Mosaic Evolution of Cognitive Skills in Mammals

R.I.M. Dunbar
Department of Experimental Psychology
Anna Watts Building
University of Oxford
Oxford OX2 1GG, UK

Susanne Shultz
Department of Earth and Environmental Sciences
Michael Smith Building
University of Manchester
Manchester M13 9PT, UK

Corresponding author: R.I.M. Dunbar [email: robin.dunbar@psy.ox.ac.uk]

Abstract

The capacity to inhibit prepotent actions (inhibitory self-control) plays an important role in many aspects of the behaviour of birds and mammals. Although a number of studies have used it as an index of foraging skills, inhibition is, in fact, also crucial for maintaining the temporal and spatial coherence of bonded social groups. Using two sets of comparative data, we show that, in primates, the capacity to inhibit behaviour when making decisions correlates better with the demands of social contexts than the demands of foraging contexts. We show that the capacity to inhibit prepotent action is unique to anthropoid primates (the Passingham-Wise Conjecture) and may be crucial for the spatio-temporal integrity of their unique bonded social groups.

Key words: primates, bonded social groups, self-control, inhibition, temporal discounting

Short title: Mosaic evolution of cognition

1. Introduction

The capacity to inhibit prepotent responses (self-control) is an important cognitive skill that plays a crucial role in many contexts. In humans, for example, it is a strong predictor of both anti-social behaviour as well as the stability of romantic relationships [1,2]. It also appears to be neurophysiologically demanding in that, in mammals at least, species differences in the ability to exercise self-control covary with brain size [3-5]. Most studies of inhibition have focussed on its role in foraging [3-4,6] on the implicit assumption that, when animals forage optimally, they have to be prepared to bypass a less valuable immediate reward in order to gain a more valuable future one [7]. Inhibition can, however, also be important in a social context for species that live in bonded social groups.

For species that form aggregations (unstable flocks or herds), differences in the rate of gut fill result in animals' time budgets getting out of synchrony [8-10], causing groups to fragment and disperse on a timescale of days [11-15]. This effect is exacerbated by the length of the foraging day. Joiner-lever models [16] remind us that, whereas small groups typically attract members, large groups lose them, partly because food patches become exhausted but also partly because of the foraging decisions that individuals make. With no centripetal force to maintain group cohesion, animals simply drift apart [11-14]. Even in herd-forming primates such as the gelada, herds are increasingly likely to fragment during the day's foraging as their size increases [17]. In contrast, some species form stable social groups (congregations) that travel and sleep together, with a composition that remains stable over many years (subject to births and deaths). These kinds of groups, in which individuals have strong bonds with each other [18-20] that form networks of interconnectedness [21], are particularly characteristic of primates. Such group face significant challenges because they have to maintain cohesion in the face of all the pressures that cause aggregations to fragment

[22]. Because these groups function primarily as defensive coalitions against external threats [5,23-25], their effectiveness is predicated on being able to maintain coherence over time so as to ensure that allies are always nearby in the event that unpredictable dangers (predators, rival groups) threaten [5,22].

To be able to maintain synchrony of activity scheduling [27], animals have to be able to suppress the desire to continue feeding when the rest of the group goes to rest (or, conversely, forego resting when everyone else wants to continue foraging). In socially flocking weaver birds (*Quelea* spp.), for example, the pressure to go to roost with the rest of the flock results in low-ranking individuals preferring to lose weight by staying with the flock rather than continue feeding unhindered at an abundant food source from which they had previously been excluded by other group-members [28]. In bonded groups, animals also need to be able to suppress the desire to steal each other's food or respond aggressively to mild threats, lest such behaviours make others less willing to come to their aid – or, worse still, leave the group.

To determine whether self-control is more important in the social or the ecological (foraging) domains, we analyse data on performance on two slightly different inhibition tasks (an A-not-B task and a Go/No-Go task, respectively) from two separate databases [3,4] for a range of primate species. Both tasks are widely used tests of the capacity to inhibit prepotent actions (i.e. inhibitory self-control) in both humans and animals. We ask whether the capacity for self-control correlates better with indices for the foraging domain or the social domain. MacLean et al. [3] also used performance on a second task (the cylinder task), which has been widely referred to it as an inhibition task [6,29-31]. In fact, it asks animals to choose between two ends of a cylinder in order to access a food reward. Because it involves understanding a causal process (one access point is blocked or longer), it is better characterized as a causal reasoning task rather than an inhibition task. We also analyse the

data for this task as it represents an important cognitive skill that provides a conceptual contrast to inhibition tasks.

As indices of foraging demand, we use the percentage of fruit in the diet and the size of the home range (or territory), both of which have frequently been used to test similar hypotheses [3-4,29-31]. Fruits are much less predictable than foliage, and are usually viewed as being a cognitively more challenging diet [32-34]. They are also more likely to vary spatially in quality, providing the ideal conditions for optimal foraging decisions. Similarly, large home ranges are assumed to be cognitively demanding in terms of the mental mapping skills and the fact that foraging animals have to choose between near and distant locations on the basis of their profitability [4,34]. In primates, both percent fruit in the diet and range size are strongly influenced by habitat conditions and hence impact on nutrient acquisition [35-39]. If inhibition relates to foraging efficiency, it should correlate positively with one or both of these indices. As social domain indices, we use mean social group size and mean day journey length. Coordination problems will increase as a function of both group size and the distance animals have to travel before converging on a sleeping site since both make it more likely that individuals' activity cycles will get out of synchrony during the course of the day's foraging [9,15]. Baboons provide an example: group fragmentation is more likely as both day journey length and group size increase (Fig. 1), with these effects acting independently (Table S3). If inhibition is primarily a social skill that influences group cohesion, it should correlate positively with one or both of these indices.

It is important to be clear about the difference between range size and day journey length since, viewed superficially, both look like foraging-relevant variables. However, functionally speaking, they are very different, and especially so for primates. Primates do not forage randomly in their environment, but rather move from one resource patch to another, often at some considerable distance [40-41]. Range size limits the number of patches

available to the animals, but it does not, of itself, determine the number of patches visited each day or the length of the day journey. Day journey length, by contrast, is a consequence, *not a determinant*, of the size of the group and the number of patches the group has to visit to satisfy its collective nutritional demand [42]. In other words, range size defines the distribution of food sources that animals can choose between and hence the choices they make on where to forage, whereas day journey length is simply the means to achieving the ecological end of visiting the required number of patches (but *not* which patches to visit). The first is a resource choice issue, the second a routing issue and it is only the second that has significant implications for maintaining group cohesion.

