Socioecological Correlates of Facial Mobility in Nonhuman Anthropoids

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ABSTRACT

Facial mobility, or the variety of facial movements a species can produce, is likely influenced by selection for facial expression in diurnal anthropoids. The purpose of this study is to examine socioecological correlates of facial mobility independent of body size, focusing on social group size and arboreality as possible evolutionary agents. Group size was chosen because facial expressions are important for group cohesion, while arboreality may limit the utility of facial expressions. Data for 12 nonhuman anthropoid species were taken from previous studies and analyzed using a phylogenetic generalized least-squares approach. Regression results indicate that group size is a good predictor of facial mobility independent of body size. No statistical support was found for the hypothesis that arboreality constrains the evolution of facial mobility. The correlation between facial mobility and group size may be a consequence of selection for more effective facial expression to help manage conflicts and facilitate bonding in larger groups. These findings support the hypothesis that the ultimate function of facial expression is related to group cohesion.

Primates rely on facial expressions for communication more so than any other mammal (Burrows, 2008). Facial displays are adaptive signals in group contexts because they provide information about the sender's immediate future behavior in a given social interaction (Andrew, 1963; van Hooff, 1967; Goosen and Kortmulder, 1979). Despite the adaptive value of facial expression, not all primates rely on this form of communication to the same degree (Gautier and Gautier-Hion, 1977; Moynihan, 1967; Redican, 1975). This is due in part to allometric constraints on facial mobility, or the variety of facial movements a species can produce (Dobson, in press). Smaller-bodied anthropoids produce fewer movements than larger species. As a result, smaller species may be limited with regard to the complexity and/or effectiveness of facial expression.

Allometric constraints on facial mobility may not be due to body size per se, but rather to size-correlated visual acuity (Dobson, in press). This is based on the observations that larger-bodied species have larger eyes and therefore greater visual acuity than smaller species (Kiltie, 2000; Ross and Kirk, 2007; Walls, 1942). If the evolution of facial expression is contingent upon preexisting adaptations of the visual system (e.g., van Hooff 1962, 1967), then smaller-bodied species would be expected to produce fewer facial movements. This assumes that the adaptive value of complex facial expression is diminished in species that have limited visual acuity. The strong interspecific correlation between body mass and facial mobility supports this hypothesis (Dobson, in press). Regardless of the reasons for this allometric effect, it is clear that body size should be considered a confounding variable in comparative studies of facial expression from a statistical perspective.

While the interspecific correlation between facial mobility and body size is strong, some species deviate from the allometric pattern. This is illustrated by comparing *Gorilla gorilla* with

Pan troglodytes. Both species produce the same number of facial movements (Table 1). However, gorillas are more than twice the size of common chimpanzees in terms of body mass (Smith and Jungers, 1997). This implies a marked contrast in size-adjusted facial mobility, with *P. troglodytes* producing a greater variety of facial movements than would be expected for an anthropoid of similar size. Moreover, common chimpanzees use a variety of complex facial displays to communicate (van Hooff, 1973; Parr et al., 2005), while visual communication in gorillas is oriented more toward bodily gestures (Pika et al., 2003). Thus, facial mobility may be influenced by selection for facial expression in species, such as *P. troglodytes*, that rely more heavily on this form of communication due to socioecological pressures (Andrew, 1963).

The purpose of this study is to build upon previous work concerning the allometry of facial mobility (Dobson, in press) by examining socioecological correlates of facial mobility in nonhuman anthropoids, independent of body size. Identifying the most likely correlates of facial mobility requires understanding the evolutionary ecology of facial expression.

Facial expressions are used in a variety of aggressive, submissive, and affinitive behavioral contexts (van Hooff, 1962, 1967; Redican, 1975, 1982). These signals appear to enhance group cohesion by facilitating conflict management and social bonding (Maestripieri, 1999). This is illustrated by the classic example of the silent bared-teeth (SBT) display, which is a common expression used by anthropoid primates (Preuschoft and van Hooff, 1997). The basic components of the SBT (van Hooff, 1967) are (1) raising the upper lip, (2) lowering the bottom lip, and (3) retracting the lip corners. The mouth is usually closed and no vocalizations are uttered. This signal is thought to be homologous to the human smile (van Hooff, 1972; Preuschoft, 1992; Waller and Dunbar, 2005; Parr et al., 2007).

