Evolution of social organization: A reappraisal for primates by using phylogenetic methods

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ABSTRACT   For many animal taxa, the extent to which phylogeny can account for the form of species' social systems has seldom been investigated formally. A quantitative phylogenetic analysis of social systems in the order Primates reveals that social organization may be strongly conserved in some lineages, even in the face of considerable ecological variability. This result has important implications for efforts to understand the evolution of animal societies and for attempts to reconstruct the social organization of early humans.

Understanding the evolution and adaptive nature of social organization is a major goal in the study of animal and human societies. Although ecological pressures and phylogenetic history are thought to contribute to the form of species' social systems (1, 2), the specific influence of phylogeny has seldom been investigated in a systematic and quantitative fashion. Here we reappraise the evolution of Primate social organization using phylogenetic methods to explicitly evaluate the phylogenetic contribution to social systems within this order.

Social Organization Defined

A phylogenetic analysis of social systems requires identifying a set of salient social organization traits and defining the alternative character states for each. Because social organization is complex, we use a set of 34 traits encompassing several major dimensions of primate social life to characterize the social systems of extant taxa (Table 1). While many of the traits and their character state definitions are self-explanatory, some warrant elaboration.

Dispersal. We define dispersal as movement out of the natal range, usually prior to first breeding. For some species where individuals may remain within part of their natal range or disperse to establish a territory elsewhere, we have coded dispersal polymorphically.

Adult Grouping Patterns. Primates group in a wide variety of ways, from the solitary foraging lorises (*Perodicticus*), to the cohesive troops of gorillas (*Gorilla*), to the flexible parties of chimpanzees (*Pan*), to the multilevel societies of some terrestrial baboons (*Papio* and *Theropithecus*). A correspondingly broad array of terms has been used to refer to these patterns (e.g., groups, parties, bands, communities, and networks). For our analyses, we have generated a set of standard definitions that can be applied across primate taxa.

We define the group as the set of individuals that commonly interact with one another (e.g., during foraging or resting). This definition encompasses the subgroups, parties, and foraging units seen in some taxa, as well as the solitary individual foragers of nongregarious species. Taxa in which individuals regularly associate with variable sets of other animals (e.g., chimpanzees) are coded polymorphically to reflect this flexibility in grouping patterns. We then examine the same-sex and opposite-sex grouping patterns of adult

males and females to assess the size and composition of groups. Lastly, we define unisex bands as stable associations of same-sex individuals that do not have persistent contact with a particular community and exclude such bands from our consideration of community structure.

Community Structure. We define the community as the set of individuals within which breeding typically occurs. For taxa grouping in stable cohesive associations [e.g., macaques (*Macaca*)], this definition is easily applied—the group and the community are identical. This definition also corresponds to the unit group or community as previously recognized for fission–fusion societies and to the bands of hamadryas and gelada baboons. The situation is less clear, however, for more dispersed nongregarious taxa [e.g., galagos (*Galago*)], where typically the home range of a resident breeding male overlaps the independent ranges of several breeding females. In these cases, we define the community as the dispersed polygynous breeding unit that includes the male and the several females whose ranges are overlapped. We then examine community structure and intercommunity relations in the following ways:

(*i*) Are males sociospatially integrated with the other community members, are they peripheral to the rest of the community, or do they typically range separately?

(*ii*) Does the community contain solitary ranging individuals, does it have no distinct substructure, or is it made up of subunits of either stable or variable composition?

(*iii*) Is the size of a typical foraging unit less than, equal to, or greater than the size of the social unit within which reproduction usually occurs?

(*iv*) Are interactions between communities territorial, tolerant, or based on a dominance/subordinance relationship?

(*v*) Which adults typically participate in intercommunity spacing?

Mating Patterns. Because for many taxa the breeding system is unclear, we consider reproductive activity with respect to mating behavior only. We consider the mating system with respect to each sex, the pattern of mating initiation, and the general mating style that characterizes the taxon.

