

## Evolution of brain size and juvenile periods in primates

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### Abstract

This paper assesses selective pressures that shaped primate life histories, with particular attention to the evolution of longer juvenile periods and increased brain sizes. We evaluate the effects of social complexity (as indexed by group size) and foraging complexity (as indexed by percent fruit and seeds in the diet) on the length of the juvenile period, brain size, and brain ratios (neocortex and executive brain ratios) while controlling for positive covariance among body size, life span, and home range. Results support strong components of diet, life span, and population density acting on juvenile periods and of home range acting on relative brain sizes. Social-complexity arguments for the evolution of primate intelligence are compelling given strong positive correlations between brain ratios and group size while controlling for potential confounding variables. We conclude that both social and ecological components acting at variable intensities in different primate clades are important for understanding variation in primate life histories.

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### Introduction

Primate life histories tend to be characterized by rather long subadult periods (Pereira and Fairbanks, 1993; Leigh, 2001), long life spans (Austad and Fischer, 1992; Hakeem et al., 1996), slow growth rates (Leigh and Park, 1998), slow fertility rates (Charnov and Berrigan, 1993), and large absolute and relative brain sizes (Rilling and Insel, 1999) compared to other mammalian orders. At the extreme are wild chimpanzee females with an age at first reproduction of about 13 years (Sugiyama, 2004) and natural-fertility hunter-gatherers that begin to reproduce around 19 years of age (Marlowe, 2005). Chimpanzees, humans, and other large primates grow nearly an order of magnitude slower than other mammals of similar size (Case, 1978; Walker et al., 2006). These “slow” life-history

traits are posited to be directly related to encephalization in the primate order in general and in great apes in particular (Kaplan et al., 2000; Deane et al., 2003). Our interest here is to evaluate different competing ideas, namely social versus foraging complexity, on the evolution of slow primate life histories. Based on previous analyses (e.g., Sawaguchi, 1992; Dunbar, 1996; Barton, 1999), but including more ecological variables, our general prediction is that various measures of relative brain size, in addition to age at first reproduction as a proxy for the end of the growth period, will be positively associated with indices of social and foraging complexity within and across primate clades.

Long juvenile periods are often interpreted as necessary to develop the sophisticated cognitive capacities requisite in complex socioecologies (Bogin, 1999; Kaplan et al., 2000). In support of this idea are strong relationships among longer juvenile periods in primates and various measures of relative brain size (Barton, 1999). Longer juvenile periods and increased learning are consistent with a social-complexity model, which is further supported by strong positive associations between relative brain-size measures and primate group

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sizes (Dunbar, 2003). In the same vein as Barton (1999), we focus on multiple regressions that allow us to simultaneously examine brain-size variation explained by diet and group size. The availability of additional ecological variables, such as home range from studies of wild primates, further strengthens our ability to separate independent predictors of brain size and age at first reproduction (Kaplan et al., 2003). We pay special attention to differences between Old and New World primates in recognition of the fact that different selective pressures may be more or less important in different primate clades. Our goal is to evaluate the relative effects of social complexity (as indexed by group size) and foraging complexity (percent fruit and seeds) on brain size and brain ratios (e.g., neocortex and executive brain ratios). We are also interested in selection for longer juvenile periods given the suggestion that these have likely coevolved with larger relative brain measures (e.g., the nonvisual neocortex; Joffe, 1997).

### *Brain evolution*

The ultimate explanation for the evolution of large relative brain sizes in primates remains unresolved. In particular, the neocortex of many primates has undergone sizable expansion, reaching its most extreme form in humans (Rilling and Insel, 1999). The neocortex is generally associated with multimodal integration, planning, inhibition, innovation, cognitive memory, and higher-order information processing (Keverne et al., 1996; Joffe and Dunbar, 1997). A number of hypotheses have been put forth to account for cerebral expansion in primate lineages. Epiphenomenal and developmental models have interpreted brain size as a by-product of large body size (Finlay et al., 2001) or as resulting from certain nutritional conditions (Broadhurst et al., 2002), respectively. In this paper, we focus on models that address potential selective pressures leading to primate cortical expansion, namely the cognitive demands associated with exploiting a skill-intensive foraging niche (Parker and Gibson, 1977) and the sociocognitive competencies of living in large social groups (Humphrey, 1976).

