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Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*

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Phylogenetic models of primate social behaviour posit that core social traits are inherent species characteristics that depend largely on phylogenetic histories of species rather than on adaptation to current socioecological conditions. These models predict that aspects of social structure will vary more between species than within species and that they will display strong phylogenetic signals. We tested these predictions in macaques focusing on dominance gradients, a relatively little studied, yet central, aspect of social structure. We used data from 14 social groups representing nine macaque species living in a variety of conditions. We examined proportions of counteraggression and two recently developed measures of dominance gradients (hierarchical steepness) for phylogenetic signals in nine phylogenetic trees constructed using (1) available genetic data sets and (2) Bayesian Markov Chain Monte Carlo (MCMC) and maximum likelihood algorithms. Hierarchical steepness and counteraggression showed significant variation between species but inconsistent variation within species. Both steepness and counteraggression showed evidence of phylogenetic signals, with results being particularly strong for one steepness measure and for counteraggression. Our results suggest that between-species variation in some core aspects of social structure are shaped by species' evolutionary relationships, despite differences in living conditions. As such, they provide broad support for the phylogenetic model.
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Understanding the origins of variation in social behaviour and social structure has been a long standing goal of animal behaviour researchers in general and nonhuman primate researchers in particular. Many aspects of primate social structure vary widely among and within species, including patterns of aggression, affiliation, conflict management, cooperation, dispersal, dominance, kin bias and mating patterns (Kappeler & van Schaik 2002). Several conceptually different models have been proposed to explain the origins of this variation, the best known of which are based on species' phylogenetic relationships (e.g. Di Fiore & Rendall 1994; Thierry et al. 2000, 2008), current socioecological adaptation (e.g. van Schaik 1989; Sterck et al. 1997) and biological markets theory (e.g. Barrett et al. 2002). However, there is no consensus regarding which of these frameworks is most useful in providing explanations for variation in social structure, or how the processes proposed by each may interact. This is partly because there have been relatively few empirical studies (e.g. Stevens et al. 2005; Majolo et al. 2008; Thierry et al. 2008; Balasubramaniam et al. 2011) testing these models. In this paper, we examine patterns of variation in one core aspect of social structure, dominance gradients (see definition below), among macaques (*Macaca* sp.) and ask whether they are consistent with predictions of phylogenetic models.

Evolutionary biologists have long stressed the importance of considering species' evolutionary relationships when exploring the origins of variation in morphological, physiological and, to a lesser extent, behavioural traits in animals (Blomberg et al. 2003;

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Rendall & Di Fiore 2007). For instance, in relation to the latter, several previous studies have traced the evolutionary origins of communicative behaviours using parsimony-based mapping approaches and previously reconstructed topologies (e.g. courtship displays: Proctor 1992; Irwin 1996; Borgia & Coleman 2000). Other more recent studies have used formal phylogenetic comparative methods and have successfully established interspecific links between communicative behaviours and phylogenetic closeness (e.g. territorial displays: Ord & Martins 2006). In comparison, the usefulness of applying phylogenetic comparative methods to examine variation in social traits and, in particular, aspects of nonhuman primate social relationships has been appreciated only recently (Thierry 2000, 2007) with the development of phylogenetic models for variation in social structure. These models (Di Fiore & Rendall 1994; Chan 1996; Matsumura 1999; Thierry et al. 2000, 2008) posit that a species' social structure is largely dependent on its evolutionary history and hence on inherent species characteristics, rather than on current social and ecological conditions. Ecological adaptation is not ruled out, but is hypothesized to have occurred primarily in the distant past. At that time, core aspects of social structure are hypothesized to have become structurally linked, constituting evolutionarily stable strategies, or ESSs (Matsumura 1999). As ESSs, these linked social characteristics are hypothesized to have become relatively unresponsive to change in ecological conditions (Matsumura 1999). As such, current variation in social structure is not expected to correlate tightly with current ecological conditions.

Because proponents of phylogenetic models posit that variation in social structure is derived from inherent species variation, aspects of social structure are predicted to show significant levels of between-species variation and relatively little within-species variation (Thierry et al. 2008). They are also predicted to display strong phylogenetic signals (Thierry et al. 2008), a pattern in which closely related species should show greater similarities in social traits than distantly related species (Blomberg & Garland 2002; Blomberg et al. 2003). Although phylogenetic signals can be due to either constant ecological conditions or evolutionary constraints, proponents of phylogenetic models favour the latter explanation based on disconnects between current ecology and social structure at the species level (Thierry 2007). Note that in the past, proponents of phylogenetic models for primate social structure sometimes used other terms, for example, 'phylogenetic inertia' (Thierry et al. 2000) in place of phylogenetic signal. However, comparative biologists now use 'phylogenetic inertia' to describe one of several possible processes that may have led to the existence of phylogenetic signals, reserving 'signal' to describe the pattern of phylogenetic similarity only (Blomberg & Garland 2002). Consistent with this, we aim to identify only patterns (signals) rather than any processes by which they may have arisen.

Thus far, evidence in support of phylogenetic signals for aspects of primate social structure has been mixed. Early studies treated social traits primarily as categorical variables (e.g. Di Fiore & Rendall 1994; Chan 1996; Thierry et al. 2000). For example, Di Fiore & Rendall (1994) found that some but not all basic patterns of female social organization, including the presence of linear dominance hierarchies, philopatry and coalitions, showed high retention indices and hence, evidence for strong phylogenetic signals. Across macaques, Thierry et al. (2000) found that seven out of 22 behavioural traits (including patterns of social play and female rank acquisition) also showed evidence for strong phylogenetic signals. More recent studies have used continuous variables, a practise that is preferable because it makes use of fine-grained variation in cross-species patterns (Garland et al. 1993; Nunn & Barton 2001). Using such an approach, Thierry et al. (2008) found strong and significant phylogenetic signals for conciliatory tendency, explicit forms of reconciliation and counteraggression (but not kin bias) across captive groups representing nine species of macaques. They also found evidence that these traits covaried between species after controlling for phylogeny, suggesting that they may be structurally linked.

Although these pioneering studies have contributed to a growing recognition of the importance of species' phylogenetic relationships in shaping social traits, one concern is that they have used previously reconstructed phylogenetic trees based on nonparametric approaches (e.g. Purvis 1995), rather than on more recently developed probability-based maximum likelihood (ML) and Bayesian Markov Chain Monte Carlo (MCMC) algorithms. These methods are advantageous because they allow for greater statistical flexibility via the incorporation of a relaxed molecular clock permitting independent rates of evolution across sites and lineages. In particular, they deliver a distribution of phylogenetic trees with nodal support values, given a model(s) of evolutionary change and, in the case of Bayesian approaches, a prior distribution (see Methods). Here we use several such newly reconstructed phylogenetic trees. Furthermore, we focus our phylogenetic analyses on a continuous measure of dominance gradients (hierarchical steepness: de Vries et al. 2006), a core aspect of macaque social structure that has not been previously examined in this manner.