Intragroup Relations. For these traits, we focus on male–male and female–female within-group social interactions and examine grooming behavior, coalition formation, dominance relations, agonism, and overall social relations.

Intersexual Relations. These traits characterizing social relations between the sexes are defined at the community level to permit coding of taxa where males and females do not commonly group together (e.g., lorises) but are still part of the same community and may thus interact and maintain social relations. Intersexual agonism may be principally directed by one sex toward the other, may be bidirectional, or may occur rarely. This includes cases where two or more same-sex adults cooperate to aggress members of the opposite sex. Intersexual dominance refers to whether or not there is a stable pattern of asymmetrical relations between the sexes.

Table 1. Social organization traits, character states, and retention indices

Social organization trait	Character state				RI
	0	1	2	3	
Dispersal					
Dispersal by males	Common	Uncommon			0.333
Dispersal by females	Common	Uncommon			0.636*
Adult grouping patterns					
Male SS grouping	No SS adults	Nonkin based	Kin based		0.250
Female SS grouping	No SS adults	Nonkin based	Kin based		0.643*
Male OS grouping	No OS adults	1 OS adult	>1 OS adult		0.455
Female OS grouping	No OS adults	1 OS adult	>1 OS adult		0.300
Unisex bands	Absent	Present			0.250
Community organization					
Sex segregation	Males integrated	Males peripheral	Males separate		0.273
Community substructure	Solo individuals	No subunits	Stable subunits	Variable subunits	0.111
Foraging unit size	< reproductive	= reproductive	> reproductive		0.400
Intercommunity relations	Territorial	Dominance/ subordinance	Tolerant		0.364
Intercommunity spacing	Males active	Females active	Both active	Neither active	0.444
Mating patterns					
Male mating system	Monogamous	Polygynous–promiscuous			0.333
Female mating system	Monogamous	Polyandrous–promiscuous			0.000
Mating initiation	By male	By female	By either		0.455
Mating style	Dominance-based or contested	Pair bond	Short term consortship	Permissive	0.250
Male intragroup relations					
Male–male grooming	Absent	Infrequent	Common		0.000
Male–male coalitions	Absent	Present			0.000
Male dominance relations	Absent	Weakly developed	Well developed		0.167
Male–male agonism	Absent	Infrequent	Common		0.333
Social relations between males	Absent	Competitive	Tolerant	Competitive/ cooperative	0.250
Female intragroup relations					
Female–female grooming	Absent	Infrequent	Common		0.600*
Female–female coalitions	Absent	Present			0.571*
Female dominance relations	Absent	Weakly developed	Well developed		0.538*
Female–female agonism	Absent	Infrequent	Common		0.538*
Social relations between females	Absent	Competitive	Tolerant	Competitive/ cooperative	0.688*
Intersexual relations					
Male-to-female grooming	Absent	Infrequent	Common		0.154
Female-to-male grooming	Absent	Infrequent	Common		0.333
Intersexual agonism	Male-to-female	Female-to-male	Both	Neither	0.500
Intersexual dominance	Male	Female	Neither		0.455
Reproductive investment					
Paternal care	Absent	Present			0.600*
Allomothering	Absent	Present			0.583*
Infanticide by males	Absent	Present			0.429
Targeted aggression by females	Absent	Present			0.375

SS, same sex; OS, opposite sex; RI, retention index. The retention index is a ratio from zero to one relating the range of possible character state changes a trait could require on any conceivable tree to the actual number of changes observed on the given tree. Values close to zero indicate a poor fit to the tree, while those close to one indicate a strong tendency for the character state to be retained once evolved. The retention index for each trait is evaluated by the formula (max − actual)/(max − min), where max is the maximum possible number of changes that a particular trait could require on any conceivable tree, min is the minimum number of changes that the trait could show on any conceivable tree, and actual is the observed number of changes in that trait on the given tree.
*Traits with retention indices >0.500.

