Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints

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Abstract Primate socioecological studies have attempted to derive general frameworks using the average behavioural traits of species or genera to place them into categories. However, with the accumulation of primate studies, it is timely to place more emphasis on understanding within-species variation in social structure. In this review we have four objectives. First, we examine within-species variation in the potential determinants of social structure, including diet, demography, predation and infanticide, and document considerable variation. Second, we present case studies of within-species variation in social structure to illustrate the potential magnitude of this variation. For example, there are cases within a single interbreeding population where multi-male, uni-male, fission–fusion and monogamous groups are found. Third, by examining widespread primate lineages that occur in a variety of habitats, we note that there are differences in the magnitude of variation in social structures across different lineages and as a result we consider phylogenetic constraints on phenotypic variation in social structure. Finally, we reflect on the implications of extensive variation in social structure. We suggest that primate social structure will represent a combination of adaptation to present-day environment and phylogenetic inertia. To advance our understanding of the relative contribution of phylogeny versus ecology we propose two approaches. One approach is to compare groups in the same interbreeding population that inhabit different ecological conditions. Any differences that are found can be attributed to ecological differences, since phylogeny should not play a role within a single population. The second approach is to study distantly related species that have similar social structures to illustrate how similar ecological pressures might be operating to select for parallel social structures.

Keywords Socioecology · Feeding competition · Phylogeny · Mating systems · Social structure · Phenotypic plasticity

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Introduction

A major component of socioecological investigation involves the study of how environmental conditions influence the social structures of animals. Socioecological studies have been a central theme in behavioural studies of primates (Gartlan and Brian 1968; Eisenberg et al. 1972; Clutton-Brock and Harvey 1977; Struhsaker and Leland 1979; Wrangham 1980; Terborgh 1983; van Schaik 1983; Dunbar 1992), and have been one of the areas where

primate studies have contributed most to theory. Early research on this topic formed the framework for many subsequent investigations (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Snaith and Chapman 2007). In these studies, social structure is considered the composition of groups and the spatial patterns of individuals, while social organization consists of the processes of social interactions as exhibited by different group members (i.e. social relationships; Rowell 1972; van Schaik and van Hooff 1983). Early studies attempted to derive general frameworks of social organization, including social structure, but a limited number of descriptive studies were available (Clutton-Brock and Harvey 1977). Consequently, as pointed out by Strier (2003, 2008) and Struhsaker (2000, 2008), species or genera were placed in categories based on the 'average' behavioural characters for each taxonomic unit, ignoring the within-specific variation in social structure. It is now clear that it is necessary to examine how different ecological pressures can lead to within-species variation in social structure (Chapman and Chapman 1999; Struhsaker 2000, 2008; Strier 2003, 2008). We make this statement as a result of three developments. First, over the last three decades there has been an impressive accumulation of data on the diets and behaviour of wild primates, enabling more informed intraspecific comparisons (Richards 1974; Struhsaker and Oates 1975; Butynski 1990; Chapman and Chapman 1990, 1999; Davies et al. 1999); for example, based on the study of 11 different groups of redtail monkeys (*Cercopithecus ascanius*) the proportion of time spent eating different plant parts was shown to vary dramatically (leaves 7–74%, fruit 13–61%, and insects 1–16%; Chapman et al. 2002a). Similarly, while seasonal variation in diet has been appreciated for some time (Clutton-Brock and Harvey 1977; Baranga 1983; Chapman 1987; Lambert 2002), recent long-term studies are demonstrating strong interannual differences in the composition of a group's diet (Altmann 1998; Chapman et al. 2002b; Struhsaker 2008). Changes in the relative proportion of the diet composed of different plant parts are likely indicative of the variables that are predicted to drive change in social structure, but further examinations using factors such as the density, distribution and defensibility of resources are needed.

