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Adrian V. Jaeggi
Emory University

Karen Kramer
University of Utah

Raymond Hames
University of Nebraska - Lincoln

Evan J. Kiely
Emory University

Cristina Gomes
University of Miami

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Authors

Adrian V. Jaeggi, Karen Kramer, Raymond Hames, Evan J. Kiely, Cristina Gomes, Hillard Kaplan, and Michael Gurven

Human grooming in comparative perspective: People in six small-scale societies groom less but socialize just as much as expected for a typical primate

Adrian V. Jaeggi[1,*], **Karen L. Kramer**[2,*], **Raymond Hames**[3,*], **Evan J. Kiely**[1], **Cristina Gomes**[4], **Hillard Kaplan**[5], and **Michael Gurven**[6]

[1]Department of Anthropology, Emory University, Atlanta, GA 30322

[2]Department of Anthropology, University of Utah, Salt Lake City, UT 84112

[3]Department of Anthropology, University of Nebraska Lincoln, Lincoln, NE 68588

[4]Department of Psychology, University of Miami, Coral Gables, FL 33124

[5]Department of Anthropology, University of New Mexico, Albuquerque, NM 87131

[6]Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA 93106

Abstract

Objectives—Grooming has important utilitarian and social functions in primates but little is known about grooming and its functional analogues in traditional human societies. We compare human grooming to typical primate patterns to test its hygienic and social functions.

Materials and Methods—Bayesian phylogenetic analyses were used to derive expected human grooming time given the potential associations between grooming, group size, body size, terrestriality, and several climatic variables across 69 primate species. This was compared against observed times dedicated to grooming, other hygienic behavior and conversation among the Maya, Pumé, Sanöma, Tsimane', Yanomamö, and Ye'kwana (mean number of behavioral scans = 23,514).

Results—Expected grooming time for humans was 4% (95% Credible Interval = 0.07%–14%), similar to values observed in primates, based largely on terrestriality and phylogenetic signal (mean $\lambda = 0.56$). No other covariates strongly associated with grooming across primates. Observed grooming time across societies was 0.8%, lower than 89% of the expected values. However, the observed times dedicated to any hygienic behavior (3.0%) or 'vocal grooming', i.e. conversation (7.3%), fell within the expected range.

Conclusions—We found (i) that human grooming may be a (recent) phylogenetic outlier when defined narrowly as parasite removal but not defined broadly as personal hygiene, (ii) there was no support for thermoregulatory functions of grooming, and (iii) no support for the 'vocal grooming' hypothesis of language having evolved as a less time-consuming means of bonding. Thus, human grooming reflects decreased hygienic needs, but similar social needs compared to primate grooming.

*Contributed equally to this work

Keywords

Comparative methods; Evolution of language; Grooming; Primates; Hunter-gatherers

Introduction

Allo-grooming (henceforth: 'grooming'), defined as one individual brushing through another's pelt and removing ectoparasites, dirt, or dead skin, is common in many nonhuman primates (henceforth: 'primates') (Lehmann et al., 2007; Grueter et al., 2013). Grooming serves two broad functions: utilitarian and social. In terms of the former, grooming reduces ectoparasite loads and therefore morbidity and mortality (Hutchins and Barash, 1976; Zamma, 2002; Akinyi et al., 2013), and increases pelt loft and consequently thermoregulatory efficiency (Mcfarland et al., 2015). Given these benefits, it is not surprising that grooming releases rewards such as endorphins (Dunbar, 2010) or oxytocin (Crockford et al., 2013), thereby motivating primates to both give and receive it, often leading to reciprocal exchange (Schino and Aureli, 2008). Once such reward systems evolved, grooming could be co-opted for building and maintaining social relationships, by trading it for other commodities such as coalitionary support or food (Schino et al., 2007; Jaeggi et al., 2013).

The amount of time primates devote to grooming varies widely across species, with some primates spending up to 18% of their time grooming (Lehmann et al., 2007; Grueter et al., 2013). Comparative analyses can therefore provide a powerful tool to determine the functions of grooming by testing for associations with variables indicating utilitarian or social benefits across species. Dunbar (1991) and later Lehmann et al (2007) found group size to be the best predictor of grooming time across some 40 species, concluding that the most important function of grooming was meeting social demands such as building and maintaining alliances, which were thought to increase with group size. In contrast, Grueter et al (2013) found no effect of group size in a larger dataset of 69 species; instead, grooming time was strongly associated with terrestriality, which these authors interpreted as reflecting greater ectoparasite exposure and consequently hygienic need. Whether thermoregulatory demands (Mcfarland et al., 2015) explain variation in grooming time across species has yet to be tested.