The meaning of the SBT depends on the species, but it is generally a submissive and/or affinitive display (Preuschoft and van Hooff, 1995, 1997). In some species of macaque, the SBT is used as a formal sign of subordination when performed by a lower-ranking individual in response to the approach of a more dominant animal (de Waal and Luttrell, 1985; Flack and de Waal, 2007). Similarly, the SBT is often a submissive signal that serves an appeasing function by inhibiting the aggressive behavior of the receiver during an agonistic encounter (Preuschoft and van Hooff, 1997). This can be followed by reconciliation and affiliation in some species (Preuschoft, 1992). In contrast, other species use the SBT only in affinitive interactions (Preuschoft and van Hooff, 1997), and never in response to aggression (Visalberghi et al. 2006; De Marco et al., 2008). For example, the use of the SBT among Tonkean macaques (*M. tonkeana*) does not correlate with measures of dominance or subordination, but facilitates social play in this species (Thierry et al., 1989). Mandrills (*Mandrillus sphinx*) and common chimpanzees (*P. troglodytes*) also use the SBT to promote peaceful interaction and social bonding in non-agonistic contexts (Bout and Thierry, 2005; Waller and Dunbar, 2005). These examples clearly illustrate the relevance of facial expression to the problem of group cohesion in primates (Maestripieri, 1999).

The problem of group cohesion itself is a function of group size. Larger groups are inherently less cohesive than smaller groups (e.g., Lehmann and Boesch, 2004), due to increased within-group competition for resources (Sterck et al., 1997) and time constraints on social bonding (Lehmann et al., 2007). Therefore, as species evolve to live in larger groups for ecological reasons, such as reducing the risks of predation (van Schaik, 1983), behaviors that facilitate group cohesion will be favored by natural selection (e.g., Dunbar, 1993). This is supported by the fact that species that live in larger groups spend more time grooming and have

larger vocal repertoires than less gregarious species (Dunbar, 1991; Kudo and Dunbar, 2001; McComb and Semple, 2005; Lehmann et al., 2007). Similarly, I suggest that facial mobility and group size have evolved in a correlated fashion as a consequence of selection for facial expression to facilitate group cohesion as group size increases. The basic prediction of this hypothesis is that facial mobility is positively correlated with social group size, controlling for body size.

Another potential factor influencing the evolution of facial mobility relates to the transmission properties of facial expression. Facial displays may be transmitted more effectively in terrestrial versus arboreal contexts (Chevalier-Skolnikoff, 1973; Redican 1975, 1982). This is because dense foliage results in visual barriers and dim lighting conditions (Kingdon, 2007; Preuschoft and Preuschoft, 1994). I hypothesize that the adaptive value of facial expression is diminished in tree-dwelling species compared to more terrestrial species, because of limited visibility in arboreal contexts. As species become more terrestrial, this constraint is released and the opportunity for complex facial expression arises. The main prediction of this hypothesis is that arboreal species produce fewer distinct facial movements than terrestrial species, controlling for body size.

To test the predictions of the aforementioned hypotheses, I will focus on social group size and arboreality as correlates of size-adjusted facial mobility. This study has broad implications for the adaptive evolution of facial expression in primates, including humans.

MATERIALS AND METHODS

Comparative data

My comparative sample consists of 12 nonhuman anthropoid species representing three superfamilies (Table 1). I defined facial mobility as the number of visually distinct facial

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movements a species can produce (Dobson, in press). Values were estimated using a subset of

the Facial Action Coding System, or FACS (Ekman et al., 2002a,b). FACS is a detailed

inventory of the observable consequences of all possible facial muscle contractions in humans

(Ekman and Friesen, 1976; Waller et al., 2006). These are referred to as action units, or AUs. I

applied FACS to video recordings of facial activity in zoo animals as a way to estimate facial

mobility for comparative purposes. For example, *Hylobates concolor* has a facial mobility

estimate of 8 AUs, while *Macaca silenus* has an estimate of 10 AUs (Table 1). Thus, by this

measure, *M. silenus* has greater facial mobility than *H. concolor*. See Dobson (in press) for

further details regarding this approach.