Second, the primate socioecological model has been refined to more fully account for the variation seen in ecological conditions and social structure, particularly with respect to folivorous primates. Food competition is expected to limit primate group size since larger groups deplete patches faster, forcing increased travel (Wrangham et al. 1993; Chapman and Chapman 2000). However, since leaves do not appear limited in distribution, many authors have assumed that food competition within folivore groups was inconsequential and that populations were not limited by the availability of food (van Schaik 1989; Isbell 1991;

but see Borries 1993; Koenig et al. 1998), and a number of studies have found no relationship between group size and day range among folivores (Clutton-Brock and Harvey 1977; Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998). Given this assumed reduction in feeding competition and the notion that individuals in larger groups are safer from predators, folivores are theoretically free to form large groups. Yet, many folivores live in surprisingly small groups. This apparent contradiction has been referred to as the folivore paradox (Steenbeek and van Schaik 2001; Koenig and Borries 2002). Recent studies have suggested that at least one folivorous species, the red colobus (*Procolobus rufomitratus*), appears to experience within-group food competition: red colobus deplete patches of preferred foods (Snaith and Chapman 2005), travel further in larger groups (Gillespie and Chapman 2001; Snaith and Chapman 2007; Snaith and Chapman 2008) and have reduced reproductive success in larger groups (Snaith and Chapman 2007; see also Koenig 2000; Borries et al. 2008). This led to a new formulation of the socioecological model, at least for the red colobus monkey, because it demonstrated that folivore group size can be limited by food availability (Snaith and Chapman 2007). Since the folivore paradox is invoked to explain why folivores typically do not form large groups, it would be best to test the generality of these findings with a species that is restricted to small groups, which the red colobus is not. Consequently, further tests of these ideas are warranted (but see Snaith and Chapman 2007 for an attempt to generalize these ideas). To demonstrate the potential generality of these ideas for predicting group size of colobus monkeys, Korstjens and Dunbar (2007) use climate as a proxy of habitat productivity and suggest that time budgets may be constraining group size since the monkeys need to spend more time resting as a result of their digestive ecology. They had previously examined this issue in a meta-analysis of spider monkey and baboons at various research sites (Dunbar 1992; Korstjens et al. 2006).

Third, building on advances in evolutionary theory and genetics there has been a realization that there is no evidence to support the idea that homoplasy (similarity between taxa that results from convergent evolution) occurs disproportionately in behavioural systems (Henzi and Barrett 2003, 2005; Rendall and DiFiore 2007). Consequently, the analysis of specific behavioural traits should be phylogenetically informative, when consideration is given to how traits may be linked (DiFiore 2003). What this means for the study of primate sociality is that the observed social structure will represent the combination of adaption to the present-day environment and phylogenetic inertia (Struhsaker 1969; Terborgh and Janson 1986; DiFiore and Rendall 1994; Thierry et al. 2000; Korstjens et al. 2002). When phylogenetic inertia is strong, the less a

social structure represents adaptations to current environmental conditions, and interspecific variation will be more attributed to phylogenetic distance. The strength of the phylogenetic inertia will operate along a continuum on individual traits or sets of linked traits. Inertia would be considered relatively strong in the case of a lineage of primates that was not recently derived and that had similar social structure over a large geographical range where habitat characters varied considerably (e.g. the genus *Macaca*—see below). The notion that phylogenetic inertia can play a large role in determining social structure was suggested early on by Struhsaker (1969), but these ideas stand in opposition to the socioecological model, which assumes that social structure is determined by environmental condition. Rarely has the relative role of phylogeny versus environment been considered with primates (but see Struhsaker 1969; DiFiore and Rendall 1994; Thierry et al. 2000).

The objectives of this paper are to (1) examine within-species variation in determinants of social structure—diet, demography and predation/infanticide, focusing on diet where our expertise lies, (2) present examples of within-species variation in social structure to illustrate the potential magnitude of this variation, (3) consider constraints on phenotypic variation in social structure and (4) reflect on the implications of extensive variation in social structure. While we focus on social structure, we do mention the implication of our deliberations on social relations, such as dominance hierarchy and coalition formation.

Variation in determinants of social structure: diet

It is a long-standing view that social structure is strongly influenced by the nature of food resources. In fact, early assessments of primate socioecology relied primarily on correlational analyses to examine the relationships between ecological and behavioural variation, and categorised primates according to group size or the number of males per group based on diet or habitat (Crook and Gartlan 1966; Eisenberg et al. 1972; Alexander 1974; Clutton-Brock and Harvey 1977). In an influential paper, Wrangham (1980) suggested that female behaviour is affected by ecological variables and food competition, while males are primarily affected by mating competition and the distribution of receptive females (see also Trivers 1972; Emlen and Oring 1977; Vehrencamp and Bradbury 1978). Wrangham (1980) proposed an ecological mechanism for the formation of female-bonded primate groups; specifically, females will live in groups when the benefits of cooperative resource defence outweigh the costs of within-group feeding competition. Females will form bonds with their relatives to

