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Sociality, ecology, and relative brain size in lemurs

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ABSTRACT

The social brain hypothesis proposes that haplorhine primates have evolved relatively large brains for their body size primarily as an adaptation for living in complex social groups. Studies that support this hypothesis have shown a strong relationship between relative brain size and group size in these taxa. Recent reports suggest that this pattern is unique to haplorhine primates; many nonprimate taxa do not show a relationship between group size and relative brain size. Rather, pairbonded social monogamy appears to be a better predictor of a large relative brain size in many nonprimate taxa. It has been suggested that haplorhine primates may have expanded the pairbonded relationship beyond simple dyads towards the evolution of complex social groups. We examined the relationship between group size, pairbonding, and relative brain size in a sample of 19 lemurs; strepsirrhine primates that last share a common ancestor with monkeys and apes approximately 75 Ma. First, we evaluated the social brain hypothesis, which predicts that species with larger social groups will have relatively larger brains. Secondly, we tested the pairbonded hypothesis, which predicts that species with a pairbonded social organization will have relatively larger brains than non-pairbonded species. We found no relationship between group size or pairbonding and relative brain size in lemurs. We conducted two further analyses to test for possible relationships between two nonsocial variables, activity pattern and diet, and relative brain size. Both diet and activity pattern are significantly associated with relative brain size in our sample. Specifically, frugivorous species have relatively larger brains than folivorous species, and cathemeral species have relatively larger brains than diurnal, but not nocturnal species. These findings highlight meaningful differences between Malagasy strepsirrhines and haplorhines, and between Malagasy strepsirrhines and nonprimate taxa, regarding the social and ecological factors associated with increases in relative brain size. The results suggest that factors such as foraging complexity and flexibility of activity patterns may have driven selection for increases in brain size in lemurs.

Introduction

Understanding the selective pressures that have influenced primate brain evolution is among the greatest challenges in biological anthropology. In recent years, there has been increasing consensus that haplorhine primates evolved larger degrees of encephalization primarily in response to the demands of living in complex social groups (Dunbar, 1998). This explanation has been coined the "social brain hypothesis." It asserts that species living in social groups must manage a wide variety of dynamic information relevant to social living, that these processes are cognitively demanding, and that an increase in sociality was an important causal factor in the evolution of large brains relative to body size (Kummer et al., 1997; Whiten, 2003; Dunbar and Shultz, 2007a).

Evidence for the social brain hypothesis has emerged in two complementary domains. First, a wealth of observational and experimental studies have documented the exceptional abilities of primates to solve social problems (for reviews, see Byrne and Whiten, 1988; Tomasello and Call, 1997). Primates, especially apes, excel in solving problems that require complex forms of social cognition, such as imitation (Horner and Whiten, 2005), theory of mind (Hare et al., 2000, 2001), social learning (Bonnie et al., 2007), and cooperation (Melis et al., 2006). A second class of studies has examined the relationship between various neuroanatomical traits and indices of sociality among primates. Most notably, Dunbar (1992) has shown that relative neocortex volume is strongly predicted by group size among haplorhine primates. This result was interpreted as reflecting an increase in cognitive demands as group size increases. Importantly, group size was implicated only as a proxy for social complexity in primates and not as the driving factor for brain evolution (Dunbar and Shultz, 2007a). Although other indices of sociality have also been shown to correlate with

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relative brain size in primates (Kudo and Dunbar, 2001; Byrne and Corp, 2004), group size remains the most robust predictor between social organization and relative brain size. Further, Pérez-Barbería et al. (2007) showed that changes in relative brain size and sociality are tightly coupled within primates, suggesting a coevolutionary relationship in which changes in one of these variables seldom occurs without corresponding changes in the other.

Has social complexity driven brain evolution in non-primate taxa? If group living is inherently complex, one should expect to see strong relationships between group size and relative brain size in a diverse range of taxa. Interestingly, recent analyses suggest that the relationship between group size and brain size may indeed be unique to haplorhine primates (Dunbar and Shultz, 2007b; Shultz and Dunbar, 2007). In a comparison of relative brain sizes across bird species and in four mammalian orders, Shultz and Dunbar (2007) showed that pairbonded social monogamy, not group size, is most closely linked to relatively large brain size in all taxa except haplorhine primates. The authors proposed that pairbonds reflect a shift away from loose social aggregations and represent the basic unit for complex negotiated social relationships. Furthermore, they proposed that early in primate evolution, haplorhine primates expanded the pairbonded relationship beyond simple social monogamy. Haplorhine primates were thus able to maintain multiple complex social relationships within the group by exploiting the basic cognitive machinery utilized in pairbonding (Dunbar and Shultz, 2007b).