Group size data were taken from Nunn and van Schaik (2001). Group size, or the mean

number of individuals in a group, is a common measure of sociality in comparative studies

(Barton 1998; Dunbar, 1992; Lehmann et al., 2007; McComb and Semple, 2005; Nunn et al.,

2003; Sherwood et al., 2005). For most diurnal anthropoids, group size is a relatively

unambiguous aspect of social organization. However, determining this value for *Ateles geoffroyi*,

Pan troglodytes, and *Papio hamadryas* can be problematic. The former two species live in

fission-fusion societies in which one large community breaks up into smaller, temporary

subgroups for the purposes of foraging (Mitani et al., 2002; Stumpf, 2007; Symington, 1990).

Similarly, Hamadryas baboons exhibit a multilevel society in which group size can be measured

at several hierarchical levels of organization, such as the one-male unit, clan, or band (Abegglen,

1984; Kummer, 1968; Stammbach, 1987). Given these considerations, I followed the

recommendations of Dunbar (1991, 1992) in defining group size at the level of the community in

species with fission-fusion grouping patterns and at the band level in species with multilevel

societies. This is based on the assumption that the highest level at which aggregations exhibit

long-term stability and cohesion is the most appropriate level of organization for analyzing group size in comparative studies.

Species were classified as arboreal or terrestrial according to Nunn and van Schaik (2001). Semi-terrestrial species (e.g., *Cercopithecus neglectus*) were lumped together with terrestrial species. Female mean body mass (g) was used as a measure of species body size. These data were taken from Smith and Jungers (1997).

Statistical analysis

Trait correlations were examined using multiple regression analysis with facial mobility as the dependent variable. The independent effects of body mass, group size, and arboreality were examined by entering all three variables into the regression model as predictors. Arboreality was dummy-coded and treated as a continuous independent variable, which is equivalent to an analysis of covariance (Cohen and Cohen, 1983). Body mass and group size were log-transformed (base 10) prior to analysis. I did not transform facial mobility because of its relatively compressed range of variation.

I incorporated phylogenetic information into the regression analysis because interspecific data are prone to violating assumptions of independence required by conventional statistical methods (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Hansen, 1996; Nunn and Barton, 2001). With regard to multiple regression, the main concern is whether or not the residuals are independently distributed (Martins and Hansen, 1997; O'Neill and Dobson, 2008). Residual independence can be attained directly by modifying the error structure of the regression using the phylogenetic generalized least-squares (PGLS) approach (Garland and Ives, 2000; Grafen, 1989; Martins and Hansen, 1997; Rohlf, 2001). This method can be used to analyze a

combination of continuous and categorical variables within an analysis of covariance framework (Martins and Hansen, 1996). The evolutionary assumptions of PGLS are outlined in detail below.

Statistical dependence among interspecific data, including regression residuals, is due to phylogenetic signal (Blomberg and Garland, 2002). Phylogenetic signal is maximized when species differences increase as a linear function of phylogenetic distance (Diniz-Filho, 2001; Hansen and Martins, 1996; Martins, 1994). This pattern is linked to a Brownian-motion model of evolution (Felsenstein 1985, 1988). Brownian motion assumes that changes at each generation accumulate at a constant rate and are independent of changes that occurred in previous generations (Blomberg et al., 2003; Díaz-Uriarte and Garland, 1996; Garland et al., 1993; Martins and Garland, 1991). As such, the degree of difference between any two species for a given trait is determined solely by the amount of time the species have been diverged from each other. Thus, the covariance among species values is phylogenetically structured, rendering the data statistically dependent (Martins, 1995). Brownian motion is compatible with genetic drift and other stochastic evolutionary processes (Felsenstein, 1988; Hansen and Martins, 1996).

