out to be infertile or unreliable (e.g. abandons its mate), the fitness costs would be catastrophic, especially in those cases where pairbonding is in principle lifelong and divorce with remating is not an easy option because there are few unpaired individuals. In such cases, mate choice is not a trivial issue. As a result, we might expect intense selection pressure for fine-tuned mate choice competences. In at least some of these respects, the demands are associated mainly with Machiavellian considerations: An individual must be able to assess the honesty and reliability of prospective mates, and make fine judgements about their future behaviour and fertility. Failure to do so may lead to reduced fitness if the individual is cuckolded by its mate or has to share the mate's rearing effort with someone else.

In principle, of course, these issues apply to all cases of mate choice to some degree, though their intrusiveness may be especially strong in the case of lifelong monogamy (that's to say, monogamy that is more than just seasonal). However, pairbondedness necessarily imposes additional purely social demands in terms of the need to coordinate and synchronize behaviour. This is perhaps most obvious in the case of birds, where the need for one member of the pair to remain on the nest to keep the eggs warm and/or guard them from nest predators means that the pair have to maintain a high level of coordination in their behavioural scheduling. An individual cannot remain away from the nest for too long, or its mate will be forced to choose between staying on the nest and starving or putting the eggs/chicks at risk by abandoning them in order to feed. Similarly, among small pairbonded antelope like klipspringer, pair members maintain a constant level of mutual attention whose function is to ensure close coordination (Dunbar and Dunbar 1980). Indeed, so

attentive are klipspringer to each other's whereabouts and behaviour that they are rarely found more than a couple of metres apart. Similarly, among the small monogamous New World cebids, mates maintain close spatial proximity both when resting and when foraging. When resting, they are often to be found sitting together with tails intertwined.

It is not obvious which of these two considerations are paramount. However, since parsimony should once again enjoin us to assume that only one factor is the principal selection pressure favouring the need for advanced cognitive abilities, two points would tend to suggest that it is the demands of behavioural coordination that are the more likely. First, mate choice is a one-off issue, and, once a decision has been made, there should be no great need for the pair to pay much attention to each other thereafter. Rather, they should simply get on with the business of rearing their offspring and ensuring their own survival. That ought to mean that the pair is together only when offspring are actually being reared. This, of course, is exactly what we see in those bird species that have annual pairbonds: The pair disperses after the clutch has fledged, and each forms a new pairbond with another mate the following year. It is notable that bird species with annual pairbonds have significantly smaller relative brain sizes than those with lifelong pairbonds (Shultz and Dunbar 2007). Second, a critical tests analysis (Table I) suggests that, at least in primates and other pairbonded mammals, it is the costs of behavioural synchrony that are the issue. More predictions of the behavioural coordination hypothesis are supported than those of the mate choice hypothesis. Of course, this does not mean that mate choice does not impose secondary selection pressures that also favour large brains. Rather, it suggests that, in the absence of the need for behavioural coordination, mate choice might not be a sufficiently intrusive problem to warrant investment in very large brains. After all, most lekking birds solve essentially the same mate choice problem with brains of very modest size (Shultz and Dunbar 2007).

One might counter this claim by raising the issue of cuckoldry: Both sexes can have a great deal at stake if their mate fails to fulfil their half of the bargain implicit in bi-parental

Table I. Critical tests analysis* of the short term (mate choice) vs long term (behavioural coordination) cognitive demands of pairbonding, with relevant evidence from three strongly pairbonded taxa.

Behavioural predictions	Hypothesis		Evidence†		
	Mate choice	Coordination	Klipspringer	Canids	Cebids
Long courtship to assess mate quality	✓	X	X	X	X?
Exaggerated cues of mate quality	✓	X	X	X	X
Close monitoring of mate	X‡	✓	✓	(?)	✓
Remain in close spatial proximity to mate	X	✓	✓	(?)	✓
Pair remain together outside breeding season	X	✓	✓	✓	✓
Sex-specific defence of pairbond	X	✓	✓	✓	✓
Behavioural synchrony between pair	X	✓	✓	?	✓

*A critical tests analysis (originally developed by Isaac Newton) uses the assumptions by which alternative hypotheses differ to generate a suite of predictions by which the hypotheses under consideration must differ (see van Schaik 1983, van Schaik and Dunbar 1990). It allows the evidence to decide unequivocally between competing explanations for a phenomenon.