Finally, Passingham & Wise [43] argue that, in primates, inhibition depends explicitly on the brain's frontal pole (Brodmann Area 10), a brain unit that is only found in anthropoid primates. The significant role of the prefrontal cortex in supporting inhibition is confirmed by neuroimaging and lesion studies in humans, albeit with a wider focus on the ventrolateral prefrontal cortex (Brodman areas 44, 45 and 46) immediately adjacent to the frontal pole [44]. Since, with the exception of a few (mostly species-poor) orders, large bonded social groups are found only in anthropoid primates [5,22,45-46], we also test the derivative hypothesis that the capacity to inhibit behaviour will be more highly developed in anthropoid primates than in other mammalian orders.

2. Methods

(a) Data

We use data from two sources [3,4] that provide experimental data on the capacity to inhibit prepotent responses in a number of primate species (see *ESM DATASET-1*). Since they involve different tasks, we analyse the two datasets separately. Mean group size for species was sourced from [47], percentage of fruit in the diet (except for *Macaca mulatta*: see

Table S4) from [33] and day journey length (in km) and home range size (in ha) from [48-49] and primary sources therein (for exceptions, see *ESM*).

To test the Passingham-Wise conjecture, we use the data given by [3] on the A-not-B and cylinder tasks for a wide range of mammalian orders as well as a selection of bird species: these data are given in *ESM DATASET-2*.

We excluded *Papio hamadryas* from the MacLean et al. dataset because of its unusually long day journey length (>7 km, 5.9 SD above the mean for all the other primates in this dataset) and a group size (mean band size=82.5) that is 4.6 SD above the average for the rest of the sample. This reflects the fact that this species lives in uniquely challenging and, for primates, dry habitats [50], and as a result has an unusual fission-fusion social system that allows it to adjust its group size flexibly to cope with the demands of foraging under these conditions [51]. In this respect, it behaves more like a herd-forming species than a conventional primate that lives in stable groups [5]. We also excluded *Canis familiaris* from the same dataset because it is a domesticated species and we cannot be sure which traits have been selected for, or what its natural social group size might have been.

(b) Statistical analysis

Although multiple regression might seem like the obvious method for testing hypotheses of this kind, the format of the standard regression model would oblige us to regress the cognitive cause (inhibition skill) on the four ecological and social outcome variables, thus reversing the natural biological causality. Doing so implies that ecological behaviour constrains or determines cognition, and can produce very different results to those obtained when the axes are reversed. In this case, the causality is quite obviously the other way around: a species' cognition constrains (i.e. statistically "causes") what it can do in terms of behavioural outcomes. A statistically more elegant approach is to use principal

components (or factor) analysis to ascertain which variables covary (i.e. cluster together). This avoids the need to presumptively specify the causal relationship between variables that may in fact have a more complex relationship.

Conventionally, comparative analyses use phylogenetic methods to control for the impact of phylogenetic inertia. We do not do so in this case because there are no phylogenetic methods designed for use with factor analysis. More importantly, in primates, the phylogenetic signals for group size, percent fruit in diet, home range size and day journey length are all close to zero [52]. This is because most of these variables are phenotypic responses to local environmental conditions rather than being species-typical: in most of these cases, the variance within species is greater than that between species [22]. When the phylogenetic signal is ~0, phylogenetic controls are not required. Indeed, previous studies have shown that, at least in primates, the inclusion or omission of phylogenetic controls does not change the results of comparative analyses for group size or any of the cognitive variables included in our analyses [3,45-46]. Finally, in only a very few cases are there samples from the same genus or even closely related genera in either of these datasets (the principal problem that phylogenetic methods exist to address). As a check, however, we calculated averages at genus level and re-ran the factor analyses.

3. Results

Bivariate correlations between the three cognitive tasks and the four ecological outcome measures are given in Table S5 and Fig. S1. The three cognitive tasks correlate with each other (though one pairing is only marginally significant); in contrast, only group size and day journey length of the ecological variables correlate significantly with each other. None of the cognitive tasks correlate with diet or range size, but they all correlate

significantly with group size and day journey length ($p \leq 0.03$; half the correlations would still be significant with Bonferroni correction).

To examine the covariation patterns among these variables, we ran separate principal components analysis for the four ecological variables with each cognitive task. With eigenvalues set to $\lambda > 1$, two factors are extracted in each case, which between them explain 72-75% of the variance (Table 1, upper panel). In each case, the inhibition task, group size and day journey are placed in one factor with very high weightings, while diet is consistently placed in a separate factor on its own. In contrast, home range size and the cylinder task are associated only weakly, and unstably, with either factor. If the cylinder task is combined with the A-not-B task in the same analysis, it loads more heavily with diet (Table 1, right hand column). Table S6 confirms that these results hold when we analyse the data at genus level.

To explore the status of home range in more detail, we reduced the eigenvalue criterion to $\lambda = 0.5$ (Table 1, lower panel). This adds a third factor which includes only home range size, for which the weightings are consistently strong. As before, both inhibition tasks load with the social variables, but the cylinder task now loads unambiguously with diet. The three factors combined explain 92-96% of the variance in the data.

Finally, we test the Passingham-Wise conjecture using the two MacLean et al. [3] tasks. Fig. 2a plots the performance on the A-not-B task for the major taxonomic groupings in their full dataset. Performance varies significantly across mammalian orders ($F_{6,19}=3.73$, $p=0.013$). It requires no statistical tests to conclude that this index of inhibition is unique to anthropoid primates, just as Passingham & Wise [43] suggested. None of the non-anthropoid taxa (birds, rodents, carnivores, elephant and prosimians) perform at better than chance level (dashed line at 33%). MacLean et al. [3] themselves confirm this: they report that there is no correlation with brain size for the non-anthropoids (phylogenetically controlled regression, $p=0.71$), whereas there is a significant ($p<0.01$) correlation between brain size and inhibition

competence in the anthropoids (see also [5]). Figure 2b plots the equivalent data for the cylinder task. In stark contrast to the A-not-B task, performance on the cylinder task does not differ significantly across the major taxonomic groups ($F_{5,25}$=2.22, p=0.084). More importantly, carnivores out-perform anthropoids on this task (albeit not significantly), with rodents running them a close second. Note that all three orders out-perform prosimian primates and birds. This strongly suggests that this task is not indexing a cognitive skill that is specific to the primates.

4. Discussion

We have shown, using two very different inhibition tasks from different databases, that inhibition (self-control) is closely correlated with two key variables that affect group coordination (group size and day journey length), but not with either of the two explicitly ecological indices (percentage of fruit in the diet and home range size). This suggests that the capacity to inhibit prepotent responses has less to do with foraging *per se* than the demands of maintaining group coordination while foraging. This concurs with human evidence that the ability to inhibit gratification strongly predicts social skills, and is directly related to disruptive anti-social behaviour and poor ability to maintain stable relationships [1-2]. In primates, including humans, this ability is associated with units in the prefrontal cortex (notably the frontal pole [43] and the adjacent inferior frontal cortex [44]), the part of the brain that evolved last during the course of mammalian evolution (the brain evolved from back to front) and has expanded most during the course of primate and human evolution.