The PGLS approach is based on an Ornstein-Uhlenbeck model of evolution (Butler and King, 2004; Felsenstein, 1988; Hansen, 1997). This model is essentially Brownian motion with the addition of a single parameter representing an "adaptive constraint" (Martins et al., 2002). Ornstein-Uhlenbeck requires that stochastic evolution be restricted by a force proportional to the difference between the trait value and a fixed primary optimum (Blomberg et al., 2003; Díaz-Uriarte and Garland, 1996; Garland et al., 1993; Martins et al., 2002). As this difference increases, the pull back towards the optimum gets stronger. This is referred to as a "rubber-band" effect (Martins et al., 2002). The strength of this effect determines the extent to which a trait will tend to resemble its optimal value or will be free to diverge in a stochastic fashion. Ornstein-

Uhlenbeck is compatible with genetic drift restricted by stabilizing selection (Felsenstein, 1988; Hansen and Martins, 1996). It is important to note that strong stabilizing selection erases phylogenetically-structured variance produced by stochastic evolution, thereby reducing phylogenetic signal (Blomberg et al., 2003; Revell et al., 2008).

The error term in PGLS regression is a variance-covariance matrix, which is weighted by a phylogenetically-informed scaling parameter (Garland and Ives, 2000; Martins and Hansen, 1997; Rohlf, 2001). This parameter is referred to as α by Martins and Hansen (1997), or more recently a_C by Martins et al. (2002). It represents the composite rubber-band effect in an Ornstein-Uhlenbeck model of correlated evolution between two or more traits (Martins et al., 2002). Given the above considerations, it is possible to interpret the magnitude of a_C with regard to different evolutionary mechanisms. When $a_C = 0$, phylogenetic signal among the regression residuals is maximized and there is no rubber-band effect. This pattern is compatible with correlated evolution by means of genetic drift. As a_C increases, phylogenetic covariance among the residuals decreases, corresponding to an increasingly strong rubber-band effect. Thus, larger values of a_C are compatible with correlated evolution restricted by strong stabilizing selection. The PGLS approach estimates regression coefficients and standard errors using the phylogenetically-informed error structure based on a_C. Felsenstein's (1985) method of independent contrasts is equivalent to PGLS under a Brownian-motion model of correlated evolution, or when $a_C = 0$ (Martins et al., 2002; Rohlf, 2001).

I performed PGLS multiple regression using COMPARE version 4.6b (Martins, 2004). The requisite phylogenetic tree was taken from a larger composite primate phylogeny (Smith and Cheverud, 2002). With regard to the species in my sample, the topology of this tree is identical to a recent "supertree" for Mammalia that includes the order Primates (Bininda-Emonds et al.,

2007). Maximum-likelihood was used to estimate a_C within the range 0 to 15.5, because values greater than 15.5 approximate the error structure of conventional, non-phylogenetic regression (Martins et al., 2002). COMPARE does not report P values, but instead provides standard errors that can be used to construct confidence intervals for hypothesis testing. If the residuals are independent, normally-distributed, and homoscedastic, then a traditional 95% confidence interval is ± 1.96 standard errors. A statistically significant effect ($P < 0.05$) is indicated by a regression-slope confidence interval that does not contain zero.

RESULTS

Figure 1 presents a scatter-plot matrix depicting the relationships among the variables of interest: facial mobility, body mass, group size, and arboreality. The three continuous variables are correlated in a positive fashion, such that larger-bodied species tend to live in larger groups and produce a greater variety of facial movements. On average, terrestrial species exhibit greater facial mobility than arboreal species, with median values of 12 and 8.5 AUs respectively. Terrestrial species also tend to be larger and live in larger social groups than arboreal species. Thus, there is no visual indication of a grade shift between terrestrial and arboreal species in any of the scatter plots. Multiple regression analysis supports these observations.