cooperatively defend access to food resources. Larger groups will outcompete smaller groups and obtain higher fitness by excluding neighbouring groups from food sources. An assumption of this ecological mechanism was that high-quality food occurs in discrete, defensible patches, and fallback foods (those eaten when preferred high-quality foods were unavailable) occur in large, uniform patches that minimize within-group competition (Wrangham 1980). When feeding sites within food patches were limited or vary in quality, competition within groups will lead to the formation of female dominance hierarchies. Non-female-bonded species were suggested to occur when preferred foods were of low quality and were uniformly distributed with a large number of feeding sites, or when species used high-quality, patchy resources and had short-term variation in group size whereby individuals respond to fluctuations in food availability and competition [e.g. chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles geoffroyi*; Symington 1990; Chapman et al. 1995; Absensio et al. 2008].

Empirical work has supported the idea that the type and intensity of food competition has important implications for group size, social behaviour, dominance relationships, and dispersal patterns in primates (Koenig et al. 1998; Koenig 2000; Stevenson and Castellanos 2000). With respect to group size, the intensity of scramble competition will increase as a function of group size, as more animals are extracting resources from depletable food patches. As a result, patches will be depleted more rapidly, and individuals will travel further, thereby expending more energy in large groups than small groups (Milton 1984; Wrangham et al. 1993; Chapman and Chapman 2000). Smaller groups will be favored when the energy spent traveling exceeds the energy obtained from the environment. Accordingly, ecological factors affect movement patterns and foraging efficiency, and therefore constrain the number of individuals that can benefit from food resources.

Implicit to this theoretical work is the notion that, if large variation in diet exists, particularly with respect to the size, quality, density and distribution of resource patches, social structure will also be highly variable. Accumulation of data on the diets of wild primate populations in the last three decades has led to growing appreciation of the magnitude of dietary variation within species, including differences among populations, among groups in a single population and within a single group over time (Butynski 1990; Chapman and Chapman 1990; Chapman and Fedigan 1990; Davies et al. 1999; Russo et al. 2005; Yepez et al. 2005); for example, redtail monkey groups (*C. ascanius*) within the same national park varied in the amount of time they spent foraging for leaves (13–35%), fruit (36–60%), and insects (15–31%; Chapman et al. 2002a). When comparing redtail monkey groups in different regions this

variation increased (leaves 7–74%, fruit 13–61%, and insects 1–16%; Chapman et al. 2002a). Even greater levels of variation were found in blue monkeys (*C. mitis*). Butynski (1990) studied four groups of blue monkeys at the same site and found that the amount of time feeding on fruit varied from 22% to 35%. Fruit intake varied among populations from 26% to 91%, and leaf intake varied from 3% to 47% (Chapman et al. 2002a). One population of blue monkeys has even been described as relying on bamboo (*Arundinaria alpina*) for 60% of its foraging time (Twinomugisha et al. 2006).

Studies among folivorous primates have also shown considerable temporal and spatial within-species dietary variation; for example, Chapman et al. (2002b) quantified dietary variability in red colobus monkeys in Kibale National Park, Uganda and compared eight groups each separated by <15 km, neighbouring groups with overlapping home ranges, and the same groups over 4 years, and revealed differences in the amount of time the groups spent eating different plant parts. The largest difference was found in the amount of time spent eating young leaves (38% maximum difference). The amount of time eating fruit varied among groups from 2% to 17%. Chapman et al. (2002b) also contrasted the diet of two red colobus groups with overlapping home ranges. Group 1 used an area of 26.4 ha, while group 2 used an area of 21.9 ha. The area of home-range overlap was 10.7 ha, which represents 41% of group 1's home range and 49% of group 2's home range. During the days that group 2 was observed it spent 70% of the time in the area of overlap, while group 1 spent 49% of its time in this area. Despite this degree of home-range overlap, diets differed; for example, group 1 ate young leaves for 64% of the feeding observations, while group 2 ate young leaves in 76% of the observations. Finally, interannual differences in diet were documented; for example, in 1994 red colobus ate young leaves during 56% of their feeding time, and this increased to 76% in 1998. There was also interannual variation in the amount of time spent eating from particular plant species. In 1994 the red colobus fed on *Albizia grandibracteata* for 11% of their feeding time, but in 1998 they fed on the same species for only 1% of their time, and there were no interannual differences in availability of the plant parts of this species.