How do humans fit into this picture? With regard to utilitarian functions, it could be argued that humans have lower needs than other primates due to loss of body hair and more controlled environments reducing ectoparasite loads, technological innovations like combs or soap increasing grooming efficiency, and the use of clothing replacing thermoregulatory functions of pelt. Human grooming time could therefore represent a phylogenetic outlier (Nunn and Zhu, 2014) if humans spend less time grooming than expected based on typical primate patterns (Prediction 1). This would be similar to decreases in feeding time due to cooking (Organ et al., 2011) and sleep duration due to increased vigilance and opportunity costs (Samson and Nunn, 2015).

In terms of social functions, it has been argued that humans would have had to spend more of their time grooming (42%) than is ecologically viable (i.e. not leaving enough time for

other activities like foraging), based on an association between group size and grooming time in primates, as well as an inferred group size of 147.8 in humans based on an association between group size and neocortex ratio in primates (Dunbar, 1993). According to this 'vocal grooming' hypothesis, conversation evolved as a more efficient, i.e. less time-consuming, way of obtaining the social benefits of grooming in large groups. We generate two predictions from this hypothesis: (i) expected grooming time for humans should fall well above the range of grooming times observed in primates (Prediction 2), and (ii) the observed conversation time should fall well below the expected grooming times (Prediction 3).

Testing these predictions requires detailed quantitative data on time spent grooming and socializing in traditional human societies who are exposed to ectoparasites but have minimal access to health care and hygiene products (high hygienic need), live in tight communities where social support is crucial for fitness (high social need), and produce their own food (high time and energy constraints). These characteristics more closely approximate the conditions of the human past than do people living in contemporary industrialized societies.

Materials and Methods

Study populations

We used time-allocation data collected in six native New World populations: the Maya of Mexico, the Tsimane' of Bolivia, and the Pumé, Sanöma, Yanomamö and Ye'kwana of Venezuela (Table 1; see ESM for ethnographic descriptions). All groups live in humid tropical environments, have limited or no access to modern health care, are self-sufficient food producers (with about 95% of all calories coming from hunting, gathering, fishing, and horticulture), and live in communities similar in size (mean=146) to what has been inferred for ancestral humans (Dunbar, 1993). The Pumé are hunter-gatherers, and the other groups depend on horticulture for the bulk of their calories but spend substantial time foraging for wild foods. All groups are exposed to similar parasite species and body hair coverage is largely limited to the head and pelvic region.

Quantifying grooming time

Human grooming can be defined narrowly as behavior targeted at parasite removal, mostly directed to someone's scalp to remove lice (*Pediculus humanus capitis*). This is the clearest homologue to primate grooming and here simply referred to as *grooming* (see Figure 1). 'Grooming' is also used more broadly colloquially to include other hygienic behaviors such as washing, bathing, or hair care, here summarized as *other hygiene*; note though that these behaviors mostly represent *auto*-grooming instead of *allo*-grooming. We define *vocal grooming* as engaging in conversation as a speaker or attentive listener.

Instantaneous scan sampling was used to quantify time devoted to each of these categories of grooming (Altmann, 1974; Hames, 1992). In all groups, observations were collected during the 11–12 hours of daylight, depending on group. Because study populations did not have access to artificial light, observations were not collected during nighttime hours. Since grooming and other hygiene require good lighting, our daytime sampling method should not

produce biased estimates of grooming time, and therefore should not impede our ability to test Prediction 1. The lack of nighttime observations does probably underestimate time spent vocal grooming, as much conversation in traditional societies occurs at night (Wiessner, 2014), thus making Prediction 3 more likely to be supported.