Results of the multiple regression analysis based on phylogenetic generalized least squares (PGLS) are presented in Table 2. The regression model explains 98% of the variance in facial mobility. Tests of normality indicate that the PGLS residuals satisfy the distributional assumptions required to use confidence intervals for hypothesis testing. The regression-slope confidence intervals for body mass and group size do not contain zero, indicating statistically significant partial effects for each variable. In contrast, differences between terrestrial and arboreal species, controlling for the effects of body mass and group size, are not statistically

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significant. The regression slope for body mass is larger than for group size. Nonetheless, group size is a significant predictor of facial mobility, controlling for body mass (Fig. 2).

These results can be interpreted in light of different evolutionary mechanisms with regards to a_C. This parameter represents the strength of the rubber-band effect in an Ornstein-Uhlenbeck model of correlated evolution (see above). If the pattern of covariance was not governed by a rubber-band effect, then the maximum-likelihood estimate of a_C would be zero. This is the expectation under a Brownian-motion model of correlated evolution. However, the estimated value of a_C in my sample is 8.44. Thus, an evolutionary mechanism akin to Brownian motion (e.g., genetic drift) cannot account for the correlated evolution of facial mobility, body size, and group size in my sample. Conversely, I cannot rule out stabilizing selection as a possible cause of this pattern of covariance because a_C is well above zero. Thus, it is appropriate to interpret my regression results within an adaptive framework.

It should be noted that a potential problem in multiple regression analysis is "shrinkage" (Darlington, 1990). This happens when the ratio of cases to variables is low (e.g., < 10:1). My analyses were based on a ratio of ~ 3:1. Thus, the parameter estimates may be unreliable. In addition, when collinearity is high among the predictor variables in a multiple regression, the coefficients may be prone to error (Petraitis et al., 1996). Despite these issues, the overall effect of sociality on variation in facial mobility appears robust (see below).

DISCUSSION

The results of this study demonstrate that social group size is a good predictor of facial mobility, independent of body size. Species that live in larger social groups tend to produce a greater variety of facial movements than expected from body size alone. This suggests that as diurnal species evolve to live in larger groups, thereby reducing the risks of predation (van

Schaik, 1983), natural selection favors increased facial mobility for more effective facial expression. Given the importance of facial displays in conflict management and social bonding (e.g., De Marco et al., 2008; Flack and de Waal, 2007; Waller and Dunbar, 2005), the correlation between facial mobility and social group size implies that the ultimate function of facial expression is group cohesion (Maestripieri, 1999).

The effect of sociality appears to go beyond group size. For example, there are marked differences in social organization between the species with the highest and lowest values of size-adjusted facial mobility (Table 3). At one end of the spectrum, *Macaca silenus*, *Papio hamadryas*, and *Pan troglodytes* have high facial mobility for their body size and live in relatively-complex multimale groups, including fission-fusion and multilevel societies (Stammbach, 1987; Menard, 2004; Stumpf, 2007). In contrast, *Hylobates concolor*, *Gorilla gorilla*, and *Cercopithecus neglectus* have low facial mobility for their body size and live in smaller unimale or two-adult groups (Fuentes, 2000; Enstam and Isbell, 2007; Robbins, 2007). Thus, the evolution of more complex grouping patterns appears to be associated with increases in the variety of facial movements a species can produce.

This pattern mirrors the results of comparative studies of vocal communication in primates, rodents, and birds (Blumstein and Armitage, 1997; Freeberg, 2006; McComb and Semple, 2005). McComb and Semple (2005) examined the evolutionary relationships between vocal repertoire size and two measures of sociality in nonhuman primates, group size and grooming time. They found that species that are more social have a greater variety of calls in their repertoire. Blumstein and Armitage (1997) examined the relationship between alarm call repertoire size and a demographic measure of social complexity in sciurid rodents. They found that species with more complex grouping patterns tend to exhibit a larger number of calls.