Selective pressures related to foraging have long been suspected to play a role in the evolution of intelligence. This argument centers on cognitive challenges associated with securing high-quality (nutrient-dense) but difficult-to-acquire food sources, which may be ephemeral and require detailed mental maps to track and locate across time and space (Parker and Gibson, 1977; Clutton-Brock and Harvey, 1980; Harvey and Krebs, 1990; Parker and McKinney, 1999). For example, the greater cognitive abilities in frugivorous compared to folivorous primates may reflect the greater challenges associated with foraging for ripe fruit versus a nearly constant supply of leaves (Milton, 1981). Additionally, more nutritionally dense, higher-quality foods are required to support metabolically expensive neural tissue (Milton, 2003). As such, the shift in hominin diet to higher-quality but more difficult-to-acquire resources would have required learning skill-intensive extracting techniques, thereby producing longer juvenile-learning periods and larger brains (Kaplan et al., 2000). Proponents

of this model point to the complex techniques employed by human hunters, who integrate many sources of information within a large area to locate many types of prey and to utilize a wide range of techniques to capture prey once located (Kaplan et al., 2000). Chimpanzees also utilize a range of complex hunting techniques (Mitani and Watts, 1999), and the great apes, in general, are capable of elaborate tool use for foraging (Boesch and Boesch, 1990; McGrew, 1992; Fox et al., 1999; Yamakoshi, 2004; Russon and Begun, 2004) and execute complex sequences for extracting food from plants (Byrne and Byrne, 1991, 1993). However, some primates are as adept at foraging as juveniles as they are as adults (Watts, 1988; Pereira and Fairbanks, 1993; Janson and van Schaik, 1993).

Interpreting the brain and higher cortical functions as adaptations for negotiating social interactions within large-group settings has been widely discussed (Jolly, 1966; Humphrey, 1976; Whiten and Byrne, 1988; Byrne and Whiten, 1988; Alexander, 1989; Dunbar, 1993, 1998, 2003; Byrne, 1995; Kummer et al., 1997; Whiten and Byrne, 1997; Heyes, 1998; Barton, 1999; Flinn et al., 2005) and offers an alternative (or perhaps complementary) scenario leading to primate encephalization. The central supposition of social-brain scenarios or “Machiavellian” intelligence is that higher cognitive functions evolved in response to selective pressures arising from social interactions with conspecifics and specifically the ability to use and manipulate social information. Monkeys are capable of rapid social learning and deception (Byrne and Whiten 1988), while the great apes are further capable of theory of mind, the reasoning about the beliefs and desires of others (Call and Tomasello, 1998).

In hominoids, particularly chimpanzees and humans, the influence of intergroup competition on social organization has been emphasized (Manson and Wrangham, 1991). Competition among subpopulations can result in coalitionary arms races, producing larger and necessarily more complex social groups (Alexander, 1989). The ability to navigate within increasingly larger social arenas filled with equally sophisticated conspecifics may have provided an autocatalytic mechanism by which social intelligence rapidly increased. Social models can be criticized on grounds that they do not account for qualitative differences among primate grades, nor do they adequately address overcoming the costs associated with living in large groups. These costs may in turn depend on ecological conditions highlighting the probable interaction of social and ecological factors on primate life histories.

A challenge to students of primate life-history evolution is to develop tests that evaluate foraging and social explanations for the evolution of long juvenile growth periods and large brains. In this paper, we develop a series of multiple regressions that examine the relative effects of group size and percent fruit and seeds in the diet on age at first reproduction and brain size while addressing interrelationships with home range and longevity. The models allow us to separate direct (perhaps causal) effects from indirect effects acting through spurious correlations with other life-history and socioecological variables. In this manner we are able to simultaneously evaluate social- and foraging-complexity hypotheses and

estimate the relative importance of each for the evolution of primate brain sizes and juvenile periods within and across clades.

## Materials and methods

### *Comparative analysis*

Comparative data can be used to better understand the selective pressures acting on brain size and juvenile periods. The analyses reported here used a primate data base containing female age at first reproduction (months), brain weight (g), maximum life span (years), body size (kg), maximum home range (km<sup>2</sup>), percent fruit and seeds in the diet, and average group size. The data base was compiled from secondary sources (Barton, 1999; Harvey et al., 1987; Smith and Jungers, 1997; Kappeler and Pereira, 2003) with an emphasis on primary field data where available (Kaplan et al., 2003; see <http://www.unm.edu/~7Ehkaplan/pnas/primatedatabase.xls> for data and information sources). In various analyses, we used a total of 67 primate species (11 strepsirrhines, 19 New World monkeys, 30 Old World monkeys, and 7 hominoids, excluding humans) for which values for each of the seven characteristics listed above were available. Where possible, we performed analyses within New World and Old World monkeys but were not able to do so for the hominoids and strepsirrhines, given small sample sizes. Therefore, in our all-primate analyses we included all 67 species. Analyses (unreported) show that omission of the strepsirrhines from the all-primate sample does not significantly alter our main conclusions.