Dominance gradients (Vehrencamp 1983) are a characteristic of linear dominance hierarchies defined conceptually as 'the extent to which one animal can exert a negative influence on another' (Henzi & Barrett 1999, page 54). Briefly, gradients are conceptualized as steep when differences in aggressive success between adjacently ranked individuals are large, and as shallow when these differences are small (Flack & de Waal 2004). Dominance gradients have been hypothesized to be central to phylogenetic models as well as socioecological and biological markets models that aim to explain variation in social structure (Sterck et al. 1997; Thierry 2000; Barrett et al. 2002). However, gradients have not been used extensively in empirical tests of these models, partly because they have been difficult to operationalize until recently. Most studies have resorted to qualitative, categorical comparisons between presumably high and low steepness based on indirect behavioural indicators (e.g. patterns of submissive interactions: Thierry 2000) or ecological differences (e.g. resource distribution: Henzi & Barrett 1999), that is, variables hypothesized to influence or result from gradients. Unfortunately, this has inserted a degree of circularity into causal and functional arguments. Barrett et al. (2002) were the first to attempt to empirically measure dominance gradients, for chacma baboons, *Papio cynocephalus ursinus*, as the slopes of plots between ratios of aggression given to that received, and ranks of individuals. However, such ratios do not provide precise measures of cardinal ranks of individuals essential for determining steepness (Flack & de Waal 2004). Later, Gammell et al. (2003) developed a measure called David's scores (David 1987) that determines an individual's aggressive success as a 'weighted sum of the individual's dyadic proportions of wins combined with an unweighted and weighted sum of its dyadic proportions of losses' (de Vries et al. 2006, page 586). de Vries et al. (2006) subsequently used David's scores to quantitatively determine dominance gradients at a group level, by measuring the absolute slopes of linear regressions between normalized David's scores and ranks of individuals. As such, de Vries's measure of hierarchical steepness presents the most comprehensive empirical measure of dominance gradients to date. Yet, so far, it has not been used to examine phylogenetic models. Here we use two versions of de Vries's measure of steepness (based on Dij and Pij indices) and levels of counteraggression to test predictions of the phylogenetic model across macaque species and across groups belonging to the same species using a comparative data set of dyadic aggressive behaviour from macaque groups living in a variety of conditions (captive, free-

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ranging and wild). Counteraggression, defined as the percentage of aggressive interactions in which the recipient of aggression immediately directs aggression back to the initial initiator, is a measure of dominance asymmetry that is closely related to steepness (see Methods).

Macaques are an appropriate genus for testing predictions related to variation in social structure. They are the most widespread primate genus geographically (Abegg & Thierry 2002), representing at least 20 extant species belonging to three distinct phyletic lineages (Groves 2001; Abegg & Thierry 2002). Apart from a few lingering discrepancies, phylogenetic relationships are well established based on several analyses using a variety of traits and methodological approaches (e.g. Purvis 1995; Tosi et al. 2003; Li et al. 2009; Chatterjee et al. 2009). All macaques have a similar basic social structure, featuring large multimale–multifemale social groups, female philopatry, male dispersal (Pusey & Packer 1987) and stable, linear female dominance hierarchies (Paul & Kuester 1987). At the same time, they show marked inter- and intraspecific variation in several behaviours related to aggression, dominance relationships and other aspects of social structure that have been conceptualized as resulting from differences in dominance gradients (Thierry 2000; Thierry et al. 2000, 2008). Using data from 14 groups representing nine species, we test the predictions that measures of steepness and counteraggression (1) show greater levels of between-species variation than between-group variation within species, as well as (2) significant and strong phylogenetic signals across multiple phylogenetic trees.

METHODS

Our study adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, and to the requirements listed in the *Guide to Ethical Information Required for Animal Behaviour Papers*. Protocols used to gather individual data sets used in the study were strictly observational. In addition, the project was approved by the Institutional Animal Care and Use Committee of the State University at Buffalo SUNY (Protocol No. ANT01070 N).

Behavioural Data Sets

After thoroughly researching the literature and contacting a wide range of macaque researchers, we assembled a broad data set of dyadic contact and noncontact aggressive behaviour and counteraggression (see Appendix for definitions) in actor–receiver matrix format for social groups that ultimately represented nine macaque species (Table 1). Sources included data from our previous studies, both published and unpublished. We searched the literature on social behaviour for the genus *Macaca* in PrimateLit from 1970 to 2011 using the following keywords: dominance, aggression, bi-directional aggression, counteraggression. Specifically, we searched for data sets that included interactions between adult females (>3.5 years of age), since females are the philopatric sex and form the core of macaque societies. When possible, we also contacted the authors of these and related articles on macaque behaviour to inquire about unpublished data sets.

Our initial assembly included 22 groups representing 12 macaque species, but several groups had to be discarded because the data were inconsistent or incomplete. In addition, it was necessary to minimize the detrimental effects of small group size and observational zeros on the calculation of steepness measures (de Vries et al. 2006). To do this, we implemented two strict criteria before including a group in the analysis. First, we only considered groups that had a minimum sample size of five adult females. Second, we only considered groups that had minimal or correctable observational zeros. Following de Vries et al. (2006, personal communication), we adopted a cautious, stepwise approach to groups that had observational zeros for more than one-third of all combinations of dyads. First, we examined whether the data were

Table 1
Information about groups and species constituting the data set

Macaca sp.	Source	Group size	Adult females	Condition	Sampling method	Mean hours/subject
*M. assamensis**	Cooper & Bernstein 2008	64	14	Wild (fed at temple)	Ad libitum (1008 h)	—
M. fascicularis	Butovskaya et al. 1995	9	7	Captive	Instantaneous scan	47
	Butovskaya et al. 1995	13	9	Captive	Instantaneous scan	50
M. fuscata	Schino et al. 2007	57	23	Captive	Focal group, complete record observation	291
	Ventura et al. 2006	25	8	Wild	Focal animal	25
M. mulatta	C. Desportes & B. Thierry, unpublished data	15	5	Captive	All-occurrences	48
	de Waal & Luttrell 1989	51–62	13	Captive	All-occurrences	675
M. nigra	K. N. Balasubramaniam, unpublished data	8	6	Captive	All-occurrences	76
M. radiata	Cooper et al. 2007	41–49	13	Wild (fed at temple)	Ad libitum (907 h)	—
M. sylvanus	R. McFarland & B. Majolo, unpublished data	19	8	Wild	Focal animal	32
M. thibetana†	Ogawa 1995	39–42	8	Wild (provisioned)	Focal animal, all-occurrences	130
	Berman et al. 2004	37–52	10	Wild (provisioned)	Focal animal	40
M. tonkeana	De Marco et al. 2010	21	7	Captive	All-occurrences	110
	Thierry 1985; Demaria & Thierry 2001	16	9	Semi-free-ranging	All-occurrences	107

Sources listed provide further information regarding living conditions. Information for unpublished data is available from the first author upon request.

* Group corrected for observational zeros by including submissive displacement interactions. A positive correlation between aggressive and submissive displacements (Kendall rank correlation: $\tau_{rw} = 0.623$, $P < 0.01$) indicated that observational zeros for this group could be reduced by including submissive displacements in the aggression matrix (see text).

† This group was treated as two separate groups in comparative analyses because they were observed several years apart: 1991–1992 (Ogawa 1995) and 2000–2002 (Berman et al. 2004).

