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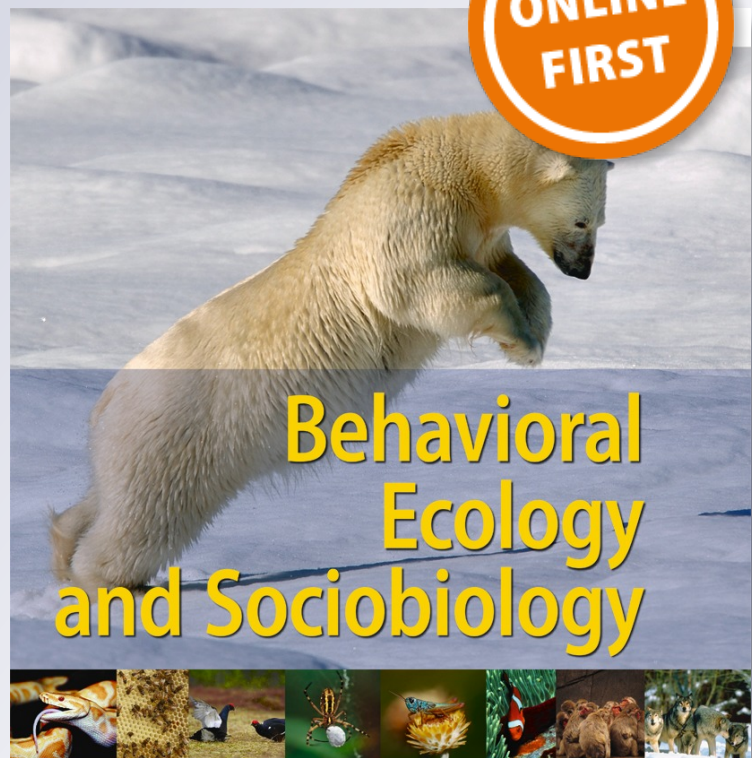
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What drives flexibility in primate social organization?

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Abstract The importance of behavioral flexibility for understanding primate ecology and evolutionary diversity is becoming increasingly apparent, and yet despite the abundance of long-term studies across diverse sampling localities, we still do not understand the myriad factors responsible for among-site variation in species' social organization. The goals of our study were to address this question via three main objectives: to quantify social organization flexibility (i.e., across-site intraspecific variation) of well-studied primate species, test the idea that closely related species exhibit similar levels of flexibility, and test hypotheses explaining variation in social organization flexibility among primate species. We obtained data for a total of 175 study sites from 32 primate species representing all major primate clades. We employed phylogenetic principal components analysis to quantify social organization flexibility for each species. We quantified the phylogenetic signal in social organization flexibility and then evaluated the best predictors of flexibility. We found that mean

group size was positively related to social organization flexibility. Large social groups may be more flexible because the foraging costs and predation risk associated with adding or subtracting individuals are lower compared to small social groups. There was some support that absolute brain size and the presence of fission–fusion dynamics were also related to high levels of social organization flexibility, suggesting that cognitive ability and/or within-site behavioral flexibility may also lead to increased variation across sites. Our results serve as an early step in understanding the patterns and processes related to social organization flexibility in primates and other social mammals.

Keywords Socioecology · Behavior · Phylogenetic generalized linear models · Biogeography · Geographic variation

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Introduction

Early comparative studies of animal behavior sought to understand the adaptive value of behavioral traits and how these traits evolved (Lorenz 1950; Tinbergen 1963). These first investigations compared behavioral patterns across species, assuming that the traits displayed by a single group or population were representative of the species' "norm"; intraspecific variation exhibited among populations was considered unimportant "noise" (Lorenz 1970; Mayr 1976). Some researchers, however, argued that intraspecific behavioral variation was due to selective forces. Leyhausen (1965), for example, proposed that the flexibility in the social behavior of feral domestic cats (*Felis domesticus*) could be used as a model system to understand behavioral variation. Soon after, several additional species were also recognized for their high degrees of behavioral flexibility (Struhsaker 1967).

Eisenberg et al. (1972) were among the first to stress the possible importance of intraspecific variation on a broad comparative scale by emphasizing the use of modal categories when describing primate social structures. Later research also incorporated intraspecific variation into the mating system theory (Emlen and Oring 1977; Oring 1982). Intraspecific variation in primates has since been examined at several different levels of analysis, including among age/sex classes, across seasons or generations (temporal) within a single site, among groups within a single site, and among sites or populations (geographic) (Table 1). However, despite its importance to understanding broad-scale patterns of diversity, studies examining intraspecific variation in primate behavior and ecology are comparatively sparse (Foster and Endler 1999; Kappeler et al. 2013), and the large majority of comparative studies have continued to focus on species' norms (e.g., mean values) at the interspecific level (Clutton-Brock and Harvey 1977; Terborgh 1983; Sterck et al. 1997; Lee 1999; Nunn 1999; Kamilar et al. 2010).

While broad-scale interspecific studies are critically important for quantifying behavioral and ecological variation and testing evolutionary hypotheses (e.g., social organization and behavior: DiFiore and Rendall 1994; allomaternal care: Ross and MacLarnon 2000; Thierry et al. 2000; Tecot et al. 2012; social organization, ecology, and life history: Kamilar and Cooper 2013), they fail to consider the variable selection pressures at the intraspecific (i.e., population) level under which primate sociality has evolved (Strier 2009). Moreover, we have little idea how intraspecific variation translates into patterns at the interspecific level (Chapman et al. 2002), or whether similar factors drive intraspecific variation across species. For instance, does increased across-site variation in environmental conditions such as temperature or rainfall lead to increased intraspecific variation in social organization? And do these factors equally influence social organization flexibility across primate species? The goal of this study is to therefore incorporate measures of *intraspecific* variation in primate social organization into a broader *interspecific* comparative analysis to ask the question: Why do some primate species

vary more in their social organizations than others? We follow the definition of social organization presented by Kappeler and van Schaik (2002), “the size, sexual composition and spatiotemporal cohesion of a society” (see “Methods” for more details).

Socioecological theory predicts that variation in primate social relationships should be explained by ecology, that is, social relationships and associated aspects of social organization should vary according to the diversity, abundance, and distribution of food resources within a given habitat (van Schaik 1989; Sterck et al. 1997; Koenig 2002). Likewise, social organization should also depend, at least in part, on the pressures exerted by the predator community (van Schaik et al. 1983), a factor which should also vary across sites when environmental conditions and associated habitats differ (Reed and Bidner 2004). Accordingly, we predict that a species' social organization should reflect the environment in which it lives, and thus, species whose distributions include more environmental variation (and by proxy, more habitat types) should display greater *social organization flexibility* (i.e., greater geographic or across-site variation in their social organizations) than those restricted to one or a few habitat types (Fig. 1). Furthermore, some species exhibit substantial spatio-temporal variation in their grouping patterns *within* a given site (i.e., fission–fusion social dynamics; *sensu* Aureli et al. 2008), patterns that have been, in part, related to environmental variables (e.g., within-site resource availability, predator pressure) (Chapman et al. 1995; Lehmann and Boesch 2005). Thus, we also predict that taxa that are typified by high levels of within-site fission–fusion social dynamics should also display relatively greater across-site variation in their social organization because their typical grouping patterns are already quite flexible.