Freeberg (2006) examined call complexity within a single species, the Carolina chickadee (*Poecile carolinensis*). He found that the complexity of the "chick-a-dee" call was correlated with group size, such that individuals living in larger groups produce a greater variety of notes in their calls on average. Thus, the correlated evolution of sociality and communication appears to be a recurrent pattern among vertebrates.

Although I did not include *Homo sapiens* in the analysis, the results of this study have implications for the evolution of human facial expression. Humans exhibit adaptations for facial expression, including universally recognized displays corresponding to six basic emotions (Ekman, 1999a,b) and a common set of facial muscles necessary to generate these displays (Waller et al., 2008). If group size is an important influence on the evolution facial expression in nonhuman anthropoids, then it follows that selection for group cohesion may be responsible for the elaboration of facial expression in humans as well. Facial expressions used in long-term, cooperative interactions are likely to have positive fitness consequences for humans (Schmidt and Cohn, 2001). For example, people who smile more often are generally perceived to be more sociable (Matsumoto and Kudoh, 1993), whereas those who do not smile effectively due to facial paralysis can experience social difficulties (VanSwearingen et al., 1999). Thus, if fossil hominins tended to live in relatively large groups from the early Pliocene onward (Dunbar, 2003), then the human lineage is likely to have experienced significant selection pressure favoring facial expression for 3.5 million years or more.

While the effect of sociality on the evolution of facial mobility is apparent, the adaptive value of increased facial mobility with regard to facial expression is less clear. There are at least three possible reasons why natural selection might favor increased facial mobility. First, a species that can produce a greater number of facial actions can generate more combinations of

movements, thereby increasing the total number of facial displays in their behavioral repertoire. Second, the addition of new movements to existing displays may also increase the intensity of the signal, allowing the receiver to better assess the strength of the sender's motivations. Last, adding facial actions to any given display may increased the conspicuousness of the signal, thereby increasing the likelihood that it is received by the target (e.g., Visalberghi et al., 2006).

A related issue concerns facial pelage color patterns, such as the permanently visible "facial flags" found among members of the genus *Cercopithecus* (Kingdon, 1980, 1988, 1992, 2007). If facial color patterns augment facial expression in the absence of enhanced facial mobility, then the correlation between facial mobility and group size might be misleading. For example, if the distinct white beard and orange brow patch of *C. neglectus* (Kingdon, 1980) increases the effectiveness of facial expression, then the relatively small group sizes characteristic of this species (Table 3) would suggest a lack of correlation between group size and facial expression effectiveness. However, according to Kingdon (1980), facial pelage in guenons did not evolve primarily to augment facial expression, but to enhance reproductive isolation as part of species-specific mate recognition systems. Any role in making facial expressions more conspicuous is a secondary consequence (Kingdon, 1988). Furthermore, elaborate facial coloring can actually obscure and detract from facial movements, such that the benefits of facial patterns must outweigh the costs of more opaque expressions (Kingdon, 2007). Thus, the evolution of complex facial color patterns is an unlikely alternative to increased facial mobility as a means of enhancing facial expression.

The results of the present study appear to contradict the results of a recent comparative analysis of facial motor control in primates. Sherwood et al. (2005) examined the relationship between facial nucleus volume and social group size in primates. The volume of the facial

nucleus is an estimate of the absolute number of motor neurons that travel to the muscles of facial expression. As such, it is a measure of the degree of facial motor control, which is presumably an important factor in the evolution of facial expression. However, Sherwood et al. (2005) did not find a statistically significant correlation between facial nucleus volume and group size. This may be explained by the fact that their sample of 47 species included various strepsirrhines, as well as the nocturnal haplorrhines *Tarsius syrichta* and *Aotus trivirgatus*. These taxa have probably not been subject to strong selection for facial expression for two reasons. First, with regard to strepsirrhines, having an upper lip tethered to the maxilla in association with a moist rhinarium may limit the variety of facial movements a species can produce (Kingdon, 1992; Martin, 1990). Second, for nocturnal species, the low-contrast lighting conditions associated with nighttime activity would likely impede quick and accurate processing of complex facial displays. Thus, when testing hypotheses regarding the evolution of facial expression, it may be important to focus on diurnal anthropoids only.