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based on either (1) a minimum mean of approximately 25 h of observation per female using all occurrences/focal animal/instantaneous scan sampling methods (Altmann 1974), or (2) at least 3 months of adequate ad libitum sampling for wild groups. Second, we ascertained whether data on dyadic submissive displacements had been collected for the group using similar sampling methods. If neither of these two subcriteria were met, we eliminated the group from the analyses because we could not be certain about whether the zeros were an artefact of insufficient observation time or genuine indicators of uncertain and/or undecided dominance relationships. If submissive displacement data were available, we next determined whether they accurately reflected the general direction of aggressive interactions between dyads by performing a Kr matrix correlation test (Hemelrijk 1990) of aggression given and submission received (using MatMan software: de Vries et al. 1993). A positive correlation indicated that the observational zeros could be reduced by including submissive displacements in the aggression matrix. Once this was done, the group was included in the analyses. Out of several groups with observational zeros, only one (see Table 1) met all three subcriteria and was ultimately included. As such, we describe results for a final data set of 14 groups representing nine species in the text. Supplementary Table S2 shows results for the phylogenetic signal analyses after excluding the corrected Assamese macaque, *Macaca assamensis*, group (i.e. for 13 groups representing eight species).

All 14 groups ultimately included in our final data set had been observed for substantial periods of time (see Table 1) and as such, had sufficient data to provide reliable and accurate scores of steepness. Most studies conducted on the captive groups used all-occurrences sampling (Altmann 1974), ranging from 48 h (rhesus macaque, *Macaca mulatta*: B. Thierry, unpublished data) to 675 h (*M. mulatta*: de Waal & Luttrell 1989). Two captive groups of longtailed macaque, *Macaca fascicularis*, had 94 and 100 30-minute scan samples (Altmann 1974), respectively. Two of the studies on wild groups followed ad libitum sampling during fixed hours of the day: on *M. assamensis*: 1008 h over 5 months (Cooper & Bernstein 2008); on bonnet macaque, *Macaca radiata*: 907 h over 12 months (Cooper et al. 2007). All other wild studies used focal animal sampling (Altmann 1974), with focal sessions lasting 10–15 min, and a mean observation time per subject ranging between 25 h (Japanese macaque, *Macaca fuscata*: Ventura et al. 2006) and 40 h (Tibetan macaque, *Macaca thibetana*: Berman et al. 2004). For *M. thibetana*, Ogawa (1995) conducted all-occurrences sampling (99.6 h) in provisioned areas and focal animal sampling (approximately 30 h/subject) in forested areas. Data on the Celebes or crested black macaque, *Macaca nigra*, group were collected by the first author at the Buffalo Zoo between February and April 2011. To ensure that we collected sufficient data, we calculated steepness scores each week for this group using cumulative data, and ceased observations after steepness scores remained stable for several consecutive weeks (i.e. after 25 h).

Behavioural Measures: Steepness and Counteraggression

We computed steepness scores from overall aggression matrices in which we entered all acts of contact and noncontact aggression, both unidirectional and bidirectional, including acts of counteraggression. The inclusion of counteraggression was necessary to produce representative measures; although counteraggression made up a very small proportion of aggressive acts among most species, it constituted a high percentage of aggressive acts for the crested (*M. nigra*) and Tonkean, *Macaca tonkeana*, macaques. Moreover, nearly all acts of counteraggression in these species involved almost simultaneous aggression by both opponents. Thus, the exclusion of counteraggression would have greatly distorted measures of steepness for these species. We also calculated levels of counteraggression separately for a comparison with steepness and with results in Thierry et al.'s (2008) study.

We calculated hierarchical steepness for each group in our data set using the GUI (Graphical User Interface) for Excel created from the steepness R package program developed by D. Leiva and H. de Vries (de Vries et al. 2006). For each aggression matrix, the program generates a matrix of dyadic dominance index (DDI) values corrected for chance (Dij scores). From these scores, it generates David's scores (David 1987) for each individual as a measure of relative aggressive success. Steepness is then measured as the absolute slopes of plots between normalized David's scores (NDS scores) and ranks of individuals (Gammell et al. 2003; de Vries et al. 2006). In addition to using Dij dominance indices, we also calculated steepness values from wins–losses matrices containing Pij dominance index scores (David 1987; de Vries et al. 2006). Pij indices are simply ratios of wins to total numbers of interactions, and (unlike Dij indices) do not take frequency of interaction into account. We used steepness scores calculated from both indices in all our analyses. For a discussion of the advantages and disadvantages of each index for use with broad comparative data sets, see Balasubramaniam et al. (2011) and the Discussion. We calculated scores for counteraggression for each individual in each group as the percentage of all aggressive interactions that involved immediate aggressive retaliation from the recipient. Group-level scores were the mean scores across individuals, and species-level scores were mean scores across groups. We examined phylogenetic signals exclusively with species-level scores to avoid a possible inflation of the samples by splitting terminal species branches into new lineages to accommodate groups within species.

Phylogenetic Trees

To test for phylogenetic signals, we used trees from the 10kTrees website (version 2: Arnold et al. 2010; Matthews et al. 2010), a recently available online resource for primate phylogenies. The website provides a maximum of 10 000 primate phylogenies generated using Bayesian MCMC methods and a generalized time-reversible (GTR+I+G) substitution model, from a concatenated data set of six mitochondrial genes and three autosomal genes available for the majority of 230 primate species in Genbank. From this database, we extracted 10 of the best supported trees available for 20 species of macaques (classification as per Groves 2001). From these extractions, we used five trees (four selected at random and one consensus tree) to carry out tests for phylogenetic signals (Supplementary Fig. S1). In addition, we also reconstructed our own trees from a concatenated nucleotide data set using Bayesian MCMC and maximum likelihood (ML) analyses. For these reconstructions, we assembled 10 genes (eight mitochondrial and two nuclear) that were available for the majority of the 20 macaque species (Groves 2001) and hamadryas baboon, *Papio hamadryas* (outgroup) in the National Center for Biotechnology Information (NCBI) database. We aligned each gene separately, using the L-INS-i algorithm in MAFFT v6.0 (Katoh & Toh 2008). Averaging across all 21 taxa, complete or partial coding regions of 8.39 genes were available per species, with six species being represented by all 10 genes (Supplementary Table S1). Individual gene alignments were controlled and edited using Geneious v5.3.4 (Drummond et al. 2008) to remove poorly aligned and/or poorly represented regions, and then concatenated to form a DNA supermatrix of 5787 sites. The data set was partitioned by gene, and substitution model selection was conducted for each partition using JModeltest v0.1.1 (Posada 2008) by comparing Akaike Information Criterion (AIC) scores. We reconstructed Bayesian trees using the software BEAST (Drummond & Rambaut 2007) after assigning (1) a single

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substitution model (GTR+I+G) for each partition (Fig. 1) and (2) separate substitution models (as determined by JModeltest results) for each gene partition (Supplementary Fig. S2). For both cases, we used an uncorrelated lognormal relaxed molecular clock to allow independent variation among branches, and placed a Yule (pure-birth process) prior on the tree. Support for each of the two maximum-clade-credibility trees (topologies identified using TreeAnnotator software, part of the BEAST package) was obtained from posterior probability distributions obtained from MCMC runs that sampled every 1000th step from 10^7 steps, after burn-in. We reconstructed a maximum likelihood tree using RAxML v7.0.4 (Stamatakis 2006) with bootstrap values (number of replicates automated) providing node support (Supplementary Fig. S3). All three trees were edited using FigTree v1.3.1 and trimmed down to the nine species for which behavioural data were available using Mesquite v2.74 (Midford et al. 2005; Maddison & Maddison 2010). We were concerned that trimming might cause some branch length information to be lost from our phylogenies. Therefore, we reconstructed a fourth tree (Supplementary Fig. S4) from the concatenated data set for just nine species (on which comparative data was available), using a Bayesian MCMC approach (described above) and a GTR+I+G model of substitution for each partition. In all, we used nine trees (five from 10kTrees and four reconstructed).