In addition, we predict that species living at sites characterized by high rainfall seasonality should exhibit relatively higher levels of social organization flexibility because variable environments may select for species with alternate ecological strategies (Moran 1992; Lee and Kappeler 2003). This hypothesis differs from the earlier environmental variation

Table 1 Types of intraspecific variation in primate behavior and ecology

Type of variation	Traits	Examples
Between age/sex classes	Ontogeny of behavior and ecology, diet, ranging, habitat use	Harrison (1983); Rose (1994); Kamilar and Pokempner (2008)
Temporal—seasonal	Diet, activity budget	Terborgh (1983); Ganzhorn et al. (2003); Brockman and van Schaik (2005)
Temporal—across generations	Social organization, demography, life history	Altmann (2000); Borries (2000); Kappeler and Watts (2012)
Geographic—among groups within a site	Social organization, life history, foraging, reproductive output	Altmann and Alberts (2003); Borries et al. (2008)
Geographic—across sites or populations	Social organization, diet, activity budget, culture	Cords (2000); Struhsaker (2000); Ossi and Kamilar (2006); Kamilar and Atkinson (2014)

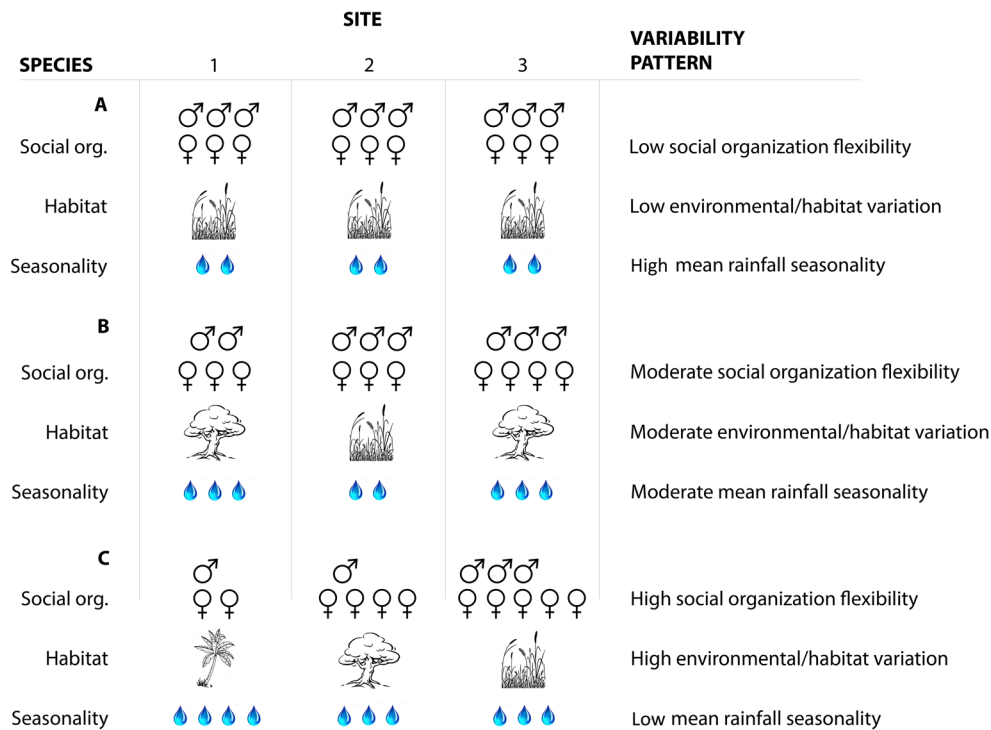


Fig. 1 Figure illustrating our dependent variable, social organization flexibility, and two of our predictor variables, environmental variation (used as a proxy for habitat variation) and mean rainfall seasonality. In this example, three species are found at three sites each. Species A exhibits the lowest level of variation in social organization (i.e., social organization flexibility), species B a moderate amount, and species C the highest amount. Increasing social organization flexibility is defined as increasing variation in group size and

composition across sites. Species A also experiences the least amount of across-site environmental variation, species B a moderate amount, and species C the highest amount. Finally, species A experiences the highest mean rainfall seasonality across sites, species B a moderate amount, and species C the lowest amount. Note that fewer rain drop symbols indicate higher rainfall seasonality. See “Methods” section for details

hypotheses because a species may be distributed among one or a few, albeit highly seasonal habitat types, and will therefore display high within-site, but little across-site environmental variation.

Group size itself may also be an important predictor of social organization flexibility. Janson and Goldsmith (1995) found that the relative costs of foraging are lower in medium- to large-sized groups than in small groups. Although they suggest that this effect is stronger in frugivorous primates (due to increased feeding competition), subsequent researchers have argued that folivorous species may also experience strong feeding competition due to their selective consumption of (young) leaves (Snaith and Chapman 2007). For this reason, we predict that primates living in large social groups should display greater social organization flexibility because large social groups have fewer costs associated with changes in group size.

Finally, beyond the far-reaching effects of a species’ ecology, previous work has tied intertaxonomic differences in social complexity, dietary flexibility, and the ability to adjust to novel situations to a species’ cognitive capacity (Clutton-Brock and Harvey 1980; Milton 1988; Dunbar 1992; Barton 2000). Thus, for our final hypothesis, we predict that larger brained species, and by proxy species having relatively higher

cognitive abilities, should display greater across-site variation in their social organizations than others.

We used a phylogenetic comparative approach to test these predictions using a sample of 32 primate species for which there are high quality data documenting their ecology and social organization from several different study sites, as well as reliable measures of both absolute and relative brain size. We first quantified intraspecific variation in social organization across studies/sites. We then examined this variation within an evolutionary context by calculating its phylogenetic signal. Finally, we tested several hypotheses explaining inter-specific variation in social organization flexibility.

Methods

Ecological and social organization data were gathered from the literature for 32 primate species from a total of 175 study sites (Electronic Supplementary Material Table 1). Our dataset included 27 haplorhines, of which 16 species were catarrhines. The species included in this analysis were selected on the basis of several criteria: (1) data were available from a minimum of three study sites; (2) sites were characterized by minimal anthropogenic disturbance (i.e., we avoided studies

in highly fragmented habitats and/or provisioned populations); (3) group size and composition could be accurately determined from published accounts; and (4) data were available for all variables (described below).

Data were obtained from a variety of publications including numerous dissertations (see [Electronic supplementary material](#)). As stated above, we minimized the inclusion of sites with substantial habitat fragmentation, though we could not guarantee that some sites exhibited some fragmentation. This is because fragmentation is quite widespread, though the level of fragmentation varies substantially and is often not quantified sufficiently, i.e., there is little consensus as to how much fragmentation is needed for a habitat to be called “fragmented.” More importantly, we did not include data from sites where the researchers believed that the degree of fragmentation substantially altered group size and/or composition outside of the natural range of variation for the species. In addition, to test the sensitivity of our results to the inclusion of two relatively highly fragmented sites (*Colobus guereza* at Limuru and *Alouatta seniculus* at El Frio), we re-analyzed our data, excluding these two data points. The re-analyzed dataset yielded nearly identical results.