Reproductive Investment. Patterns of reproductive investment are defined using four traits that characterize, for each sex, the nurturant and competitive components of reproductive effort. We define paternal care as the absence or presence of direct contributions by adult males to the survival of offspring (e.g., provisioning or carrying). Our definition does not include such indirect forms of investment as territory maintenance or vigilance. By targeted aggression we refer to the behavior of females' focusing aggression on specific other females or their infants, presumably to compromise the reproductive performance of those females.

Data Collection and Analyses

Data were compiled from an extensive review of the primary literature and from taxon review chapters in primate behavior texts (e.g., refs. 3–6) (the data matrix and a complete list of the references used to compile the matrix

is available upon request). Attention was limited to studies of wild or free-ranging populations; data from captive studies were not included. Data were first collated at the species level and then collapsed into genus level codings because of computational limitations inherent in the computer software used for analyses. All species for which data were available on >70% of the traits were included. To perform some analyses, it was necessary to specify an outgroup for comparison. Because some uncertainty exists as to what is the most appropriate outgroup for primates, our coding was developed from two major sources: (i) field studies of tree shrews (7, 8)—commonly regarded as a sister taxon to the Primates—and (ii) a hypothesized "general mammalian" social condition (9, 10). The coding is consistent with what a number of researchers have presumed the ancestral primate condition to be (11, 12).

We first used the PAUP computer program (13) to undertake a cladistic analysis, unconstrained by phylogenetic information about the taxa being considered, to reveal how primate genera cluster together solely on the basis of derived similarity in their social systems. The large number of taxa in our data set prohibited the use of exact algorithms for this task; instead, we used the heuristic search option of PAUP, which is designed to deal with such large data sets. One of the potential limitations of a heuristic search is that it does not guarantee that globally optimal minimum length trees are found. To circumvent this problem, we conducted 50 heuristic searches for parsimonious trees of minimum length to be confident of locating a globally optimal tree.

For all searches, traits were assigned equal weight, and all character states were left unordered and allowed to reverse freely. Searches were conducted as follows: Each search was started from a different random seed, proceeded by stepwise addition, and used the tree bisection-reconnection algorithm to generate a set of 500 trees of the same minimum length. Of the 50 searches, 31 yielded minimum length trees of length 385 and no search yielded trees of length greater than 390. This compares to a set of 1000 randomly generated trees based on the same data that yielded an average length of 570, with no tree shorter than length 532. For each of the 31 searches yielding minimum length trees of length 385, we constructed a single consensus tree by a 90% majority rule criterion. These 31 trees were then used to construct a single consensus tree by 75% majority rule that identifies the most consistent pattern of clustering of primate taxa on the basis of derived similarity in social systems (Fig. 1).

The striking result of this analysis is the marked uniformity in patterns of social organization revealed among the Old World monkeys (superfamily Cercopithecoidea): 9 of the 10 genera in this taxon (Fig. 1) cluster together as a highly derived group relative to all other primates. This cluster was observed in 100% of the minimum length trees generated (n = 15,500 trees). The only remaining cercopithecoid genus, the red colobus monkey (Piliocolobus), lies only a short distance away. Also clustering with the cercopithecoids are three genera from two of the other primate superfamilies: capuchin monkeys (Cebus), ring-tailed lemurs (Lemur), and sifakas (Propithecus). The tight grouping of cercopithecoid taxa at the derived pole of this cladogram indicates that their social systems are not only very similar to one another but also very different from those of most other primates. The pattern seen in the cercopithecoids contrasts with the greater variability in social organization seen among genera in the other primate superfamilies.

