The Evolution of Self-Control

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Abstract

The capacity to inhibit prepotent actions (self-control) plays a potentially important role in many aspects of the behaviour of birds and mammals. A number of studies, for example, have used it as an index of foraging skills. Inhibition is, however, also crucial for maintaining the temporal and spatial coherence of bonded social groups. Using 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 argue that the capacity to inhibit prepotent action has been crucial for the evolution of bonded social systems in primates and some other mammals.

Key words: primates, bonded social groups, day journey, group size, inhibition, causal reasoning

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1. Introduction

The capacity to inhibit prepotent actions (self-control) has often been interpreted as an index of foraging skill: when animals forage optimally, they have to be prepared to bypass a less valuable immediate reward to gain a more valuable future one [1,2]. Inhibition can, however, also be important in a social context, especially 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 [3-5], causing groups to fragment and disperse [6-10]. Bonded social groups (congregations) face significant challenges in this respect: because they function as defensive coalitions against external threats [11-14], 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. The core problem these species face is the need to maintain synchrony of activity scheduling [15]. Animals have to be able to suppress the desire to continue feeding when the rest of the group go to rest (or forego resting when everyone else wants to continue foraging). They may also need to be able to suppress the desire to steal another animal's food or respond aggressively to a mild threat, lest such behaviour make others less willing to come to their aid.

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 [1,2] for a range of primate species. Both tasks are considered to be reliable tests of the capacity to inhibit prepotent actions (i.e. self-control). We ask whether the capacity for self-control correlates better with indices for the foraging domain or the social domain. As indices of foraging, 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 [1,2,16-18]. Fruits are much less

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predictable than foliage, and are usually viewed as being a cognitively more challenging diet

70   [18,19]. Similarly, large home ranges are assumed to be cognitively demanding in terms of

the mental mapping skills involved in foraging decisions [18] since foraging animals have to

choose between locations on the basis of their profitability [2]. 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

75   problems will increase as a function of both group size (greater likelihood of individuals'

activity cycles getting out of synchrony) and day journey length (more opportunity for

individuals' activity schedules to get out of synchrony even when group size is small) [15]. If

inhibition is primarily a social skill, it should correlate positively with one or both indices.

Passingham & Wise [20] argue that inhibition depends explicitly on the brain's

80   frontal pole (Brodmann Area 10) and that this brain unit is only found in anthropoid primates.

Since, with the exception of a few (mostly species-poor) orders, large bonded social groups

are found only in anthropoid primates [21,22], we also test the derivative hypothesis that the

capacity to inhibit behaviour will be more highly developed in anthropoid primates.

85   2. Methods

We use data from two datasets [1,2] that provide experimental data on the capacity to

inhibit prepotent responses in primates. We analyse the two datasets separately. Mean group

size for species was sourced from [23], percent fruit in the diet from [24] and day journey

length (in km) and home range size (in ha) from [25,26]. The data are provided in the *ESM*.

90   For the reasons given in the *ESM* **[provided at end of MS for convenience]**, we use

principal components analysis with varimax rotation to determine whether variables cluster

together (i.e. co-vary). We do not use phylogenetic methods because (a) none exist for use

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with factor analysis and (b) many previous studies have shown there is no phylogenetic signal in these data (see *ESM*).

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3. Results

Fig. 1 plots the bivariate relationships with inhibition score in the two datasets. For both indices, inhibition correlates significantly with group size (MacLean: r=0.614, p=0.007; Stephens: r=0.737, p=0.004) and day journey length (MacLean: r=0.653, p=0.003; Stephens: r=0.846, p<0.001), but not with diet (MacLean: r=0.038, p=0.886; Stephens: r=0.151, p=0.639) or home range size (MacLean: r=0.450, p=0.070; Stephens: r=0.256, p=0.447). With eigenvalues set to $\lambda>1$, principal component analysis extracts two dimensions for both datasets, which between them explain 74.0% and 72.3% of the variance, respectively (lefthand columns in Table 1). In both cases, inhibition, group size and day journey are placed in one factor with very high weightings (mean = 0.903), while diet is placed in a factor on its own. Home range size, however, is associated only weakly with either factor. To explore the status of home range in more detail, we reduced the eigenvalue criterion to $\lambda=0.5$: this adds a third factor which includes only home range size (mean weighting = 0.889). The three factors combined explain 93.9% and 90.5% of the variance in the data, respectively. This suggests that diet and range size are unrelated to inhibition capacities, or to each other.