The data were analyzed with species as independent data points and using independent contrasts, which adjust for phylogenetic effects (Nunn and Barton, 2001) because closely related species may be similar simply because they share a recent ancestor (Felsenstein, 1985; Garland et al., 1992; Losos, 1999). The independent contrasts module of PDTree by Garland and colleagues (1993, 1999; Garland and Ives, 2000), used primarily with the phylogenetic tree and branch lengths of Smith and Cheverud (2002) and secondarily from Purvis (1995), was used to construct independent contrasts. These were analyzed and graphed using SPSS software and Pascal (see below). All variables were log-transformed (base 10) prior to analysis. Diagnostics available in PDTree were examined to ensure homoscedasticity in residuals and that branch lengths were statistically appropriate.

### *Other relative brain-size measures or “brain ratios”*

Since body size can change independently of brain size (Willner, 1989; Deacon, 1990), it has been suggested that various brain ratios are preferable to using whole-brain or brain-component size while controlling for body size (Dunbar, 1998). Brain ratios are relative measures of brain volume for areas of higher cognitive functions (i.e., neocortex) scaled to the remainder of the brain or a more ancestral brain region. We used the following brain ratios: (1) neocortex ratio

[neocortex / (whole brain – neocortex); Dunbar, 1992], (2) neocortex ratio that adjusts for the cerebellum [neocortex / (whole brain – cerebellum – neocortex); Reader and MacDonald, 2003], (3) nonvisual neocortex ratio [(neocortex – V1) / (whole brain – neocortex); Joffe, 1997], (4) nonvisual neocortex ratio that adjusts for the cerebellum [(neocortex – V1) / (whole brain – cerebellum – neocortex)], and (5) executive brain ratio [(neocortex + striatum) / (mesencephalon + diencephalon); Reader and Laland, 2002]. The best measure of relative brain size is still debated (Barton, 1999; Deaner et al., 2000), but we included ratios that exclude the cerebellum to avoid the problem that larger neocortices could be driven by diminished cerebella (Reader and MacDonald, 2003). The brain ratios were taken from Reader and MacDonald (2003), who relied principally on the primate brain-component volumes (corrected for species-typical values) of Stephan and colleagues (1970, 1981, 1988).

Unfortunately, the available sample size for different brain ratios was only 23–33 primate species depending on the ratio, which is small for the assumptions of ordinary least squares regression. Small sample size is also a problem for the regression analyses conducted within Old and New World monkeys. Therefore, we calculated *p*-values for our parameter estimates using resampling with replacement, or bootstrapping, techniques (Efron, 1979; Yu, 2003) with a Pascal program. The original data distributions were resampled with replacement in 10,000 bootstrap replications for each independent variable while holding the other variables constant. The *p*-value was defined as the proportion of iterations in which the slope fitted to random data was absolutely larger than the slope through the observed data (Davison and Hinkley, 1997). Contrary to the recommendations of some (Deaner et al., 2000), we found similar or often better model results for all the brain ratios when they were log-transformed, but this could be partially a function of resampling, which is less affected by distributions of the original data (Mitchell-Olds and Shaw, 1987).

## Results

### *Age at first reproduction*

We report results in three related sections of dependent variables—length of the juvenile period, brain size, and brain ratios. First, age at first reproduction, which approximates the cessation of the growth period (at least for females), was regressed on body size, group size, life span, and the ecological variables. Group size has a strong positive effect on longer juvenile periods in Old World monkeys and across the primate order (Table 1). Home range has a negative effect on age at first reproduction for Old World monkeys. This interesting but difficult to interpret result was also mentioned by Deaner and colleagues (2003). Taken together these results (positive group size and negative home-range effect) imply that age at first reproduction in Old World monkeys is later when population density is high given that  $\log(\text{population density}) \sim \log(\text{group size}) - \log(\text{home range})$ .

Table 1  
Multiple-regression models of age at first reproduction (dependent variable) for 1) Platyrrhini, 2) Cercopithecoidea, and 3) all primates (including Hominoidea and Strepsirrhini)