In the same general area of Kibale National Park, Harris and Chapman (2007) studied six groups of neighbouring black-and-white colobus (*Colobus guereza*), and found considerable intergroup variation in diet; for example, the overall percentage of mature leaves in the diet differed by more than fourfold among groups (11.7–50.2%) and that of fruit in the diet differed by more than 11-fold among groups (1.6–17.7%). Monthly variation in different plant parts was also highly variable; for example, for one group the use of mature leaves ranged among months from 5.9%

to 91.6%. Similarly, folivorous Hanuman langurs (*Semnopithecus entellus*) had a very flexible diet, which varied from 19% to 86% leaves, and at times 25% of their diet was insects (Koenig and Borries 2001, 2002). This variation in diet corresponded to variation in group size, the number of males per group (i.e. uni-male versus multi-male), the tendency for male or female dispersal, and infanticide (Treves and Chapman 1996; Koenig and Borries 2001, 2006).

To know if such differences in diet select for different social structures one would ideally have information on diet, the nature of the competitive regimes and social structure. However, when diets are as variable as has been documented here, it would lead one to suspect that such differences as those described here could lead to variation in social structure in many primate species.

Variation in determinants of social structure: demography

It has long been recognized that demographic factors can influence social structure (Altmann and Altmann 1979). As discussed above, for many species, evidence suggests that the upper limit of group size is constrained by travel costs. Larger groups deplete food patches more quickly (i.e. more mouths to feed) and are forced to travel to more patches. When the travel costs associated with the increase in group size becomes prohibitive, smaller groups become advantageous (Wrangham et al. 1993; Chapman and Chapman 2000). For species where this was the case, ecological factors determined the social structure in a group by influencing the number of animals in the group: a simple demographic factor; for example, if ecological conditions only permit groups of very small size, then the species will adopt a monogamous social structure. Robbins et al. (1991) demonstrated such a demographic effect by contrasting the social structure and group size of gibbons (*Hylobates muelleri*) and spider monkeys (*Ateles geoffroyi*): two taxonomically distant species with similar diets, body size, and locomotor patterns. Gibbons have a monogamous social structure where the pair of adults travel with their pre-adult offspring, while spider monkeys live in a fission–fusion social structure. Robbins et al. (1991) demonstrated that the density of spider monkey foods were highly variable among months. When the density of their foods were comparable to the more stable gibbon food resources, spider monkeys travelled in similarly sized groups to gibbons (spider monkeys 3.5 members, gibbons 3.4 members; Robbins et al. 1991).

As Strier (2008) notes, both multi-male and uni-male social structures are documented for a number of species, and examples include black howler monkeys (*Alouatta pigra*;

van Belle and Estrada 2006), red howlers (*Alouatta seniculus*; Pope 1991) and mountain gorillas (*Gorilla beringei*; Robbins 2001). This may be the effect of the demographic factor of group size on social structure, or the effects of population density relative to carrying capacity (Pope 1991). Variation in differences of dispersal patterns has been described for hylobatids (Fuentes 2000) and gorillas (Bradley et al. 2004) that live under different demographic conditions (Strier 2008), which led to different behavioural patterns; for example, documented dispersal networks in western lowland gorillas (*G. gorilla*) may explain the frequent nonaggressive encounters between neighbouring lowland gorilla groups (Tutin 1996; Bradley et al. 2004), while those between mountain gorillas were typically aggressive (Harcourt and Stewart 2007). In western lowland gorillas, males in neighbouring groups were often related (Bradley et al. 2004).

Similarly, ecological pressures that influence the sex ratio of primate populations potentially affect group size and social structure. In a study of 102 primate species, Silk and Brown (2008) demonstrated that birth sex ratio was skewed in favour of the dispersing sex as predicted by the local resource competition hypothesis (Clark 1978). This hypothesis suggests that, when individuals of one sex disperse while the other sex remains in the mother's home range, sex ratio will be biased in favour of the sex that disperses from the natal area. In spider monkeys the bias in the sex ratio increased with decreasing resource availability, and became extremely skewed in the least productive habitats (Chapman et al. 1989a, b). For many primates, populations occupying harsh environments will likely reduce their group size, and for female-dispersing species that typically occur in multi-male multi-female groups, uni-male groups will become more common (Shino 2004).