This assertion raises critical questions about the relationship between social organization and relative brain size in ancestral primates. Although it is debated whether or not the ancestral primate social organization was a dispersed multi-male system (Müller and Thalmann, 2000) or a dispersed pairbonded system (Fietz, 1999; Mutschler et al., 2000), several strepsirrhine species have social organizations that may closely resemble the ancestral social system (Fietz, 1999; Fietz et al., 2000). In light of the fact that the last common ancestor between strepsirrhines and haplorhines lived approximately 75 Ma (Yoder et al., 1996; Horvath et al., 2008), comparative studies between these groups are useful in inferring the antiquity of major trends found in either lineage. Do strepsirrhines show the same relationships between relative brain size and sociality as haplorhines, or are haplorhines relatively derived in this regard?

The well-documented relationship between group size and relative brain size in haplorhine primates has thus far not been detected in strepsirrhines (Barton, 1996). Strepsirrhines living in large social groups do not appear to have relatively larger brains than strepsirrhines living in small social groups. However, previous studies examining this relationship have included relatively few species, making this result difficult to interpret. It is possible that a larger sample will reveal that strepsirrhine group sizes predict relative brain sizes in a similar fashion to haplorhine primates. This result would suggest that sociality was a critical selective pressure in primate brain evolution as early as 75 Ma. Recent studies indicate that there may be more cognitive overlap between haplorhines and strepsirrhines than was previously thought (Merritt et al., 2007). Furthermore, comparative analyses of cognition within strepsirrhines indicate that sociality (specifically group size) does predict cognitive ability within some domains such as transitive reasoning (MacLean et al., 2008).

Nonetheless, there are reasons to believe that sociality has imposed differing cognitive demands on strepsirrhines and haplorhines. For example, in her initial formulation of the social intelligence hypothesis, Jolly (1966) noted that relatively few lemur species reveal the social complexity found in haplorhines. Furthermore, strepsirrhines seem to lack the majority of complex sociocognitive abilities recorded for haplorhines in laboratory tasks (Genty and Roeder, 2006). It is therefore possible that strepsirrhines have not undergone selection for many of the complex sociocognitive abilities found in haplorhines, implying that strepsirrhines closely resemble ancestral primates in terms of cognition and brain organization. This argument is strengthened if strepsirrhines do not show the robust association between group size and brain size found in haplorhine primates.

Strepsirrhine social groups also differ from those of haplorhines with smaller social groups and high incidences of pairbonding (Jolly, 1998). Do pairbonded strepsirrhines have large brains relative to non-pairbonded species, as is the case in many nonprimate taxa? If strepsirrhine sociality parallels that of the ancestral primate social organization, then tests of the relationships between brain size and social organization in strepsirrhines could provide important data regarding the social selective pressures that were active early in primate brain evolution.

An alternative set of possibilities stipulates that strepsirrhine brain evolution has been predominantly influenced by nonsocial ecological pressures. Indeed, both diet and activity pattern have been shown to have robust relationships with relative brain size in primates even when parceling out the influence of sociality (Barton, 1996; Fish and Lockwood, 2003). Therefore, these factors require analysis as potential alternative predictors of relative brain size in our sample.

We examined the relationships between group size, pairbonding, diet, activity pattern, and relative brain size in a sample of 19 lemur species. Lemurs are a radiation of strepsirrhine primates found exclusively on Madagascar and its surrounding islands. We tested two hypotheses regarding the relationship between encephalization and sociality. First, we considered the social brain hypothesis. This hypothesis holds that group living has been a driving factor in brain evolution and predicts that species that live in large social groups have relatively large brain sizes compared to species that live in smaller social groups. We also tested the pairbonding hypothesis (Dunbar and Shultz, 2007b), which has been developed to explain the patterns of encephalization found in a diverse range of nonprimate taxa. The pairbonding hypothesis holds that socially monogamous pairbonds represent a relatively complex and calculated social organization, and predicts that species exhibiting a pairbonded social organization will have relatively larger brains than non-pairbonded species.

We also explored the relationship between ecology and relative brain size by including both diet and activity pattern as predictors of relative brain size in our analysis. Following the logic of Aiello and Wheeler (1995) and the results of Harvey et al. (1980), Barton (1996), and Fish and Lockwood (2003), we predicted that predominantly frugivorous species would have relatively larger brains than folivorous species. Although previous analyses of activity pattern and brain size have shown that diurnal primates have relatively larger neocortices than nocturnal primates (Barton, 1996), this result included data from both strepsirrhines and haplorhines; thus, it is unclear whether or not this trend is robust within strepsirrhines. Further, Barton (1996) included only diurnal and nocturnal species and did not consider cathemeral species. Therefore, we investigated diurnality, nocturnality, and cathemerality as potential predictors of relative brain size in this analysis.