Comparative data

The largest available dataset on grooming time in primates is that of Grueter et al (2013), which contains terrestriality, group size, and body size as covariates. This dataset has received critique because (i) it lacks several covariates that were included in the smaller Lehmann et al (2007) dataset (e.g. neocortex ratio, predation pressure, dispersal patterns), and because (ii) it includes extreme outliers and uses debatable definitions of group size (Dunbar and Lehmann, 2013). On the other hand, Grueter et al were careful to include only wild, unprovisioned populations, which is crucial for testing Prediction 2 as observed grooming times are subject to other time constraints like foraging, and therefore by definition ecologically viable. We followed best scientific practice of including the most data available and used the Grueter dataset, but addressed the above criticisms by (i) first running our phylogenetic model on the Lehmann dataset to test if any of its unique covariates contributed to explaining grooming time across primates, and (ii) repeating analyses on the Grueter dataset without the extreme outliers and/or with different definitions of group size.

An additional problem for both datasets is the correlation between group size and terrestriality, as group size tends to be larger in terrestrial primates due to increased predation pressure (van Schaik, 1983). Indeed, group size is significantly larger for terrestrial primates in the Lehmann dataset (t=3.21, df=18.2, P<0.01), and in the Grueter dataset when group size is defined at the level of bands and communities (t=2.35, df=24, P<0.05) although not when defined as one-male units and foraging parties, respectively (t=1.22, df=30.7, P=0.23) (even when outliers are excluded). This collinearity complicates the interpretation of terrestriality and group size effects, as either factor appears to eclipse the other depending on the specific sample. This has led to opposing views on whether primate grooming is best explained by hygienic or social benefits (Lehmann et al., 2007; Dunbar and Lehmann, 2013; Grueter et al., 2013). Here, our primary concern is not to resolve this debate, but rather to derive the most accurate expectations for human grooming time. Hence, we repeated all analyses without terrestriality as a covariate to give group size a chance to contribute to the expectations for human grooming time.

To test for thermoregulatory benefits of grooming (Mcfarland et al., 2015) we added several covariates to the Grueter dataset related to climate (Table S1). Specifically, we extracted geographic location for each of the study populations (see Grueter et al's Table S1) and mapped climatic data obtained from worldclim.org (Hijmans et al., 2005) to these locations. Due to the high collinearity among climate variables, we then used variance inflation factors (VIFs) in a backward elimination procedure to reduce the number of covariates (Zuur et al., 2010). Specifically, a full model with all covariates (group size, body size, terrestriality, latitude, altitude, and 12 other climate variables - BIO1 – BIO12) was fit, the covariate with the highest VIF was removed, the reduced model was fit, etc. until all VIFs <3. The climate

covariates retained were latitude, altitude, mean diurnal temperature range (BIO2), isothermality (BIO3), and annual precipitation (BIO12).

Phylogenetic analyses

To derive expectations for grooming time in humans, we used Bayesian phylogenetic prediction following the method and R code provided by Nunn and Zhu (2014). This analysis uses a Markov chain approach to efficiently sample different possible statistical models and generate a distribution of expected values that takes uncertainty in the model and phylogeny into account. Specifically, at each iteration a phylogenetic regression model is fit to a comparative dataset excluding the species of interest (here humans), drawing a selection of covariates from the full candidate model (see below) according to their ability to explain variation in the dependent variable (i.e., grooming), e.g. iteration 1: group size+terrestriality, iteration 2: terrestriality+latitude+altitude, etc. Similarly, one phylogenetic tree out of a large sample is randomly drawn at each iteration. The model then uses the resulting regression coefficients, the estimated phylogenetic signal, and the observed value of the covariates for the species of interest (e.g. human group size = 146, terrestriality = yes, etc.) to calculate an expected value for human grooming time. Summarizing across many iterations, a distribution of expected values is generated. This distribution can be summarized in terms of its *credible intervals* (CI), i.e. the interval containing a certain percentage of samples (e.g. 95%), against which the observed value can be compared. Furthermore, since 95% is an arbitrary cut-off, we present the proportion of values in this distribution that are greater/ lower than the observed value, i.e. the *posterior probability* that the observation is greater/ lower than expected. To conform to the assumption of normality, proportion of time spent grooming was arc-sine square root transformed; group size and body size were log transformed. Thus, the candidate model was:

$$\arcsin(\sqrt{(\text{proportion of time spent grooming})}) \sim \log(\text{group size}) + \log(\text{body size}) + \text{terrestriality} + \text{latitude} + \text{altitude} + \text{mean diurnal temperature range} + \text{isothermality} + \text{annual precipitation}$$

A sample of 100 phylogenetic trees was downloaded from the 10ktrees website version 3 (Arnold et al., 2010), and minor adjustments were made to the dataset to match the available species (see ESM). Each analysis was run for 200,100 iterations with a burnin of 100; every 100th iteration was sampled to obtain a posterior distribution of 2,000 model selections, parameter estimates, and expectations for human grooming time. Plotting time series of parameter estimates confirmed that the Markov chains had converged.