The large majority of the 175 sites in our dataset are based on habituated or semi-habituated groups (most at long-term research sites and/or sites where dissertation data were collected on the group(s) or groups that the authors stated were reliably counted (e.g., *Chlorocebus aethiops* at Lolui Island; *Ptilocolobus badius* at Sonjo), with a small number of sites yielding data through relatively extensive surveys (e.g., *Alouatta pigra* at Tikal National Park; *Gorilla gorilla* at Mbeli Bai; *C. guereza* at Kyambura Gorge). Two exceptions to these criteria are relatively short-term studies of *C. guereza* at Arusha and *Pithecia pithecia* at Saraca-Taquera National Forest. We tested the sensitivity of our results to the short-term data by re-analyzing the dataset without these populations. Again, these analyses yielded nearly identical results.

Several primate clades have undergone extensive taxonomic revisions during the last several years, resulting in the elevation of subspecies and populations to species level status (e.g., Rylands and Mittermeier 2009; Mittermeier et al. 2010). As there is little consensus about the relationship between biological and taxonomic diversity, we chose to employ a taxonomic scheme that was most appropriate for our research question. Specifically, the goal of our paper was to examine variation among closely related taxa and not to make assessments regarding species designations. We therefore adhered to a “lumper” taxonomy to maximize the availability of within-species data. In biological terms, this can be thought of as designating populations to the same species if they have experienced gene flow in the present or recent past. Our taxonomic arrangement was adapted from Davies and Oates (1994) for the colobine species, Jolly (1993) for *Papio*, and Fleagle (1999) for the remaining taxa. To further investigate

the sensitivity of our results to taxonomy, we re-ran our analyses while removing taxa that have since undergone substantial taxonomic revisions (and were therefore more likely to have been influenced by the use of a lumpers taxonomy), including *Cercocebus agilis*, *Papio hamadryas*, and *Eulemur fulvus*. The re-analyses generated qualitatively similar results to our original analyses and led us to the same conclusions.

Quantifying across-site variation in social organization

For our dependent variable, *social organization flexibility*, we quantified the across-site variation in a species’ social organization, which we define as “the size, sexual composition and spatiotemporal cohesion of a society” (sensu Kappeler and van Schaik 2002) (Fig. 1). For nearly all species, group cohesion data were unavailable at the site level. Our calculations of social organization flexibility were thus limited to the intraspecific variation present in group size and sexual composition across sampling localities. However, while we do not explicitly incorporate group cohesion into our measure of social organization flexibility, we broadly consider the ability for certain taxa to exhibit regular fission–fusion social dynamics in our predictors of social organization flexibility (see below).

We first collated site-specific data for four variables related to a species’ social organization: (a) group size, (b) number of adult males in the group, (c) number of adult females in the group, and (d) adult sex ratio. We defined group size as social group size in species with cohesive grouping patterns and as total community size in species having high levels of fission–fusion social dynamics. We did not question the sources’ definition of an adult individual and variation in this definition may introduce error in the dataset. We used mean values for sites with data from multiple social groups. With these data, we then used two methods to quantify social organization flexibility.

Our first method calculates the weighted multivariate variance for each species, a technique adopted from paleontological research that has been used to examine multidimensional morphospace (Wills et al. 1994) (see [Electronic supplementary material Table 2](#) for example). For our purposes, this method is particularly useful for two reasons. First, variation-based methods such as this are less biased by sample size; using this method thereby reduces the likelihood that our estimation of a species’ social organization flexibility is simply a result of the number of research sites included per species. Second, this method accounts for co-variation among variables, e.g., group size and the number of females. Using the data points from all species across all sites, we conducted a principal components analysis (PCA) based on a correlation matrix. The principal component scores were weighted based on their respective component’s eigenvalue. This is essentially weighing the PCA scores based on the amount of variance

explained by their respective component. For each species, we calculated the variance of the weighted principal component scores from their respective study sites. This was done for each principal component and then summed across components for a species-specific weighted multivariate variance (i.e., social organization flexibility) score. This approach has been applied to cranial variation in primates (Fleagle et al. 2010) as well as ecological variation (Kamilar 2006a).

By contrast, our second approach quantifies social organization flexibility by calculating the coefficient of variation for each species' respective PCA scores. Whereas the aforementioned variance method quantifies variation in an absolute sense, this second method allowed us to better account for the relative variation in group size among species. Consider, for example, two species that are each represented by three sites; one species has associated group sizes of 3, 4, and 5, while the second species has associated group sizes of 25, 26, and 27. Although the group size variances of these two species are the same (variance = 1), the relative amount of variation in group size is quite different. Adding or subtracting one individual from a group of 26 represents a much smaller change (i.e., percent difference) compared to a group of four individuals. Using this method, the coefficient of variation (CV) quantifies variability by calculating the standard deviation divided by the sample mean. Variation in group size is thus scaled to mean group size. In essence, this approach better represents the relative cost of adding or subtracting individuals from a group. Because group size heavily loads on PCA axis 1, we calculated the CV for each species' respective PCA axis 1 scores. By doing so, we are capturing nearly all of the variation in group size, while also keeping this variable directly comparable to our first multivariate variance approach.

Because we used a dataset that included several species, the correlation matrix which served as the basis for our PCA may have been influenced by phylogenetic effects (Catlett et al. 2010). We therefore used the method developed by Revell (2009) to incorporate phylogenetic information into the PCA, thereby producing phylogenetically adjusted PCA scores. We used a primate consensus tree generated from the 10 K tree website (Arnold et al. 2010), which was modified to include multiple tips per species, with each tip representing a different site. Polytomies were created for sites within species because site-specific phylogenetic information was unavailable for most species. All variables were transformed into *z* scores and subsequently log (base 10)-transformed before being entered into the PCA. These data transformations better fit the assumptions of the analyses. The phylogenetic PCAs were conducted with the `phyl.pca` function in the `phytools` package (Revell 2012) for R (R Development Core Team 2012).

Finally, we explored the possibility that using a different number of social groups per site to calculate the site-specific group size and composition values influenced our calculations of social organization flexibility. In theory, among-site

variation in group size and composition may be higher for species with sites only containing single study groups due to increased sampling error within a site. Yet, we examined the relationship between the mean number of study groups per site versus the amount of social organization flexibility exhibited by a species and found no significant relationship.

Quantifying phylogenetic signal in social organization flexibility

We calculated phylogenetic signal, or the degree to which a trait (e.g., social organization flexibility) is correlated to phylogeny, by using Blomberg's *K* (Blomberg et al. 2003; Kamilar and Cooper 2013). *K* is measured on a scale from 0 to no theoretical maximum (though values are often not much greater than 1), with 0 indicating that the trait is random with respect to phylogeny, and 1 indicating that the trait perfectly follows a Brownian motion model of evolution (i.e., closely related species exhibit similar trait values and this similarity declines with increasing phylogenetic distance). We randomized the data 1,000 times to generate a *p* value associated with *K*. We used a species level primate consensus tree generated from the 10 K tree website (Arnold et al. 2010). The data were analyzed using the `phytools` package (Revell 2012) for R (R Development Core Team 2012).

Predictors of social organization flexibility

Six predictor variables were included for each species: (1) across-site environmental variation, (2) mean annual rainfall seasonality, (3) absolute brain size, (4) relative brain size, (5) mean group size, and (6) fission–fusion (presence/absence).