Variation in determinants of social structure: predation and infanticide

It has been frequently speculated that the risk of predation (Alexander 1974; Terborgh 1983; van Schaik 1983; van Schaik and van Noordwijk 1989) and infanticide (Treves and Chapman 1996; Crockett and Janson 2000; Steenbeek and van Schaik 2001) influences group size and composition. Unfortunately, these speculations are difficult to verify quantitatively since predation and infanticide are rare events, may be deterred by the presents of an observer and are often clustered in time (Cheney and Wrangham 1987; Isbell 1990; Borries 2000; Crockett and Janson 2000); for example, Cheney and Wrangham (1987) estimated that the yearly predation rate in 24 primate populations was 3%.

Some of the best quantifications of predation come from studies of predators; for example, based on observations of the chimpanzees, Teelen (2008) reported the predation rate of red colobus by chimpanzees (*Pan troglodytes*) from the Ngogo site in Kibale National Park. Between 1995 and 2002 the off-take of red colobus averaged 217 animals per year, representing between 15% and 53% of the population within the territory of the chimpanzee community. In contrast, in over 33,000 h of observation of red colobus at the Kanyawara site in Kibale, only two predation events of infants have been observed (Chapman et al., unpublished data) and observations of the well-habituated chimpanzee community in Kanyawara also reported that predation rate on red colobus were low compared with that at Ngogo (Watts and Mitani 2002). However, despite this large difference in predation rate, there was no evidence for differences in average red colobus group size and the composition of groups were similar between these two sites (Ngogo: Teelen 2008, Kanyawara: Chapman, unpublished data), suggesting that predation rate is highly variable within a species and that the role of predation on social structure is not well understood.

In contrast to the chimpanzee example, the predation rate by African crowned eagles (*Stephanoaetus coronatus*) in Tai Forest, Ivory Coast was negatively correlated with group size among arboreal primates (Shultz et al. 2004). Unfortunately, there are relatively few long-term evaluations of predation rates at the community level. However, it seems probably that predation by eagles (Struhsaker and Leakey 1990; Mitani et al. 2001) could lead to increases in group size, and species that typically exhibited a uni-male social structure could adopt a multi-male multi-female social structure when predation rates were high.

As with predation, diet and demography, accumulating evidence suggests that the rate of infanticide is highly variable (Borries and Koenig 2000); for example, in some multi-male groups, no or less than 10% of all infants born fall victim to infanticide, and infanticide accounted for less than 20% of all infant mortality (Broom et al. 2004). Species that fall into this category include *Macaca* spp., *Papio anubis* and *P. cynocephalus*. In contrast, in another group of species more than 10% of all infants born die as a result of infanticide, accounting for over 30% of infant mortality (Broom et al. 2004). Species that fall into this category include *P. ursinus*, *Propithecus diadema* and *Semnopithecus entellus*.

In addition, to the rate of infanticide being variable, different authors have advocated that infanticide plays varying roles in influencing primate social structure; for example, Crockett and Janson (2000) found that the rate of infanticide increased with group size in red howlers (*Alouatta seniculus*), but only until the group was large enough to create paternity confusion, at which point

competition amongst group members became more costly. However, the authors concluded that, before the level of competition within the group imposed a significant cost, infanticide avoidance could constrain group size. Similarly, Steenbeek and van Schaik (2001) suggested that, among Thomas' langurs (*Presbytis thomasi*), group size was limited by the risk of infanticide because larger groups were more at risk of male takeover. In contrast, Treves and Chapman (1996) found that infanticide avoidance did not limit group size in different populations of hanuman langurs, but that increasing group size may have been a counterstrategy to prevent takeovers and infanticide. Thus, it is possible that not only is the rate of infanticide variable, but that the role it plays in influencing social structure may also be variable and suggests that more information is needed and it may be helpful to evaluating the relative strengths of a set of selective pressures at influencing social structure.