Data Analysis

We used ANCOVA to examine within-species variation, and both ANCOVA and mixed model analyses (SPSS v16.0; Field 2009) to examine between-species variation in hierarchical steepness (prediction 1). Ideally, we would have preferred to do nested analyses of groups within species, but we had only two groups per species for five species, and one group each for four species (see Table 1). Therefore, we performed within-species analyses separately. To examine between-species differences, we selected one representative group at random for species that showed no significant within-species differences in steepness (longtailed macaques, *M. fascicularis*; rhesus macaques, *M. mulatta*; Tibetan macaques, *M. thibetana*; Tonkean macaques, *M. tonkeana*), and one group at a time for species that showed significant differences (Japanese macaques, *M. fuscata*). In each ANCOVA test, we examined whether the slopes of regression lines (i.e. the hierarchical steepness scores) for each group (or species) varied significantly from one another. Normalized David's scores (NDS scores) were the dependent variable, group (or species) was a fixed factor, and rank was a covariate. A significant interaction between rank and group (or species) would indicate significant differences in steepness. In the mixed model analysis, NDS scores were the dependent variable,

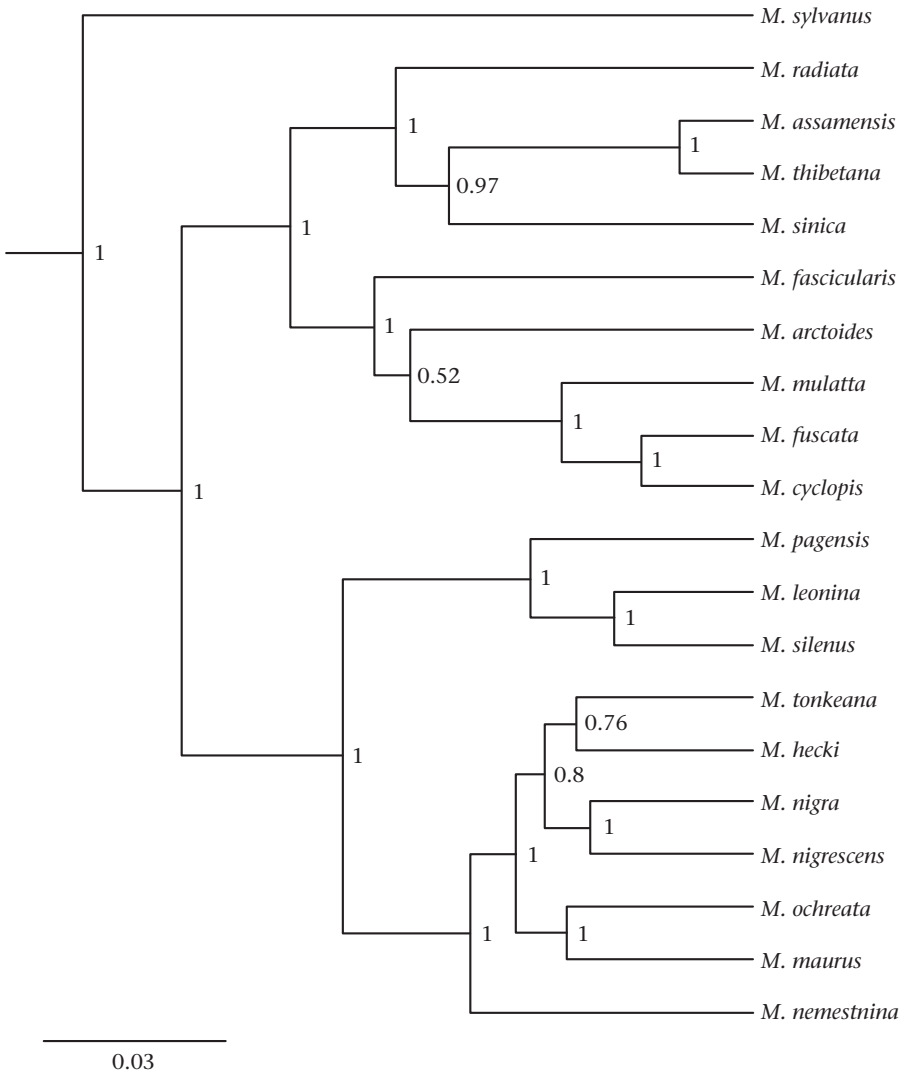

Figure 1. Maximum-clade-credibility tree obtained from Bayesian Markov Chain Monte Carlo (MCMC) runs sampled every 1000th step from 10^7 steps using the same generalized time-reversible (GTR+I+G) substitution model for each gene partition for 20 macaque species. Values at nodes represent posterior probabilities.

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and species and rank were covariates. Note that specifying species as a fixed factor in this SPSS program leads to inaccurate results (Field 2009, page 744). None the less, this analysis determined whether the introduction of a variance of slopes (steepness) term by assigning species as a level-two variable significantly improved the fit of the data to this structured model compared to an unstructured model that did not consider a variance of slopes.

For counteraggression, we used Mann–Whitney *U* tests to examine within-species differences, and one-way ANOVAs to examine between-species differences (prediction 1). As with steepness, we selected one representative group at random for species that showed no significant within-species differences (*M. mulatta*, *M. thibetana* and *M. tonkeana*) and one group at a time for species that showed significant differences (*M. fascicularis*, *M. fuscata*) to examine between-species differences.

Because our behavioural scores (steepness and counteraggression) were not related to group size and/or number of subjects (i.e. adult females; see Results), it was unnecessary to control for these factors. We thus tested for phylogenetic signals using raw species-level behavioural scores of hierarchical steepness (based on Dij and Pij indices) and counteraggression, and for each of our nine phylogenetic trees. We examined whether our behavioural traits showed phylogenetic signals (prediction 2) using the Phylogenetic Signal package (Blomberg et al. 2003) and specifically, the Matlab code PHYSIG_LL.m. This program (Blomberg et al. 2003) computes mean squared errors (MSE) and log likelihood (LL) scores that indicate how well our comparative data fit a given phylogeny as compared to a star phylogeny of no species relationships. MSEs are computed by transforming raw species-level behavioural scores in matrix format using an n^*n (n being the number of species or terminal taxa) variance–covariance matrix whose elements contain phylogenetic branch length information from a candidate tree. MSE scores calculated for this 'phylogenetically transformed' data set for each candidate tree are then compared to similar scores (MSE*) computed for data sets and a 'star' phylogeny of contemporaneous tips. A lower MSE relative to MSE* indicates that most of the variation in the tip data is accurately described by the candidate tree. The LL score indicates how well a candidate phylogeny fits our species-level behavioural scores compared to the fit of the same data sets to a star phylogeny. A higher likelihood score for a candidate tree model compared to a star phylogenetic tree model indicates a stronger phylogenetic signal for that candidate tree.

The program then generates a test statistic (K) that indicates the strength of the phylogenetic signal relative to the amount of signal that may be expected under a Brownian motion model of evolution for a given tree. K is inversely related to mean squared errors (MSE) from phylogenetically transformed data sets, and may be defined as the value of the ratio between the MSE of the tip data (MSEo) and the MSE of the phylogenetically transformed data (MSE) scaled over the value of the same ratio that is expected under a Brownian motion model of evolution. Therefore, a value of $K > 1$ indicates strong evidence for closely related species to show greater similarities in behavioural scores than is expected under a Brownian motion model. In contrast, $K << 1$ indicates a weak signal that is uncorrelated with phylogeny, and evidence for homoplasy or adaptive evolution. $K \sim 1$ indicates moderate signal that is close to the amount of signal expected under Brownian evolution.