†Relevant data for klipspringer derive from the author's own field studies in Ethiopia and Kenya (see Dunbar and Dunbar 1980; Roberts and Dunbar 2000); evidence for canids and cebids based on the literature.

‡Dunnoek males manage to monitor the level of mate fidelity by simply keeping track of the proportion of time for which the mate is out of sight during the egg-laying period (Davies 1992); however, this applies only during a very narrow time window. Consequently, in pairbonded mammals, close monitoring should only occur during the (often brief) mating season.

care. Conversely, the opportunity to acquire extra sirings (for males) or better quality sperm (for females) through extrapair copulations might select for Machiavellian skills. However, whatever the advantages of extrapair sirings may be, it is worth noting that dunnock males manage to solve the problem of cuckoldry by dint of an exceptionally simple rule of thumb (how long the female was out of view during the egg-laying period: Davies 1992), using a brain of quite modest size. In contrast, the pressure for close social coordination on a daily basis for months or even years on end might seem to be more demanding cognitively than a one-off decision about mate quality.

One final piece of evidence against the suggestion that the need for bi-parental care itself was the key factor selecting for large brains is that game theory analyses of the evolution of monogamy in callitrichid primates suggest that pairbonding must have evolved before bi-parental care (Dunbar 1995). The costs to the female of opting for twinning are too great in the absence of reliable bi-parental care, and at the same time there is no advantage to the male in offering paternal care if the female is unable to twin. However, if the male is willing to pairbond with the female for some other reason (e.g. defence against infanticide or predation on the offspring), then this creates a window of opportunity for the female to up her reproductive investment and opt for twinning. Hence, a reproductive system of twins-with-paternal-care is only viable if the male is already associating with the female for reasons other than offering paternal care. Once the male is locked into a pairbond, paternal care is a marginal additional cost that offers a significant benefit in fitness for the male. And that in turn makes it feasible for the female to bear the cost of twinning.

An alternative hypothesis that needs to be considered is that the large brains of pairbonded species are related to the need for more sophisticated food finding in order to make bi-parental care effective for rearing altricial young. However, whatever its merits, this explanation is not supported by two key observations. First, among birds, species that form lifelong pairbonds have significantly larger brains than species that form annual pairbonds, despite the fact that the foraging costs of rearing young each year are essentially the same (Shultz and Dunbar 2007). Second, ungulate species that live in monogamous pairs show the same pairbond effect on brain size despite the fact that ungulates do not have bi-parental care. Moreover, pairbonded species of ungulates do not specialize on higher quality diets than non-pairbonded species of similar body mass: Rather, specialization on high quality diets is a consequence of small body size, irrespective of mating system (Jarman 1974).

The most likely interpretation of these findings, then, is that the demands of pairbonding were the critical factor responsible for triggering the evolution of large brains in both the birds and the mammals. These demands are reflected in the need to coordinate one's behaviour with that of one's mate. An important feature of behavioural coordination in these cases is that individuals must be able to anticipate the mate's needs in order to ensure that both members of the pair are able to meet their nutritional and other requirements (e.g. have sufficient rest time to process food and control heat load by resting), as well as ensure effective parental care on the appropriate occasions. Being attentive to the mate's needs so as to ensure that he/she can achieve his/her daily nutrient intake has many of the hallmarks that would be recognized as theory of mind in humans. In effect, pairbonded species have to be able to engage in perspective-taking, a phenomenon that is widely accepted as being a prerequisite for mentalizing (or theory of mind: Hare et al. 2001, 2006). Hence, pairbonded monogamy can perhaps be seen as laying the foundations for the kinds of advanced social cognition found (albeit in limited form) in primates and (perhaps uniquely in full-blown form) in humans.

Lest this be misunderstood, let me be clear that I am not implying that pairbonded birds and ungulates have theory of mind, but rather that they have had to evolve at least some of the elements that underpin full-blown theory of mind in humans. Put another way, it is in these species in particular that we should look for the precursors of theory of mind. It is also important to appreciate that this claim is explicitly about pairbonded relationships, not about monogamous mating systems as such: Monogamous mating systems can arise from a number of causes (including mate guarding: e.g. Brotherton and Komers 2003), and need not necessarily involve pairbonding.