## Case studies: within-species variation in social structure

While few primate species have been studied to the extent where it is possible to accurately contrast the potential predictors of variation in social structure, there are a handful of studies that specifically examined this, and these studies suggest substantial intraspecific variation; for example, Sinha (2005) and Sinha et al. (2005) provided a detailed description of variability in social structure in bonnet macaques (*Macaca radiata*). Bonnet macaques are usually described as living in relatively large multi-male multi-female social groups (mean group size 25.7 ± 3.7 SE), where males within a group are tolerant of each other, and males are the dispersing sex (Sinha et al. 2005). In stark contrast, groups in Bandipur–Mudumalai Wildlife Sanctuary in southern India were small (10.6 ± 1.2 SE), typically uni-male, males were very intolerant of other males, males herded receptive females, and females dispersed among groups. Sinha et al. (2005) speculated that this social structure has resulted from high-quality food provisioning by tourists along the road. Since the food was spatially and temporally clumped, it led to high levels of competition among females in multi-male groups. This led to group fission, whereby smaller groups were monopolized by a single male, resulting in uni-male groups. Provisioning creates food sources that are spatially clumped and monopolisable, so unlike typical nonprovisioned populations, in provisioned populations linear dominance hierarchies among females are often found. Provisioned food is typically available year round. This reduces food and mating seasonality, thus females are more monopolisable, leading to uni-male groups. In addition, predators are typically reduced or absent in areas with

frequent human presence. If the males serve a role in predator defense, this reduction will permit smaller groups, which may also contribute to the formation of uni-male groups (Treves and Chapman 1996). The adoption of a linear dominance hierarchy in langurs has also been described in undisturbed areas where food resources were clumped (Koenig et al. 1998; Koenig and Borries 2006). Similarly, Nakagawa (2008) contrasted two populations of patas monkeys (*Erythrocebus patas*) and documented that, in situations where food resources were clumped, they formed linear dominance hierarchies, but when resources were dispersed they did not.

Several lemur species, including sifakas (*Propithecus diadema*) have been considered "idiosyncratic" or "puzzling" because, within a single population, several different types of social structures are found (Wright 1999; Kappeler 2000; Pochron and Wright 2003). Pochron and Wright (2003) quantified the sex ratio of sifaka groups during the mating season for 15 years. Of 45 groups observed, 29% were polyandrous, 27% were pairs, 24% were polygynandrous, and 20% were polygynous. The animals were more likely to remain in the same mating system than expected from random, infant survival was equal amongst the different types of social structures and the number of females in a group did not predict the number of males in a group, counter to a general trend in primates (Andelman 1986; Nunn 1999). Pochron and Wright (2003) suggested that for sifakas predator avoidance selected for grouping and that feeding competition may limit group size, but since mating readily occurs among groups, mating and foraging groups may be different and the neighbourhood may serve as a "mating group". This is made possible because this species has a very restricted breeding season. If this explanation is correct, there would be little selection for the composition of the group, which would explain the wide variety of social structures that are observed.

By contrasting the social structure of groups in the same population but inhabiting areas with different ecological conditions, the effect of varying ecological conditions can be evaluated directly, since phylogeny will have no impact. To evaluate this let us turn to our own work on red colobus in Kibale National Park, Uganda. This population is known to adopt four social structures: multi-male multi-female, uni-male, monogamous, and fission–fusion. The majority of the red colobus groups have a multi-male multi-female composition and are relatively stable in composition (Struhsaker 1975, 1997). However, two large groups (74 and 127 members) were known to repeatedly fission into smaller subgroups for periods lasting from several hours to several days; the size and composition of subgroups were not constant over time (Snaith and Chapman 2008). Subgroups were defined as a portion of the group that was