Methods

We compiled extensive, high quality data from numerous sources covering a number of potentially important social and ecological parameters. More specifically, we obtained data on group size from several sources, including Kappeler and Heymann (1996), Kappeler (1997), Atsalis (2000), Fietz et al. (2000), Sterling and McCreless (2006), Eberle and Kappeler (2006), Lahann (2007a), and Rasoloharijaona et al. (2008). We also extracted social organization data from Jolly (1998), Overdorff (1998), Fietz (1999), Fuentes (2002), Bayart and Simmen (2005), Lewis and Kappeler (2005), Grassi (2006), Erhart and Overdorff (2008), and Rasoloharijaona et al. (2008). Data on activity patterns were compiled from Kappeler and Heymann (1996), and diet data were extracted from numerous references, including Richard (1977), Ganzhorn (1988), Harcourt and Thornback (1990), Sterling (1994), Kappeler and Heymann (1996), Sauther et al. (1999), Tan (1999), Britt (2000), Lehman and Mayor (2004), Gould and Sauther (2006), and Lahann (2007b). For the purpose of analysis, species were classified as either primarily folivorous or primarily frugivorous.

Measurements of endocranial volume (ECV) and body weight were taken from the data compiled by Kirk (2006) and Isler et al. (2008). Isler et al. (2008) found an isometric relationship between brain mass and endocranial volume, indicating the maintenance of proportion between cranial capacity and brain mass. The intercept of their regression equation was 0.036, which accords well with studies that found that the specific gravity of brain tissue is 1.036 (Stephan et al., 1981). Therefore, we calculated brain mass by adjusting endocranial volumes by a factor of 1.036 g per cubic centimeter.

It is well documented that brain size scales with significant negative allometry relative to body size in primates (Jerison, 1973; Stephan et al., 1981; Barton, 2006). To evaluate the scaling pattern in this sample, we calculated the slope of a reduced-major-axis (RMA) regression of log brain mass (g) against log body mass (g). To quantify shape relationships between brain mass and body mass in this sample, we created dimensionless brain shape ratios for each species (Darroch and Mosimann, 1985; Jungers et al., 1995). The brain shape ratio is brain mass/body mass. In all, we analyzed data for brain mass, body mass, shape ratio, group size, pairbonding, activity pattern, and diet for each species (Table 1). We used the y-axis residuals from the RMA regression of brain mass on body mass as our measure of relative brain size to examine the relationship between relative brain size and the social and ecological variables. As such, we explicitly treat the component of brain size that is correlated with body mass as a confounding effect (Smith, 2005).

Because closely related species may share traits through phylogenetic inertia rather than independent evolution, it is inappropriate to treat species as individual data points in broad comparative analyses (Felsenstein, 1985). This confound can be controlled through techniques such as independent contrasts, which account for similarity as a result of common descent by incorporating phylogenetic information into the analysis. However, the use of independent contrasts has also been criticized on the grounds that this technique may yield misleading results under several scenarios. Notably, the use of contrasts may fail to recognize functional grade shifts in the relationships between two variables and can be problematic if phylogenetic inertia has differentially affected the variables in an analysis (Martin et al., 2005). Further, the phylogenetic inertia for which independent contrasts are designed to control may already be largely accounted for in analyses that incorporate multiple regression or residual values, as in the current study. Therefore, we conducted statistical comparisons using both independent contrasts and raw data wherever possible.

We used Horvath et al.'s (2008) lemur phylogeny and set branch lengths to be equal because divergence dates were not available for all nodes included in the analysis. The Mesquite computer program (Maddison and Maddison, 2007) with the PDAP package (Midford et al., 2003) was used to compute standardized contrasts, which were then used to test for associations between group size and relative brain size using an RMA regression forced through the origin. The BRUNCH algorithm of the C.A.I.C. computer package was used to calculate standardized contrasts and test for an association between the continuous variable of relative brain size and the discrete variables of pairbonding and diet (Purvis and Rambaut, 1995). All analyses on raw data were performed in JMP® 7.0.1.

Results

Brain scaling

The RMA regression of log brain mass on log body mass revealed significant negative allometry of brain size relative to body size in this sample, with a slope of 0.73 (95% C.I. = 0.64–0.83) (Fig. 1). Note that much of the variation in ECV is explained by variation in body size ($R^2 = 0.94$). The brain shape ratios (Table 1) also demonstrate that overall, small-bodied lemurs have larger brains relative to their body size than do large-bodied lemurs. Species with high brain shape ratios also tend to have positive residuals (*Microcebus rufus*, *Eulemur coronatus*, *E. mongoz*, *Hapalemur griseus*, and *Daubentonia*

Table 1
Raw Data for Species Evaluated.