Much like our dependent variable, our first predictor variable, across-site environmental variation, was a multivariate composite of four environmental measures for each species across the study sites included in our dataset. We obtained climate data to quantify the environmental variation experienced by each species from the same sites in which we have social organization data. Climate variables included (a) mean annual rainfall, (b) rain seasonality as measured by the *r* statistic (Batschelet 1981), (c) mean minimum, and (d) mean maximum monthly temperature. These four variables were entered into a PCA and then the weighted multivariate variance based on the PCA components was calculated for each species. This is the same method described for calculating social organization flexibility. Environmental data for each site were obtained from the WorldClim climate database (Hijmans et al. 2005). The WorldClim database has been frequently used in comparative ecology studies to quantify abiotic conditions and, therefore, as a proxy for habitat characteristics (e.g., Graham et al. 2012; Kamilar et al. 2012; Kamilar and Beaudrot 2013). Furthermore, these data have been well correlated with habitat types on the ground (e.g.,

Kamilar et al. 2010). The climate data were extracted for the geographic location of each site using ArcGIS 9.0.

Our second predictor variable, mean annual rainfall seasonality, was calculated as the average r value across all study sites for the respective species in the dataset. R is a circular statistic that varies from 0 to 1, with 0 indicating an equal amount of rainfall during every month of the year and a value of 1 indicating that all rain falls within a single month. This variable differs from the across-site environmental variation variable because a species could be consistently found in seasonal habitats, which would yield a high mean r value. Yet, this would also yield a relatively low across-site environmental variation score (see Fig. 1 for example).

Mean group size, our third predictor variable, was calculated as the mean group size for a species based on their across-site dataset. Furthermore, we designated four species as exhibiting regular fission–fusion social dynamics (predictor variable four): *Ateles belzebuth*, *Ateles geoffroyi*, *Pan troglodytes*, and *Varecia variegata*. These four species were coded as a “1” for the fission–fusion variable, with the remaining species being coded as a “0.” The species we have designated as fission–fusion all exhibit a similar form of group cohesion (fission–fusion dynamics that occur on a daily basis) that is relatively well understood and is considered the norm for the species. More subtle forms of fission–fusion group cohesion exist (Aureli et al. 2008) but are less well documented/understood in terms of whether it is a species’ typical trait and/or how frequently it occurs when it is present in a population. Not accounting for other species that may show some form of fission–fusion groupings should increase our type II error when investigating a possible relationship between fission–fusion and across-species variation in group size and composition. For baboons (*Papio hamadryas* sensu lato), we constrained our sample to include only savanna populations to reduce the potential confounding effect of including *P. hamadryas* sensu stricto groups that exhibited substantially different social cohesion characteristics.

Finally, we defined species absolute and relative brain size based on female brain size data from Isler et al. (2008). Relative brain size data were generated from the Isler et al. (2008) dataset and calculated as phylogenetic residuals (resulting from a phylogenetic reduced major axis regression (pRMA) of female brain size versus female body mass). The pRMA model was performed using the `phyl.RMA` function in the `phytools` package (Revell 2012) for R (R Development Core Team 2012).

Phylogenetic models predicting social organization flexibility

We used three approaches to determine which variables best predict species’ social organization flexibility. First, we conducted a series of bivariate linear models between each predictor variable and our measure of social organization

flexibility. Second, if more than one predictor variable was statistically significant ($p < 0.05$), then we conducted additional models that simultaneously included these “significant” variables. Finally, we also performed a full model analysis that included all predictor variables. We note that the full model should be interpreted with caution considering the ratio of predictor variables (six) to total sample size (32 species). Conducting analyses including more than one predictor variable allowed us to investigate the importance of each independent variable while accounting for the effects of the other predictors. To check for high degrees of multicollinearity in our models, we calculated variance inflation factor (VIF) values for all predictors that were used in models with more than one independent variable. VIF values were low in all cases. VIF values were below 1.5 for variables in models with two or three predictors. VIF values were below 2.2 for all variables in the full model.

We used Akaike’s Information Criterion with the small sample size correction (AICc) (Burnham and Anderson 2002) for selecting the best models that explained social organization flexibility. This method has several advantages over a stepwise modeling approach, including relying less on the importance of p values. Most importantly, AICc ranks models by balancing the explanatory power of the model versus the number of predictors in the model (with the latter possibly leading to overfitting the model). The model with the lowest AICc value is considered the best and all models within two AICc units of this best model are also treated as equally good (Burnham and Anderson 2002). Using AICc (and related metrics) for model selection is becoming increasingly common in comparative biology research (Kamilar et al. 2010, 2013; Garamszegi 2011; Tecot et al. 2012).

The goal of our study was to predict why some primate species exhibit more social organization flexibility than others. Therefore, we needed to utilize a phylogenetic comparative method to accommodate our interspecific dataset. Comparative studies have benefited from the implementation

Table 2 Results of phylogenetic principal components analysis quantifying intraspecific social organization flexibility

	Comp 1	Comp 2	Comp 3	Comp 4
Component loadings				
Group size	−0.915	0.172	0.365	−0.002
No. of adult females	−0.927	0.278	−0.245	−0.055
No. of adult males	−0.779	−0.609	−0.131	0.064
Adult sex ratio	−0.061	0.994	−0.075	0.055
Component eigenvalues				
Eigenvalue	2.308	1.466	0.216	0.010
% variance	57.7	36.6	5.4	0.3
% cumulative variance	57.7	94.3	99.7	100.0

of statistical methods that reduce the nonindependence of residuals in models that include data from evolutionarily related species (Felsenstein 1985; Nunn 2011). The method that has gained the most acceptance and use is phylogenetic generalized least squares models with Pagel's lambda (Pagel 1999; Freckleton et al. 2002). Lambda varies continuously from 0 to 1. A value of 0 indicates that the error structure of the model is completely independent of phylogeny, resulting in a model that is equivalent to a standard linear model. A lambda value of 1 indicates that the model's residuals perfectly follow a Brownian motion model of evolution, being equivalent to an

analysis using phylogenetically independent contrasts. We used a likelihood approach to determine lambda. We obtained a consensus tree from the 10 K trees website (Arnold et al. 2010) that included all the species in our study. We produced diagnostic plots for each analysis to examine if the assumptions of the analyses were met. We considered species with phylogenetic residuals greater than an absolute value of 3 to be an outlier. If outliers were present, then we re-ran the analysis without the outlier species. All phylogenetic generalized linear models were conducted with the caper package (Orme et al. 2012) for R (R Development Core Team 2012).