We next input a primate phylogeny (14–17) and used the MACCLADE computer program (18) to chart the locations of changes in social organization variables along the primate evolutionary tree. Fig. 2 depicts the phylogeny used and indicates the number of character state changes—averaged across all equally parsimonious reconstructions of character
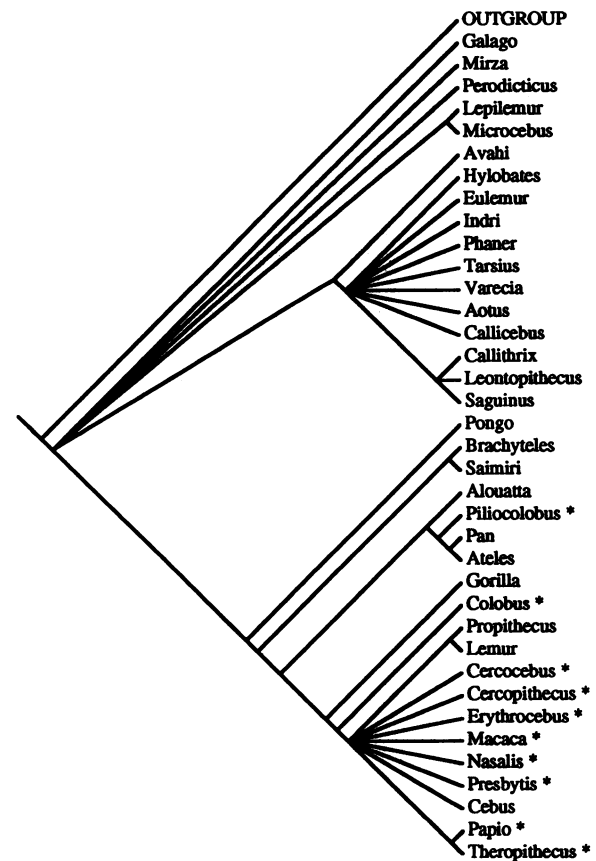

FIG. 1. Relationships among primate genera based on social system similarity. Genera with similar social systems group closer together. Those further from the social system of the outgroup are more derived.
*Cercopithecoid genera.

state evolution—occurring along each branch of the tree. Note that by averaging the amount of change across all reconstructions, no assumptions are made about whether reversals or parallelisms are favored in character state evolution. Internal nodes on the figure are labeled to reflect hypothetical ancestral taxa.

Fig. 2 emphasizes the highly derived nature of cercopithecoid social systems: an average of 15.8 changes occurs in the evolution of the stem cercopithecoid from the stem primate, whereas an average of only 9.1 changes characterizes the evolution of the stem hominoid, 8.2 changes characterizes that of the stem ceboid, and 4.7, 2.9, and 1.9 changes characterize those of the stem tarsioid, lemuroid, and lorisoid, respectively. Because calculations of average amounts of change consider the maximum number of changes that can occur along each branch (including ambiguous changes where the character states of ancestral and descendant taxa cannot be assigned definitively), it may be more informative to consider only those traits that change unambiguously. A total of 9 unambiguous changes is involved in the evolution of the stem cercopithecoid, while no more than 2 changes are required in the evolution of any other superfamily. Importantly, 7 of the 9 unambiguous changes that occur in the evolution of the Cercopithecoidea do so along a single branch of the tree, as they diverge from their last common ancestor with the apes.

Understanding Old World Monkey Social Systems

The uniform and derived nature of cercopithecoid social organization revealed in these analyses indicates that the
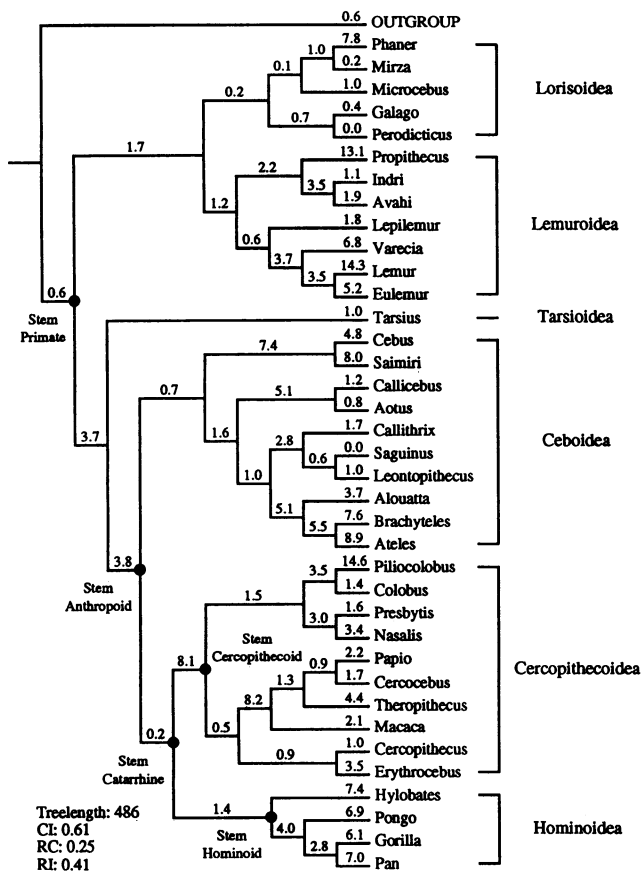
FIG. 2. Primate phylogenetic tree and branch lengths. Numerical values indicate the average number of character state changes occurring along each branch of the tree. Ancestral taxa are labeled at internal nodes. CI, consistency index; RI, retention index; RC, rescaled consistency index. This phylogeny was derived from studies using both morphological and molecular data.