MacLean et al. [1] also used performance on a second task (the cylinder task), referring to it as a second inhibition task. In fact, it asks animals to choose between two ends of a cylinder in order to access a food reward, and so is better characterized as a causal reasoning task rather than an inhibition task. We re-ran the principal components analysis with the two MacLean cognitive tasks (A-not-B and cylinder tasks) and the same four predictor variables. With eigenvalues set at $\lambda=0.5$ (to give a three-factor solution), we obtain the results in the righthand columns in Table 1. The three factors account for 90.4% of the

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variance between them (with the first two factors accounting for 76.1%). As before, the A-not-B inhibition task clusters with group size and day journey length, while home range size

120   forms a separate factor of its own. In contrast, the cylinder task clusters strongly with percent fruit in the diet. This latter correlation makes sense since, as much as anything, fruit acquisition is an extraction task – an animal has to figure out how to extract the food item from a matrix (e.g. seeds from within a casing, flesh from within an inedible peel).

Finally, we test the Passingham-Wise conjecture using the data given by [1]. Fig. 2a

125   plots the performance on MacLean's A-not-B inhibition task separately 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 allow us to conclude that this index of inhibition is unique to anthropoid primates. None of the non-anthropoid taxa (birds, rodents, carnivores, elephant and prosimians) perform at better than chance levels (dashed

130   line at 33%). MacLean et al. [1] 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 [27]).

Figure 2b plots the equivalent data for the MacLean cylinder task. In stark contrast to

135   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 outperform anthropoids on this task (albeit not significantly), with rodents running them a close second (and both of them significantly outperforming prosimian primates). This strongly suggests that this task is not indexing a cognitive skill that is specific to the primates, as we might

140   suspect given that it indexes causal reasoning rather than inhibition.

Discussion

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We show, with two independent datasets and two very different inhibition tasks, that self-control is closely correlated with two key socially-relevant variables (group size and day journey length) but not with either of the two ecological indices (percentage of fruit in the diet and home range size). This suggests that the capacity to inhibit prepotent responses is primarily associated with social rather than ecological demands. 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 each day. 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. Fig. 2a confirms that this capacity is unique to anthropoid primates, as suggested by Passingham and Wise [16], and is probably associated with the fact that bonded social groups are uniquely characteristic of anthropoid primates [21,22]. Of the non-anthropoid species studied by [1], only elephants have bonded sociality above the level of monogamous pairbonds; however, they have a fission-fusion social system that does not depend on maintaining cohesion in large social groups [28]. In contrast, a causal reasoning task exhibits less taxonomic specificity and is correlated with at least some aspects of food-finding.

A longstanding distinction has been drawn between species that have stable social groups (congregations) and those that live in unstable herds (aggregations, or fission-fusion social systems). The former are characterized by intense affiliative relationships between individuals, mediated in primates by social grooming [29] and the constant monitoring of social partners [30]. These kinds of bonded social groups are characteristic of anthropoid primates and a handful of other mammalian orders (notably elephants, equids, tylopods, delphinids), but otherwise are found only in the form of monogamous pairs in both mammals and birds [21,22]. The capacity to inhibit and modulate behaviour is crucial for the continued viability of bonded social groups. Although this has not been widely explored in animals,

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there is considerable evidence from humans that the inability to inhibit prepotent responses is responsible for disruptive anti-social behaviour and poor ability to maintain stable

170   relationships [31,32].

The level of coordination required may also involve 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 and the ability to persuade others to adjust their behaviour, all of which are also dependant on the frontal pole [20]. In some Old World monkeys, for

175   example, individuals make explicit bids, or suggestions, about direction of group travel (often signalled by specific behaviours), while others 'vote' on their preferences before arriving at a consensus [33-35]. These kinds of signals depend on animals being able to infer the intentions of the signaler and interpret the meaning of a signal. The capacity to coordinate behaviour and the capacity to manage relationships also depend on the ability to understand

180   other individuals' mindstates and intentions (mentalizing), a cognitive skill that is probably also confined to the anthropoid primates [36]. In humans, mentalizing competences are correlated both with the size of an individuals' friendship network [37-39] and with the volume of the brain's default mode neural network [40-41], a brain connectome involving both the frontal and temporal lobes and the limbic system that humans share with at least the

185   cercopithecine monkeys [42-44].