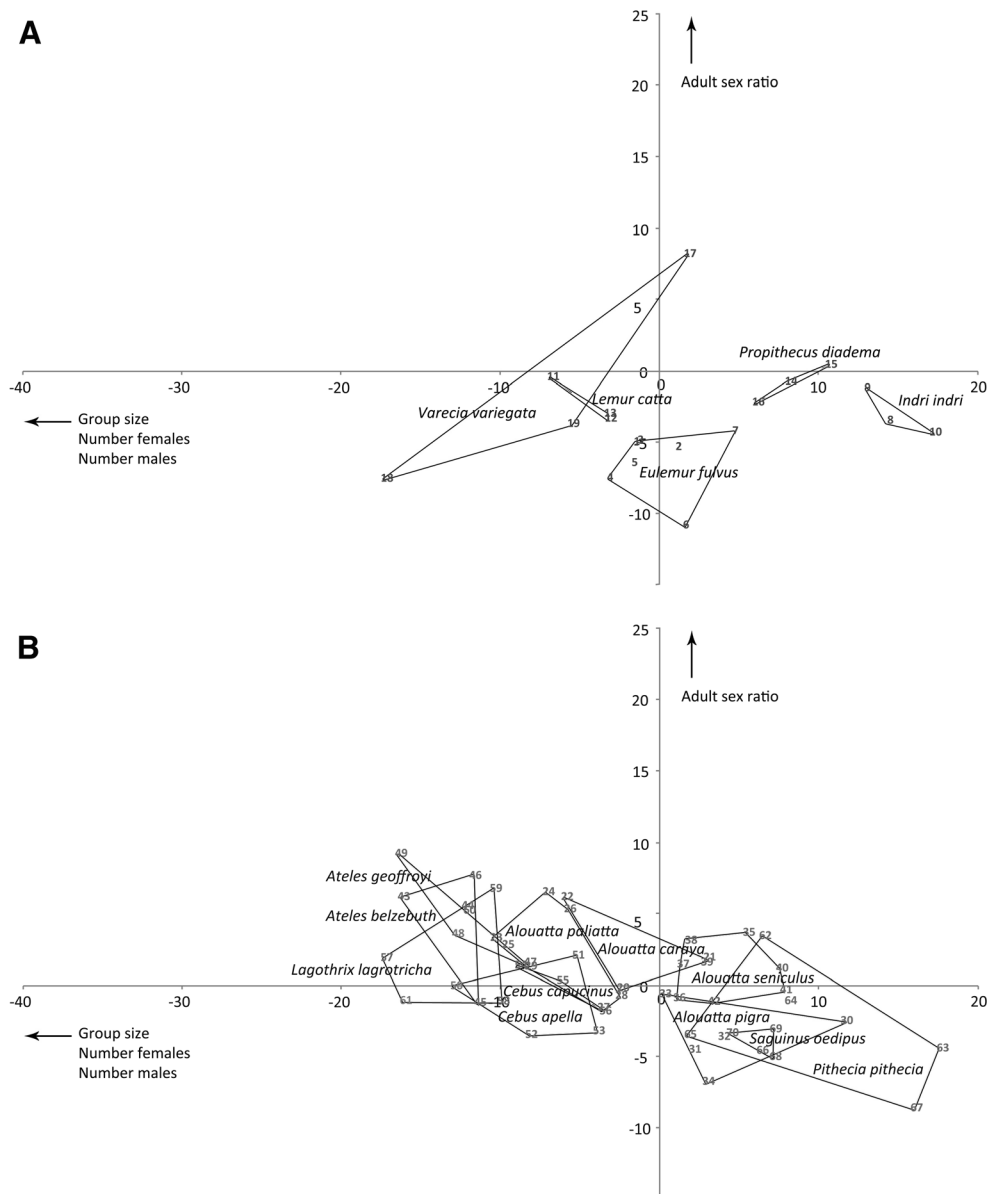


Fig. 2 Plot of phylogenetic principal components analysis (pPCA) representing social organization flexibility across 32 primate species. Plots are separated by phylogenetic group (lemurs (a), platyrrhines (b),

cercopithecines (c), colobines (d), and apes (e)) to enable better visualization of the results, though each plot represents the same multivariate space. Details about the pPCA results can be found in Table 1

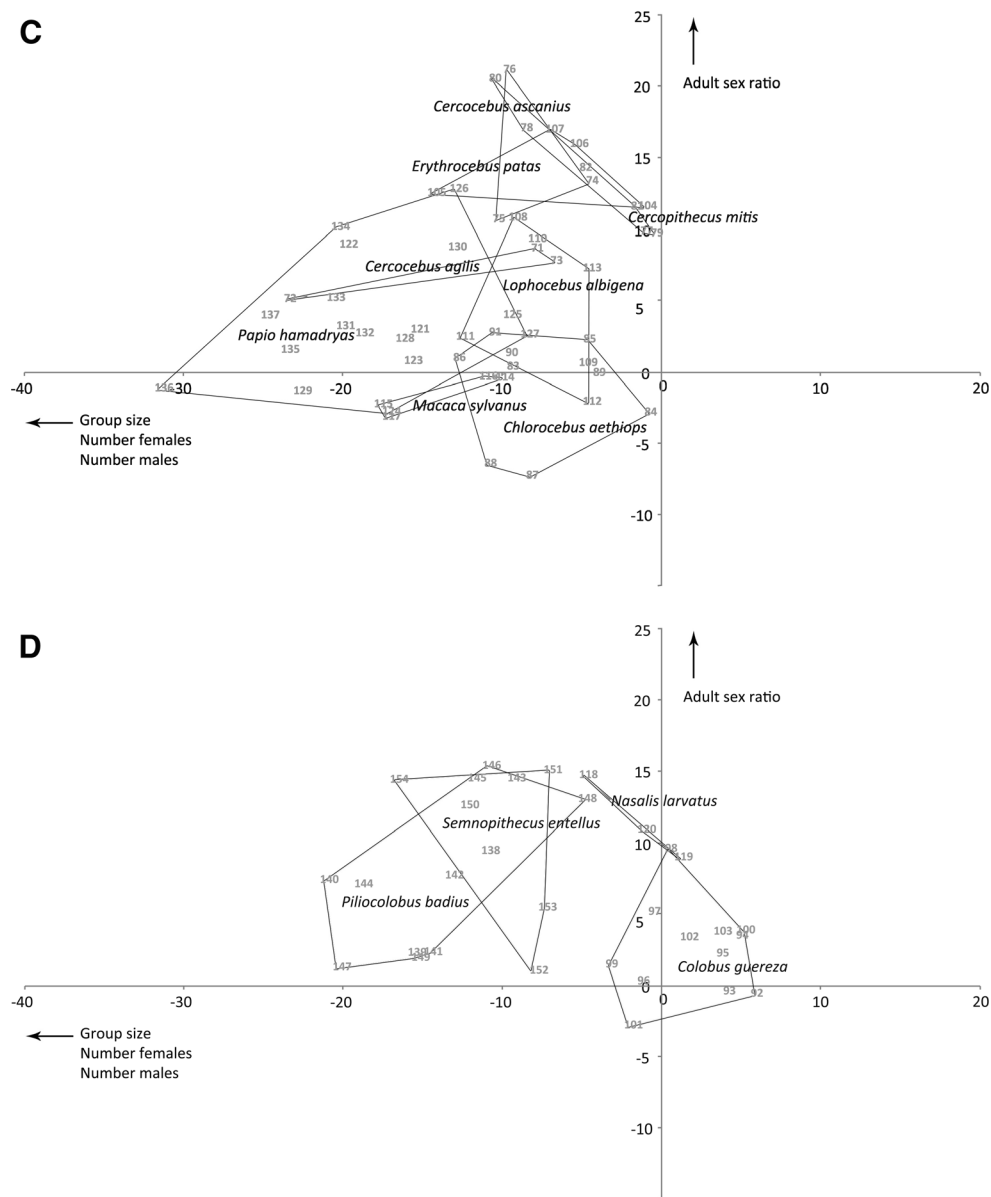


Fig. 2 (continued)

All continuously measured variables were log-transformed before analysis. Variables were transformed to better meet the assumptions of the analyses.

Results

Quantifying social organization flexibility and phylogenetic signal

Our social organization phylogenetic PCA produced two components that exhibited eigenvalues greater than 1 and

explained more than 94 % of the variation in the dataset. Group size and the number of adult males and females loaded most heavily on component 1, with adult sex ratio loading heavily on component 2 (Table 2; Fig. 2a–e).

