



Evolution of Primate Social Systems

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We review evolutionary processes and mechanisms that gave rise to the diversity of primate social systems. We define social organization, social structure and mating system as distinct components of a social system. For each component, we summarize levels and patterns of variation among primates and discuss evolutionary determinants of this variation. We conclude that conclusive explanations for a solitary life and pair-living are still lacking. We then focus on interactions among the 3 components in order to identify main targets of selection and potential constraints for social evolution. Social organization and mating system are more closely linked to each other than either one is to social structure. Further, we conclude that it is important to seek a priori measures for the effects of presumed selective factors and that the genetic contribution to social systems is still poorly examined. Finally, we examine the role of primate socio-ecology in current evolutionary biology and conclude that primates are not prominently represented because the main questions asked in behavioral ecology are often irrelevant for primate behavior. For the future, we see a rapprochement of these areas as the role of disease and life-history theory are integrated more fully into primate socio-ecology.

KEY WORDS: social organization; mating system; social structure; social relationships; sexual selection; life history; socio-ecology.

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INTRODUCTION

The stunning diversity of primate social systems has been described and analyzed in reviews by Crook and Gartlan (1966), Eisenberg *et al.* (1972), Clutton-Brock (1974), Clutton-Brock and Harvey (1977), van Schaik and van Hooff (1983), Terborgh and Janson (1986), Wrangham (1987), Dunbar (1988), Janson (2000), and Strier (2000a). Aspects of this diversity include spacing, grouping and mating patterns, as well as variability in patterns and quality of social relationships. Moreover, diversity in social systems is not only evident among species but also exists within species (Sterck, 1999) and even within populations (Goldizen, 1987a; Richard, 1978), though in comparison with other vertebrates (Lott, 1991) documentation is relatively poor. We do not attempt another review of this diversity, but instead systematically examine the evolutionary forces that have generated and shaped it.

A prerequisite for this endeavor is clarification of how social systems or any of their component parts evolve. After all, definitions and characteristics of social systems focus on traits of groups and not on individuals, the latter of which are the targets of natural and sexual selection (Goss-Custard *et al.*, 1972; *cf.* Rowell, 1993). We therefore need a theoretical framework that relates fitness-relevant behavior of individuals, such as foraging, predator avoidance, mating and parental care, to the defining characters of a social system.

This link is provided by the socio-ecological model (Crook, 1970; Emlen and Oring, 1977; Terborgh and Janson, 1986), which recognizes that social systems represent emergent properties of individual behavioral interactions and strategies (Hinde, 1976). The underlying behavior of individuals towards conspecifics, in turn, is probably largely shaped by ecological factors, such as the distribution of risks and resources in the environment and their interactions (Elgar, 1986; Emlen, 1994; Mangel, 1990; Terborgh and Janson, 1986; van Schaik, 1983, 1989; Vehrencamp, 1983; Wrangham, 1980). However, the social organization and demographic conditions created by individual behaviors also impose constraints on the behavioral options of these same individuals, leading to complex feedback loops (Janson, 1986; van Schaik, 1996).

Males and females are treated separately in the model because their fitness is limited by different factors ultimately related to sexual differences in potential reproductive rates and the resulting intersexual conflict (Clutton-Brock and Parker, 1992, 1995). Accordingly, the model assumes that the distribution of females is primarily determined by the distribution of risks and resources in the environment, whereas males distribute themselves primarily in response to the temporal and spatial distribution of receptive females. The resulting demographic categories broadly determine the kinds of social

relationships possible, as well as the operational sex ratio, which is an important predictor of sex roles, reproductive strategies and the intensity of mating competition (Emlen and Oring, 1977; Kvarnemo and Ahnesjö, 1996; Sterck *et al.*, 1997).

DEFINITIONS AND TARGETS OF SELECTION

Despite considerable theoretical progress and increasing knowledge about the diversity of primate societies over the last two decades, confusion about targets of selection, combined with a lack of clear definitions, continue to hamper analyses of primate social systems. Accordingly, we begin by defining 3 different elements of social systems that had earlier been identified as fundamental and distinct components (Rowell, 1979, 1993; Struhsaker, 1969).

The distinctions among social organization, social structure and mating system are important because they are not necessarily congruent. Each of them alone is insufficient to characterize adequately a social system comprehensively because they are shaped by different selection pressures, even though they are not entirely independent of one another. For example, speaking of polygynous groups confuses two distinct aspects of the social system when one only refers to group composition (Clutton-Brock, 1989a; Davies, 1991; Müller and Thalmann, 2000). Moreover, a particular social organization does not necessarily reflect the logically corresponding mating system (Cords, 1988, 2000).

Because the 3 elements have been defined and named differently, sometimes by the same authors, and their labels have been used interchangeably in the past (*cf.* Barton *et al.*, 1996; Charles-Dominique, 1978; Eisenberg *et al.*, 1972; Hill and Lee, 1998; Janson, 1988; Müller and Thalmann, 2000; Rowell, 1988; Struhsaker, 1969; van Schaik and van Hooff, 1983; Whitehead, 1997; Wrangham, 1987), we propose consistent use of the following definitions.