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 [10]. In contrast, studies of structural coordination during foraging

190   have been more common for herding ungulates [6-9], perhaps because these have fission-fusion social systems and group fragmentation is hence more intrusive. In ungulates, desynchrony of activity budgets as a consequence of differential gut-fill due to differences in

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body size has been identified as the major cause of group dispersal [6-9]. In one of the few studies to explore this in primates, King & Cowlishaw [10] found that, in baboons, activity

195   synchrony decreased across the day, although the degree of desynchrony was modified by local environmental factors (resource patchiness and local predator riskiness).

Taken together, these studies suggest that maintaining synchronized activity schedules is the main factor causing groups to fragment and disperse. Overcoming this is a very significant challenge to maintaining group cohesion. The principal reason for

200   maintaining cohesion is predation risk. Shultz et al. [12,45] have shown, for mammals generally, that group size is the principal factor mitigating predation risk. King & Cowlishaw [10] found that the riskiness of a location was a key factor enforcing synchrony.

Author contributions

The authors contributed equally.

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Declaration of Interests

The authors declare no competing interests.

References

215   1. 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.

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

220   3. Conradt, L., 1998. Measuring the degree of sexual segregation in group-living animals. *Journal of Animal Ecology* 67: 217-226.

4. Conradt, L. & Roper, T.J. (2000). Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society, London*, 267B: 2213-2218.

5. Conradt, L., Krause, J., Couzin, I.D. and Roper, T.J., 2009. "Leading according to need" in
225   self-organizing groups. *American Naturalist* 173: 304-312.

6. Ruckstuhl, K.E. & Kokko, H. (2002). Modelling sexual segregation in ungulates: effects of group size, activity budgets and synchrony. *Animal Behaviour* 64: 909-914.

7. Ruckstuhl, K.E. & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews* 77: 77-96.

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

9. Dunbar, R.I.M. & Shi, J. (2008). Sex differences in feeding activity results in sexual segregation of feral goats. *Ethology* 114: 444-451.

10. King, A.J. & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons.
235   *Animal Behaviour* 78: 1381-1387.

11. van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour* 87: 120-144.

12. 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.

240   13. 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.

14. Ashton, B.J., Kennedy, P. & Radford, A.N. (2020). Expanding the social intelligence hypothesis: interactions with outsiders as drivers of cognitive evolution. *Nature*
245   *Communications* (in press).

15. King, A.J. & Sueur, C. (2011). Where next? Group coordination and collective decision making by primates. *International Journal of Primatology* 32: 1245-1267.

16. Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evol*ution 22: 469-493.

250   17. 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.

18. Clutton-Brock, T.H. & Harvey, P.H. (1980). Primates, brains and ecology. *Journal of Zoology* 190: 309-323.

255   19. Reader, S.M. & Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Science s, USA*, 99: 4436-4441.

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

21. Shultz, S. & Dunbar, R.I.M. (2007). The evolution of the social brain: Anthropoid primates
260   contrast with other vertebrates. *Proc. R. Soc. Lond.* 274B: 2429-2436.

22. 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.

23. 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.

24. 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.

25. Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Struhsaker, T.T. & Wrangham, R.W. (eds.). (2008). *Primate Societies*. Chicago: University of Chicago Press.

26. Campbell, C.J., Fuentes, A., Mackinnon, K.C., Bearder, S. & Stumpf, R. (Eds.) (2016). *Primates in Perspective*. Oxford: Oxford University Press.

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

28. 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.

29. Lehmann, J., Korstjens, A. & Dunbar, R.I.M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour* 74: 1617-1629.

30. Dunbar, R.I.M. & Shultz, S. (2010). Bondedness and sociality. *Behaviour* 147: 775-803.

31. 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.

32. 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.

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

34. 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.

35. 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.

36. 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.