Finally, the program performs a randomization test to determine whether a phylogenetic signal is significant, by comparing the MSE of contrasts from terminal species scores with the MSEs of contrasts from permuted data sets generated by scattering terminal (tip) data randomly. The signal will be significant if 95% of permuted data sets show higher MSEs in contrast scores than the original data set. Note that the randomization test is independent of the estimation of the strength of the signal (i.e. it is possible that a phylogenetic signal may be significant even if $K < 1$, or if MSE and LL scores are lesser and greater, respectively, for candidate trees compared to star phylogenies). In other words, strength and significance are both different, but weakly dependent, ways to assess phylogenetic signals.

All statistical tests were two-tailed, with the critical P value set at 0.05.

RESULTS

Group-level scores for steepness based on Dij and Pij measures and counteraggression are shown in Table 2 for all 14 groups in our data set. Dij Steepness scores were similar and relatively high for Tibetan (*M. thibetana*), rhesus (*M. mulatta*), Japanese (*M. fuscata*) and longtailed (*M. fascicularis*) macaques, were moderately high for Assamese (*M. assamensis*) and bonnet (*M. radiata*) macaques, and were moderate to low for Barbary (*Macaca sylvanus*), Celebes crested (*M. nigra*) and Tonkean (*M. tonkeana*) macaques. Pij steepness measures showed similar variations (Fig. 2) but tended to be relatively more similar between species showing high and moderately high Dij scores. Celebes crested (*M. nigra*) and Tonkean macaques (*M. tonkeana*) showed very high levels of counteraggression, whereas scores were relatively low for other species. Pij steepness scores were positively correlated with (Pearson correlation: $r_{12} = 0.97$, $P < 0.01$) and consistently higher than Dij scores (Wilcoxon signed-ranks test: $T = 0$, $N = 14$, $P < 0.01$), as expected, owing to differences in how these indices are calculated (de Vries

Table 2
Scores of hierarchical steepness (based on Dij and Pij indices) and counteraggression (mean ± SD percentage) for 14 macaque groups representing nine species

Macaca sp.	Source	Steepness (Dij)	Steepness (Pij)	% Counteraggression (mean±SD)
M. assamensis	Cooper & Bernstein 2008	0.65	0.80	6.06±5.99
M. fascicularis	Butovskaya et al. 1995	0.94	0.98	1.09±0.86
	Butovskaya et al. 1995	0.79	0.85	10.30±7.86
M. fuscata	Schino et al. 2007	0.56	0.68	7.14±3.90
	Ventura et al. 2006	0.92	0.99	0.18±0.34
M. mulatta	C. Desportes & B. Thierry, unpublished data	0.65	0.80	0±0
	de Waal & Luttrell 1989	0.78	0.92	4.43±6.64
M. nigra	K. N. Balasubramaniam, unpublished data	0.49	0.53	50.80±24.70
M. radiata	Cooper et al. 2007	0.60	0.83	3.72±5.89
M. sylvanus	R. McFarland & B. Majolo, unpublished data	0.45	0.64	1.98±2.75
M. thibetana	Ogawa 1995	0.87	0.96	0.76±0.85
	Berman et al. 2004	0.80	0.92	0.53±0.49
M. tonkeana	De Marco et al. 2010	0.22	0.28	61.7±26.7
	Thierry 1985; Demaria & Thierry 2001	0.20	0.27	59.2±13.1

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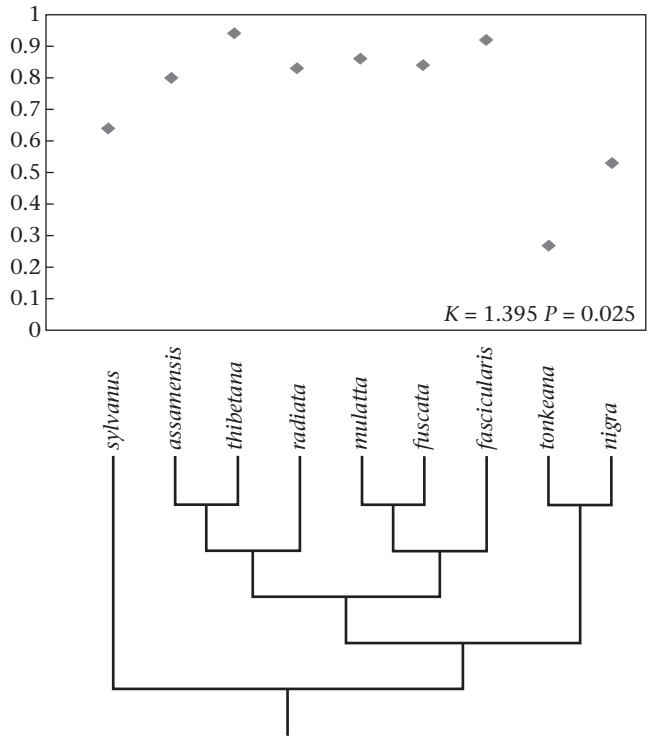

Figure 2. Pij steepness measures associated with terminal species mapped onto our generalized time-reversible (GTR+I+G) substitution model-based Markov Chain Monte Carlo (MCMC) tree (from Fig. 1) trimmed to nine species. Results from the PHYSIG_LL analyses that indicate the strength (K) and significance (P) of the phylogenetic signal for Pij steepness are also indicated for this tree.

et al. 2006; see also Discussion). Furthermore, counteraggression scores were significantly negatively correlated with both Dij steepness (Pearson correlation: $r_{12} = -0.801$, $P < 0.01$) and Pij steepness ($r_{12} = -0.905$, $P < 0.01$). This was expected given the inclusion of counteraggression data in the calculation of steepness scores. Species-level behavioural scores were unrelated to mean group size or the mean number of females (see Table 3).

Variation Within and Between Species (Prediction 1)

Results for within-species variations in steepness and counteraggression are summarized in Table 4. We found significant variation in steepness scores for only one out of five species for which we had data for more than one group. This exceptional species (Japanese macaques: *M. fuscata*) showed a significant interaction between rank and group (ANCOVA: Dij-based scores: $F_{1,27} = 11.084$, $P = 0.003$; Pij-based scores: $F_{1,27} = 6.991$, $P = 0.013$), indicating that the slopes of NDS scores and ranks (i.e. steepness) varied significantly between groups. We found significant within-species differences in counteraggression for two species: Japanese macaques (Mann–Whitney U test: $U = 5.0$, $N_1 = 23$, $N_2 = 8$, $P < 0.001$) and longtailed macaques (*M. fascicularis*) ($U = 4.0$, $N_1 = 9$, $N_2 = 7$, $P = 0.002$).

Based on these results, we selected groups for our between-species analyses by randomly choosing one group from each species (four in all for steepness, and three for counteraggression) for which there were no significant within-species differences in scores. For steepness, we selected one Japanese macaque group at a time and thus performed two sets of between-species analyses. ANCOVA and mixed model analyses performed for each of the two sets showed evidence for significant between-species variation in steepness for both Dij- and Pij-based scores (Table 5). ANCOVA results showed significant relationships between NDS scores and species × rank. Mixed model analyses showed that the incorporation of a variance of slopes (steepness) term after structuring the data using species as a level-two variable significantly improved the fit of the data to the model, as indicated by chi-square analyses of differences in likelihood scores. For counteraggression, we selected one Japanese macaque and one longtailed macaque group at a time and thus, performed between-species analyses for all four emerging combinations. ANOVA results showed significant between-species differences in levels of counteraggression for all four combinations (Table 6).