We now know from both reaction time experiments and neuroimaging studies that this kind of intentional-based social cognition is cognitively very demanding, not only in terms of neural activity while processing tasks but also in terms of neural allocation to these functions (Birch 2007; see also Dunbar 2003a). These results parallel recent findings suggesting that species differences in executive function skills (on which social cognitive skills must ultimately depend) correlate with brain volume in primates (Lee 2006; Deaner et al. 2007; Shultz and Dunbar, unpublished).

The evidence reviewed here thus suggests that the cognitive demands of relationships (at least as instantiated in the form of pairbonds) may be very significant, and that these in turn translate into wetware. It is important to remind ourselves that brain tissue is exceptionally expensive in energetic terms (Mink et al. 1981; Aiello and Wheeler 1995; Kaufman 2003; Isler & van Schaik 2006; Karbowski 2007). Brain tissue consumes about 10 times more energy than an equivalent mass of skeletal muscle, mainly because the costs of having to replenish neurotransmitters is very high. Thus the costs of evolving a large brain are substantial, and significant benefits are needed to offset these costs so as to make a large brain worth an animal's while – a point that often seems to be overlooked in discussions of brain evolution. This is particularly relevant in the contrast between primates and other species: Irrespective of whether there is a relationship between brain size and any ecologically relevant behaviour among mammals in general, we still have to explain why primates need so much bigger brains than, say, deer or meerkats to solve the same ecological problems. Primates must be doing something else with their big brains.

Why are primates so different?

The apparent contrast between anthropoid primates and other species in the way brain size relates to sociality raises the question as to why primates seem to be so different to other mammalian and avian taxa. It seems that something happened very early on during the course of primate evolution to switch the social brain process from a qualitative to a quantitative mode. (It remains a possibility that some other non-primate lineages might also exhibit a primate-like quantitative relationship between brain size and social group size – elephants, equids and delphinids are the likely candidates – but there are insufficient data available for these taxa for a detailed comparative analysis to be undertaken at present. However, the point is that this transition seems to have been rare.)

What this phase shift seems to have involved is a generalization of the pairbond relationship from a reproductive mate to other members of the social group (Dunbar and Shultz 2007). Doing so would naturally yield a set of intense (albeit non-reproductive) 'pairbonds' with a number of individuals (in effect, 'friends': Silk 2002). In contrast to reproductive mates, however, the number of such non-reproductive 'pairbonds' is limited

only by group size, which would account for the quantitative relationship between group size and brain size found in primates.

This suggests that primate sociality is of a rather different kind to that found in most other mammalian taxa, being characterized by more strongly bonded relationships. Indeed, Shultz and Dunbar (2007) showed that anthropoid primate societies were characterized by a significantly higher proportion of female-bonded social groups (i.e. groups in which females had close, bonded relationships in which dyads maintained close spatial proximity on a long-term basis, interacted frequently with each other and came to each other's aid against other group members). Relationships of this kind were, by comparison, rare among carnivores, artiodactyl ungulates and prosimian primates, even though conventional reproductive pairbond relationships were relatively common.

The fact that prosimian and anthropoid primates seem to differ in the frequency of bonded relationships suggests that this phase shift in bondedness occurred close to the point of origin of anthropoid primates during the Eocene. Quite why such a shift in social structure was required remains, at present, unclear, although it is possible that it had something to do with the shift in diet from insectivory to frugivory that occurred at this juncture (Barton 1998; Dunbar, in press).

In sum, then, my suggestion here has centred around the claim that increases in brain size were triggered by the cognitive demands of pairbonds (themselves necessitated by the requirements for biparental care), and that these cognitive mechanisms were generalized to non-reproductive individuals by early anthropoid primates in order to facilitate bonded social groups, thereby giving rise to the familiar group-size-to-brain-size relationship of the social brain hypothesis. I have suggested that it was the cognitive demands of maintaining close pairbonds that was responsible for this, and that these provided the precursor for the evolution of social cognition that takes its ultimate form in theory of mind in humans.

Declaration of interest: The author reports no conflicts of interest. The author alone is responsible for the content and writing of the paper.

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This paper was first published online on iFirst on 2 July 2009.