# The Social Role of Inhibition in Primates and Other Animals

**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 correlates better with the demands of social contexts than the demands of foraging contexts, whereas a more generalised capacity for causal reasoning correlates with both social and foraging contexts. In addition, we confirm the Passingham-Wise Conjecture that the capacity to inhibit prepotent action is unique to anthropoid primates, and suggest that it 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]. Many studies have emphasised a role for inhibition in foraging [3-4,6]: when animals forage optimally, they have to be able to bypass a less valuable immediate reward in order to gain a more valuable future one [7]. However, inhibition can also be important in a social context for species that live in bonded social groups. These groups face severe coordination problems during foraging [8-10]. In order to maintain group cohesion, individuals need to be able to inhibit the inclination to continue feeding when others want to rest (or rest when others want to feed). Failure to do so results in groups becoming scattered, and eventually fragmenting.

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 [11-13], causing groups to fragment and disperse on a timescale of hours [8,14-17]. Joiner-leaver models [18] remind us that, whereas small groups typically attract members, large groups lose them, especially when food patches become exhausted or the stresses of group-living become too great [19]. In such groups, individuals maintain weak (or simply casual) relationships with other members of group. With no centripetal force to maintain group cohesion, animals simply drift apart [14-17] such that group membership varies on a daily basis. Even in herd-forming primates like the gelada, herds are increasingly likely to fragment during the day's foraging as their size increases [20]. In contrast, species that form stable social groups (congregations) that travel and sleep together are demographically stable over many years (subject to births and deaths). These groups, individuals have strong bonds with each other [21-23] that create networks of

interconnectedness [24]. Such groups, which are particularly characteristic of primates, face significant challenges because they have to maintain cohesion in the face of the pressures that cause aggregations to fragment [8].

The central problem that bonded groups face is the risk that individuals' activity budgets get out of synchrony, since that leads to groups dispersing. Mechanisms are needed to suppress the tendency for an individual to continue with an activity (e.g. feeding) when the rest of the group wants to do something else [25-28]. 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 [29]. In bonded groups, animals also need to minimise actions that will destabilise groups and cause individuals to leave the group [9]. This requires individuals to be willing, for example, to suppress the desire to steal each other's food and to avoid escalating agonistic contests.

So far, however, no attempt has been made to determine whether the capacity to inhibit behaviour is more important in the social or the ecological domain, or equally important to both. The answer bears on the debate over domain-general versus domain-special cognition, and hence whether cognition itself is under selection. To determine whether self-control is more important in the social or the ecological (foraging) domains, we analyse data on performance on two widely used inhibition tasks (Go/No-Go task and A-not-B task) sourced from two separate databases [3,4] for a range of primate species. MacLean et al. [3] also used performance on an additional task (the cylinder task) as an index of self-control. Although widely used as a test of self-control [6,30-32], doubts have been expressed as to whether this task actually indexes inhibition [32]. The cylinder task asks animals to choose between two ends of a tube in order to access a food reward, one of which is more

accessible than the other (either because one end is blocked or because the reward is nearer one end). This suggests that it might, in fact, be better characterized as a causal reasoning task. If so, it may be a proxy for generalised reasoning rather than specialised cognition, and may hence be used in a wider range of contexts than is self-control.

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 [3-4,33-34]. Fruits are much less predictable than foliage, and are usually viewed as being a cognitively more challenging diet [35]. They also vary spatially in both quality and quantity, 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 profitability [3,4]. In primates, both percent fruit in the diet and range size are strongly influenced by habitat conditions and hence impact on nutrient acquisition [36-40]. If inhibition relates to foraging efficiency, performance on such tasks should correlate positively with one or both of these ecological indices: the more patchy the resource distribution, the more animals will need to be able to inhibit the temptation to stay with a proximate resource rather than delay reward to go to a richer one that is further away.