37. Stiller, J. & Dunbar, R.I.M. (2007). Perspective-taking and memory capacity predict social network size. *Social Networks* 29: 93-104.

38. 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.

39. 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.

40. 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.

41. Powell, J., Lewis, P.A., Roberts, N., García-Fiñana, M. & Dunbar, R.I.M. (2014). 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.

42. 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.

43. 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.

44. 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.

45. 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.

Legends to Figures

330   Fig. 1. Predictors of inhibition. (a) Percent fruit in diet, (b) mean home range area, (c) mean group size and (d) mean day journey length for individual species plotted against performance on inhibition tasks. Filled symbols and solid line: Stevens (2014), N=13 species; unfilled symbols and dashed line: MacLean et al. (2014), N=21 species. Lines are LSR regressions.

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Fig. 2. Performance on two cognitive tasks for different taxonomic groups. (a) Mean ($\pm$2se) percentage success on the A-not-B inhibition task for the major taxonomic groups. The dashed horizontal line denotes the chance response rate at 33% (for a task in which the animal chooses between three locations). (b) Mean ($\pm$2 se) percentage success on the cylinder

340   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 MacLean et al. (2014).

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Table 1. Factor loadings (with varimax rotation) for the six variables for each of the two datasets. Bold font indicates variables that load together on the same factor.

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|	Stevens	(2014)			MacLean	et al.	(2014)	
	Go-no-	Go task		A-not-B	task only	A-not-B	and	Cylinder
Factors:	1	2		1	2	1	2	3
Cylinder task						0.528	**0.712**	0.355
Indifference	**0.917**	0.245		**0.855**	0.053	**0.694**	0.087	0.547
% fruit	0.055	**0.984**		0.020	**0.971**	-0.120	**0.971**	-0.007
Group size	**0.904**	-0.194		**0.900**	0.031	**0.902**	0.060	0.158
Day journey (km)	**0.949**	-0.015		**0.895**	-0.018	**0.970**	-0.030	0.057
Range size (ha)	0.256	0.077		0.498	0.028	0.125	0.085	**0.954**

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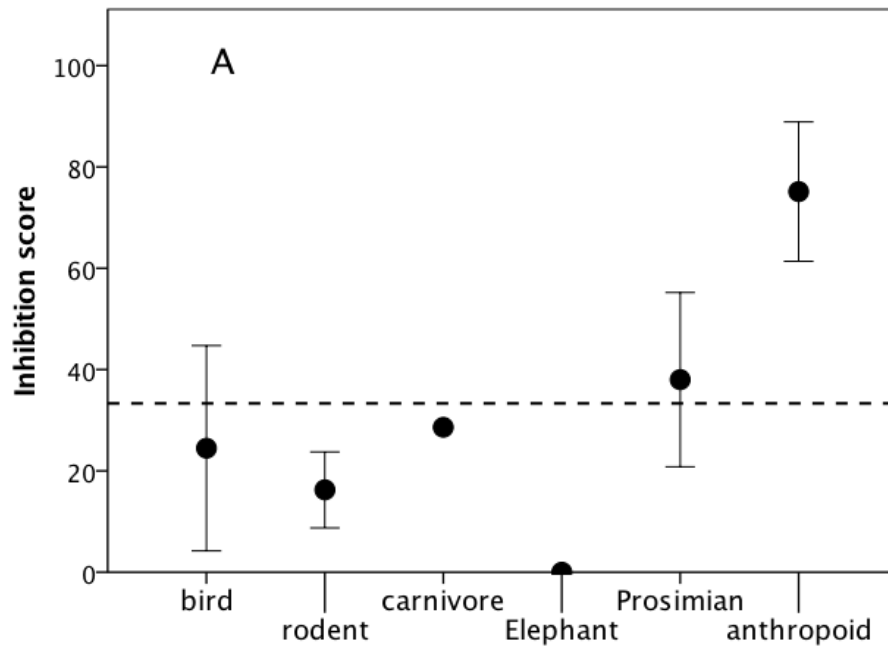
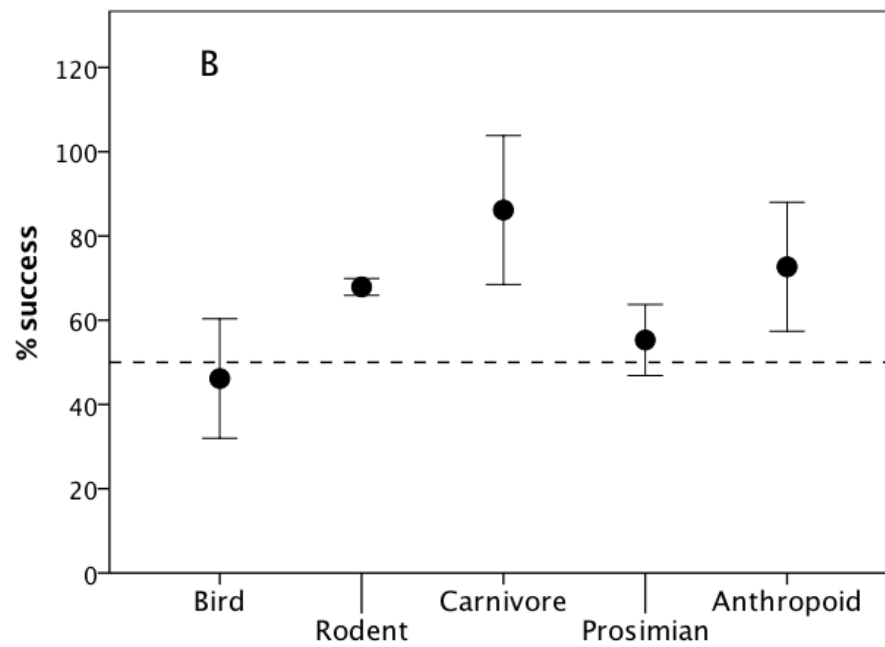14