Fig. 1 To advance our understanding of the relative contribution of phylogeny versus ecology one can study very distantly related species that do not share a close common ancestor but that have similar social structures to illustrate how ecological pressures might be operating (**a**, **b**), in this case spider monkeys (*Ateles* sp.) and chimpanzees (*Pan troglodytes*) in similar forest habitats. Alternatively, another valuable approach will be to make comparisons when phylogeny plays a relatively small role, which can be done by contrasting groups in the same interbreeding populations but found under different ecological conditions. In this case a fictitious baboon species is contrasted in a forest habitat and a savanna habitat (**c**, **d**)
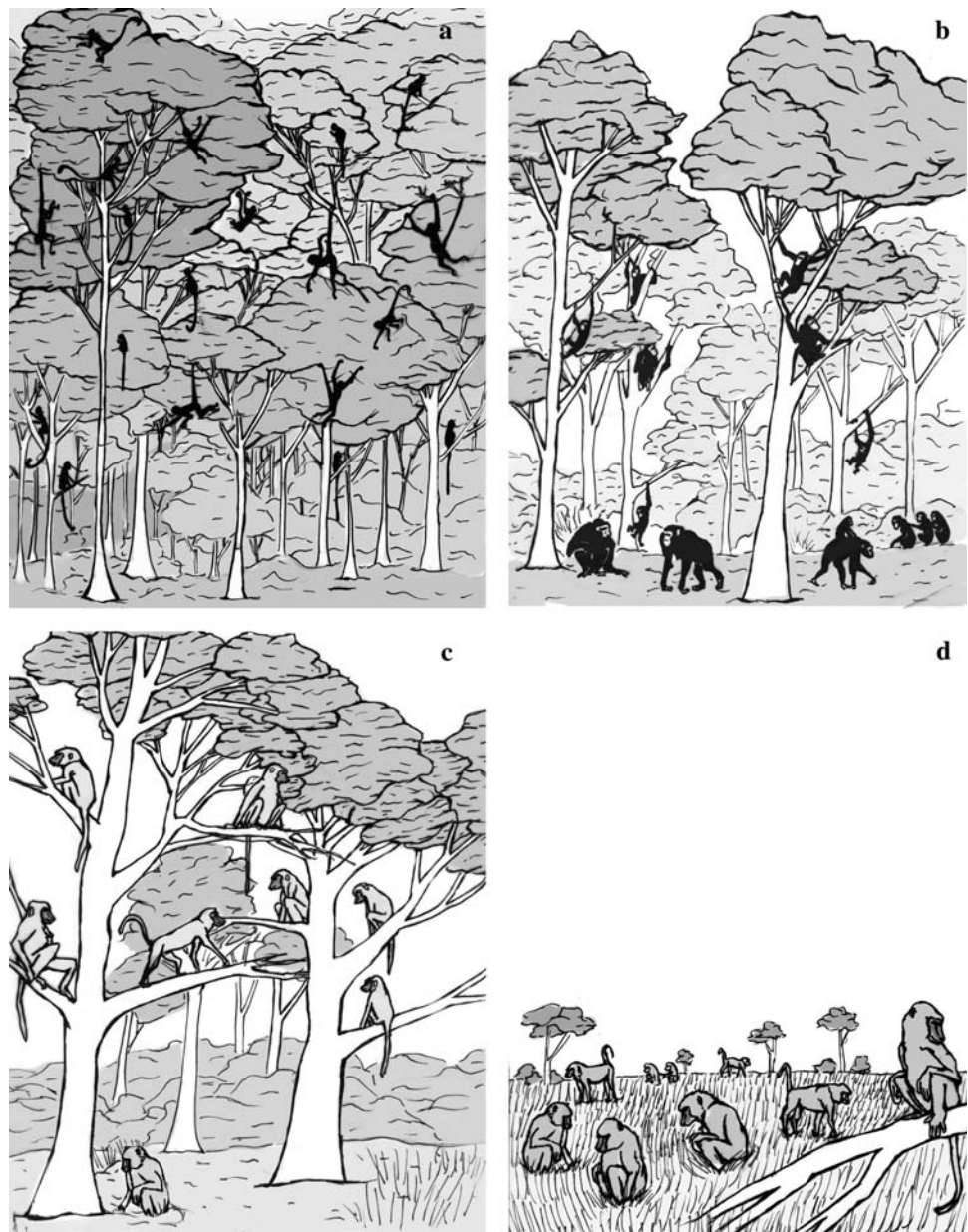
separated from the rest of the group by more than 300 m, with no group members scattered in between. One of these groups has been followed for 6 years and has been known to adopt this social structure throughout this period, thus it does not appear to represent a group that is in the process of dividing (see also Marshall et al. 2005). This social group was found in the same area as a number of multi-male multi-female groups and there were no apparent ecological differences in the home ranges of groups that have these different social structures; the only difference between the different types of groups was that the group that regularly divides was much larger than the other multi-male/multi-female groups. In addition, just outside of the park along a

riverine strip of forest subject to the harvesting of canopy-level trees and apparently ecologically depauperate, two groups have been observed: one group had a uni-male social structure while the other took on a monogamous social structure (Chapman et al. 2002b). These groups (3 and 11 members) were observed for two years and appeared to have a stable adult composition, although we were unable to individually recognize the females. It would appear that the type of social structure was dependent on group size, which was a pattern that has been documented in the past (Andelman 1986; Nunn 1999); however, these groups have adopted different types of social structures and were found in a single population.