Species	Brain Mass (g)	Body Mass (g)	Shape Ratio	Pairbonded	Group Size	Diet	Activity Pattern
Avahi laniger	10.22	1207	0.008	yes	2.5	FO	N
Cheirogaleus major	6.02	400	0.015	no	5.5	FR	N
Cheirogaleus medius	2.69	140	0.019	yes	3	FR	N
Daubentonia madagascariensis	46.46	2555	0.018	no	2	FR	N
Eulemur coronatus	21.39	1180	0.018	no	8.4	FR	C
Eulemur fulvus	26.70	2292	0.012	no	9.2	FR	C
Eulemur macaco	25.40	2390	0.011	no	8.4	FR	C
Eulemur mongoz	20.90	1212	0.017	yes	3.5	FR	C
Eulemur rubriventer	27.18	2388	0.011	yes	3.2	FR	C
Hapalemur griseus	14.60	709	0.021	no	2.6	FO	C
Indri indri	36.06	6335	0.006	yes	3.1	FO	D
Lemur catta	23.73	2210	0.011	no	15.3	FR	D
Lepilemur mustelinus	9.90	777	0.013	no	2	FO	N
Microcebus murinus	1.69	65	0.026	no	7.2	FR	N
Microcebus rufus	1.78	45	0.040	no	2	FR	N
Mirza coquereli	6.00	312	0.019	no	2	FR	N
Propithecus diadema	41.23	6130	0.007	no	5.1	FO	D
Propithecus verreauxi	27.15	2955	0.009	no	6	FO	D
Varecia variegata	33.28	3599	0.009	yes	5.3	FR	D

FO = Folivore, FR = Frugivore, N = Nocturnal, C = Cathemeral, D = Diurnal.

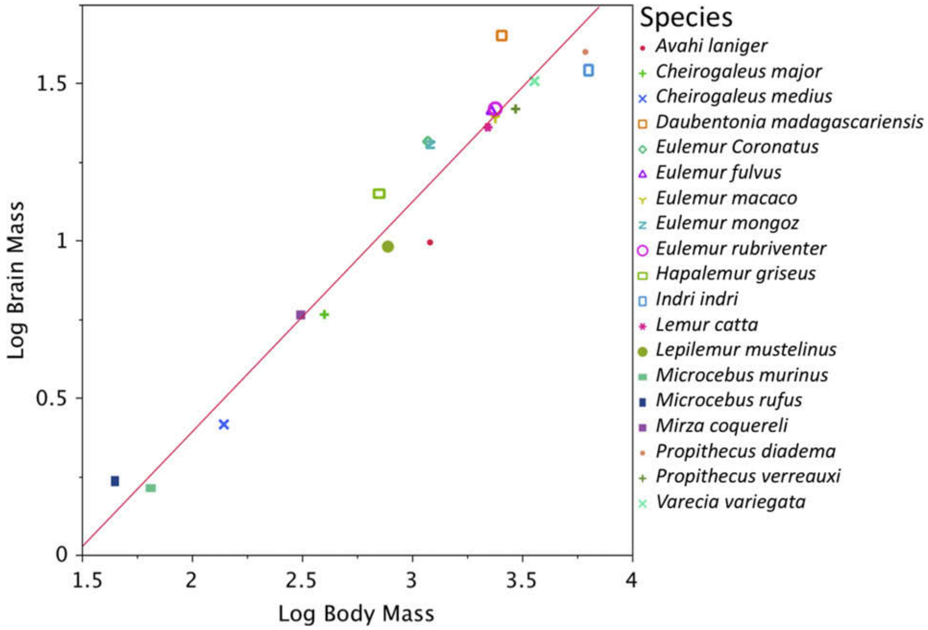

Figure 1. Reduced major axis regression of brain size against body size, $R^2 = 0.94$, $y = -1.06 + 0.73x$, $p < 0.05$. Slope 95% confidence interval: 0.64–0.83.

madagascariensis). *D. madagascariensis* is notable for having a high brain shape ratio and the largest positive residual value for ECV at a fairly large body size. *Indri indri* is notable for having the lowest brain shape ratio and a large negative residual value for ECV.

Group size and pairbonding

The RMA regression (forced through the origin) of the contrasts of relative brain size against the contrasts of group size was not significant, though the trend is in the opposite direction from that predicted by the social brain hypothesis because lemur species with large social groups tend to have relatively small brains (Fig. 2; $R^2 = 0.17$, $p > 0.05$). The RMA regression on the raw data (not controlled for phylogeny) for these variables yielded a similar result ($R^2 = 0.009$, $p > 0.05$).