Despite strong support for the hypothesis of correlated evolution between facial mobility and group size, the issue of arboreality as a constraint on facial mobility is not resolved. While terrestrial species tend to produce a greater variety of facial movements than arboreal species on average, this effect is not statistically significant at the 0.05 level. One explanation is that arboreality is correlated with body size, such that larger species tend to be more terrestrial. Given that body size and facial mobility are strongly correlated, it may be difficult to separate the independent effects of arboreality and body size. Furthermore, I treated arboreality as a dichotomy between arboreal and terrestrial (e.g., Nunn and van Schaik, 2001). Broad categorizations such as these may not be sensitive enough to demonstrate statistical associations in phylogenetic comparative analyses (Garland et al., 1993). Moreover, the sample sizes for each

group are relatively small thereby limiting statistical power. Thus, my data only weakly support the hypothesis that arboreality is a constraint on the evolution of facial expression (e.g., Chevalier-Skolnikoff, 1973; Redican, 1975).

ACKNOWLEDGEMENTS

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TABLE 1. Comparative data

Species	Facial mobility[a]	Body mass[b]	Group size[c]	Arboreality[d]
Alouatta caraya	8	4,300	7.9	yes
Ateles geoffroyi	9	7,290	22.7	yes
Cercopithecus neglectus	7	4,130	6.7	no
Colobus guereza	9	9,200	9.9	yes
Gorilla gorilla	13	71,500	15.8	no
Hylobates concolor	8	7,620	5.2	yes
Macaca silenus	10	6,100	16.6	yes
Pan troglodytes	13	33,700	47.6	no
Papio hamadryas	11	9,900	37.8	no
Pithecia pithecia	5	1,580	2.6	yes
Saguinus oedipus	3	404	5.3	yes
Trachypithecus obscura	9	6,360	13.7	yes

[a] Number of visually distinct facial movements (action units) from Dobson (in press).

[b] Female body mass (g) from Smith and Jungers (1997).

[c] Average social group size from Nunn and van Schaik (2001).

[d] Classification based on the amount of time spent on the ground. "Yes" = exclusively arboreal.

"No" = semi-terrestrial or terrestrial. Data from Nunn and van Schaik (2001).

TABLE 2. Results of multiple regression based on phylogenetic generalized least squares[a]

R^2	Predictor	Slope (b)	Standard error	Confidence interval[b]
0.98	Body mass	3.91	0.36	3.20, 4.62
	Group size	2.64	0.53	1.60, 3.68
	Arboreality	-0.23	0.36	-0.94, 0.48

[a] Dependent variable: facial mobility. See text for details.

[b] 95% confidence limits for b (lower, upper). Calculated as $b \pm 1.96$*standard error. Assumptions of normality for regression residuals cannot be rejected based on one-sample Kolmogorov-Smirnov test ($P > 0.05$). Intervals that do not overlap zero indicate a statistically significant partial effect.

TABLE 3. Social patterns for the species with the highest and lowest values of size-adjusted

facial mobility

Species[a]	Group size[b]	Grouping pattern(s)[b]
Highest		
Macaca silenus	12-43	Multimale/multifemale
Papio hamadryas	42-82	Multilevel society
Pan troglodytes	15-150	Fission-fusion society
Lowest		
Cercopithecus neglectus	3-13	Unimale/multifemale, two-adult group
Gorilla gorilla	2-40	Unimale/multifemale
Hylobates concolor	2-11	Two-adult group

[a] Species listed in descending order of size-adjusted facial mobility. Based on residuals

calculated from ordinary least-squares regression with body mass as the independent variable.

[b] References: *C. neglectus* (Enstam and Isbell, 2007); *G. gorilla* (Robbins, 2007); *H. concolor*

(Fuentes, 2000); *M. silenus* (Menard, 2004); *P. troglodytes* (Stumpf, 2007); *P. hamadryas*

(Stammbach, 1987).