Phylogenetic Signals (Prediction 2)

Figure 2 shows a representative phylogeny for the nine species we analysed along with their Pij steepness scores. All three measures (Dij steepness, Pij steepness and counteraggression) showed evidence for phylogenetic signals, with Pij steepness and counteraggression showing particularly strong evidence (Table 7). PHYSIG_LL results indicate that the K statistic was high for all three measures. K values were consistently greater than one for Pij steepness and counteraggression, indicating that they showed more signal than expected under a Brownian motion model of evolution. They approached one for Dij steepness, indicating moderately strong signals similar to those expected under Brownian evolution (Table 7). For all three measures and all nine trees, mean squared errors (MSE) of phylogenetically transformed scores were lower than MSEs for a star phylogeny (MSE*) with contemporaneous tips (Table 7). In other words, after taking phylogenetic branch length information into consideration, between-species differences were lower (and hence, more similar) for closely related species than expected for a star phylogeny that did not incorporate species' evolutionary relationships. In addition, log likelihood (LL) scores fitting each of our candidate phylogenies were consistently higher than scores for a star phylogeny with contemporaneous tips, for all three measures, indicating a better fit of the data on phylogenies. Results from the randomization tests were somewhat weaker. Although Pij steepness and counteraggression showed significant phylogenetic signals across all nine trees, Dij steepness showed significant signals for two phylogenies, and approached significance for five other phylogenies ($P < 0.07$) (Table 7).

Overall, results for both steepness and counteraggression were highly consistent across all nine phylogenetic trees (Table 7). Therefore, we found no reason to determine the most statistically robust tree to interpret our results. Repeating the analyses for 13 groups across eight species (after eliminating the manipulated Assamese macaque group) showed even more robust results (Supplementary Table S2). K statistics were consistently greater than one for steepness (Dij and Pij) and counteraggression for all phylogenetic trees. Furthermore, MSEs for phylogenetically transformed data sets were consistently lower and likelihood scores for data fitting a given phylogeny were consistently greater

Table 3
Pearson correlations between behavioural traits, and group size and number of adult females

	r_7	P (two-tailed)
Steepness (Dij) vs group size	0.322	0.398
Steepness (Pij) vs group size	0.475	0.196
Counteraggression vs group size	−0.528	0.144
Steepness (Dij) vs subjects	0.294	0.442
Steepness (Pij) vs subjects	0.414	0.267
Counteraggression vs subjects	−0.483	0.187

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Table 4
ANCOVA and Mann–Whitney *U* test results for between-group variation in hierarchical steepness and counteraggression in five species of macaques

Macaca sp. (N_1, N_2)*	Steepness (Dij)	ANCOVA NDS vs (group × rank)			Steepness (Pij)	ANCOVA NDS vs (group × rank)			Mean±SE counteraggression	Mann–Whitney *U*	
		F	*df*	*P*		*F*	*df*	*P*		*U*	*P*
M. fascicularis (9, 7)	0.94	2.51	1, 12	0.14	0.98	2.81	1, 12	0.12	1.09±0.86	4.00	**0.01**
	0.79				0.85				10.30±7.86		
M. fuscata (23, 8)	0.92	11.08	1, 27	**0.01**	0.99	6.99	1, 27	**0.01**	0.18±0.34	5.00	**0.01**
	0.56				0.68				7.14±3.9		
M. mulatta (13, 5)	0.65	1.54	1, 14	0.24	0.80	1.29	1, 14	0.28	0±0	15.00	0.09
	0.78				0.92				4.43±6.64		
M. thibetana (10, 8)	0.80	1.19	1, 14	0.29	0.92	0.15	1, 14	0.70	0.53±0.49	33.50	0.57
	0.87				0.96				0.76±0.85		
M. tonkeana (9, 7)	0.20	0.27	1, 12	0.61	0.27	0.01	1, 12	0.92	59.2±13.1	26.00	0.61
	0.22				0.28				61.7±26.7		

NDS: normalized David's scores. Significant *P* values are shown in bold.
* N_1 and N_2 indicate the number of adult females in the two groups.

than corresponding scores for a star phylogeny with contemporaneous tips. Finally, randomization tests showed consistently significant signals for Pij steepness and counteraggression, and significant signals in seven out of nine phylogenetic trees for Dij steepness (and nonsignificant tendencies for two other trees, $0.05 < P < 0.06$).

DISCUSSION

Evolutionary biologists have long stressed the importance of considering species' phylogenetic relationships while examining the origins of morphological, life-history and behavioural traits (e.g. Harvey & Pagel 1991; Brooks & McLennan 1991; Nunn & Barton 2001; Blomberg et al. 2003). Nevertheless, the application of formal phylogenetic comparative methods to social traits and, in particular, to aspects of primate social structure has occurred only relatively recently (Di Fiore & Rendall 1994; Chan 1996; Matsumura 1999; Thierry et al. 2000, 2008). Our study builds on these few pioneering efforts by using continuous data for a range of macaques and probability-based algorithms to reconstruct more accurate phylogenetic trees from up-to-date genetic data sets, by including groups and species not previously examined, and by focusing on recently developed operational measures of hierarchical dominance gradients. The examination of dominance gradients is significant because they are hypothesized to be central to several models that attempt to explain variation in primate social structure. Briefly, we tested two major predictions of the phylogenetic model using a data set of 14 social groups representing nine species. Our results generally support the predictions. Both hierarchical steepness and counteraggression varied significantly between species, but only inconsistently within species. In addition, measures of steepness and counteraggression showed strong and consistent evidence for phylogenetic signals. Below, we discuss each of our findings in depth.

Table 5
Between-species variation in hierarchical steepness

Macaca fuscata group selected	ANCOVA: NDS vs species*rank			Mixed model analyses variance of slopes (steepness)		
	F	*df*	*P*	Var (slope)j	χ^2_2	*P*
Ventura et al. 2006 (8 adult females)						
Steepness (Dij)	32.78	8, 70	0.001	0.049	250.5	0.001
Steepness (Pij)	20.86	8, 70	0.001	0.047	269.4	0.001
Schino et al. 2007 (23 adult females)						
Steepness (Dij)	9.83	8, 77	0.001	0.034	316.7	0.001
Steepness (Pij)	9.38	8, 77	0.001	0.035	309.9	0.001

ANCOVA and mixed model analyses results for two sets of analyses performed after selecting one *M. fuscata* group at a time. NDS: normalized David's scores.

