

## **ELECTRONIC SUPPLEMENTARY MATERIAL TO ‘UNDERSTANDING OF PRIMATE BRAIN EVOLUTION’, BY R. I. M. DUNBAR & SUSANNE SHULTZ**

### **METHODS**

#### *(a) Measures of relative brain size*

The data for primate brain size, based on fresh tissue volume, were taken from [Stephan \*et al.\* \(1981\)](#). In primates, both relative neocortex size and the ratio of the neocortex to the rest of the brain have been demonstrated to be more tightly associated with social complexity than relative total brain size ([Dunbar 1992, 1998](#)). Additionally, the neocortex is associated with executive functions and complex behaviours ([Keverne \*et al.\* 1996](#)) and is the region that has undergone the most evolutionary change in mammals ([Finlay \*et al.\* 2001](#); [de Winter & Oxnard 2001](#); [Barton & Harvey 2000](#)). As other studies have questioned the validity of neocortex residuals ([Deaner \*et al.\* 2000](#)) and ratios ([Nunn & Barton 2001](#)), we evaluated several measures of relative cognitive capacity including total brain size, three different measures of relative neocortex size and cerebellum size.

#### *(b) Phylogenetic controls*

Individual species cannot be assumed to be independent data points because closely related species are likely to share traits by decent rather than by parallel adaptation ([Harvey & Pagel 1991](#)). Thus, we used a phylogenetically controlled generalized least squares analysis (PGLS) to estimate all relative brain (and component) sizes. PGLS analyses allow the degree of phylogenetic autocorrelation to be identified and controlled for ([Harvey & Pagel 1991](#)). This is accomplished by attaching a covariance matrix of relatedness to each model as an error term. The amount of variation explained by the covariance matrix can thus be interpreted as an indication of the level of phylogenetic autocorrelation in the data. This can be quantified with Pagel's  $\lambda$ , which uses an optimization process that estimates the overall degree of phylogenetic autocorrelation; where  $\lambda = 0$  when there is no autocorrelation and  $\lambda = 1$  when the data follow the assumptions of Brownian motion and species traits covary proportionally with their degree of relatedness ([Paradis \*et al.\* 2004](#)). The PGLS analyses were executed in R ([Grafen 1989](#)) using the APE (Analysis of Phylogenetics and Evolution) package ([Ihaka & Gentleman 1996](#)) and code provided by R.P. Duncan. The primate phylogeny used in this analysis follows [Purvis \(1995\)](#); we assumed that branch lengths were proportional.

Relative brain sizes were calculated as residuals from the following linear regression equations. Total brain size was estimated by the deviation from a log-transformed body/log-transformed brain regression. Relative neocortex size was estimated as the deviation from three different regression lines: (i) log-transformed neocortex/log-transformed total brain size, (ii) log-transformed neocortex/log-transformed (total brain minus neocortex), and (iii) log-transformed neocortex/log-transformed medulla. The last estimate was included because the neocortex represents the relative proportion of the brain allocated to higher cognitive capacity, whereas the medulla represents the part of the brain devoted to maintenance functions. Relative cerebellum size was calculated by a regression of log-transformed cerebellum versus log-transformed (total brain size minus cerebellum).

(c) *Behavioural and ecological characteristics*

We compiled a database of several characteristics that relate to primate social complexity including social group size, social systems, dispersal (from Smuts *et al.* 1987; Dunbar 1992), and coalition formation (from Plavcan *et al.* 1995). We use group size as a proxy of social complexity, as the number of potential relationships increases with group size. Species were classed into one of four increasingly complex social systems: solitary (adults generally forage and rest individually), monogamous (one breeding adult of each sex in regular association), harem (one adult breeding male and several to many adult females in regular association), multi-male (more than one resident adult male and multiple to many adult females). We documented which sex (or both) typically disperses from the natal range as a measure of bonding within the group (with those cases where both sexes disperse assumed to be the least bonded group). Coalition formation was defined as whether same sex coalition formation had been observed in the species.

We included data on several life-history characteristics including body size, longevity, juvenile period (data from Ross & Jones 1999; Ross 1992; Harvey *et al.* 1987) and basal metabolic rate (Armstrong 1985). To determine whether metabolic rates were higher or lower than would be expected for species of a given body size, residual BMR was estimated from a regression of BMR against log-transformed body size.

We also chose a suite of ecological characteristics that measure environmental complexity and could be linked to brain size. Unfortunately, we do not have an equivalent measure of ‘innovation’ or flexibility that has been associated with large brains in birds (Grant *et al.* 1992). As day range and home range can be linked to competition, we could predict that species with longer day ranges (or larger home ranges) need to have better spatial ability, better memory and more flexible decision-making about how they move through their environment (data from Kolb & Wishaw 1996). The activity was defined as a dichotomous variable with species classed as either primarily diurnal or nocturnal: activity period is known to correlate with brain size in primates, mainly owing to the computational costs of colour vision for diurnal primates (Barton 1998). For strata use, species were classified into either primarily arboreal or as terrestrial if they regularly used the ground for locomotion between feeding/resting sites. We assume that terrestrial species are exposed to more risk, but that arboreal species have to contend with a more complex three-dimensional habitat. Habitat use was likewise defined as a dichotomous variable with species classed as occurring primarily in open/mixed habitats or being constrained to closed forest. The quality and availability of data on diet composition across species varies widely; therefore, we chose to use a simple dichotomy between relatively high quality (fruit and insects) versus relatively low quality (predominately leaves).

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