Figure 1

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Figure 2

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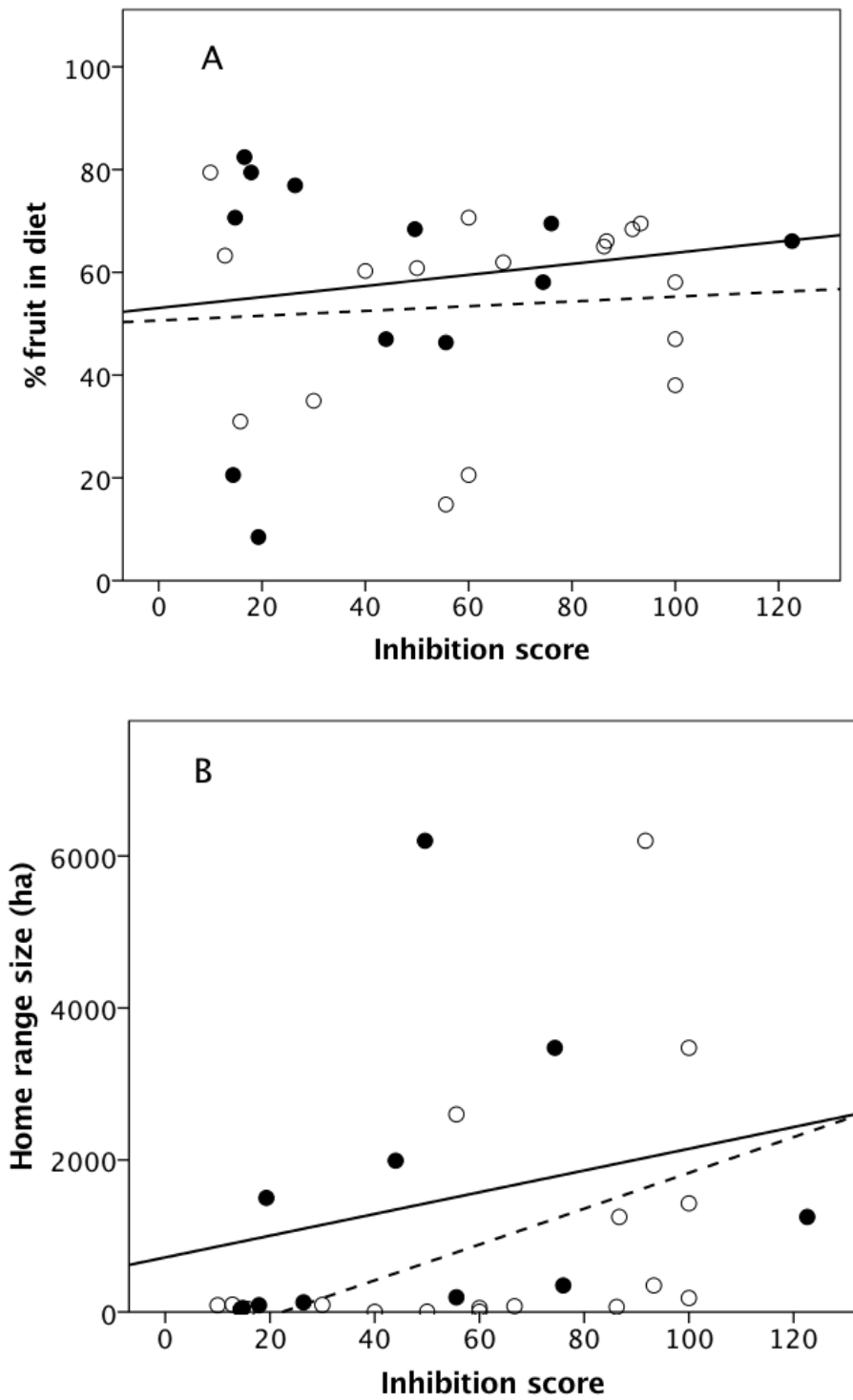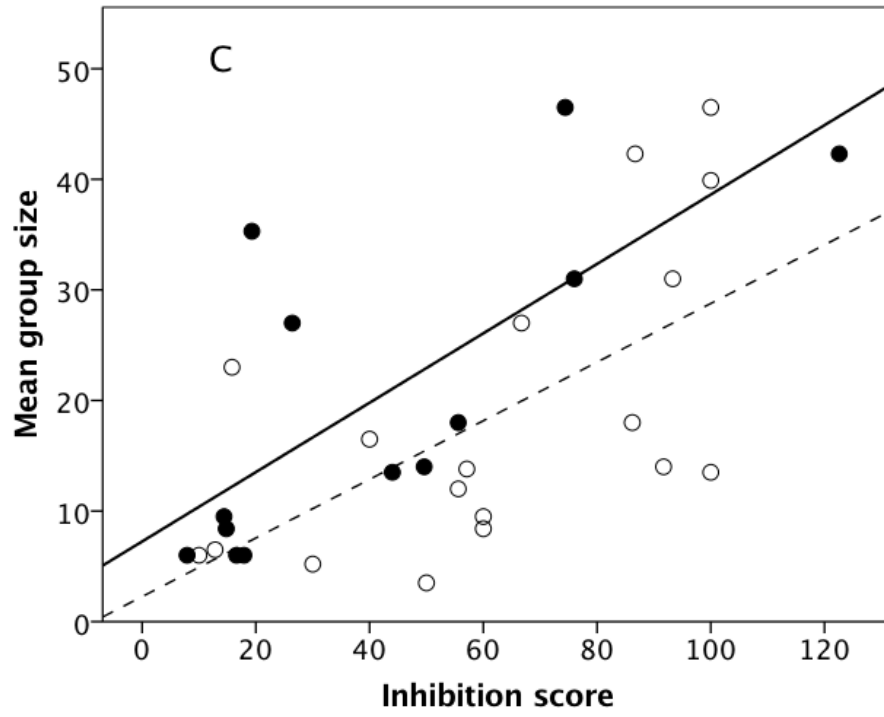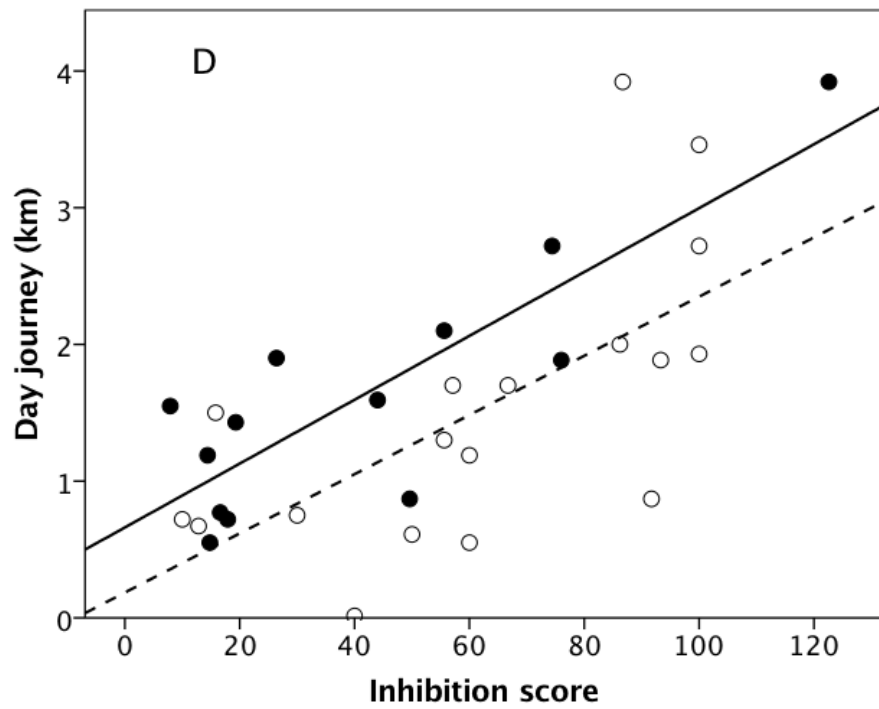
390   **Electronic Supplementary Material**