Species that exhibited the lowest levels of social organization flexibility included *Hylobates lar*, *Saguinus fuscicollis*, *Lemur catta*, and *Indri indri*. Species that displayed the highest levels of within-species variability in social organization included *V. variegata*, *C. agilis*, *P. troglodytes*, and *P. hamadryas* (Fig. 2; Electronic Supplementary Material Table 3). We found that social organization flexibility exhibited a low to moderate amount of phylogenetic signal ($K=0.364$) that was significantly greater than 0 ($p=0.038$) (Fig. 3).

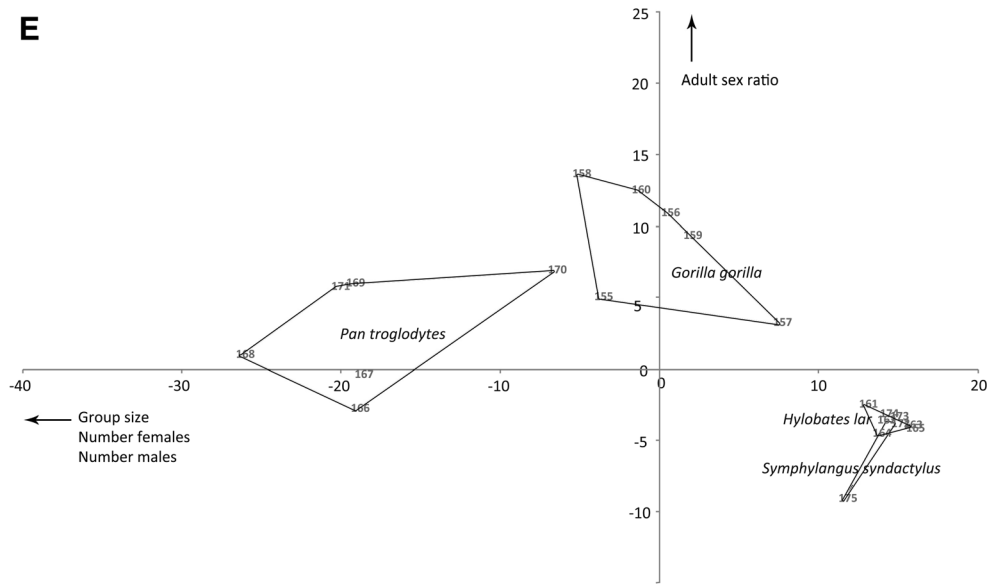


Fig. 2 (continued)

Predicting social organization flexibility

Three of our six predictor variables were statistically significant predictors of social organization flexibility when using bivariate PGLS models (Tables 3 and 4). These predictors included absolute brain size, group size, and the presence of fission–fusion social dynamics, which were all positively related to the degree of social organization flexibility. Group size was the best predictor, exhibiting a p value of <0.001 and the lowest AICc value within each set of the models (Fig. 4). The bivariate models varied greatly in terms of their Pagel's lambda values, ranging from a low of 0 to a high nearing 1. Our results were consistent regardless of our method to quantify social organization flexibility (Tables 3 and 4). In other words, species with high mean group size values show more across-site variation in social organization from an absolute perspective (defined by the weighted variance measure) and also scaled to group size (via the coefficient of variation metric).

We conducted four additional PGLS models that contained various combinations of our three best predictor variables (Tables 3 and 4). All four models produced p values <0.05 , yet the importance of the individual variables within these models varied substantially. Group size was the only variable that was significantly related to social organization flexibility. Both absolute brain size and fission–fusion dynamics exhibited p values that were statistically significant or approached $p=0.05$ in the model that did not contain group size (model 8 in Tables 3 and 4). The full model was statistically significant ($p=0.003$ and $p<0.001$ depending on our

measure of flexibility), yet only one variable (group size) within the model was a significant predictor of social organization flexibility.

In terms of model selection, the PGLS model with the lowest AICc value only contained group size as the lone predictor (Tables 3 and 4). Two additional models exhibited AICc values within (or nearly within) two units of this best model and should be treated as similarly well-supported. These two models were absolute brain size + group size (model 7 in Table 3) and group size + fission–fusion (model 9 in Table 4). *Cebus capucinus* was an outlier in several models, though re-running the analyses without this species produced similar results.

Discussion

The goal of this paper was to answer the question—why do some primate species exhibit more social organization flexibility than others? We found that mean group size was the most consistent predictor of social organization flexibility (i.e., across-site variation in social organization) followed by absolute brain size and the presence of regular fission–fusion social dynamics. This was true regardless of our method of quantifying social organization flexibility (using a weighted multivariate variance or coefficient of variation approach). Interestingly, the importance of these variables is independent of the other predictors, including our measures of environmental variation.

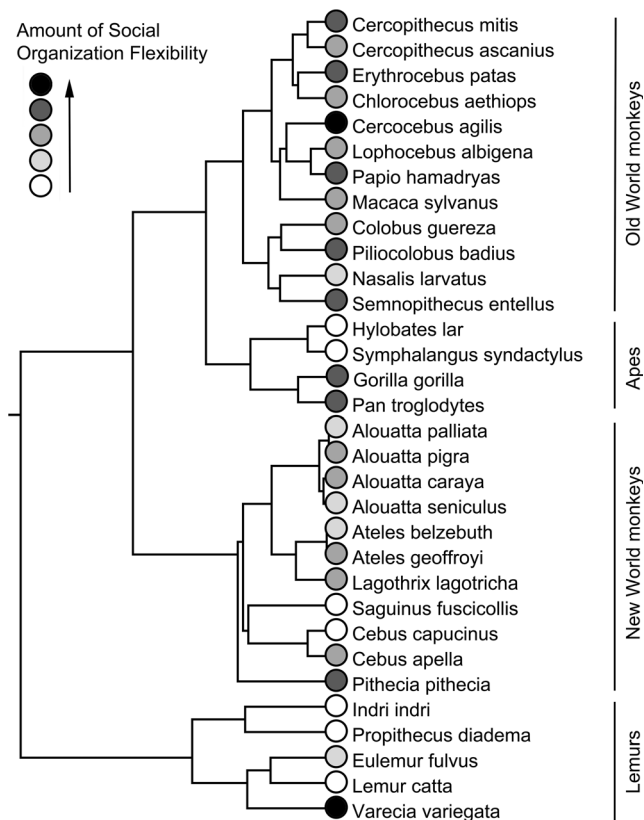


Fig. 3 Amount of social organization flexibility in a phylogenetic context

Social organization flexibility in a phylogenetic context

We found a significant phylogenetic signal associated with a species' social organization flexibility, indicating that closely related species often display similar levels of flexibility. Taxa with the least flexibility in their social organizations include four of five lemur species, some New World monkeys (*S. fuscicollis* and *C. capucinus*), one colobine (*Nasalis larvatus*), and both hylobatid species (*H. lar* and *Symphalangus syndactylus*). Taxa exhibiting moderate flexibility comprised many New World monkeys (especially the atelids) and some Old World monkeys. Old World monkeys and great apes showed the greatest social organization flexibility. In addition, a New World saki monkey (*P. pithecia*) and the ruffed lemur (*Varecia*) also exhibited substantial flexibility.