Model	Species as data points		Independent contrasts			
	$\beta$	<i>p</i>	$\beta$	<i>p</i>	$\beta$	<i>p</i>
1) New World monkeys ( <i>n</i> = 19)						
(Intercept)			(No Intercept)			
Body size	<b>0.723</b>	<b>0.001</b>	<b>0.575</b>	<b>0.035</b>	0.492	0.058
Group size*	<b>-0.307</b>	<b>0.034</b>	-0.442	0.078		
Life span	0.308	0.058	0.498	0.076	0.366	0.171
Home range*	<b>0.295</b>	<b>0.043</b>	0.357	0.247		
Fruit + seed	-0.146	0.327	-0.159	0.449	-0.060	0.738
Density					-0.250	0.390
2) Old World monkeys ( <i>n</i> = 30)						
(Intercept)			(No Intercept)			
Body size	<b>0.660</b>	<b>0.002</b>	0.214	0.109	0.068	0.532
Group size*	<b>0.940</b>	<b>&lt;0.001</b>	<b>0.495</b>	<b>0.001</b>		
Life span	-0.114	0.519	0.185	0.186	<b>0.343</b>	<b>0.036</b>
Home range*	<b>-1.155</b>	<b>&lt;0.001</b>	<b>-0.550</b>	<b>0.002</b>		
Fruit + seed	-0.109	0.546	0.366	0.143	0.464	0.118
Density					<b>0.319</b>	<b>0.044</b>
3) All primates ( <i>n</i> = 66)						
(Intercept)			(No Intercept)			
Body size	<b>0.672</b>	<b>&lt;0.001</b>	0.146	0.185	0.126	0.263
Group size*	0.011	0.907	<b>0.329</b>	<b>0.006</b>		
Life span	<b>0.396</b>	<b>&lt;0.001</b>	<b>0.297</b>	<b>0.007</b>	<b>0.385</b>	<b>&lt;0.001</b>
Home range*	-0.171	0.193	<b>-0.355</b>	<b>0.006</b>		
Fruit + seed	0.053	0.424	<b>0.379</b>	<b>&lt;0.001</b>	<b>0.411</b>	<b>&lt;0.001</b>
Density					<b>0.278</b>	<b>0.015</b>

Notes: All variables were log-transformed prior to analysis. Standardized regression coefficients,  $\beta$ , and resampling-generated *p*-values (*p* < 0.05 are in bold) are given for regressions in which species values were treated as data points and for those in which independent contrasts were used as data points. \*Denotes potential problem with collinearity, i.e., the home-range/group-size effects do not hold with omission of one or the other. Log(density) equals log(group size) – log(home range).

One might suspect that this effect may be driven by collinearity between group size and home range (Deaner et al., 2000) because both effects drop out when the other variable is omitted. However, if we collapse group size and home range into a single population density variable, the result is strong and positive on longer juvenile periods and avoids the problem of collinearity. One interpretation is that higher resource competition is associated with higher population density, which leads to longer periods of growth and is consistent with risk-aversion in juvenile primates (Janson and van Schaik, 1993). In the upcoming regression models, either home range or group size is a significant parameter (but not both simultaneously) and so we no longer need to invoke population density as a method to avoid collinearity problems.

Longevity tends to be strongly associated with age at first reproduction within and across primate clades (Table 1). This result supports one of the most salient predictions of life-history theory that higher adult mortality selects for earlier reproduction (Harvey and Zammuto, 1985; Stearns, 1992; Charnov, 1993). Additionally, the effect of diet on juvenile periods shows some support for an ecological model of longer

learning periods needed for more complex foraging skills, though this relationship does not appear to hold for New World monkeys.

### Brain size

We performed similar analyses with brain size as the dependent variable. In New World monkeys, relative brain size is best predicted by maximum life span regardless of whether species values or independent contrasts were used as data points (Table 2). This pattern does not hold, however, in Old World monkeys, in which diet is a strong predictor with species as data points, but home range is the strong predictor with independent contrasts. This intraorder variation between Old and New World monkeys makes analyses of a composite primate data base challenging because there is likely to be a blurring of grade shifts when analyzing across clades (Martin, 2003; Martin et al., 2005). It raises the red flag that important selective effects may be different across primate clades. Unfortunately, small numbers of hominoids and strepsirrhines prohibit analyses within these clades. Allman and colleagues (1993) found a positive association between life span and brain mass while controlling for body size within haplorhines but not within strepsirrhines. We confirm this relationship for New World monkeys since only home range (and not life span) is more strongly associated with brain size in Old World monkeys.