In contrast, and perhaps not surprisingly, a causal reasoning task (the cylinder task) correlates better with diet (and hence food-finding abilities) and is at best only weakly correlated with sociality. The lack of any clear differences in performance on this task between the mammal and bird taxa reinforces the suggestion that the cylinder task is a

generalised cognitive skill whose primary function is related to foraging rather than to complex social decision-making. Nonetheless, it is worth observing that, in general, birds and prosimians performed less well on the cylinder task than rodents, carnivores and anthropoid primates. The latter probably engage in far more manipulation and processing of their food than the former [53]. Although several authors have claimed that birds perform just as well as apes and monkeys [6,29-31], the species concerned (parrots, corvids, passerines) are all ones with large brains (for birds) and well known for their sophisticated cognitive abilities and the capacity to manipulate food items. They are not a statistically random sample of birds as a taxon. This result adds weight to the suggestion that inhibition and causal reasoning have evolved independently of each other, and represent a clear case of the mosaic evolution of cognitive skills and their underlying neural bases.

These results feed into the longstanding distinction has been drawn between species that have stable social groups (congregations) and those that live in unstable herds (aggregations, flocks or fission-fusion social systems). The former are characterized by intense affiliative relationships between individuals, mediated in primates by social grooming [54] and the constant monitoring of social partners [55]. These kinds of bonded social groups are characteristic of anthropoid primates and only a handful of other mostly species-poor mammalian orders (notably elephants, equids, tylopods, and delphinids), but otherwise are found only in the form of monogamous pairbonds in other mammalian and avian orders [45-46]. The capacity to inhibit and modulate behaviour is crucial for the continued viability of bonded social groups just as it is of pairbonds, but in this bonded species it ensures that groups remain together because grooming partners synchronise their movements.

Although there has been a great deal of interest in the decision processes involved in coordinated travel in primates in particular, most of this has focused on the *initiation* of travel episodes rather than the coordination of movement *during* foraging, mainly because the first

is much easier to quantify [15]. Moreover, primate groups do not often fragment, making it difficult to study something that does not often happen. In contrast, studies of structural coordination during foraging have been more common for herding ungulates [11-14], perhaps because these have fission-fusion social systems and group fragmentation is hence more intrusive. In ungulates, desynchronisation of activity budgets as a consequence of differential gut-fill due to differences in body size has been identified as a major cause of group fragmentation [11-14]. In one of the few studies to explore this in primates, King & Cowlishaw [15] found that, in baboons, activity synchrony decreased across the day, although synchrony might be re-established by local environmental factors (converging on a resource patch or heightened predator risk).

Group coordination during travel is likely to be particularly important whenever there is a requirement to maintain group cohesion, especially for species that travel long distances in predator-risky environments. This is not to say that inhibition may not play a role in some aspects of foraging, but rather to say that its principal evolutionary driver is more likely to have been the social challenges introduced by bonded sociality, and hence that its use in foraging contexts is an exaptation. Fig. 1a confirms that this capacity is unique to the anthropoid primates, as suggested by Passingham and Wise [43], and is probably associated with the fact that, at least for the present sample of mammals, bonded social groups are uniquely characteristic of this taxon [5,45-46]. Of the non-anthropoid species studied by [3], only elephants have bonded sociality above the level of monogamous pairbonds; however, elephants have a fission-fusion social system that does not depend on maintaining cohesion in large social groups [56], which may explain why, uniquely, they scored poorly on the inhibition task (Fig. 1a). In contrast, a causal reasoning task (the cylinder task) exhibits less taxonomic specificity and is more explicitly correlated with food-finding. This dissociation in

the primary functions of different cognitive skills clearly points towards a mosaic view of brain evolution [57].

The level of coordination required to maintain the coherence of bonded groups is likely associated with other more sophisticated forms of cognition, such as the ability to understand other individuals' intentions, the ability to realise the consequences of one's actions, the ability to plan ahead and the ability to persuade others to adjust their behaviour, all of which also seem to be dependant on the frontal pole [43]. In some Old World monkeys, for example, individuals make explicit bids, or suggestions, about direction of group travel (often signalled by specific behaviours), with other group members then 'voting' on their preferences in order to arrive at a consensus [51,58-60]. The capacity to infer the intentions of the signaller and to interpret the meaning of a signal is dependent on mentalising, a cognitive skill that is also confined to the anthropoid primates [61]. In humans, mentalizing skills of this kind are correlated both with the size of an individual's social network [62-63] and with the volume of the brain's combined mentalising and default mode neural networks [64-65], a brain connectome involving both the frontal, parietal and temporal lobes and the limbic system and their substantial white matter connections that humans share with at least the cercopithecine monkeys [66-68]. A likely explanation is that both mentalising and inhibition are required to maintain bonded social groups.

Acknowledgments

SS's research is funded by a Royal Society University Research Fellowship (UF160725).

References

1. Moffitt, T., Caspi, A., Rutter, M. & Silva, P. (2001). *Sex Differences in Antisocial Behaviour: Conduct Disorder, Delinquency, and Violence in the Dunedin Longitudinal Study*. Cambridge: Cambridge University Press.
2. Pearce, E., Wlodarski, R., Machin, A. & Dunbar, R.I.M. (2019). Exploring the links between dispositions, romantic relationships, support networks and community inclusion in men and women. *PloS One* 14: e0216210.
3. MacLean, E.L., Hare, B., Nunn, C.L., Addessi, E., Amici, F., Anderson, R.C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, USA, 111: E2140-E2148.
4. Stevens, J.R. (2014). Evolutionary pressures on primate intertemporal choice. *Proceedings of the Royal Society, London*, 281B: 20140499.
5. Dunbar, R.I.M. & Shultz, S. (2021). Social complexity and the fractal structure of social groups in primate social evolution. *Biological Reviews* 96: 1889-1906.
6. Kabadayi, C., Taylor, L. A., von Bayern, A. M., & Osvath, M. (2016). Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. Royal Society Open Science, 3(4), 160104.
7. Stephens, D.W & Krebs, J.R. (1986). *Foraging Theory*. Princeton: Princeton University Press.
8. Conradt, L., 1998. Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology* 67: 217-226.
9. Conradt, L. & Roper, T.J. (2000). Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society, London*, 267B: 2213-2218.
10. Conradt, L., Krause, J., Couzin, I.D. and Roper, T.J., 2009. “Leading according to need” in self-organizing groups. *American Naturalist* 173: 304-312.
11. Ruckstuhl, K.E. & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour* 64: 909-914.
12. Ruckstuhl, K.E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77: 77-96.
13. Calhim, S., Shi, J. & Dunbar, R.I.M. (2006). Sexual segregation among feral goats: testing between alternative hypotheses. *Animal Behaviour* 72: 31-41.
14. Dunbar, R.I.M. & Shi, J. (2008). Sex differences in feeding activity results in sexual segregation of feral goats. *Ethology* 114: 444-451.
15. King, A.J. & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour* 78: 1381-1387.
16. Krause, J. & Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.
17. Dunbar, R.I.M. & Dunbar, P. (1975). *Social Dynamics of Gelada Baboons.* Basel: Karger.
18. Silk, J. B. (2002). Using the'F'-word in primatology. *Behaviour* 139: 421-446.
19. Dunbar, R.I.M. & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147: 775-803.
20. Massen, J., Sterck, E., & de Vos, H. (2010). Close social associations in animals and humans: functions and mechanisms of friendship. *Behaviour* 147: 1379-1412.
21. Kudo, H. & Dunbar, R.I.M. (2001). Neocortex size and social network size in primates. *Animal Behaviour* 62: 711-722.
22. Dunbar, R.I.M. & Shultz, S. (2021). The infertility trap: the fertility costs of group-living in mammalian social evolution. *Frontiers in Ecology and Evolution* 9: 634664.
23. van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120-144.