FIGURE LEGENDS

Fig. 1. Scatter-plot matrix depicting the patterns of correlation between facial mobility, body mass, group size, and arboreality in 12 nonhuman anthropoids. Closed circles indicate terrestrial and semi-terrestrial species. Open circles indicate species that are exclusively arboreal.

Fig. 2. Scatter plot illustrating the relationship between facial mobility and social group size after controlling for the effects of body size. Values represent ordinary least-squares residuals based on bivariate regression with body mass as the independent variable. The species are: Ac = *Alouatta caraya*; Ag = *Ateles geoffroyi*; Cn = *Cercopithecus neglectus*; Cg = *Colobus guereza*; Gg = *Gorilla gorilla*; Hc = *Hylobates concolor*; Ms = *Macaca silenus*; Pt = *Pan troglodytes*; Ph = *Papio hamadryas*; Pp = *Pithecia pithecia*; So = *Saguinus oedipus*; To = *Trachypithecus obscura*.
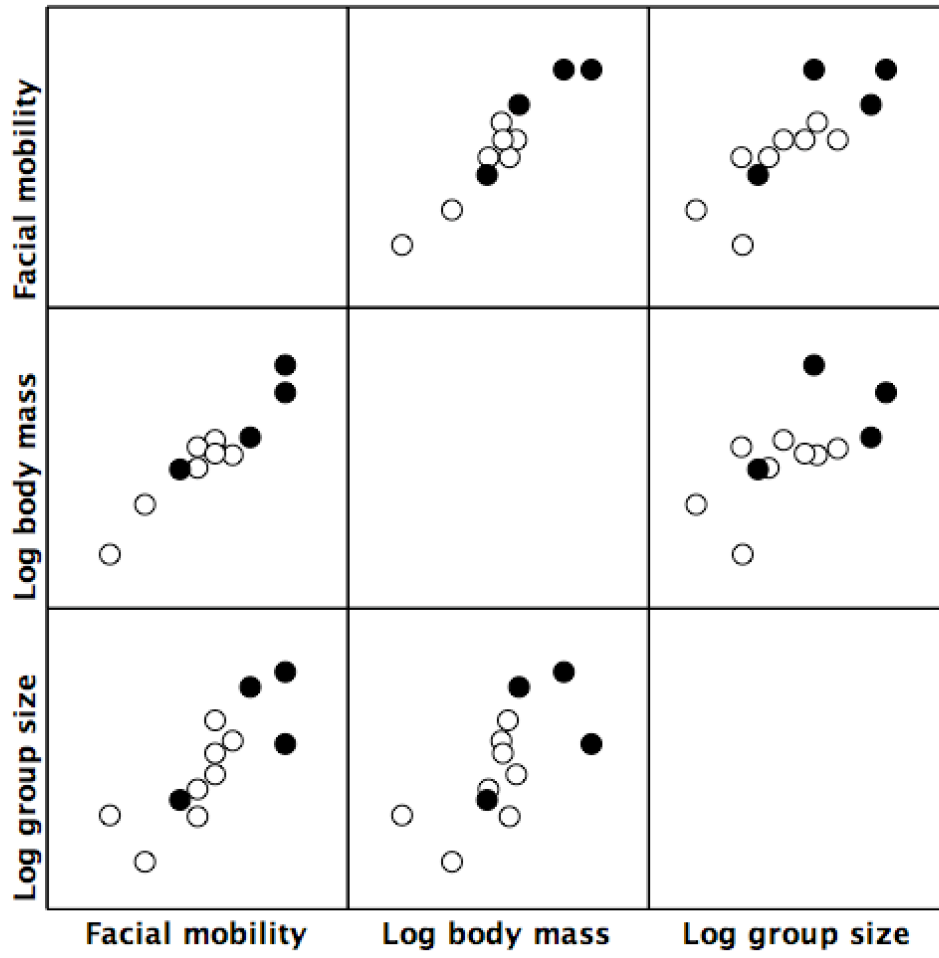
Fig. 1

Fig. 2