Figure 3 shows the distribution of values for relative brain size in pairbonded and non-pairbonded species. In the case of two-state categorical variables, C.A.I.C. generates contrasts for the predictor variable at each node being analyzed. If the dependent variable is related to the categorical predictor, the mean of these contrasts differs from 0, either positively or negatively depending on the direction of the relationship. Contrasts with a mean value of 0 indicate that the dependent variable shows no relationship with the categorical predictor. A t-test comparing the mean of the contrasts for pairbonding and relative brain size indicated that these variables are not related ($t_6 = -1.13$, $p > 0.05$). Similarly, a Wilcoxon signed-rank test comparing raw residuals (not controlled for phylogeny) between pairbonded and non-pairbonded species revealed no difference between these groups ($\chi^2{}_1 = 1.73$, $p > 0.05$).

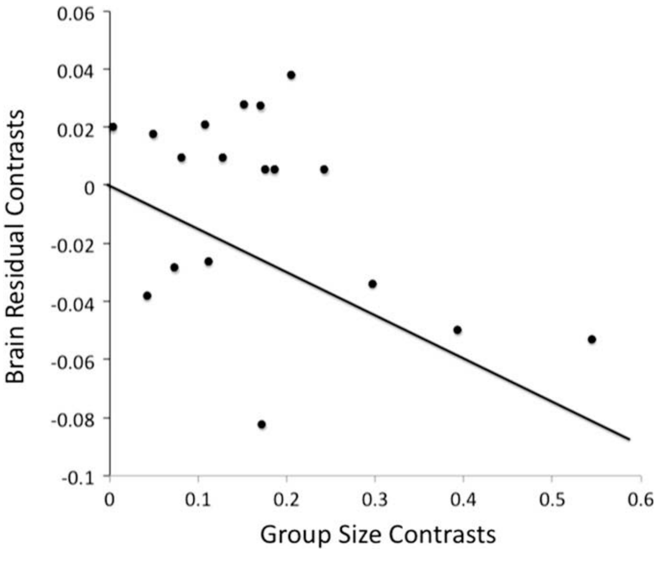

Figure 2. Reduced major axis regression of phylogenetic independent contrasts for relative brain size against contrasts for group size, $R^2 = 0.17$, $y = -0.16x$, $p = 0.09$. Line is forced through the origin. These variables are unrelated in lemurs.

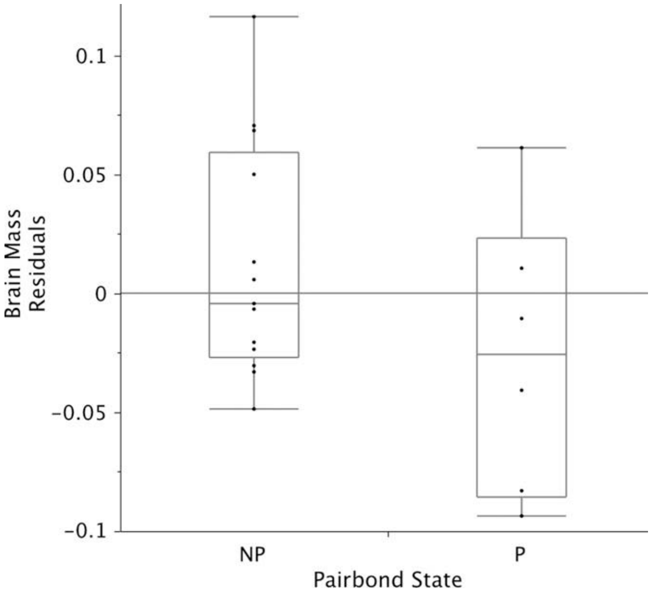

Figure 3. Brain mass residuals for pairbonded (P) and non-pairbonded (NP) species. Relative brain size does not differ significantly between these groups.

Diet and activity pattern

Frugivorous species tend to have a larger relative brain size than folivorous species (Fig. 4). A Wilcoxon signed-rank test comparing the species values across these two categories revealed significant differences ($\chi^2_1 = 4.43$, $p < 0.05$). However, this result is closely tied to phylogeny. Therefore, it was only possible to generate 3 independent contrasts for dietary category and a t-test comparing the mean of the contrasts was not significant ($t_2 = 0.11$, $p > 0.05$).