24. Shultz, S., Noe, R., McGraw, S. & Dunbar, R.I.M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society, London*, 271B: 725-732.
25. Shultz, S. & Finlayson, L. V. (2010). Large body and small brain and group sizes are associated with predator preferences for mammalian prey. *Behavioral Ecology* 21: 1073-1079.
26. Dunbar, R.I.M., MacCarron, P. & Robertson, C. (2018). Tradeoff between fertility and predation risk drives a geometric sequence in the pattern of group sizes in baboons. *Biology Letters* 14: 20170700.
27. King, A.J. & Sueur, C. (2011). Where next? Group coordination and collective decision making by primates. *International Journal of Primatology* 32: 1245-1267.
28. Dunbar, R.I.M. & Crook, J.H. (1975). Aggression and dominance in the weaver bird, *Quelea quelea*. *Animal Behaviour* 23: 450-459.
29. Kabadayi, C., Krasheninnikova, A., O'Neill, L., van de Weijer, J., Osvath, M., & von Bayern, A. M. (2017). Are parrots poor at motor self-regulation or is the cylinder task poor at measuring it? *Animal Cognition*, 20(6), 1137-1146.
30. van Horik, J. O., Langley, E. J., Whiteside, M. A., Laker, P. R., Beardsworth, C. E., & Madden, J. R. (2018). Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society, London* 285: 20180150.
31. Isaksson, E., Urhan, A. U., & Brodin, A. (2018). High level of self-control ability in a small passerine bird. Behavioral ecology and sociobiology, 72(7), 1-7.
32. Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evol*ution 22: 469-493.
33. Powell, L.E., Isler, K. and Barton, R.A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society, London*, 284B: 20171765.
34. Clutton-Brock, T.H. & Harvey, P.H. (1980). Primates, brains and ecology. *Journal of Zoology* 190: 309-323.
35. Bronikowski, A. M., & Altmann, J. (1996). Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioral Ecology and Sociobiology*, *39*(1), 11-25.
36. Hill, R.A. & Dunbar, R.I.M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evol. Ecol.* 16: 579-593.
37. Lehmann., J., Korstjens, A.H. & Dunbar, R.I.M. (2008). Time and distribution: a model of ape biogeography. *Ethol. Ecol. Evol.* 20: 337-359.
38. Ménard, N., Motsch, P., Delahaye, A., Saintvanne, A., Le Flohic, G., Dupé, S., Vallet, D., Qarro, M. & Pierre, J-S. (2013). Effect of habitat quality on the ecological behavior of a temperate-living primate: time-budget adjustments. *Primates* 54:217–228.
39. Dunbar, R.I.M., Cheyne, S., Lan, D., Korstjens, A.H., Lehmann, J. & Cowlishaw, G. (2019). Environment and time as constraints on the biogeographical distribution of gibbons. *Amer. J. Primat.* 81: e22940.
40. Altmann, S.A. & Altmann, J. (1970). *Baboon Ecology*. Basel: Karger
41. Sigg, H. & Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia Primatologica* 36: 40-75.
42. Dunbar, R.I.M., Korstjens, A.H. & Lehmann, J. (2009). Time as an ecological constraint. *Biol. Rev.* 84: 413-429.
43. Passingham, R.E. & Wise, S.P. (2012). *The Neurobiology of the Prefrontal Cortex: Anatomy, Evolution and the Origin of Insight.* Oxford: Oxford University Press.
44. Aron, A.R., Robbins, T.W. & Poldrack, R.A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*(4), 170-177.

45. Shultz, S. & Dunbar, R.I.M. (2007). The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proc. R. Soc. Lond.* 274B: 2429-2436.
46. Shultz, S. & Dunbar, R.I.M. (2010). Encephalisation is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proceedings of the National Academy of Sciences, USA*, 107: 21582-21586.
47. Dunbar, R.I.M., MacCarron, P. & Shultz, S. (2018). Primate social group sizes exhibit a regular scaling pattern with natural attractors. *Biology Letters* 14: 20170490.
48. Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Struhsaker, T.T. & Wrangham, R.W. (eds.). (1987). *Primate Societies*. Chicago: University of Chicago Press.
49. Campbell, C.J., Fuentes, A., Mackinnon, K.C., Bearder, S. & Stumpf, R. (Eds.) (2008). *Primates in Perspective*. Oxford: Oxford University Press.
50. Kummer, H. (1968). *Social Organisation of Hamadryas Baboons*. Basel: Karger.
51. Sigg H, Stolba A. 1981. Home range and daily march in a hamadryas baboon troop. *Folia Primatologica* 36: 40-75.
52. Kamilar, J.M. & Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society, London*, 368B: 20120341.
53. Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., van Schaik, C. P. & Isler, K. (2016). Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific Reports* 6: 1-9.
54. Lehmann, J., Korstjens, A. & Dunbar, R.I.M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour* 74: 1617-1629.
55. Dunbar, R.I.M. & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147: 775-803.
56. Moss, C.J., Croze, H. & Lee, P.C. (2011). *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Chicago: University of Chicago Press.
57. Barton, R. A. & Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature*, *405*(6790), 1055-1058.
58. Sueur C, Petit O. 2010. Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. *Animal Cognition* 13:239-48.
59. Sueur C, Deneubourg JL, Petit O. 2011. From the first intention movement to the last joiner: macaques combine mimetic rules to optimize their collective decisions. *Proceedings of the Royal Society, London*, 278B: 1697-704.
60. Stoltz, L.P. & Saayman, G. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Annals of the Transvaal Museum* 26: 99-143.
61. Devaine, M., San-Galli, A., Trapanese, C., Bardino, G., Hano, C., Saint Jalme, M., Bouret, S., Masi, S. & Daunizeau, J. (2017). Reading wild minds: a computational assay of theory of mind sophistication across seven primate species. *PloS Computational Biology* 13: e1005833.
62. Stiller, J. & Dunbar, R.I.M. (2007). Perspective-taking and memory capacity predict social network size. *Social Networks* 29: 93-104.
63. Powell, J., Lewis, P.A., Roberts, N., García-Fiñana, M. & Dunbar, R.I.M. (2012). Orbital prefrontal cortex volume predicts social network size: an imaging study of individual differences in humans. *Proceedings of the Royal Society, London*, 279B: 2157-2162.
64. Lewis, P.A., Rezaie, R., Browne, R., Roberts, N. & Dunbar, R.I.M. (2011). Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage* 57: 1624-1629.
65. Powell, J., Lewis, P.A., Dunbar, R.I.M., García-Fiñana, M. & Roberts, N. (2010). Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia* 48: 3554-3562.