Group size and life span are strong predictors of relative brain size across primates. However, adjusting for phylogeny causes these effects to diminish and home range becomes the single most important predictor. In most of our results, we

Table 2  
Multiple regression models of brain size (dependent variable) for 1) New World monkeys, Old World monkeys, and 3) all primates

Model	Species as data points		Independent contrasts	
	$\beta$	<i>p</i>	$\beta$	<i>p</i>
1) New world monkeys ( <i>n</i> = 19)				
(Intercept)			(No Intercept)	
Body size	<b>0.767</b>	<b>&lt;0.001</b>	<b>0.787</b>	<b>0.003</b>
Group size	0.038	0.514	0.101	0.300
Life span	<b>0.224</b>	<b>0.007</b>	0.199	0.073
Home range	0.092	0.117	0.122	0.153
Fruit + seed	-0.012	0.828	-0.134	0.293
2) Old World monkeys ( <i>n</i> = 30)				
(Intercept)			(No Intercept)	
Body size	<b>0.891</b>	<b>&lt;0.001</b>	<b>0.667</b>	<b>&lt;0.001</b>
Group size	0.065	0.352	-0.132	0.108
Life span	0.056	0.426	0.062	0.290
Home range	0.087	0.208	<b>0.359</b>	<b>0.003</b>
Fruit + seed	<b>0.159</b>	<b>0.049</b>	0.002	0.948
3) All primates ( <i>n</i> = 67)				
(Intercept)			(No Intercept)	
Body size	<b>0.812</b>	<b>&lt;0.001</b>	<b>0.780</b>	<b>&lt;0.001</b>
Group size	<b>0.083</b>	<b>0.035</b>	0.015	0.822
Life span	<b>0.178</b>	<b>&lt;0.001</b>	0.084	0.168
Home range	0.002	0.969	<b>0.191</b>	<b>0.009</b>
Fruit + seed	0.043	0.102	-0.054	0.334

Notes: See Table 1.



found consistency between models using species as data points and models using independent contrasts. The two biggest exceptions are the brain-size models in Table 2 for Old World monkeys and all primates. Given the problem of a large number of closely related cercopithecines in Old World monkeys, which is ameliorated with phylogenetic analysis, we lean towards putting more confidence in the independent-contrast results (but see Martin et al., 2005). Thus, given these results, there is little evidence in support of the social-complexity model for the evolution of longer juvenile periods and larger relative brain sizes in primates or within monkey clades. Results better support an ecological component acting on larger brain size through larger home ranges (Fig. 1). However, this result is not found in the brain-ratio analyses, where group size is consistently the strongest predictor (see below).

We omitted age at first reproduction from the brain-size model and brain size from the age-at-first-reproduction model. Age at first reproduction does show some association with brain size when entered as another independent variable. However, we believe that the length of the juvenile period is best considered a choice (dependent) variable, as it is one of the most important life-history decisions an organism faces. The advantage of this method is that we can test for coevolution between brain size and juvenile periods. The correlation of the age-at-first-reproduction residuals from Table 1 with the brain residuals from Table 2 is positive ( $r = 0.376$ ,  $p = 0.002$ ,  $n = 67$ ) using species values as individual data points. However, within New World monkeys, there is no relationship between brain size and age-at-first-reproduction residuals, and with independent contrasts, the relationship becomes negative and nonsignificant ( $r = -0.206$ ,  $p = 0.107$ ,  $n = 66$ ). Therefore, primates fail the strong test for an association between brain size and age at first reproduction (cf.

Deaner et al., 2003). This result suggests that juvenile periods and brain size may not have been subjects of strong and direct coevolution (Leigh, 2004).

One problem with using relative brain size (residuals of log brain size by log body size) as a dependent variable is that these measures appear incongruent with field study results that show high levels of cognitive complexity in great apes (Russon and Begun, 2004; Ross, 2004). Out of a list of 100 primates, gorillas rank 86th, chimpanzees 57th, and orangutans 39th on the scale of highest-to-lowest relative brain size, whereas capuchin and squirrel monkeys take up the top ranks after humans. Therefore, alternative neural measures may better index higher cognitive abilities.

### Brain ratios

A series of regressions were performed with other relative brain measures that we call brain ratios. Five brain ratios were examined as functions of body size, group size, longevity, home range, and diet using species values as data points and independent contrasts (Tables 3–7). Age at first reproduction was omitted from most brain-ratio models due to near-zero partial correlations with all except for the two nonvisual neocortex ratios, in which the relationship is strong and positive (Joffe, 1997). We report the results of a total of ten regression procedures (five ratios each with species values and contrasts). Group-size and life-span effects are invariably positive. Importantly there is a rough convergence of the different models across all five ratios with species values as data points and independent contrasts.