Results

The covariates unique to the Lehmann dataset did not contribute substantially to explaining variation in grooming time across primates (Table S2). Neocortex ratio was included in less than 5% of the models, with an overall parameter estimate of b=0.00 (95% CI=0.00–0.00). Dispersal was included in 10.3% of models (b=0.01, 95% CI=0.00–0.05), predation in 2% (b=0.00, 95% CI=0.00–0.00), and one-male groups in 2.6% (b=0.00, 95% CI=0.00–0.00). Thus, the expectations for grooming time from the Lehmann dataset mostly derived from covariates that are also included in the larger Grueter dataset (group size, body size,

terrestriality), and we proceeded with this larger dataset and the candidate model as specified above.

Table 2 presents the parameter estimates from the analysis of the Grueter dataset. Terrestriality was the dominant predictor of grooming time across species, with social (group size) and climatic factors (latitude, altitude, temperature range, isothermality, precipitation) contributing little. There was significant phylogenetic signal in the model (mean λ = 0.56, 95% CI = 0.22 – 0.86). Hence, expectations for grooming time in humans were largely based on terrestriality and phylogeny.

Figure 2 shows grooming time in primates as a function of group size and terrestriality, with the observed values for human groups plotted for comparison. Figure 3 shows the posterior distribution of expected grooming time in humans (arcsin sqrt mean = 0.20, 95% CI = 0.03 – 0.38; untransformed mean=4.1%, 95% CI = 0.07% – 14.00%), as well as observed grooming times in primates, and the observed mean times devoted to grooming, other hygiene, and vocal grooming across all six human societies (see also Table 1). In weak support of Prediction 1, observed grooming time (0.80%) was lower than 89% of the expected values; in other words, the posterior probability of human grooming representing a phylogenetic outlier was 0.89. However, when considering grooming and other hygiene together (3.0%), the observed value was lower than only 63% of the expected values, providing less support for Prediction 1. Contra Prediction 2, expected grooming time for humans fell well within the range observed in primates. Contra Prediction 3, people in our six societies did not devote less time to conversation (7.3%) than they were expected to devote to grooming, as observed conversation time fell below only 22% of the expected values (posterior probability = 0.22). These results did not change qualitatively when excluding terrestriality as a covariate, excluding outliers, and/or changing the definition of group size for multilevel and fission-fusion societies (Tables S3–9) though expected grooming times were slightly lower when excluding terrestriality. Considering each group separately reveals some variation in the posterior probability of grooming as a phylogenetic outlier, being higher in more acculturated groups (Maya 0.94, Ye'kwana 0.94, Sanöma 0.93, Yanomamö 0.91, Tsimane' 0.85, Pumé 0.78).

Discussion

We presented detailed quantitative data from six traditional societies on time allocated to behaviors that are functionally equivalent to primate grooming, including parasite removal, other hygienic behavior, and conversation, or 'vocal grooming'. Given the best data available for primate grooming time and careful phylogenetic analyses with various robustness checks, we derived expectations for time spent grooming in humans. With regard to Prediction 1, human grooming might represent a phylogenetic outlier when defined narrowly as parasite removal, but not when defined broadly as any hygiene behavior. Contra Prediction 2, expected human grooming time was not greater than grooming times observed in other primates. Contra Prediction 3, observed conversation time was not lower than expected grooming time, hence 'vocal grooming' was not less time-consuming than grooming. What does this mean for the proposed functions of grooming, broadly defined?

Humans allocated substantially less time to grooming than expected for a typical primate, although this was not true when other hygienic behavior was included. Thus, human *allo*-grooming for parasite removal seems to represent a phylogenetic outlier, consistent with the fact that humans have less body hair, and most of the study populations have some access to efficient grooming technology (combs, etc.). Other recent studies provided stronger evidence for outlier status of human feeding time (Organ et al., 2011) and sleep duration (Samson and Nunn, 2015) as these observed times fell entirely outside the range of expected values. Given our weaker results, combined with the variation across our study populations and the fact that the least acculturated Pumé hunter-gatherers with little sanitary technology are arguably most representative of ancestral conditions, any deviation from typical primate grooming time seems to be fairly recent. This might be consistent with the surprisingly recent divergence of human head and body lice, which indicates loss of body hair about 72,000 years ago (Kittler et al., 2003). Enabled by a reduced hygienic need and new technology, humans spend more time *auto*-grooming (washing, bathing, haircutting, etc.); cross-culturally, traits that can be improved by 'grooming' such as shiny, well-kept hair and smooth skin are rated as attractive (Cunningham et al., 1995), hence more time investment in such behaviors could be adaptive. Thus, humans appear to have recently deviated from other primates by shifting their grooming from parasite removal to beautification, reflecting reduced hygienic need and increased investment in mate attraction.