66. Sallet J., Mars, R.B., Noonan, M.P., Andersson, J.L., O'Reilly, J.X., Jbabdi, S., Croxson, P.L., Jenkinson, M., Miller, K.L. & Rushworth, M.F.S. (2011). Social network size affects neural circuits in macaques. *Science* 334: 697–700.
67. Sallet, J., Mars, R.B., Noonan, M.A., Neubert, F.X., Jbabdi, S., O'Reilly, J.X., Filippini, N., Thomas, A.G. & Rushworth, M.F.S. (2013). The organization of dorsal prefrontal cortex in humans and macaques. *Journal of Neuroscience* 33: 12255-12274.
68. Mars, R. B., Foxley, S., Verhagen, L., Jbabdi, S., Sallet, J., Noonan, M. P., Neubert, F-X., Andersson, J., Croxson, P., Dunbar, R.I.M., Khrapitchev, A., Sibson, N., Miller, K. & Khrapitchev, A. A. (2016). The extreme capsule fiber complex in humans and macaque monkeys: a comparative diffusion MRI tractography study. *Brain Structure and Function* 221: 4059-4071.

Legends to Figure

Fig. 1. Fissioning index for individual *Papio* baboon populations as a function of day journey length. Unfilled symbols: group size <35; grey symbols: group size 35-75; filled symbols: group size >75. For definition of fissioning index, see Table S2. The data are given in Table S1.

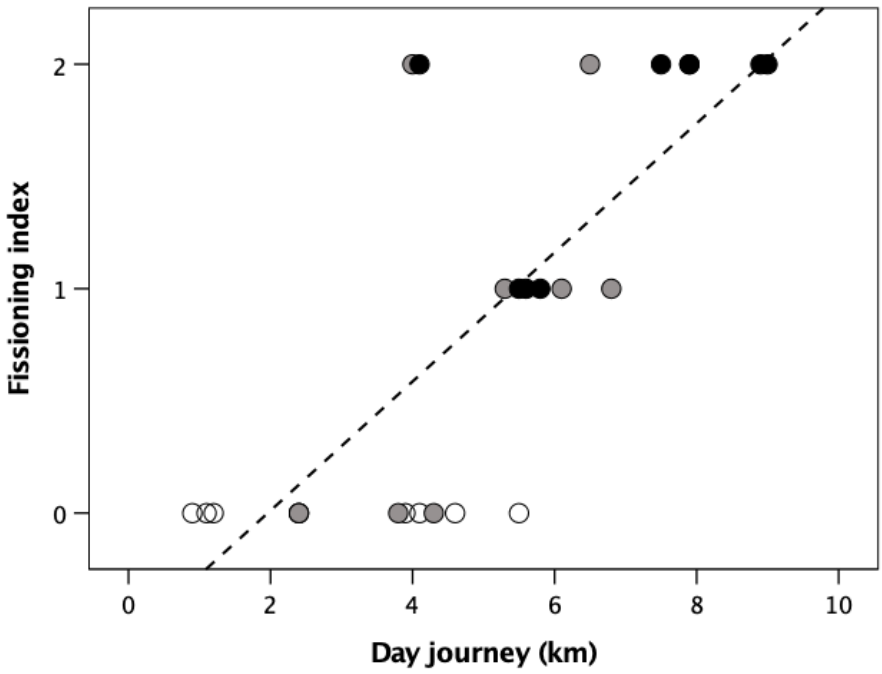
Fig. 2. Performance on two cognitive tasks for different taxonomic groups. (a) Mean (±2se) percentage success on the A-not-B inhibition task for the major taxonomic groups. The dashed horizontal line denotes the chance response rate at 33% (for a task in which the animal chooses between three locations). Data from [3,4]. (b) Mean (±2 se) percentage success on the cylinder task for the major taxonomic groups. The dashed horizontal line denotes the chance response rate at 50% (for a task in which the animal chooses between one of two locations). Data from [3].

ask

Table 1. Factor loadings (with varimax rotation) for the five variables for each of the three inhibition tasks and for both inhibition tasks in the MacLean et al. sample. Bold font indicates variables that load together on the same factor.