Our results are consistent with previous studies that have also found a phylogenetic component associated with aspects of social organization at the interspecific (Shultz et al. 2011) and intergeneric levels (DiFiore and Rendall 1994). It is important to note that while our predictive analyses "controlled for" phylogeny, phylogenetic signal can be quantified in a trait itself (in this case, social organization flexibility). Using PGLS analyses account for phylogenetic autocorrelation in model residuals, not in the traits themselves.

We found that Old World monkeys exhibit high levels of social organization flexibility, perhaps not surprising considering that many cercopithecines are considered ecological generalists (macaques and baboons in particular). While our results may initially appear contradictory to DiFiore and Rendall (1994), who found lower than expected variation in Old World monkey social behavior and organization given the species' varied environmental conditions, their analysis was conducted at the genus level and, thus, did not explicitly account for inter- and intraspecific variation. Consequently, the contrasting results between our study (focused on the subgeneric level) and theirs (focused on the generic level) clearly illustrate the different biological patterns present at varying taxonomic or phylogenetic scales.

Predicting social organization flexibility

The relationship between mean group size and social organization flexibility may be related to the costs of adding group members at small group sizes. Janson and Goldsmith (1995) found that relative ranging costs, a proxy for changes in relative fitness due to adding an individual to a social group, were higher for frugivores in small social groups and decreased as group size increased. Therefore, it is possible that species with relatively larger groups show greater social organization flexibility because of the lower relative costs associated with altering group size. By contrast, if the relative cost of adding an individual to a small group is great, then this should constrain social organization flexibility in species with relatively small group sizes.

Group size (and social organization) is also often related to mating system. In species that have evolved a system of territoriality and social monogamy (e.g., gibbons, siamangs, indri, some *Saguinus*), we tend to see less social flexibility. Opie et al. (2013) found that social/mating system (along with harem polygyny) is a derived state which likely evolved alongside social organization. Therefore, we may expect that monogamous species would exhibit little flexibility in social organization across localities.

In addition to group size, there was some support that absolute brain size and the presence of fission–fusion dynamics were also related to high levels of social organization flexibility, suggesting that cognitive ability and/or group cohesion may also lead to increased variation across sites. Previous studies have suggested that limited cognitive ability, especially neocortex size, is an important constraint on sociality and group size (Dunbar 1992). Although we did not directly incorporate data on neocortex size into our analyses, we did find that brain size, a correlate of neocortex size (Deacon 1990; Aiello and Dunbar 1993), was positively associated with social organization flexibility. This result is not surprising, as larger brains are thought to increase a species' ability to remember the identities of social partners and to

Table 3 Results of phylogenetic models predicting social organization flexibility based on a weighted multivariate variance approach

Model	Predictor	Slope	<i>t</i> value	<i>p</i> value	<i>r</i> ²	Lambda	AIC
1	Environmental variation	0.152	1.313	0.199	0.054	0.000	35.45
2	Mean rain seasonality	0.188	0.524	0.604	0.009	0.959	34.80
3	Absolute brain size	0.661	2.295	0.029	0.149	0.947	29.96
4	Relative brain size	0.621	0.867	0.393	0.024	0.951	34.33
5	Fission–fusion	0.418	2.086	0.022	0.127	0.926	30.94
6 ^a	<i>Group size</i>	<i>0.801</i>	<i>5.062</i>	<i><0.001</i>	<i>0.461</i>	<i>0.000</i>	<i>17.49</i>
7 ^a	Combined model A			<0.001	0.465	0.000	19.50
	Absolute brain size +	0.092	0.485	0.631			
	Group size	0.761	4.218	<0.001			
8	Combined model B			0.016	0.219	0.936	29.58
	Absolute brain size +	0.538	1.870	0.071			
	Fission–fusion	0.317	1.589	0.112			
9 ^a	Combined model C			<0.001	0.462	0.000	19.70
	Group size +	0.785	4.547	<0.001			
	Fission–fusion	0.045	0.252	0.802			
10 ^a	Combined model D			<0.001	0.466	0.000	21.46
	Absolute brain size +	0.089	0.459	0.649			
	Group size +	0.748	3.895	<0.001			
	Fission–fusion	0.038	0.213	0.833			
11	Full model			0.003	0.505	0.000	27.96
	Environmental variation	0.086	0.860	0.398			
	Mean rain seasonality	−0.313	−0.762	0.453			
	Absolute brain size	0.185	0.801	0.431			
	Relative brain size	−0.690	−1.248	0.224			
	Fission–fusion	0.036	0.192	0.849			
	Group size	0.844	3.771	0.001			

Sample size equals 32 species for all models. The model with the lowest AIC value is considered best and all models within two AIC units are considered equally good. These models are in italics. Note that model 7 is 2.01 AIC units from the best model

^a *Cebus capucinus* was an outlier in several analyses. Re-analyzing the dataset without this species produced similar results

navigate among their associated social relationships (reviewed in Dunbar 1998). Consequently, this same cognitive ability may allow species to adjust their social organization in response to local conditions, including variation in habitat structure, predator communities, dietary resources, and/or demographic characteristics. Of course, it is also possible that in species where demographic variability leads to frequent changes in group composition across sites, selection pressures may lead to increased cognitive ability and/or the adoption of fission–fusion social dynamics. It is currently not possible to disentangle correlation from causation at this time.

Once group size exceeds the ecological or cognitive limits of the species, groups are expected to either fission or adopt fission–fusion social dynamics (Dunbar 1996). That is, there is likely some threshold at which expanding group size or increased cognitive complexity (Isler and van Schaik 2009) can become prohibitively costly. Larger groups can suffer

from increased feeding competition (Janson 1988, 1992), and/or increased conspicuousness to predators (Stephens and Krebs 1986) or increased risk from infanticidal males (Borries 1997; Crockett and Janson 2000). Thus, the ability or tendency for large groups to fission under particular social or ecological conditions may therefore allow certain species more flexibility in their social organization across sites (e.g., ruffed lemurs: Vasey 2003) and also within sites across seasons or interannually (e.g., Schaffner et al. 2012). Confidently identifying the mechanisms shaping spatiotemporal patterns in group cohesion is difficult to ascertain without quality data related to predation risk and resource availability. Unfortunately, these data are not available for most species at most sites.

Contrary to expectations, we did not find a statistically significant effect of environmental variation on social organization flexibility, though the relationship was in the expected direction. For the taxa included in this study, primate species

Table 4 Results of phylogenetic models predicting social organization flexibility based on a coefficient of variation approach