Figure 5 shows relative brain size as a function of activity pattern. A Kruskal-Wallis test confirms that relative brain size differs significantly across activity pattern categories ($\chi^2_2 = 7.10$, $p < 0.05$). In addition, Bonferroni corrected post-hoc tests indicated that cathemeral species have relatively larger brains than diurnal species ($\chi^2_1 = 7.50$, $p < 0.0167$), and that no other groups differ significantly.

Discussion

These analyses find no evidence of a relationship between our measures of social complexity (group size and pairbonding) and relative brain size in a sample of 19 lemur species. Moreover, these results hold regardless of whether or not the analyses are performed on raw data or independent contrasts. The weak trend apparent in the regression of relative brain size contrasts and group size means that low statistical power is clearly one potential explanation for the non-significant regression. The problem of low power affects any study aiming at identifying subtle or weak trends in restricted taxonomic groups, such as the Malagasy strepsirrhines. We estimate that sample size would need to increase to greater than 50 species in order to increase statistical power to 0.95. However, it is also important that the trend in these data is in the opposite direction of that predicted by the social brain hypothesis: the tendency is for relative brain size to *decrease* as group size increases. This finding suggests that increasing the number of strepsirrhine taxa sampled by including galagids and lorisids would not change the direction of the trend toward decreasing relative brain size with increasing group size.

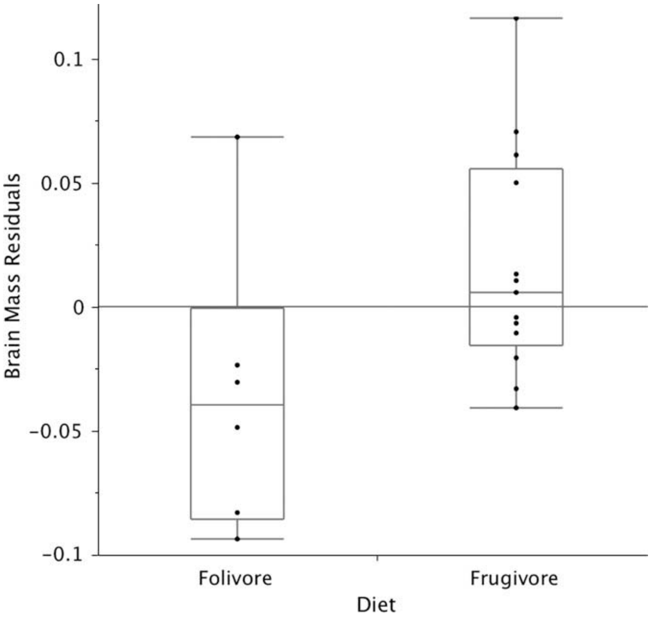

Figure 4. Brain mass residuals for folivorous and frugivorous species. Frugivorous species have significantly larger relative brain sizes than folivorous species.

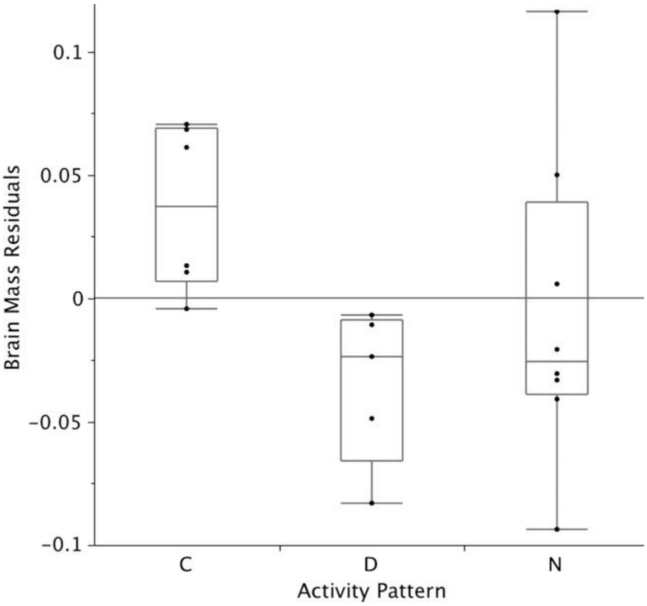

Figure 5. Brain mass residuals for cathemeral (C), diurnal (D), and nocturnal (N) species. Cathemeral species have relatively larger brains than diurnal species but no other groups differ significantly.

We did, however, find significant relationships between activity pattern and relative brain size, as well as diet and relative brain size, in the raw data statistical comparisons. In these cases, neither result was verifiable by independent contrasts. Specifically, frugivorous lemurs have relatively larger brains than folivorous lemurs and cathemeral species have relatively larger brains than diurnal (but not nocturnal) species. It is noteworthy that there is likely some overlap in these effects as all but one cathemeral species is frugivorous. However, the diet comparison considers all 19 species and thus consists of data primarily from noncathemeral species, which as a group make up less than 1/3 of species evaluated.