We found no comparative support for a thermoregulatory function of grooming (Mcfarland et al., 2015) as grooming time did not associate with latitude, altitude, diurnal temperature range, isothermality, or annual precipitation across primates (Table 2). Increasing pelt loft improves protection against heat as well as cold (Mcfarland et al., 2015), and primates may have responded to selection pressures for improved thermoregulation primarily by varying pelt length or thickness rather than through behavioral means. This could make it difficult to detect any associations between climatic variables and grooming time. Associations of grooming times and climate data across populations that do not differ in pelt characteristics, such as different populations of the same species or the same population over time may provide better comparative tests of thermoregulatory function.

Expected grooming time for humans fell well within the range of that observed for other primates (Figure 2, Figure 3) and can therefore be considered ecologically viable. In fact, the grooming time originally predicted for humans (42%, CI = 28% – 66%) based on associations with group size and neocortex ratio (Dunbar, 1993) falls entirely outside of the 95% credible interval of our expectations, even though the value of group size used for humans was virtually the same in both analyses. This difference may be partly explained by our expectations being largely derived from terrestriality and phylogeny, with only small effects of group size (Table 2). However, even when using the smaller Lehmann dataset, in which group size is the predominant factor (Table S1), the expected human grooming time (11%, CI = 3% – 25%) falls largely within the range observed for other primates. In addition, there was no indication that vocal grooming was a more efficient, i.e. less time-consuming, way of investing in social relationships, as originally postulated by Dunbar (1993). In line with this, Nakamura (2000) found that grooming cliques among chimpanzees were similar in size to human conversation cliques, i.e. in principle providing the same bonding efficiency. These results cast doubt on the original version of the vocal grooming

hypothesis according to which language evolved as a means to bond large social groups that could not be viably held together by grooming alone (Dunbar, 1993). Instead, our results suggest that conversation replaced the social functions of grooming 1:1 (i.e., the same amount of time is spent talking than expected from primate grooming), making language more likely an exaptation for social bonding, rather than the original target of selection. However, our results are silent with regard to other forms of bonding like laughter, dance, or ritual which trigger some of the same rewards as grooming and may well help to foster cooperation in large groups (Dunbar, 2012).