Model	Predictor	Slope	<i>t</i> value	<i>p</i> value	<i>r</i> ²	Lambda	AIC
1	Environmental variation	−0.033	−0.483	0.632	0.008	0.947	19.07
2	Mean rain seasonality	0.505	1.863	0.072	0.104	0.936	15.77
3	Absolute brain size	0.552	2.653	0.012	0.190	0.880	12.56
4	Relative brain size	0.859	1.623	0.086	0.081	0.906	16.54
5	Fission–fusion	0.434	2.987	0.006	0.229	0.853	11.05
6 ^a	<i>Group size</i>	<i>0.791</i>	<i>9.785</i>	<i><0.001</i>	<i>0.761</i>	<i>0.000</i>	<i>−25.46</i>
7 ^a	Combined model A			<0.001	0.761	0.000	−23.18
	Absolute brain size +	0.004	0.040	0.968			
	Group size	0.790	8.531	<0.001			
8	Combined model B			0.001	0.325	0.882	9.01
	Absolute brain size +	0.415	2.055	0.049			
	Fission–fusion	0.348	2.406	0.022			
9 ^a	<i>Combined model C</i>			<i><0.001</i>	<i>0.765</i>	<i>0.000</i>	<i>−23.60</i>
	<i>Group size +</i>	<i>0.772</i>	<i>8.794</i>	<i><0.001</i>			
	<i>Fission–fusion</i>	<i>0.056</i>	<i>0.617</i>	<i>0.542</i>			
10 ^a	Combined model D			<0.001	0.765	0.000	−21.60
	Absolute brain size +	−0.001	−0.001	0.994			
	Group size +	0.772	7.871	<0.001			
	Fission–fusion	0.056	0.605	0.55			
11	Full model			<0.001	0.777	0.000	−14.33
	Environmental variation	0.009	0.171	0.866			
	Mean rain seasonality	0.023	0.108	0.915			
	Absolute brain size	0.070	0.590	0.561			
	Relative brain size	−0.285	−1.000	0.327			
	Fission–fusion	0.045	0.467	0.644			
	Group size	0.798	6.905	<0.001			

Sample size equals 32 species for all models. The model with the lowest AIC value is considered best and all models within two AIC units are considered equally good. These models are in italics

^a *Cebus capucinus* was an outlier in several analyses. Re-analyzing the dataset without this species produced similar results

with populations living in several different habitat types were equally as flexible in their social organizations as those found in only a narrow range of habitats. This result was unexpected, given that resource availability is among the primary factors thought to influence primate social organization. Several studies have shown that environmental factors are intimately tied to plant diversity and abundance (Murphy and Lugo 1986; Chapman et al. 1999). Because almost all primates rely on plant parts as their major dietary constituent, then environmental factors influencing variation in habitat characteristics such as plant diversity, abundance, and distribution should have a significant impact on a species' behavioral ecology, including its population density and biomass (Oates et al. 1990), the size and composition of social groups (Snaith and Chapman 2007; Teichroeb and Sicotte 2009; but see Chapman and Pavelka 2005), and the resulting patterns (i.e., degree and type) of intra- and intergroup food competition

(van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig 2002). Thus, one might expect species living in diverse habitats with varying degrees of resource availability to exhibit correspondingly diverse responses in terms of group size, composition, and feeding competition. For example, there is evidence to suggest that variation in resource availability, and perhaps also predator pressure, has helped to shape the size and composition, as well as the nature of social relationships and ranging patterns across various chimpanzee communities (discussed in Lehmann and Boesch 2005). Communities characterized by high resource abundance (and low predator pressure) supported larger communities of more socially bonded individuals than sites with lower/more patchily distributed resources (and greater predation threat).

In addition to shaping the vegetative characteristics of a locale, environmental factors may also be related to the predator community at a site. If different habitat types contain

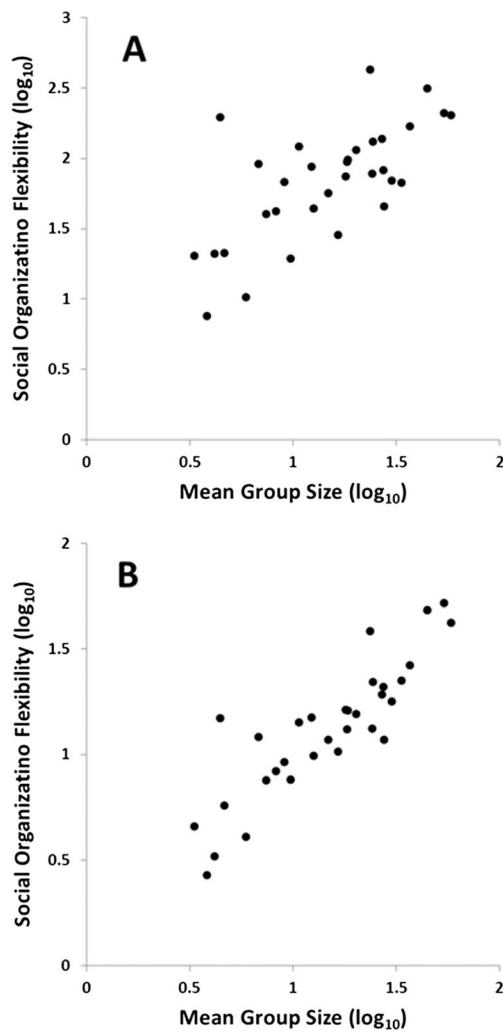


Fig. 4 The relationship between mean group size and social organization flexibility across primates. **a** Social organization flexibility was quantified based on a weighted multivariate variance approach. **b** Social organization flexibility was quantified based on a coefficient of variation approach

different types and abundances of predators, then this would directly impact the social organization of the primates inhabiting those locations. In fact, predation risk has been argued as a primary force driving the formation of animal social groups (Crook 1970; Alexander 1974; Terborgh and Janson 1986). Unfortunately, predation pressure is difficult to measure, particularly on a large, comparative/cross-site scale (Janson 2003). Likewise, although there is a large body of literature detailing the human exploitation of primates (Oates 2013), it is equally difficult to quantify intersite human hunting pressure, despite its demonstrated impact on primate grouping patterns (e.g., Papworth et al. 2013).

Although our environmental variables have been successfully used in the past to predict various aspects of primate biology (Hemingway and Bynum 2005; Nunn et al. 2005;

Ossi and Kamilar 2006; Kamilar and Beaudrot 2013), incorporating climate data from years that did not specifically match our social organization data (as these data were often absent from the literature) may have introduced a significant amount of “error” that obscured any relationship, especially given our relatively small sample size.

All species exhibit at least some constraints to their social organization variation (Chapman and Pavelka 2005; Ossi and Kamilar 2006; Chapman and Rothman 2009; Thierry 2013). Therefore, some species may be found in a wide range of habitats and environmental contexts and display social organization variation across these environments, yet the degree to which social organization varies may not match the degree of environmental variation. For instance, baboons are found in a wide array of habitats and vary in their social organization (Kamilar 2006b), though no population is known to regularly form monogamous social groups or groups with a highly skewed adult sex ratio. In addition, a previous study showed that across-population variation in *Eulemur* social organization was best predicted by phylogeny and not local environmental factors (Ossi and Kamilar 2006). Taxonomically broader studies also found that many components of social organization are correlated to phylogeny (DiFiore and Rendall 1994; Kamilar and Cooper 2013). Finally, other researchers place less importance on ecological factors for directly driving variation in mammal (including primate) social structure (Lukas and Clutton-Brock 2013). They argue that variation in the ability of males to defend access to females is a more important factor leading to variation in social systems and, consequently, social organization. Our results may lend support to certain aspects of this idea.

This current paper complements previous studies in that we found at least some degree of social organization flexibility in many species, though even these species have limits to this variation (Ossi and Kamilar 2006; Kappeler et al. 2013; Thierry 2013). Our findings improve our understanding of the factors driving social organization flexibility in primates and begin to address the possible reasons for why some species exhibit more flexibility than others. Future work would benefit from the inclusion of additional site-specific variables, such as resource availability; the presence, density, and diversity of predator communities; and anthropogenic pressures such as hunting, as well as climatic variables specific to the region at the time of the study.

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