The lack of a relationship between group size and relative brain size is consistent with Barton's (1996) analysis of a different, smaller sample of strepsirrhines. He found that relative neocortex size was unrelated to group size in strepsirrhines. Independence between group size and relative brain size in this sample is also evident upon visual inspection of data plots (Fig. 1). The three species with the largest group size in our sample fall directly on the regression line of brain size against body size (*Eulemur fulvus, Eulemur macaco, Lemur catta*).

These results indicate meaningful differences in the factors associated with relative brain size between Malagasy strepsirrhines and haplorhine primates, as well as between Malagasy strepsirrhines and other nonprimate taxa. Haplorhine primates show a strong positive relationship between group size and relative brain size, and this relationship is thought to reflect the increased cognitive demands of living in large complex social groups (Shultz and Dunbar, 2007). It is presumed that the number of inter-individual relationships increases as the number of individuals in a group increases. Under this scenario, managing information about these relationships is critical to any group member's success and leads to increased relative brain size (Dunbar and Shultz, 2007a). The need to manage a large number of relationships arises when the relationships among group members are relatively stable and individualized in nature as they are among haplorhine primates. However, many nonprimate species (e.g., bison) form large aggregations that do not impose such cognitive demands, apparently because complex, meaningful social relationships between all members of the group are lacking. The absence of a relationship between group size and relative brain size in Malagasy strepsirrhines raises the possibility that strepsirrhine groups, and their inter-individual relationships, are fundamentally less complex and cognitively demanding than haplorhine groups. This notion is supported by the fact that strepsirrhine social interactions tend to be dyadic, without the complex alliances that are common to haplorhine species (Nakamichi and Koyama, 1997). As noted, few of the sociocognitive abilities exhibited by haplorhine primates in laboratory tests of social cognition have been detected in strepsirrhines (Genty and Roeder, 2006). Together, these data suggest that lemurs may more closely resemble insectivores who show very weak social brain relationships (Dunbar and Bever, 1998), than haplorhines in terms of the relationships between socioecology and encephalization.

In addition to their differences from haplorhines, Malagasy strepsirrhines do not show the robust relationship between pairbonding and relative brain size that is common to birds, bats, ungulates, and carnivores. Among these nonprimate taxa, relatively large brains are associated with pairbonded social monogamy. This relationship is thought to reflect evolutionary movement away from loose social aggregations toward more complex individualized relationships that require complex cognition. Although many strepsirrhine species have a pairbonded social organization, it does not appear to require a substantial increase in relative brain size.

The fact that strepsirrhines differ from both haplorhines and other nonprimate taxa is consistent with their unique phylogenetic position. While strepsirrhines exhibit all of the fundamental traits that differentiate primates from other orders, they also contrast strongly with monkeys and apes in many aspects of social behavior and cognition. The results presented here provide further evidence that the major changes in primate brain evolution linked to sociality took place after the divergence of strepsirrhines and haplorhines approximately 75 Ma. These results also bear interestingly on the hypothesis that haplorhine primate societies evolved by expanding on more primitive pairbonded social structures. While it is true that many strepsirrhine species have a pairbonded social organization, the data presented here suggest that these pairbonds do not warrant an increase in relative brain size. Thus, even though haplorhine societies may have evolved from pairbonded societies, the strepsirrhine data do not support the hypothesis that pairbonding provided an evolutionary head start for the increases in relative brain size associated with group living within the primate order.

The results of our analysis suggest that the best predictors of relative brain size in Malagasy strepsirrhines are nonsocial ecological variables that perhaps capture variation related to foraging complexity and flexibility. Specifically, diet appears to be closely linked with relative brain size in that frugivorous species have relatively larger brains than folivorous species. This result can be interpreted in several ways. First, it is noteworthy that frugivorous diets are generally of a higher quality than folivorous diets because fruits require less metabolically expensive processing in the gut than plant matter (Lambert, 1998). Frugivorous species may therefore have more energy to commit to the development and maintenance of a large brain, regardless of the selective pressure to have one (Aiello and Wheeler, 1995). Secondly, it has been shown that primates with relatively large brains have an especially expanded parvocellular layer of the lateral geniculate nucleus, a part of the visual pathway which is responsible for relaying information about color (Barton, 1998). Barton has argued that this trait may represent an adaptation to frugivory, as color provides essential information about the quality of many fruits. Another possibility is that frugivory in itself is a cognitive challenge, and that frugivorous primates require unique cognitive adaptations to subsist on fruit-heavy diets. Milton (1981) first remarked that the patchy distribution and transient availability of many tropical fruits pose substantial challenges for memory and spatial representation of a primate's environment. It is possible that all of the above factors have played some role in the selection for relatively large brains in frugivorous primates. It is also noteworthy that although relationships between relative brain size and frugivory have been found throughout primates (Barton, 1996, 1998; Fish and Lockwood, 2003) and in other orders (Harvey et al., 1980), this relationship is closely tied to phylogeny in our sample, and we were unable to identify this pattern through independent contrasts due to a very limited number of nodes at which contrasts could be generated.