In respect of the social domain, our focus is on the stresses that coordination problems impose on group stability and the role that inhibition is likely to play in ensuring that animals stay together during foraging. For social species, the larger its groups and the longer its day journeys the more important inhibition will be for maintaining group cohesion As social domain indices, we use mean social group size and mean day journey length. Coordination problems increase as a function of both group size and the distance animals have to travel after leaving a point of convergence (e.g. a sleeping site or waterhole) since both make it more likely that individuals' activity cycles will get out of synchrony [8,12]. Baboons

provide a well studied example: group fragmentation is more likely as both day journey length and group size increase (Fig. 1), with these effects acting independently (Tables S1-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 here since, viewed superficially, both look like foraging-relevant variables. However, functionally 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 [41-42]. Range size determines the number of patches available to the group, but 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, the distribution of resource patches and the number of patches the group has to visit to satisfy its collective nutritional demand [43]. 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 of 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 [44] argue that, in primates, inhibition depends explicitly on the brain's frontal pole (Brodmann Area BA10), a brain unit that is found only in anthropoid primates. The significant role of the prefrontal cortex (and, in particular, the ventrolateral prefrontal cortex) in supporting inhibition is confirmed by neuroimaging and lesion studies in humans [45]. Since, with the exception of a few (mostly species-poor) orders (equids, delphinid, tylopods), large bonded social groups are found only in anthropoid primates [5,24,46-47], 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. In contrast, to the extent that the cylinder task indexes causal reasoning (and hence a form of generalised cognition), we might expect competence on this task to occur more widely outside the primates.

## 2. Methods

*Data*

We use data from two sources [3,4] that provide experimental data on the capacity to inhibit prepotent responses for a number of primate species. Since they involve different tasks using different metrics, we analyse the two datasets separately. Mean group size for species was sourced from [48], percentage of fruit in the diet (except for *Macaca mulatta*: see Table S4) from [34] and day journey length (in km) and home range size (in ha) from [49-50] and primary sources therein (for exceptions, see *ESM*). *Daubentonia* and *Papio hamadyas* were omitted from the MacLean et al. [3] dataset for the reasons given in the *ESM*. The data are given in *ESM DATASET-1*.

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 sample of bird species. These data are given in *ESM DATASET-2*.

*Statistical analysis*

Although multiple regression might seem 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 causality (cognitive capacity determines, or constrains, behaviour). 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 more complex relationships. Having identified natural complexes in this way, we then use mediation analysis to identify causal relationships.

Conventionally, comparative analyses use phylogenetic methods to control for the impact of phylogenetic inertia. We do not use these methods in this case because there are no phylogenetic methods designed for use with factor analysis or for handling complex causal relationships. 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 [51]. 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 [24]. 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 [3,46-47]. 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. To examine the covariation among these variables, principal components analyses were run with the five behavioural and ecological variables separately for each cognitive task. With eigenvalues set to $\lambda>1$, two factors were extracted for all three cognitive tasks, explaining 72-75% of the variance (Table

1). The two inhibition tasks, group size and day journey length consistently load together on the same factor with high weightings, while diet is placed in a separate factor. In contrast, the cylinder task loads equally on both factors, suggesting a more generalised form of cognition. When the A-not-B and cylinder tasks are both included in the same analysis, the cylinder task loads more strongly with diet (Table 1, right hand column). In all four analyses, range size loads only weakly on either factor, and sometimes on both factors at the same time. Table S6 confirms that these results hold when the data are analysed at genus level, indicating that phylogeny does not influence the results.

To evaluate the relationship between inhibition and its associated social variables in more detail, we ran a mediation analysis with the A/~B task as the independent variable and group size and day journey length alternately as dependent variable and mediator. A Sobel test indicates that a model with group size as mediator and day journey as dependent variable (Fig. 2) yields a significant model ($z=2.893$, $p=0.0038$). This model is significantly better than one with group size as the dependent variable and day journey as the mediator ($z=0.022$, $p=0.982$) or one with inhibition as the dependent variable ($z=0.070$, $p=0.944$). This suggests that the capacity to inhibit behaviour (self-control) determines group size, and group size then determines day journey length.