Following the results of Deaner and colleagues (2000), most of the brain ratios used here show strong relationships with body size, rendering any bivariate analyses ignoring this important confounding variable suspect. Moreover, in each of the ten models, group size is one of the strongest predictors. This pattern is surprisingly robust given the mostly spurious correlations documented for group size and brain size in Table 2. Life span is an important predictor of executive-to-brainstem ratio and is positive in the other regressions, though it tends to be weaker than group size. Home range shows a modest correlation with neocortex ratio, but like percent fruit and seeds in the diet, it is never significantly different from zero in any of the ten brain-ratio models. Therefore,

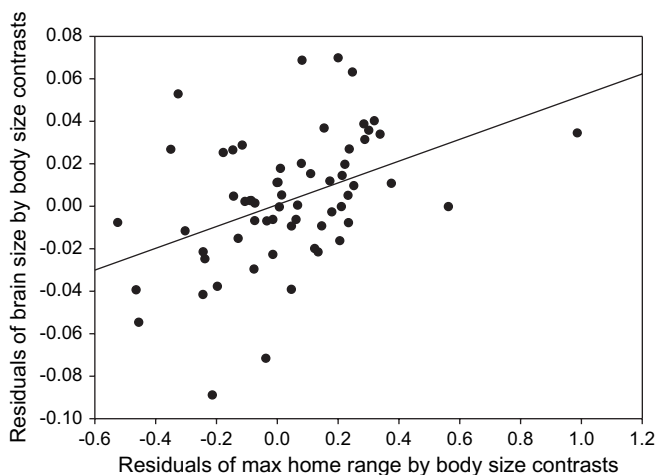


Fig. 1. Relationship between the independent contrasts of brain size and maximum home range after removing the statistical effect of body size on each ( $n = 66$  nodes for primates of all grades;  $r^2 = 0.1863$ ). A stronger effect is visible within Old World monkeys (Table 2). Using an alternative body-size data base (Kappeler and Pereira, 2003) to calculate home-range residuals gives essentially identical results, indicating that the relationship is not spuriously driven by errors in body sizes that affect both variables.

Table 3

Multiple-regression model of neocortex ratio (dependent variable) for primates of all grades

Model	Species as data points		Independent contrasts	
	$\beta$	$p$	$\beta$	$p$
All primates ( $n = 32$ )				
(Intercept)			(No Intercept)	
Body size	<b>0.267</b>	<b>0.013</b>	0.313	0.131
Group size	<b>0.405</b>	<b>0.001</b>	<b>0.320</b>	<b>0.039</b>
Life span	<b>0.285</b>	<b>0.007</b>	0.115	0.612
Home range	0.086	0.412	0.293	0.095
Fruit + seed	0.067	0.547	0.016	0.907

Notes: See Table 1.

Table 4  
Multiple-regression models of neocortex ratio without cerebellum (dependent variable) for primates of all grades

Model	Species as data points		Independent contrasts	
	$\beta$	$p$	$\beta$	$p$
All primates ( $n = 33$ )				
(Intercept)			(No Intercept)	
Body size	<b>0.402</b>	<b>&lt; 0.001</b>	<b>0.504</b>	<b>0.009</b>
Group size	<b>0.311</b>	<b>0.002</b>	0.263	0.074
Life span	<b>0.318</b>	<b>0.001</b>	0.149	0.405
Home range	0.051	0.586	0.181	0.269
Fruit + seed	0.032	0.743	-0.054	0.714

Notes: See Table 1.

we conclude that brain ratios are much more strongly related to social complexity, as opposed to foraging or ecological complexity.

The final step in the analysis compared observed human ratios to those expected for a primate of our size and adjusting for a long human life span and a typical human group size. Using the regressions in Tables 3–7, we calculated expected human values with liberal estimates of body size (65 kg), life span (120 yr), and group size ( $n = 150$ ). Observed human values are considerably higher than those expected from the nonhuman primate regressions (Table 8). For example, the human nonvisual neocortex ratios and the executive-to-brainstem ratio are three to four times larger than expected. Observed chimpanzee values are also high, as are those for other apes.

### Discussion

After addressing problems with collinearity associated with group size and home range, we conclude that diet and life span are the best predictors of longer juvenile periods, tentatively supporting a foraging-complexity model. However, neither group size nor percent fruit and seeds in the diet have significant effects on relative brain size. This result contrasts with previous work supporting a correlation between brain size and diet across primates (Clutton-Brock and Harvey, 1980; Foley and Lee, 1992), including studies in which multiple regression was used to demonstrate that diet and group size

Table 5  
Multiple-regression model of nonvisual neocortex ratio (dependent variable) for primates of all grades

Model	Species as data points		Independent contrasts			
	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$
All primates ( $n = 23$ )						
(Intercept)			(No Intercept)			
Body size	0.142	0.211	0.420	0.060	0.077	0.587
Group size	<b>0.389</b>	<b>0.003</b>	<b>0.453</b>	<b>0.009</b>	<b>0.474</b>	<b>0.003</b>
Life span	<b>0.359</b>	<b>0.004</b>	0.376	0.174	0.115	0.542
Home range	0.136	0.225	0.012	0.999	-0.027	0.810
Fruit + seed	0.086	0.495	0.083	0.474	-0.060	0.660
Age at first reproduction					<b>0.656</b>	<b>0.001</b>

Notes: See Table 1.