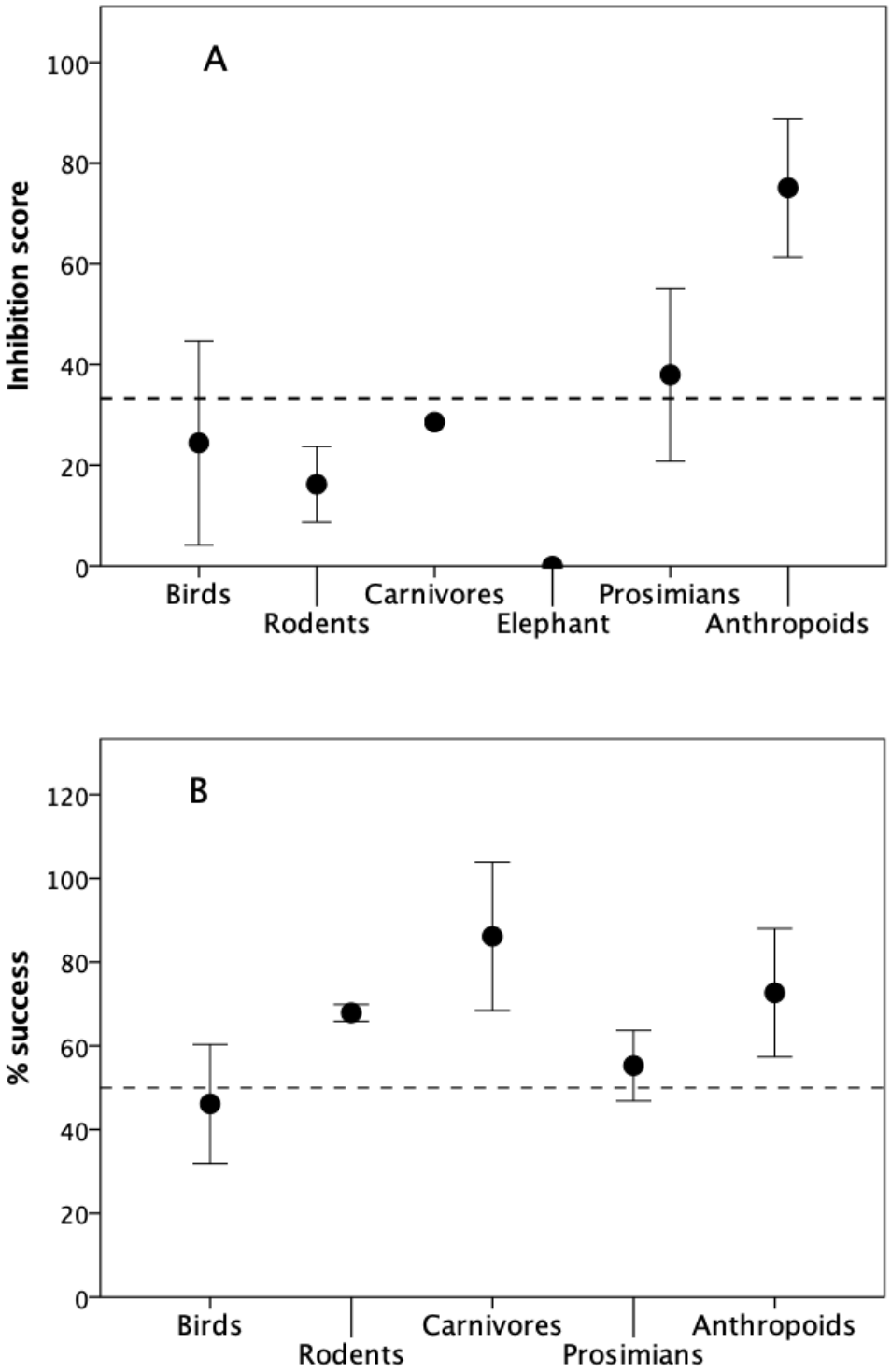
	Stevens (2014) Go/No-go task			A-not-B task			MacLean et al. (2014) Cylinder task			A/~B and cylinder tasks		
Extraction based on λ = 1.0												
Factors:	1	2		1	2		1	2		1	2	
Cylinder task							**0.693**	**0.626**		0.593	**0.740**	
Inhibition task	**0.898**	0.249		**0.855**	0.053					**0.849**	0.189	
Diet (% fruit)	-0.018	**0.778**		0.020	**0.971**		-0.137	**0.936**		-0.156	**0.931**	
Group size	**0.885**	0.102		**0.900**	0.031		**0.923**	-0.114		**0.888**	0.030	
Day journey	**0.969**	-0.090		**0.895**	-0.180		**0.897**	-0.186		**0.915**	-0.091	
Range size	0.148	**0.714**		0.498	0.208		**0.569**	0.244		0.485	0.356	
Variance explained	74.9%			72.3%			75.1%			75.7%		
Extraction based on λ =0.5												
Factors:	1	2	3	1	2	3	1	2	3	1	2	3
Cylinder task							0.572	0.348	**0.658**	0.528	0.355	**0.712**
Inhibition task	**0.904**	0.146	0.195	**0.729**	0.472	0.023				**0.694**	0.547	0.087
Diet (% fruit)	0.036	0.062	**0.994**	0.009	0.012	**0.999**	-0.181	-0.032	**0.952**	-0.120	-0.007	**0.971**
Group size	**0.875**	0.188	-0.041	**0.926**	0.120	0.100	**0.916**	0.228	-0.030	**0.902**	0.158	0.060
Day journey	**0.975**	-0.097	-0.042	**0.962**	0.026	-0.092	**0.961**	0.070	-0.060	**0.970**	0.057	-0.030
Range size	0.099	**0.991**	0.065	0.131	**0.969**	0.010	0.151	**0.979**	0.048	0.125	**0.954**	0.085
Variance explained		96.2%			90.5%			92.5%			89.6%	

Figure 1



535

Figure 2


A
Inhibition score
100
80
60
40
20
0
Birds
Rodents
Carnivores
Elephant
Prosimians
Anthropoids
B
% success
120
100
80
60
40
20
0
Birds
Rodents
Carnivores
Prosimians
Anthropoids

The Evolutionary Significance of Self-Control

R.I.M. Dunbar and **Susanne Shultz**

Electronic Supplementary Material

Supplementary Data

Table S1. Group size, day journey length and the fissioning index for a sample of baboon study sites

Site	Group size	Day journey (km)	Fissioning index†	Source
*Awash Station, Ethiopia	83.0	6.5	2	Nagel 1973
*ErerGota, Ethiopia	83.0	8.9	2	Sigg & Stolba 1981
*Awash Filoha, Ethiopia	190.0	7.5	2	Swedell 2001
Mt Assirik, Senegal	247.0	7.9	2	Byrne 1981; Sharman 1982
Siminti, Senegal	70.8	4.0	2	Zinner et al. 2021
Gashaka NP, Nigeria	28.4	2.4	0	Sommer & Ross 2010
Metahara, Ethiopia	87.0	5.8	1	Aldrich-Blake et al. 1971
Bole Valley, Ethiopia	19.0	1.2	0	R. Dunbar (unpublished)
Mulu, Ethiopia	22.0	1.1	0	R. Dunbar (unpublished)
Awash Falls, Ethiopia	71.0	5.3	1	Nagel 1973
Budongo Forest, Uganda	37.5	3.8	0	Paterson 1976; pers. comm.
Chololo, Kenya ‡	102.0	5.6	1	Barton 1990
Gilgil, Kenya ‡	49.0	4.3	1	Harding 1976
Chololo STT 1986, Kenya	102.0	5.6	1	Barton 1990
Chololo PHG 1995, Kenya	25.0	4.6	0	Kenyatta 1995
Gombe NP, Tanzania	43.0	2.4	0	J. Oliver (pers. comm.)
Amboseli NP, Kenya [Hook]	46.5	6.1	1	D. Post (pers.comm.)
Ruaha NP, Tanzania	72.0	6.8	1	Collins 1984
Mikumi NP (1995), Tanzania	18.0	3.9	0	Hawkins 1999
Giants Castle, S. Africa	11.8	0.9	0	Henzi et al. 1992; R. Byrne (pers. comm.)
Cape Point, S. Africa	85.0	7.9	2	Davidge 1978
Honnet, S. Africa	77.0	9.0	2	Stoltz & Saayman 1970
Suikerbosrand, S. Africa	78.0	4.1	2	Anderson 1981
R. Kuiseb, Namibia	15.5	4.1	0	Brain 1990
Tsaobis, Namibia	34.3	5.5	0	King et al. 2008; G. Cowlishaw (pers. comm.)