Finally, we test the Passingham-Wise conjecture using the two MacLean et al. [3] tasks. Fig. 3a 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 [44] 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 in the anthropoids (see also [5]). Figure 3b 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 ($F_{5,25}=2.22$, $p=0.084$). Indeed, 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), 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 with the demands of maintaining group coordination whilst foraging. This concurs with human evidence that the ability to inhibit gratification strongly predicts social skills, with poor capacity to do so being directly related to disruptive anti-social behaviour and poor ability to maintain stable relationships [1-2], both of which are indicative of an inability to negotiate compromises. In primates, including humans, this ability is particularly associated with units in the prefrontal cortex (notably the frontal pole [44] and the adjacent inferior frontal cortex [45]), the part of the brain that expanded most during the course of primate and human evolution – and is most dependent for full adult functionality on experience and learning during socialisation.

The causal reasoning task (the cylinder task) gives more ambiguous results, loading with diet (and hence food-finding abilities) in some cases but on both factors in other cases. The lack of any clear difference 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 specifically 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 (or behavioural prediction in the case of carnivore hunters) and processing of their food than the former [52]. Although several authors have claimed that birds perform just as well as apes and monkeys on this task [6,30-32], 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 the birds. Nonetheless, this result adds weight to the suggestion that inhibition and causal reasoning have evolved independently of each other, and represent a clear case of mosaic evolution in cognitive skills and their underlying neural bases.

The mediation analysis makes it clear that by far the best model of the causal relationships between the three variables in the social cluster is that capacity to inhibit prepotent actions determines group size, and group size then determines day journey length. Biologically, this makes more sense than any alternative model. This suggests that self-control plays a crucial role in managing group size and its constituent social relationships rather than influencing day journey length directly.

These results feed into the longstanding distinction 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 [53] and the constant monitoring of social partners [54]. These kinds of bonded relationships are characteristic of anthropoid primates, but otherwise are found only and only a handful of

other mostly species-poor mammalian orders which live in modest-sized groups (notably elephants, equids, tylopods, and delphinids) and in the monogamous pairbonds of other mammalian and avian orders [46-47]. The capacity to inhibit and modulate behaviour is crucial for the continued viability of bonded social groups just as it is for pairbonds in that it ensures that the individuals remain together and hence synchronise their movements. Fig. 1a confirms that this capacity is unique to the anthropoid primates, as suggested by Passingham and Wise [44], 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 [5,46-47]. 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 [55], which may explain why, uniquely, they scored poorly on the inhibition task (Fig. 1a).

The level of coordination required to maintain the coherence of bonded groups is also likely to be associated with other specialised 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 dependent on the frontal pole [44]. 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 [28,56-59]. 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 [60]. In humans, mentalizing skills of this kind are correlated both with the size of an individual's social network [61-62] and with the volume of the brain's mentalising and default mode neural networks [63-65], 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 [66-67]. A likely explanation is that both mentalising and inhibition are required to maintain bonded social groups.

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## 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. Mediation analysis of the relationship between the three variables in the social cluster in Table 1. A model with day journey length as the dependent variable gives a significantly better fit than one with group size as the dependent variable. βs are standardised slopes; $\beta_{med}$ gives the standardised slope from the multiple regression equation with both independent variables.

Fig. 3. 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].

Table 1. Factor loadings (with varimax rotation) for the five variables (excluding grooming) for each of the three inhibition tasks.

| | Stevens (2014) | | | | MacLean et al. (2014) | | | |
|---|---|---|---|---|---|---|---|---|
| | Go/No-go task | | A-not-B task | | Cylinder task | | A/~B and cylinder tasks | |
| 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 |
| 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 |
| Diet (% fruit) | -0.018 | **0.778** | 0.020 | **0.971** | -0.137 | **0.936** | -0.156 | **0.931** |
| Range size | 0.148 | **0.714** | 0.498 | 0.208 | **0.569** | 0.244 | 0.485 | 0.356 |
| N | 13 | | 18 | | 17 | | 14 | |
| Variance explained | 74.9% | | 72.3% | | 75.1% | | 75.7% | |

Extraction based on $\lambda = 1.0$. Bold font indicates variables that have a strong positive load on the same factor.