Constraints on phenotypic variation in social structure

In contrast to studies just discussed, there are numerous studies of members of the *Macaca* genus that have found little or no variation in social structure and female social relationships despite the fact that members of this genus are found in variable ecological conditions (Yamagiwa and Hill 1998; Matsumura 1999; Hanya et al. 2008; but see Nakagawa 1998 for a difference among populations in grooming frequency and Sinha et al. 2005 above); for example, Hanya et al. (2008) compared the competitive regimes and female social relationships of Japanese macaques (*Macaca fuscata*) at two elevations on Yakushima that differed in fruit availability. Counter to predictions of the socioecological model, no differences in the direction and concentrations of grooming or linearity in dominance rank were found. However, Zhang and Watanabe (2007) documented relaxed dominant relationships of Japanese macaques on Shodoshima Island, which they speculated facilitated the formation of large resting groups, which may be an adaptive behaviour against the cold weather. They speculated that this paralleled subtle differences among species within the genus and suggested that members of the *Macaca* genus may be conservative in some traits (Zhang and Watanabe 2007).

Variation among baboon species in the tendency to form coalitions offers a clear example of how behaviours can be phylogenetically constrained. Barrett and Henzi (2002) presented evidence that, under the ecological conditions found at the time that the baboon races diverged (Henzi et al. 1999), most groups would contain only one adult male. Consequently, the conditions to form male coalitions could not have been selected for. Even though multi-male groups are common today, males do not form coalitions in the population studied by Barrett and Henzi. A similar argument can be made for females; because of the small cohort size in females and the low availability of potential partners (i.e. females with young infants tend to be peripheral and not available to form coalitions), coalitionary behavioural strategies are not selected for (Barrett and Henzi 2002). As a result, females do not form coalitions today, even though female cohort size is larger than the cohort size of other baboon races that do form coalitions (Barrett and Henzi 2002).

Implications for within-species variation in social structure

To understand what factors lead to an observed social structure, some traits will be responses to current ecological or social factors (e.g. demography and infanticide), while others will be constrained by phylogeny. The striking similarity between spider monkey and chimpanzee social structure, whose last common ancestor was prior to 26 million years ago (Hartwig 2007), suggests that in some instances ecological responses can produce remarkably similar social structures. Both of these species have similar association patterns (Symington 1990; Chapman et al. 1995; Sayer and Lovejoy 2008; Aureli et al. 2008), territorial patterns that involve male boundary patrols (spider monkeys, Aureli et al. 2006; chimpanzees Wilson et al. 2004), lethal intergroup attacks (spider monkeys, Campbell 2006; Valero et al. 2006; chimpanzees, Watts 2004), patterns of female-directed aggression (spider monkeys, Campbell 2003; chimpanzees Wrangham et al. 2006) and rely on food resources with similar characteristics (Chapman et al. 1995). Interestingly, such similarities in social structures between species that are very distantly related questions the validity of using chimpanzees as models to reconstruct the social structure of early humans (Moore 1996).

It would be intriguing to investigate what traits allow some species to be phenotypically plastic, while others remain phylogenetically constrained. To advance our understanding of the relative contribution of phylogeny versus ecology one valuable approach would be to make comparisons when phylogeny plays no role. This comparison can be done by contrasting groups in the same interbreeding populations found under different ecological conditions (Fig. 1c, d). This evaluation highlights the need for interdemic comparisons or long-term studies that span periods of ecological change (Chapman, Rothman, and Struhsaker, unpublished data; Butynski 1990; Altmann et al. 2002). Alternatively, one can study species that are very distantly related but that have similar social structures to illustrate how ecological pressures might be operating (Fig. 1a, b).

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