Data

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We exclude *Papio hamadryas* from the MacLean et al. (2014) dataset because of its unusually long day journey length (>7 km = 5.9 SDs above the mean for all the other species in this dataset). Hamadryas baboons live in a very challenging and, for primates, unusually dry habitat (Kummer 1968), and its unusual fission-fusion social system allows it to adjust its
400   group size flexibly to cope with the demands of foraging under extreme environmental conditions (Sigg & Stolba 1981). As a result, it behaves more like a herd-forming species.

Canis familiaris is also excluded because it is a domesticated species.

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Regression analysis

Although multiple regression would be the conventional way to test hypotheses of this kind, the format of a standard regression model would oblige us to regress the cognitive cause
410   (inhibition skill) on the four ecological and social outcome variables, thus reversing the natural biological causality. Doing so often produces very different results because it implies that ecological behaviour constrains or determines cognition, when the causality is obviously the other way around: it is cognition that constrains (i.e. "causes") behavioural outcomes, not the behavioural outcomes that constrain cognition.

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In addition, standard least squares (LSR) regression (which was designed for experimental contexts where X-axis values are pre-specified and therefore known exactly) assumes that the values on the X-axis are known without error (Kendall & Stuart 1979). If the error variances on the X- and Y-axes are approximately equal, then the resulting estimated regression slope
420   will be lower than it actually is (Rayner 1985). A statistically more elegant approach is to use principal components (or factor) analysis to ascertain which of the variables covary (i.e. cluster together). This avoids the need to presumptively specify the causal relationship between variables.

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Phylogenetic methods

There are no phylogenetic methods designed for use with factor analysis. However, this is less problematic than it might seem for three reasons. First, the phylogenetic signal for group
430   size, percent fruit in diet, home range size and day journey length are all close to zero (Kamilar & Cooper 2013). Second, previous studies have shown that, 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 (Shultz & Dunbar 2007, 2010; MacLean et al. 2014). Third, in only a very few cases are there samples from the same genus
435   or even closely related genera in either of these datasets (the principal problem for which phylogenetic methods were developed).

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References

Kamilar, J.M. & Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society, London*, 368B: 20120341.

445 Kendall, M.G. & Stuart, A. (1979). Functional and structural relationship. In: *The Advanced Theory of Statistics*. Vol. 2. *Inference and Relationships*, pp. 391-409. London: Griffin.

Kummer, H. (1968). *Social Organisation of Hamadryas Baboons*. Basel: Karger.

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:
450 E2140-E2148.

Rayner, J.M.V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *Journal of Zoology* 286: 415-439.

Shultz, S. & Dunbar, R.I.M. (2007). The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society, London,* 274B: 2429-2436.

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

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

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