Activity pattern is also closely related to relative brain size in this sample. Specifically, cathemeral species have relatively larger brains than diurnal, but not nocturnal species. Cathemerality, first described by Tattersall (1987), is an activity pattern in which animals are active intermittently throughout the 24-hour cycle. Although the adaptive value of cathemerality remains unclear, it has been suggested that it may provide a flexible behavioral strategy through which animals could regulate thermoregulation, obtain access to transient food sources, and limit exposure to predation and interspecific competition (Curtis and Rasmussen, 2002). From a cognitive perspective, it is this flexibility that is most interesting. Indeed, much of what separates intelligent behavior from highly canalized instinct is the degree to which an organism can flexibly solve problems, adapting to its changing environment on demand. Whether or not cathemerality bears any relationship to brain size in other mammals has not yet been determined, although the question warrants further investigation.

It is also important to note that the lack of an association between relative brain size and either pairbonding or group size in strepsirrhines does not imply that these factors have not influenced the evolution of cognition in this lineage. Rather, we can only conclude that these factors have not led to marked differences in relative brain size. Therefore, it is still possible that sociality has selected for cognitive adaptations in strepsirrhines that are not detectable simply by comparing relative brain size. One possible technique for probing this question further from an anatomical approach is to test whether or not particular brain regions, or neural pathways thought to be associated with sociality, reveal a finer picture than that which can be detected simply by measuring overall brain size (Barton, 2006). This seems to be a particularly promising route of inquiry for Malagasy strepsirrhines given that so much of the variation in total brain size in our sample can be accounted for by variation in body size ($R^2 = 0.94$). Although brain size is expected to be linked to body size in all taxonomic comparisons (Bauchot, 1978), the amount of variation explained within any clade may differ substantially. For example, in a large-scale evaluation of brain to body scaling in 309 extant placental mammal species, Martin (1981) found that body size explained 92% of variation in brain size. Within primates, Isler et al. (2008) found that body size explained 95% of variation in brain size in a sample of 176 species. However, the amount of variation explained differed considerably among primate groups. Body size explained 96% of the variation in brain size in prosimians, 93% of the variation in cercopithecines, and 98% of the variation in hominoids. In contrast, body size explained only 90% of the variation in callitrichines, 77% of the variation in non-callitrichine platyrrhines, and 55% of the variation in colobines. Other analyses of narrow clades within the strepsirrhines echo the high R^2 reported in our study; when examining brain to body scaling in galagos and lorises, Jungers and Olson (1985) reported an R^2 of 0.97. In such cases where there is little residual variation in overall brain size, it may be especially important to look for variation within brain components, restricting analysis to those brain regions implicated in social cognition (or other cognitive abilities of interest).

A second useful approach involves direct behavioral tests of cognition, comparing relatively social to less social species. For example, a recent study comparing the abilities of a highly social lemur species with dominance hierarchies to a species with a much simpler social organization revealed that the more social species outperformed the less social species on a task requiring transitive reasoning (MacLean et al., 2008). The ability to make transitive inferences has now been linked to sociality (Bond et al., 2003; MacLean et al., 2008) and the prediction of dominance hierarchies (Paz-y-Miño et al., 2004; Grosenick et al., 2007) in a number of species and likely represents a cognitive adaptation to living in organized social groups. Notably, the difference in performance between the lemur species in this study is inconsistent with their relative degrees of encephalization. That is, although the more social ring-tailed lemurs outperformed the less social mongoose lemurs on the cognitive task, the less social mongoose lemurs actually exhibit a greater degree of encephalization.

At the broadest level, the evolution of cognitive complexity is likely to be accompanied by corresponding increases in relative brain size. Measures of these changes in relative brain size are undoubtedly an important metric for gauging large-scale cognitive changes between taxa. These broad analyses can be supplemented by more refined neuroanatomical measures and behavioral tests with extant species in attempt to understand the selective pressures that influence particular cognitive capacities. Ultimately, when taken together, these complementary lines of research will help to unravel the factors that have driven cognitive evolution across species.

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