Table 6  
Multiple-regression model of nonvisual neocortex ratio without the cerebellum (dependent variable) for primates of all grades

Model	Species as data points		Independent contrasts			
	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$
All primates ( $n = 23$ )						
(Intercept)			(No Intercept)			
Body size	<b>0.266</b>	<b>0.011</b>	<b>0.561</b>	<b>0.010</b>	<b>0.311</b>	<b>0.042</b>
Group size	<b>0.332</b>	<b>0.003</b>	<b>0.362</b>	<b>0.013</b>	<b>0.378</b>	<b>0.008</b>
Life span	<b>0.373</b>	<b>0.001</b>	0.382	0.098	0.192	0.251
Home range	0.101	0.296	-0.022	0.824	-0.051	0.667
Fruit + seed	0.053	0.605	0.045	0.637	-0.059	0.626
Age at first reproduction					<b>0.478</b>	<b>0.004</b>

Notes: See Table 1.

independently explain variation in brain size (Barton, 1999) and neocortex ratio (Dunbar, 1996). On the other hand, our results are consistent with those of Kaplan and colleagues (2003). Here, group size affects brain size indirectly through its positive associations with longevity and home range, often omitted in studies that detect correlations between brain size, diet, and group size. In our analyses, there is a strong relationship between relative brain size and home range (Fig. 1). The default expectation of a relationship between group size and brain size was not supported, potentially because relative brain size is not a good measure of intelligence given that selection acts on body size independently of brain size (case in point, gorilla). Importantly, group size is most strongly and consistently related to all of the various brain ratios.

Most of the results presented here are concordant with previous comparative analyses. For example, Dunbar (1993, 1998, 2003) found a significant correlation between neocortex ratio and group size within and across primate grades (see also Deaner et al., 2000). Kaplan and colleagues (2003) also demonstrated that, across primates, the neocortex (with the rest of brain weight entered as an instrument) correlates most strongly with group size. We find that the executive-to-brainstem and other neocortex ratios also tend to correlate more strongly with group size than with any ecological variable.

Our three main variables of interest—length of the juvenile period, brain size, and brain ratios—appear to be driven by different socioenvironmental factors, namely diet/life span

Table 7  
Multiple-regression model of executive-to-brainstem ratio (dependent variable) for primates of all grades

Model	Species as data points		Independent contrasts	
	$\beta$	$p$	$\beta$	$p$
All primates ( $n = 30$ )				
(Intercept)			(No Intercept)	
Body size	<b>0.403</b>	<b>&lt; 0.001</b>	<b>0.586</b>	<b>&lt; 0.001</b>
Group size	<b>0.231</b>	<b>0.007</b>	<b>0.328</b>	<b>0.008</b>
Life span	<b>0.400</b>	<b>&lt; 0.001</b>	<b>0.340</b>	<b>0.017</b>
Home range	0.094	0.226	0.045	0.733
Fruit + seed	0.007	0.930	0.035	0.776

Notes: See Table 1.

Table 8  
Comparison between observed brain ratios in humans and those expected from primate regressions (chimpanzee brain ratios are included for comparison)

Brain ratio	<i>Pan troglodytes</i>	<i>Homo sapiens</i>	
		Predicted	Observed
Neocortex ratio	2.4–3.2	2.2	3.1–4.1
Neocortex ratio without cerebellum	4.5–6.2	3.5	5.3–9.3
Nonvisual neocortex ratio	3.1	1.4	4.0
Nonvisual neocortex ratio without cerebellum	5.9	2.3	9.1
Executive-to-brainstem ratio	31.8	13.7	58.5

(Table 1), home range (Fig. 1), and group size (Tables 3–7), respectively. We could not find a convincing link between the residuals of age at first reproduction and those of brain size. Moreover, most of the brain ratios did not exhibit an association with age at first reproduction, with the exception of the nonvisual neocortex ratio with and without the cerebellum, where the correlations with longer juvenile periods are quite strong. This finding is consistent with the results of Joffe's (1997) study, who found strong relationships between various measures of the length of the juvenile period and the nonvisual neocortex ratio. In sum, there may be a suite of semi-independent effects of socioenvironmental parameters on different aspects of primate life histories, namely diet/life span → juvenile period, home range → brain size, and group size → brain ratios. The links among these different effects are surprisingly weak, which cautions against any all-encompassing coevolutionary argument for slower primate life histories. The few examples of links across these different relationships are age at first reproduction → nonvisual neocortex ratio and life span → executive-to-brainstem ratio.