In conclusion, we found that (i) human grooming may be a (recent) phylogenetic outlier when defined narrowly as parasite removal, but not when defined broadly as personal hygiene, (ii) there was no comparative support for a thermoregulatory function of grooming across primates, and (iii) there was no support for the 'vocal grooming' hypothesis, at least in its original formulation of conversation as more efficient bonding in large social groups not viably held together by grooming. Thus, human grooming reflects decreased hygienic needs, but similar social needs than primate grooming.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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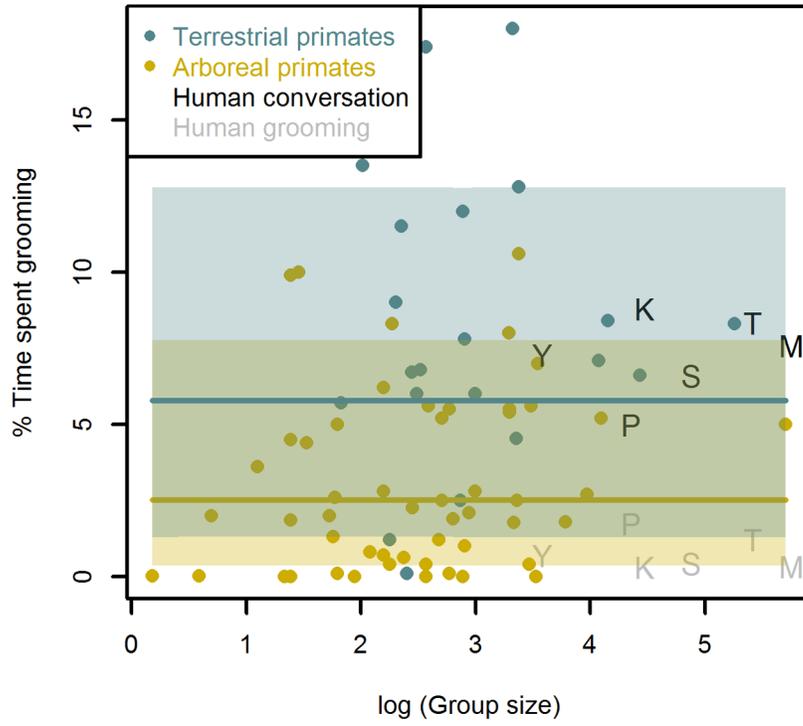
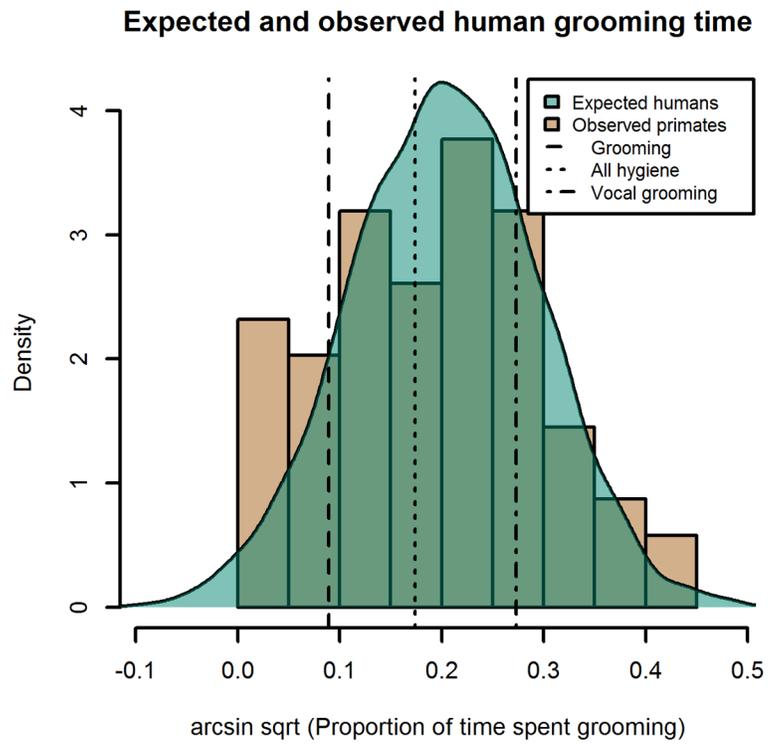**Figure 1.**

Figure 2.

Figure 3.

Table 1

Summary of the study populations, covariates, and grooming times

Group	N scan samples	Group size	Female body size (kg)	Grooming[c] (%)	Other hygiene[c] (%)	Conversation[c] (%)
Maya	18,591	316	50.3	0.32	4.19	7.59
Pumé	14,694	78	50.7	1.79	2.34	4.98
Sanöma	9,889	132[a]	43.4	0.44	1.68	6.59
Tsimane'	70,574	226[b]	54.1	1.21	2.16	8.33
Yanomamö	8,252	35	45.4	0.70	1.25	7.29
Ye'kwana	19,088	88	52.1	0.31	1.54	8.80
Mean	23,514	146	49.3	0.80	2.19	7.26

[a] Average of two communities

[b] Average of six communities

[c] Calculated as (number of scan samples spent in this activity/total scan samples)*100

Table 2

Summary of the Bayesian phylogenetic model for grooming time across primates

Covariate	Mean estimate	Lower 95% CI	Upper 95% CI	% models included in
Intercept	0.20	0.04	0.54	100
Log (group size)	0.00	0.00	0.00	0.95
Log (body size)	−0.00	−0.04	0.00	12.85
Terrestriality	0.08	0.00	0.15	86.30
Latitude	0.00	0.00	0.00	0.15
Altitude	0.00	0.00	0.00	0.05
Mean diurnal temperature range	0.00	0.00	0.00	0.05
Isothermality	−0.00	0.00	0.00	0.40
Annual precipitation	0.00	0.00	0.00	0.00