Variation Within and Between Species

We found strong evidence that both steepness and counteraggression varied significantly between species. In contrast, we found significant within-species variations in counteraggression for only two (Japanese and longtailed macaques) out of five species for which we had data for more than one group. Only one species (Japanese macaques) showed significant differences for both steepness and counteraggression. Although definitive conclusions await a larger sample of groups, particularly those belonging to the same species, our findings appear to be consistent with the prediction that between-species variation is greater than within-species variation, and are similar to the findings of Thierry et al. (2008) for counteraggression and conciliatory tendencies. Also consistent with this prediction, the two Japanese macaque groups in our study belonged to two different subspecies (*M. fuscata yakui*: Ventura et al. 2006; *M. fuscata fuscata*: Schino et al. 2007). On the other hand, they also were the only groups of the same species that showed marked intraspecific differences in size and living conditions. Although we found no evidence to suggest that group size was related to variation in steepness across species (Table 3), it is possible that it may have affected steepness within species (Sterck et al. 1997; Stevens et al. 2005; Balasubramaniam et al. 2011). Similarly, the importance of living condition is not clear in view of the fact that the two Tonkean macaque groups had similar steepness scores despite the fact that one was captive (Orangerie Zoo: De Marco et al. 2010) and the other lived in a forested enclosure of approximately 0.5 ha (Thierry 1985; Demaria & Thierry 2001). Finally, given that the two longtailed macaque groups were of similar size and housed in very similar living conditions (Butovskaya et al. 1995), it is unclear why there were significant differences in counteraggression between these groups. Further clarification of these issues should become possible as suitable data from additional groups become available.

Table 6
ANOVA results for between-species variation in counteraggression for four sets of analyses performed after selecting one *Macaca fascicularis* group and one *Macaca fuscata* group at a time

Groups of *M. fascicularis* and *M. fuscata* selected (number of adult females)	One-way ANOVA		
	F	*df*	*P*
Butovskaya et al. 1995 (7); Schino et al. 2007 (23)	64.98	8, 86	0.001
Butovskaya et al. 1995 (7); Ventura et al. 2006 (8)	57.87	8, 71	0.001
Butovskaya et al. 1995 (9); Schino et al. 2007 (23)	59.72	8, 88	0.001
Butovskaya et al. 1995 (9); Ventura et al. 2006 (8)	53.15	8, 73	0.001

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Table 7
Summary of results from PHYSIG_LL analyses performed for steepness (Dij and Pij) and counteraggression across nine phylogenetic trees

Behavioural trait	MSE	MSE*	LL	LL*	P†	K
10kTrees_tree 1						
Steepness (Dij)	0.042	0.044	2.037	1.816	0.077	0.851
Steepness (Pij)	0.032	0.047	3.293	1.509	0.009	1.162
Counteraggression	212.32	539.76	-36.35	-40.55	0.022	1.857
10kTrees_tree 2						
Steepness (Dij)	0.04	0.044	2.279	1.816	0.066	0.914
Steepness (Pij)	0.03	0.047	3.538	1.509	0.013	1.258
Counteraggression	214.45	539.76	-36.4	-40.55	0.021	1.884
10kTrees_tree 3						
Steepness (Dij)	0.039	0.044	2.406	1.816	0.046	0.94
Steepness (Pij)	0.03	0.047	3.56	1.509	0.011	1.264
Counteraggression	214.32	539.76	-36.39	-40.55	0.03	1.899
10kTrees_tree 4						
Steepness (Dij)	0.039	0.044	2.367	1.816	0.053	0.942
Steepness (Pij)	0.031	0.047	3.446	1.509	0.006	1.234
Counteraggression	221.23	539.76	-36.54	-40.55	0.024	1.842
10kTrees_consensus						
Steepness (Dij)	0.04	0.044	2.203	1.816	0.067	0.895
Steepness (Pij)	0.031	0.047	3.371	1.509	0.013	1.201
Counteraggression	217.45	539.76	-36.46	-40.55	0.04	1.852
MCMC_GTR+I+G						
Steepness (Dij)	0.04	0.044	2.299	1.816	0.068	0.987
Steepness (Pij)	0.031	0.047	3.358	1.509	0.022	1.296
Counteraggression	248.41	539.76	-37.06	-40.55	0.029	1.755
MCMC_partitioned						
Steepness (Dij)	0.04	0.044	2.201	1.816	0.059	0.958
Steepness (Pij)	0.032	0.047	3.28	1.509	0.016	1.254
Counteraggression	245.49	539.76	-37.01	-40.55	0.028	1.733
MCMC_GTR+I+G_9 species						
Steepness (Dij)	0.042	0.044	1.983	1.816	0.074	0.915
Steepness (Pij)	0.034	0.047	3.006	1.509	0.025	1.395
Counteraggression	265.54	539.76	-37.36	-40.55	0.03	1.66
ML						
Steepness (Dij)	0.043	0.044	1.926	1.816	0.113	1.031
Steepness (Pij)	0.036	0.047	2.694	1.509	0.045	1.291
Counteraggression	308.31	539.76	-38.03	-40.55	0.025	1.561

MSE: mean squared errors; MSE*: MSEs for star phylogeny; LL: log likelihood; LL*: log likelihood for star phylogeny. MCMC: Bayesian Markov Chain Monte Carlo; ML: maximum likelihood; GTR+I+G: generalized time-reversible substitution model.
† Indicates significance level from randomization tests.

Phylogenetic Signals

Several lines of evidence suggest that both hierarchical steepness and counteraggression display substantial phylogenetic signals, although the evidence was somewhat weaker for Dij-based steepness scores than Pij-based scores and counteraggression. The *K* statistics were probably the best indicators because they corrected for tree size and shape (Blomberg et al. 2003). For all nine trees, values of *K* for Pij steepness and counteraggression were greater than one, indicating stronger phylogenetic signals than expected under a Brownian motion model of evolution for both traits. Those for Dij scores were slightly less than one, indicating evidence for phylogenetic signals approaching amounts expected under Brownian evolution. MSE and LL scores were also uniformly indicative of strong phylogenetic signals for all three measures. Finally, results from randomization tests also showed significant signals for Pij steepness and counteraggression, and primarily nonsignificant trends for Dij steepness. However, the power of this test is influenced by sample size and was only 30–35% in this case (nine species: Blomberg et al. 2003). It is entirely conceivable that a future analysis incorporating data from more species may yet produce significant results for Dij steepness as well. Our data set was restricted to groups representing nine of the 20 extant species of macaques due to (1) the strict criteria we adopted for calculating accurate behavioural scores (see Methods) and (2) the nonavailability of empirical behavioural data for some species (e.g. northern pigtailed macaque, *Macaca leonina*; Mentawai macaque, *Macaca pagensis*) to date. As such, final conclusions await the availability of data from additional species.

It is possible that the somewhat weaker signals displayed for Dij steepness than Pij steepness could also be due to differences in the way the two indices (Dij and Pij) are calculated. Dij indices (unlike Pij indices) are calculated after taking into consideration differences in the total number of interactions between aggressors (i) and recipients (j) (de Vries et al. 2006; see also Methods). They therefore correct for possible distortions in proportions of wins produced by one-off interactions between dyads. For instance, the victor in a dyad in which one individual wins 10 interactions and the other none, a (10,0) dyad, would have a higher wins–losses index (Dij score) than the victor in a (1,0) dyad, but would have the same Pij score. Such a correction minimizes possible errors due to inadequate observation time when for example, a (1,0) dyad may actually mask a (1,1) relationship. However, it can also be argued that it confounds the effects of activity levels and direction of interaction. Thus, Dij scores may be a less adequate indicator of steepness in some instances, for example, when some dyads interact infrequently but in a consistent manner. At the same time, because it weighs one-off interactions less, we argue that the Dij index may be more useful for species in which there are frequent reversals in aggressive success (Balasubramaniam et al. 2011; see also Bang et al. 2010), relatively low levels of aggression asymmetry and/or high levels of counteraggression (e.g. Sulawesi macaques: *M. nigra* and *M. tonkeana*). Although we only used groups that had been observed for substantial amounts of time, our data set included both types of species (i.e. those that showed consistent asymmetry and those with low asymmetry). We therefore measured steepness using both Dij and Pij indices. The fact that we

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generally found only minor differences in the results suggests that our overall approach to identifying phylogenetic signals for steepness and counteraggression was fairly robust.

