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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.

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-