* *Papio hamadryas* † see Table S2
‡ based on a comparison of group size and the mean number of individuals within 10m of a focal adult

Table S2. Fissioning index

Index	Definition
0	Group relatively compact during foraging, and always sleeps together; not explicitly described as becoming widely dispersed (>200m) during foraging
1	Group becomes dispersed during foraging (mean spread >200m), but always sleeps together
1	Group fragments during foraging, with sub-groups moving independently, and may sleep at separate sites

For each study site, index is based on descriptions of foraging patterns given by primary sources

Fissioning index correlates significantly with both group size (τ=0.642, N=26, p<0.001) and day journey length (Kendall's τ=0.655, N=26, p<0.001). A multiple regression with fissioning index as dependent variable and group size and day journey as independent variables yields a significant overall equation (r^2=0.615, $F_{2,23}$=20.995, p<0.0001), with both variables making significant independent contributions (group size: standardised β = 0.341, t_{23}=3.414, p=0.043; day journey: standardised β = 0.545, t_{23}=3.414, p=0.002). This suggests that day journey length has a stronger effect on fission risk than group size on its own.

To determine whether there is an interaction effect between the two independent variables, we transformed group size and day journey length to standard normal deviates, and reran the regression with an interaction effect. The results are given in Table S3. There are independent effects, of approximately equal weight, due to the two main variables and no interaction effect.

Table S3. Regression analysis of fission index

Variable	slope	standardised β	df	t	p
Overall model:	r^2=0.664, $F_{3,22}$=14.47, p<0.0001				
SD(group size)	0.481	0.546	22	2.20	0.039
SD(day journey)	0.373	0.423	22	2.17	0.041
Interaction	-0.182	-0.207	22	-1.07	0.295

Diet data

We sourced our data on diet from Powell et al. (2017) rather than DeCasien et al. (2017) because we considered their data compilation generally more reliable. However, the value of 8.5% that they give for *Macaca mulatta* seems to be based on just one idiosyncratic high altitude study site, despite the fact that data from other study sites are available. Other more typical habitats have much higher values of frugivory for this species. We searched for diet data for this species on GoogleScholar and located a further five studies (Table S4).

Table S4. Diet data for *Macaca mulatta*

Study site	Country	% fruit in diet	Source
Taihangshan Reserve	China	36.5	Cui et al. (2018)
Nonggang Reserve	China	30.0	Tang et al. (2016)
*Murree Hills	Pakistan	8.5	Goldstein & Richard (1989)
Buxta Tiger Reserve	Bangladesh	74.9	Sengupta & Radhakrisha (2015)
Asola-Bhatti Sanctuary	India	5.7	Ganguly & Singh Chauhan (2018)
Siwalik Hills	India	63.0	Lindburg (1977)
Mean		**37.2%**	

* Site on which Powell et al. (2014) based their estimate.

Powell et al. (2014) do not give a value for percent of fruit in diet for *Saguinus oedipus*. We use the value given for this species by Garber (1984).

We did not use Powell et al. (2017) as a source of data for day journey length or home range size because, although their values for day journey correlate significantly with those we compiled from Smuts et al. (1987) and Campbell et al. (2008) (r=0.887, p=0.003), those for range size, in particular, appear to be based on a very selective subsample of study sites. Our sources are based on a wider range of primary sources, and are likely to be more representative.

Supplementary analyses

Bivariate correlations

Bivariate correlations between all the variables are given in Table S5, and those between the cognition variables and each of the ecological variables are plotted in Figure S1.

Table S5. Bivariate correlations.

	A-not-B	Cylinder	Diet	Group size	Day journey	Home range
Go/no-go	r=0.605 p=0.064 N=10	r=0.700 p=0.036 N=9	r=0.206 p=0.544 N=11	r=0.676 p=0.022 N=11	r=0.866 p=0.001 N=11	r=0.258 p=0.444 N=11
A-not-B		r=0.664 p=0.007 N=15	r=-0.072 p=0.758 N=21	r=0.637 p=0.002 N=21	r=0.603 p=0.004 N=21	r=0.461 p=0.041 N=20
Cylinder			0.428 p=0.076 N=18	0.519 p=0.027 N=18	0.512 p=0.030 N=18	0.443 p=0.066 N=18
Diet				-0.086 p=0.695 N=23	-0.197 p=0.366 N=23	-0.065 p=0.769 N=23
Group size					0.813 p<0.001 N=24	0.365 p=0.087 N=23
Day journey						0.242 p=0.265 N=23

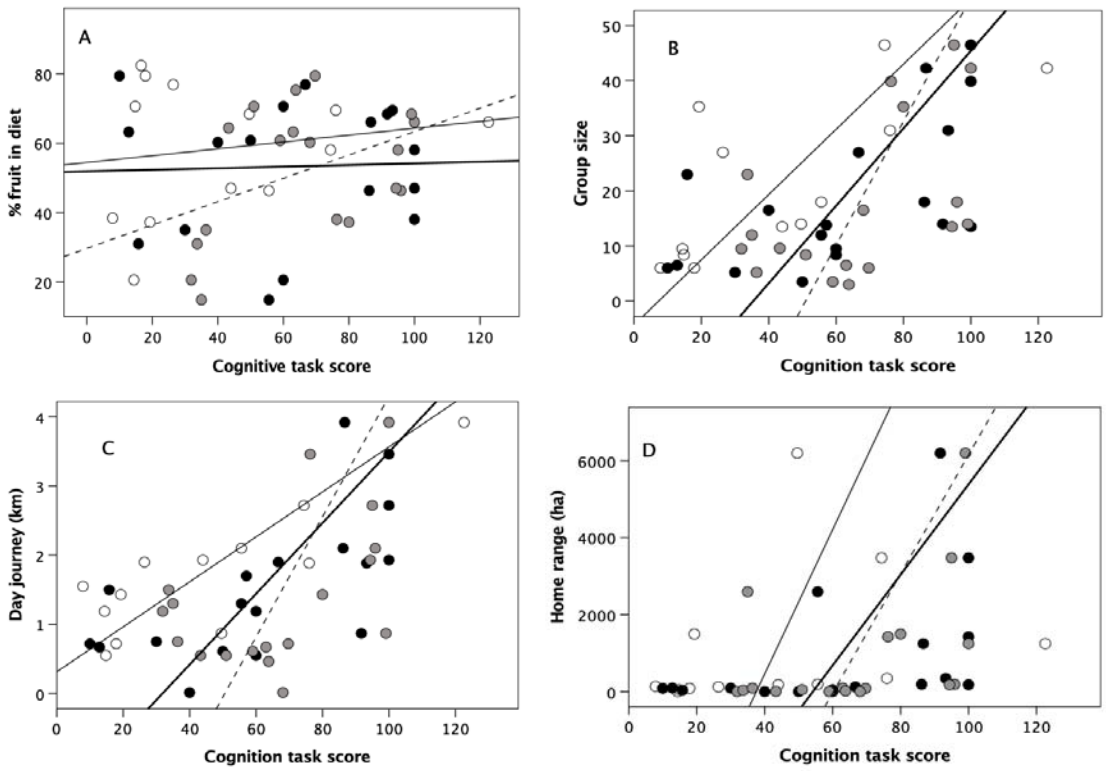


Figure S1. Cognition score as predictor of (a) diet (% fruit), (b) mean group size, (c) mean day journey length (km), and (d) mean home range area (ha) for individual species. Unfilled circles, thin solid line: MacLean et al. A-not-B task; grey circles, dashed line: MacLean et al. cylinder task; filled circles, thick line: Stevens Go/No-go task. Lines are LSR regressions.