social systems of these primates are highly unusual. All but one of the unambiguous changes that characterize the evolution of the cercopithecoids pertain to female relationships and grouping patterns. Thus along the branch leading to the Old World monkeys, the following social organization traits evolve: female philopatry, females grouping with same-sex kin, strong female grooming relationships, well-developed female dominance relations, allomothering, and the existence of both competitive and cooperative relationships among females. This suite of character states is found in nearly all extant cercopithecoids. Additionally, female–female coalitions and female–female agonism are common among the Cercopithecoidea. The social organization traits to which all of these characteristics pertain show eight of the nine highest retention indices across the phylogenetic tree (Table 1). The retention index measures how conserved a trait is across a given tree; high retention indices indicate that once particular character states for a trait evolve, they tend to persist in descendant taxa. This fact helps to explain the marked uniformity in social systems among cercopithecoid primates revealed by our cladistic analysis.

Notably, the set of social organization traits characterizing cercopithecoid primates appears to hinge on female philopatry. Where adult females remain in their natal range and group with female kin, the potential for strongly differentiated female relationships arises. Females will be predisposed to behave cooperatively with kin, forming strong affiliative relationships with them (as shown by frequent social grooming, allomothering, and support in coalitions), and to compete

with nonkin (leading to interfemale aggression and well-developed dominance relations) (19).

While this suite of character states is highly correlated with female philopatry, it is not always manifest as a unitary complex; in other taxa, some of these character states are seen in the absence of female philopatry, while not all occur in the presence of female philopatry. For example, among female-dispersal species, strong female grooming relationships and female–female coalitions are seen in bonobos (Pan paniscus), and allomothering is normative among tamarins. Furthermore, two of the three genera that cluster with the cercopithecoids in the social system cladogram (Lemur and Propithecus) show some, but not all, of the character states in this suite. While both are female philopatric and group with female kin, sifaka females groom only infrequently, do not show allomothering, and tolerate but do not obviously cooperate with one another, and ring-tailed lemur females are competitive but do not form coalitions and show little evidence of cooperation even within matrilines.

The uniformity in Old World monkey social systems is particularly interesting in the light of the fact that extant cercopithecoids are the most ecologically diverse primate taxa (3, 15)—they cover the largest geographical range of any nonhuman primates, occur in the most extensive variety of habitat types (including dry open savannas, tropical rainforests, and snow-covered subalpine regions), show a corresponding diversity of substrate use and locomotor patterns (from strict terrestriality to strict arboreality), and include species specialized for folivory (colobines), gramnivory (hamadryas and gelada baboons), frugivory (Cercopithecus), and broad omnivory (macaques). Their remarkable similarity in patterns of social organization, in the face of considerable ecological diversity, suggests that there has been an important phylogenetic influence on the social systems of cercopithecoid primates. Social organization in this group has been strongly conserved over evolutionary time despite radiation into a variety of adaptive niches.