#### *Social, ecological, or socioecological?*

The strong positive effect of home range on brain size may support an ecological foundation underlying larger brain size. However, larger home ranges may also introduce increased social complexity at the intergroup level through more contact with other groups of conspecifics. Regardless, home range does covary strongly with both longevity and group size and should be included as a potential confounding variable in any regression. Otherwise, one runs the risk that the omission of home range confounds the true relationship between group size and brain size or some brain ratio. The positive association between group size and longevity creates a similar effect whereby omission of longevity increases the correlation between group size and brain size. Because of strong covariance among the variables of interest and consequent risk of obtaining spurious results, multiple regression methods are often preferable to bivariate correlations that only control for body size. This admonition is a most important consideration when overall brain size is the dependent variable.

We suggest that associations between group size and relative brain size are spurious. It is probable that there exists more than one causal pathway to larger brain size and later

ages at first reproduction in particular primate taxa. Ecological and social hypotheses can be difficult to separate because development of higher cortical function for one purpose can be applied in other domains. For example, long juvenile learning periods can serve the dual purpose of mastering skills needed to compete in adult social arenas (e.g., mating and social-manuevering) and also to master complicated foraging tasks (e.g., frugivory and carnivory).

An interesting test case is the sympatric fruit-eating spider monkey and the more folivorous howler monkey. It has been suggested that the spatiotemporal demands for locating ripening fruit relative to a ubiquitous supply of leaves has led to the evolution of a spider-monkey brain about twice the size of that of a howler monkey (Milton, 1981). Spider monkeys exhibit a complex fission-fusion social system (Symington, 1990), also seen in chimpanzees, which perhaps has selected for increased cognitive capacity in contrast to howler monkeys. Dunbar (2003) suggests that complex fission-fusion social relationships, created by a combination of ripe-fruit foraging and large community sizes, have driven intelligence (and nonvisual neocortical expansion) in hominoids.

It is possible that certain primate socioecologies select for increases in brain size based more on social demands, whereas others tend to promote larger brains because of foraging complexities (including tool use), leading to the weak correlations among diet, group size, and brain size demonstrated in this study. Across the primate order, there is mixed evidence for the coevolution of larger brains, longer juvenile periods, and longer life spans (Charnov and Berrigan, 1993; Kaplan and Robson, 2002; Kaplan et al., 2003). The specifics of social and/or ecological pressures are likely to vary across the primate order, especially when comparing phylogenetic grades (Sawaguchi, 1992). Indeed, we found that life span appears to be a more important determinant of brain size in New World monkeys, whereas home range is more important in Old World monkeys. This difference potentially relates to complete arboreality in the New World monkeys and the larger body size and terrestrial strategies among Old World species.

Following the patterns documented here, human life-history characteristics appear qualitatively similar, yet the specifics of selection pressures involved since the human-chimpanzee split remain unresolved. Evaluating the marginal benefits of social versus foraging returns to investment in brain size (Dunbar, 2003) between closely related taxa appears to be an especially informative avenue for future investigations. Analyzing what humans and other primates are doing during the long juvenile period and how this translates into adult behavior and fitness benefits should also prove valuable (Altmann, 1998; Walker et al., 2002; Maestripiere and Ross, 2004). Many cognitive and motor skills are gained quickly during childhood, but not mastered as easily if the learning process begins later (e.g., language; Kim et al., 1997). Documenting sensitive periods of time when the brain is primed for the learning of important life skills (e.g., foraging and social tasks; Bock, 1995, 2002) can elucidate how selective pressures have shaped cognitive architecture. Substantial neurophysiological changes that occur into young adulthood (e.g., Cabana et al.,

1993; Pujol et al., 1993; Benes et al., 1994; Pfefferbaum et al., 1994; Durston et al., 2001) may also offer clues to the importance of long human learning periods.

## Conclusions

Our regression models suggest that group size is strongly associated with indices of neocortical expansion and higher executive-to-brainstem ratios across primates while controlling for a number of potentially important ecological confounds. This result is strong support for social complexity as the main driving factor behind primate intelligence. On the other hand, several results point to strong ecological components acting on primate life histories. For example, life span tends to be a significant correlate of the executive-to-brainstem ratio. The two most notable ecological effects are home range on larger brain sizes and diet/life span on longer juvenile periods. In conclusion, differential life-history strategies probably result from a mix of social and ecological selective pressures acting at different intensities in particular primate clades. There is no evidence for a single prime-mover of slow life-history strategies in primates. We suspect that life-history variation will be best explained by detailed socioecological information within and across closely related primate species.

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