Genus level analysis

Although there is negligible phylogenetic signal in any of the data and analyses of the data with and without phylogenetic control yield identical results (MacLean et al. 2014; Stevens 2014), we nonetheless checked whether phylogenetic inertia might distort our results by re-analysing the data as genus-level averages. In fact there are only three genera with more than a single species sampled in either of the two datasets. The results are given in Table S6. As before, a factor analysis with λ=1 explains 70-74% of the variance, with the Go/No-Go and A-not-B tasks loading with group size and day journey length as before, and the cylinder task loading with diet and home range size. The only difference is that range size loads more strongly with diet on factor 2 on both datasets than was the case with the original sample.

Table S6. Factor loadings (with varimax rotation and λ>1) for the five variables for each of the two datasets for mean genus-level data. Bold font indicates variables that load together on the same factor.

	Go/No-go task		A-not-B task		Cylinder task	
Factors:	1	2	1	2	1	2
Cognitive task	**0.774**	0.583	**0.853**	0.236	0.225	**0.902**
Diet	-0.252	**0.893**	-0.224	**0.801**	-0.648	**0.666**
Group size	**0.865**	-0.170	**0.783**	-0.333	**0.880**	0.216
Day journey	**0.881**	0.106	**0.853**	-0.188	**0.805**	0.277
Range size	0.200	**0.562**	**0.517**	**0.543**	0.231	**0.581**
Variance explained	74.4%		70.5%		73.3%	

References

Aldrich-Blake, F. P. G., Bunn, T. K., Dunbar, R. I. M., & Headley, P. M. (1971). Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia Primatologica* 15: 1-35.

Anderson, C. M. (1981). Subtrooping in a chacma baboon (Papio ursinus) population. *Primates* 22: 445-458.

Barton, R. A. (1990). *Foraging strategies, diet and competition in olive baboons* (Doctoral dissertation, University of St Andrews).

Brain, C. (1990). Spatial usage of a desert environment by baboons (Papio ursinus). *Journal of Arid Environments* 18: 67-73.

Byrne, R. W. (1981). Distance vocalisations of Guinea baboons (Papio papio) in Senegal: an analysis of function. *Behaviour* 78: 283-312.

Campbell, C.J., Fuentes, A., Mackinnon, K.C., Bearder, S. & Stumpf, R. (Eds.) (2008). *Primates in Perspective*. Oxford: Oxford University Press.

Collins, D. A. (1984). Spatial pattern in a troop of yellow baboons (Papio cynocephalus) in Tanzania. *Animal Behaviour*, *32*(2), 536-553.

Cui, Z., Shao, Q., Grueter, C. C., Wang, Z., Lu, J. & Raubenheimer, D. (2019). Dietary diversity of an ecological and macronutritional generalist primate in a harsh high-latitude habitat, the Taihangshan macaque (*Macaca mulatta tcheliensis*). *American Journal of Primatology* 81: e22965.

Davidge, C. (1978). Ecology of baboons (*Papio ursinus*) at Cape Point. *African Zoology* 13: 329-350.

DeCasien, A.R., Williams, S.A. & Higham, J.P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution* 1: 0112.

Ganguly, I. & Chauhan, N. S. (2018). Dietary preference and feeding patterns of the urban rhesus macaque *Macaca mulatta* (Mammalia: Primates: Cercopithecidae) in Asola-Bhatti Wildlife Sanctuary in India. *Journal of Threatened Taxa* 10: 12907-12915.

Garber, P. A. (1984). Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi*. *International Journal of Primatology* 5: 1-15.

Goldstein, S. J. & Richard, A. F. (1989). Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *International Journal of Primatology* 10: 531-567.

Harding, R. S. (1976). Ranging patterns of a troop of baboons (Papio anubis) in Kenya. *Folia Primatologica*, *25*(2-3), 143-185.

Hawkins, D.M. (1999). *Individual time budgets of yellow baboons in Mikumi National Park, Tanzania: Group size and environment.* PhD thesis, University of Liverpool.

Henzi, S. P., Byrne, R. W., & Whiten, A. (1992). Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. *International Journal of Primatology* 13: 601-629.

Kenyatta, C.G. (1995). *Ecological and social constraints on maternal investment strategies*. PhD thesis, University College London.

King, A. J., Douglas, C. M., Huchard, E., Isaac, N. J., & Cowlishaw, G. (2008). Dominance and affiliation mediate despotism in a social primate. *Current Biology* 18: 1833-1838.

Lindburg, D. G. (1977). Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in North India. In: T.H. Clutton-Brock (ed) *Primate Ecology*, pp. 223-250. London: Academic Press.

MacLean, E.L., Hare, B., Nunn, C.L., Addessi, E., Amici, F., Anderson, R.C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, USA, 111: E2140-E2148.

Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19: 104-165.

Paterson, J.D. (1976). *Variations in ecology and adaptation of Ugandan baboons Papio cynocephalus anubis*. PhD thesis, University of Calgary.

Powell, L.E., Isler, K. & Barton, R.A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society, London*, 284B: 20171765.

Sengupta, A. & Radhakrishna, S. (2015). Fruit trait preference in rhesus macaques (*Macaca mulatta*) and its implications for seed dispersal. *International Journal of Primatology* 36: 999-1013.

Sharman, M. J. (1982). *Feeding, ranging and social organisation of the Guinea baboon. PhD thesis*, University of St Andrews.

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

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Struhsaker, T.T. & Wrangham, R.W. (eds.). (1987). *Primate Societies*. Chicago: University of Chicago Press.

Sommer, V., & Ross, C. (Eds.). (2010). *Primates of Gashaka: Socioecology and Conservation in Nigeria's Biodiversity Hotspot* (Vol. 35). Berlin: Springer.

Stoltz, LP & Saayman, G. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Annals of the Transvaal Museum* 26: 99-143.

Swedell, L. (2002). Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia Primatologica* 73: 95-103.

Stevens, J.R. (2014). Evolutionary pressures on primate intertemporal choice. *Proceedings of the Royal Society, London*, 281B: 20140499.

Tang, C., Huang, L., Huang, Z., Krzton, A., Lu, C. & Zhou, Q. (2016). Forest seasonality shapes diet of limestone-living rhesus macaques at Nonggang, China. *Primates* 57: 83-92.

Zinner, D., Klapproth, M., Schell, A., Ohrndorf, L., Chala, D., Ganzhorn, J. U., & Fischer, J. (2021). Comparative ecology of Guinea baboons (Papio papio). *Primate Biology* 8: 19-35.