**Figure 1**

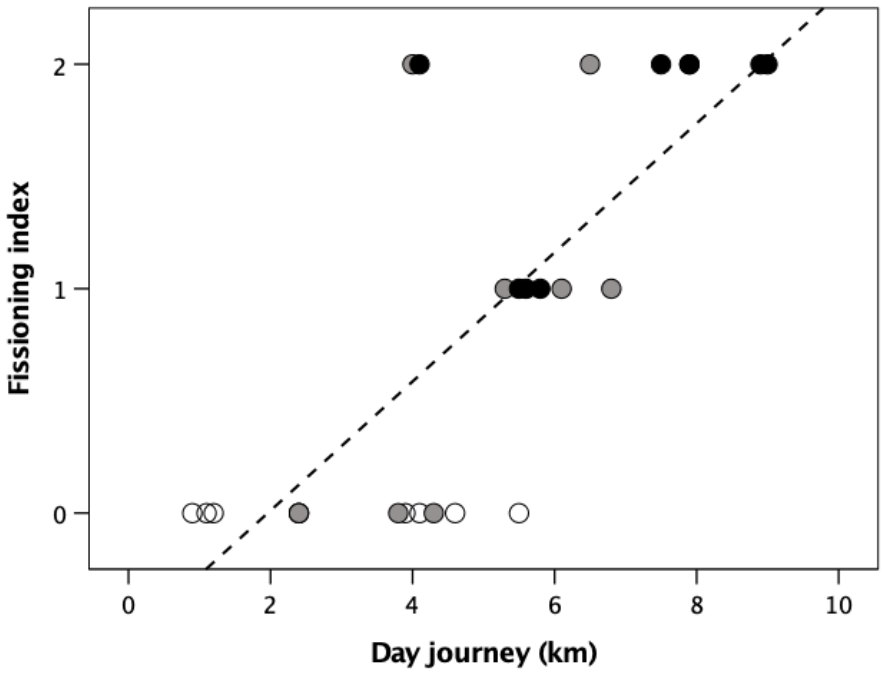


**Figure 2**

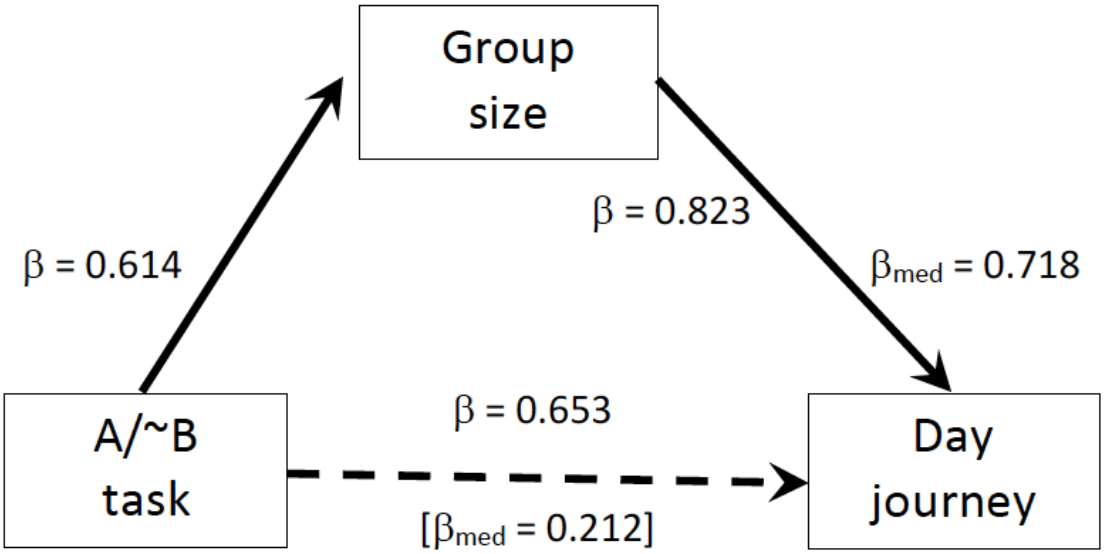
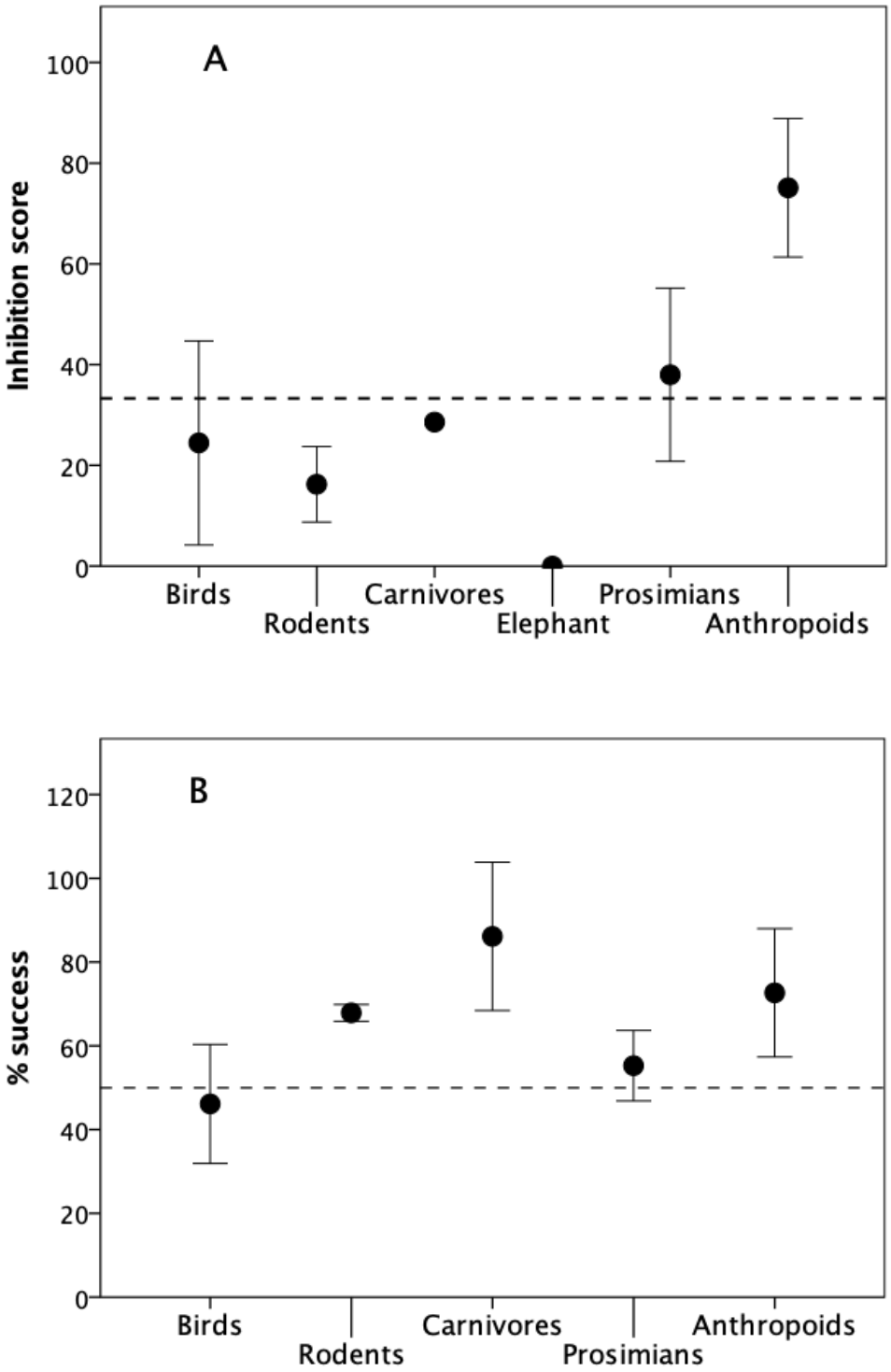

Group size
β = 0.823
β = 0.614
βmed = 0.718
A/~B task
β = 0.653
Day journey
[βmed = 0.212]

**Figure 3**


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