Our results for counteraggression are consistent with Thierry et al. (2008), who also found a phylogenetic signal for this measure. However, unlike Thierry et al.'s (2008) study, we included groups living in a wide range of conditions, from captive to wild. As such, our findings of strong phylogenetic signals add to a growing body of evidence (Thierry et al. 2000, 2008) that core aspects of macaque social structure, including hierarchical steepness and counteraggression, have been influenced by species' evolutionary relationships. Additionally, the fact that variation in housing/living condition did not apparently mask evidence for phylogenetic signals is particularly noteworthy in a genus with a history of highly successful phylogeographic radiations into a wide variety of environmental conditions (Hoelzer & Melnick 1996; Abegg & Thierry 2002). It suggests that these characteristics, at least in macaques, may be subject to evolutionary constraints and are not simply the product of historically stable environmental conditions. Nor is it likely that our results are due to correlations between phylogeny and current ecological conditions; a number of studies of macaques (Okamoto & Matsumura 2002; Menard 2004) and of primates in general (Cheney 1992; Boinski 1999; Koenig 2002) have described a lack of correspondence between social traits and ecological conditions (or between social traits and competitive regimes associated with particular ecological conditions).

Whether or not social behaviours show consistent phylogenetic signals in other taxonomically diverse primate genera awaits future research. In other genera, studies on phylogenetic signals thus far have by and large tended to focus more on global patterns of social organization (Di Fiore & Rendall 1994) than on empirical measures of individual or group-level social behaviours, and the results have varied. For example, Ossi & Kamilar (2006) showed that core aspects of social organization in the genus *Eulemur*, including group sizes and sex ratios, correlate with phylogenetic distances. Contemporary Asian colobines show three forms of social organizations (Grueter & van Schaik 2010), the most predominant of which are also the ancestral single-male/multifemale units (Yaeger & Kirkpatrick 1998). The other forms (i.e. strictly modular one-male units and multimale/multifemale organizations) appear to have evolved independently from this ancestral state (Grueter & van Schaik 2010). Given that all the colobines can persist on abundantly available, evenly spread folivorous diets, it is unlikely that variation in social organization has been influenced primarily by variation in resource distribution (Yaeger & Kirkpatrick 1998; but see Snaith & Chapman 2005). On the other hand, both within- and between-species variation in three forms of social organization in baboons (*Papio* sp.), non-female-bonded and lone-foraging units, modular single-male units and multimale/multifemale groups, appear to be more closely related to ecological factors such as food distribution, predation and environmental differences/changes (e.g. Barton et al. 1996; Henzi & Barrett 2003). Squirrel monkeys (*Saimiri* sp.) show even more divergent patterns of social organization that seem closely related to subtle variations in ecological conditions (Boinski 1999).

To our knowledge, comparative data on social traits related to agonistic or affiliative behaviours across a broad range of species in the above genera have not been examined within a phylogenetic framework. It is further uncertain whether, as in the case of macaques, comprehensive, systematically collected data sets on multiple species representing these taxa are available. It is conceivable that the existence and strength of signals for social behavioural traits may vary from taxon to taxon given variation in the phylogenetic basis of basic social organization. In both colobines (e.g. Korstjens et al. 2002; Koenig et al. 2004) and baboons (e.g. Barrett et al. 2002; Henzi et al. 2009), between-group comparative studies of such traits thus far have been predominantly based on either socioecological (Sterck et al. 1997; Koenig 2002) or biological markets (Noe & Hammerstein 1994, 1995) frameworks, and have seldom considered more than two species in the same analysis. Future work needs to discern whether social behaviours also show phylogenetic signals in these taxa using quantitative approaches and reliable phylogenetic trees.

One strength of our findings is that our results were consistent across multiple phylogenetic trees that were constructed from up-to-date genetic data and construction approaches. The use of up-to-date and reliable trees is important given recent revisions in tree typologies for some primate taxa. For instance, revisions in phylogenetic relationships between *Papio* sp. (e.g. Chatterjee et al. 2009; Zinner et al. 2009) have led to the rejection of the earlier hypothesis (Purvis 1995) that hamadryas baboons (*P. hamadryas*), which show single-male/multifemale organizations (Kummer 1968), are basal to other baboons. Such revisions may be significant in understanding the evolutionary origins and divergence patterns of comparative traits. In this regard, comparative biologists are increasingly recognizing the usefulness of Bayesian probability-based approaches for tree reconstruction (Huelsenbeck et al. 2001; Pagel & Lutzoni 2002; Arnold et al. 2010; see Introduction for advantages). We thus suggest that future comparative studies pay adequate attention to deciphering species relationships by using resources such as 10kTrees and/or by attempting similar reconstructions of probability-based trees, rather than relying on outdated topologies available in the literature.

Phylogeny and Socioecology

Taken together, our results provide strong support for the influence of phylogeny in shaping counteraggression and hierarchical steepness in macaques, core aspects of social structure. Thus, they provide strong support for the phylogenetic model. However, our results should not be interpreted to rule out the influence of current ecological circumstances, especially given our limited sample size of groups belonging to the same species.

For the last decade or so, phylogenetic and socioecological models have often been characterized as being in competition with one another (e.g. Sterck et al. 1997; Isbell & Young 2002; Koenig 2002; Thierry 2007; Koenig & Borries 2009). This is in spite of the fact that major proponents of both models suggest that both phylogeny and current ecological conditions are likely to influence behaviour. Recent empirical findings support this view as it relates to kin bias. Berman & Thierry (2010) found that female kin bias in three species of macaques, rhesus (*M. mulatta*), Tibetan (*M. thibetana*) and Tonkean, varied significantly both (1) across species with phylogeny/social style and (2) within species with current socioecological conditions (group size). Their results suggested that kin bias reflects a social reaction norm, in which species respond similarly to socioecological factors, but have inherently different ranges of response to the same conditions (Berman & Thierry 2010). Other aspects of social relationships may also show significant within-species flexibility. For example, Schino & Aureli (2008) showed that across eight groups of Japanese macaques, steeper dominance hierarchies were associated with more grooming being directed up the hierarchy, and that a trade-off occurred between the tendency to groom up the hierarchy and the degree of grooming reciprocation. Whether or not patterns of variation in hierarchical steepness are consistent with the idea of species reaction norms, and to what extent different aspects of social structure show different degrees of within-species variation awaits future research.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2012.02.012.

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Appendix: Definitions of Behaviours

Dyadic Aggression

We analysed frequencies of contact and noncontact aggression. Types of aggression included open-mouth threat gestures or any of its components (i.e. staring, raised eyebrows, lowered jaw, ground slapping), lunges, chases, slaps, grabs and bites. Only total frequencies of aggression were analysed, since some specific subcategories of aggression differed somewhat across different studies. Simultaneous acts of aggression given by the same individual were scored as a single aggressive interaction. If a series of aggressive exchanges took place over time and were interspersed, for example, by the recipient temporarily escaping, each exchange was recorded as a separate aggressive interaction.

Submissive Displacements

We included silent bare-teeth displays and supplantations in which the submissive individual either fear-grinned at, and/or moved away from an approaching dominant individual.

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