One highly unparsimonious explanation for the extreme similarity in Old World monkey social systems is that each genus has independently evolved the same pattern of social organization as a product of adaptation to similar environmental pressures. Indeed, Lemur, Cebus, and Propithecus seem to have independently converged on a social system like that of the cercopithecoids. However, it is not clear what set of selective pressures might be responsible for these convergences, nor is it clear in the case of the Cercopithecoidea what aspects of ecology might explain their similar social systems. This does not mean that some potent, but as-yet-unknown, ecological similarity could not unite all these taxa, rather that for the cercopithecoids it is much more parsimonious to assume that their similarity is due to the retention of social organization features from a common ancestor and is not the product of multiple independent evolutionary events.

Another alternative explanation may lie in the fact that the Old World monkey radiation is a relatively recent phenomenon—perhaps there has not been sufficient time for differentiation of social organization within the Cercopithecoidea. However, although the greatest diversification in cercopithecoid taxa at the species level seems to have occurred during the last five million years, fossil evidence indicates that the two subfamilies, Cercopithecinae and Colobinae, began diverging much earlier, probably in the early Miocene (18–20 million years ago) and certainly by the late-middle Miocene (11 million years ago) when the first unmistakable colobine, Mesopithecus, appears (20). Moreover, if we compare the timing of this radiation with that of the radiation of ateline primates in the New World [Alouatta, Ateles, Brachyteles: beginning ≈10 million years ago (21)] or of the hominoids in the Old World [Pongo, Pan, Gorilla: beginning 12–15 million

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years ago (22)], we see that in both of these groups considerable social system diversity has evolved in a comparable period of time.

Furthermore, the period of cercopithecoid radiation has proved sufficient to permit significant differentiation of the two subfamilies with respect to locomotor, gastrointestinal, and dental morphology associated with their dietary specializations (folivory vs. frugivory/omnivory) (15), while social organization has remained largely unchanged. In view of their morphological differentiation, it seems unlikely that recency of radiation is a sufficient explanation for the strongly conserved social systems of Old World monkeys.

In sum, then, it appears that the form of extant Old World monkey social systems has been phylogenetically conserved. In saying this, we do not mean to contradict well-established links between ecology and social organization. Indeed, it is likely that the social organization of the cercopithecoid ancestor itself evolved in response to some set of ecological pressures faced in the middle Miocene. However, in general, the evolutionary process involves descent with modification, and in the absence of modification, one must conclude that similarities among closely related taxa reflect shared ancestry. Phylogeny, then, is an important explanatory principle for understanding shared characteristics and should be the null hypothesis in all tests of similarity or differentiation among taxa. In the case of the Cercopithecoidea, we cannot reject the null hypothesis that similarity in social organization is due to retention of characteristics possessed by a common ancestor.

Implications for the Study of Human Sociality

One important reason for investigating the social organization of nonhuman primates is that it may help us to reconstruct the social systems of early humans (23–27). Past attention has focused on two groups of primates as referents for early hominid sociality: the great apes because of their close phylogenetic affinity to modern humans and certain species of Old World monkeys because they live in savanna–woodland environments presumed to be similar to those faced by early hominids. Our analyses suggest, however, that the use of cercopithecoid sociality as a model for that of early hominids may be unjustified. First, we demonstrate that the social systems of cercopithecoids are remarkably similar despite the diverse ecologies of these taxa, a fact that obscures any causal relation between environment and social organization for this superfamily and thus weakens the socioecological rationale for using Old World monkeys as referents for early hominids. Moreover, we show that the derived nature of cercopithecoid social systems hinges on strict female philopatry. Female philopatry is a derived trait characteristic only of the cercopithecoids and a handful of other primate species, while female dispersal appears to be the primitive condition for primates in general (28); the fact that female philopatry is typical of neither extant hominoids nor most traditional human societies (29) further questions the relevance of using cercopithecoids to model early human sociality. We conclude that models that explicitly adopt a phylogenetic perspective and incorporate information on the social systems of extant apes are likely to provide more accurate reconstructions of the social organization of early humans (e.g., refs. 26 and 27).

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