The society (= social unit; social system) is the set of conspecific animals that interact regularly and more so with each other than with members of other such societies (Struhsaker, 1969). It is usually easy to recognize a society, but with animals that form parties of variable composition (fission-fusion) or are largely solitary, recognition is a challenging task. Primatologists have recognized the following aspects of societies: social organization, mating system, and social structure.

Social organization describes the size, sexual composition and spatiotemporal cohesion of a society. Traditionally, 5 fundamental social organizations are recognized: an animal either lives alone, or it is associated with

either one or several members of the same and or opposite sex (Kappeler, 1999a). Obviously, this categorization only coincides with the definition of social organization if spatial dispersion of individuals corresponds with social boundaries. Specifically, whether an animal is solitary or gregarious is just one aspect of social organization, and not a distinguishing feature, but for practical reasons we retain this categorization.

The mating system has a social and a genetic component. The social mating system describes one subset of social interactions, namely mating couples, whereas the reproductive consequences of mating interactions, i.e., the genetic mating system, can only be determined via genetic studies.

Social structure refers to the pattern of social interactions and the resulting relationships among the members of a society.

These definitions and the resulting categories focus on adult males and females and do not consider infants and juveniles, presumably because of the historical focus on mating systems (Crook and Gartlan, 1966), even though they obviously also contribute importantly to a social structure. Together, these three components define the essentials of a society of a taxon.

Social Organization

The most basic characterization of primate societies has traditionally been based on social organization alone (Clutton-Brock and Harvey, 1977; Crook and Gartlan, 1966; Eisenberg *et al.*, 1972). At this level, 3 fundamental types of social organization can be distinguished: neighborhood and solitary, pair-living, and group-living species.

Solitary Primates: Neighborhood Systems

The key aspect for the definition of solitary species is the fact that “the general activity, and particularly, the movements of different individuals about their habitat are not synchronised” (Charles-Dominique, 1978, p. 139). Thus, solitary individuals typically forage alone (Bearder, 1987), in contrast to gregarious animals, in which ≥ 2 individuals synchronize their activity in space and time (Boinski and Garber, 2000). Recognition of solitary foragers as a category of social organization is therefore justified if they also form a distinct social unit. The term solitary does not imply that they do not maintain social relationships or lack complex social networks; these traits simply describe other elements of the social system (Bearder, 1987, 1999; Charles-Dominique, 1978; Sterling and Richard, 1995; but see e.g., Radespiel, 2000; Thalmann, 2001). Similarly, it is neither necessary nor useful

to introduce mating system terminology to characterize social organization, e.g., dispersed polygyny, and it also seems unnecessary to confine the term solitary to taxa without social relations outside the breeding season (*cf.* Müller and Thalmann, 2000).

The reason for the confusion about solitary species is that we know so little about their social life. With the exception of the orangutan, all solitary primate species are nocturnal. As a result, the pioneering field studies may have focused on what could be measured under these difficult circumstances, rather than on what should be measured to characterize the social organization of solitary foragers. Fortunately, a methodological consensus that could establish a standard for the study of solitary primates is emerging (Sterling *et al.*, 2000). Until the 1990s, our conceptions about the diversity of their social systems were largely based on reports from a few pioneering studies, summarized by Bearder (1987). Since then, the number of long-term field studies of solitary primates, particularly lemurs, has grown almost exponentially, prompting several recent reviews (Bearder, 1999; Kappeler, 1997a; Müller and Thalmann, 2000; Sterling *et al.*, 2000; van Schaik, 1999). Given the emerging picture of increasing diversity, we are still far from a complete overview, especially because the social systems of all Asian and most African strepsirhines remain poorly studied (Bearder, 1999) and those of 10 newly described species of cheirogaleids (Groves, 2000; Rasoloarison *et al.*, 2000) are among those still completely unknown.

Existing studies revealed that the major axes organizing the social diversity of solitary primates are (1) extent of range overlap with members of the same and opposite sex and (2) occurrence of sleeping groups and their sexual composition (Bearder, 1987; Kappeler, 1997a; Müller and Thalmann, 2000). Home range overlap is highly variable, both within and between sexes, and male ranges tend to exceed those of females (Müller and Thalmann, 2000), but in a few cases, the ranges of one male and one female coincide. Only when we know more about the nature and size of these still largely obscure basic units from exploratory studies in relatively small and randomly chosen study plots can systematic investigations of the more interesting level of social organization at the population level be designed. Hence, perhaps the currently safest generalization is that many solitary foragers live in neighborhoods (Richard, 1985), in which individuals do not live in distinct social units but are decreasingly familiar with others that overlap increasingly less with their own home ranges. Unless populations are structured into discrete nuclei (Martin, 1972), recognition of discrete societies and hence social organization may be impossible.

A third axis with potentially important relationships with social structure and mating systems remains largely unexplored. It concerns the genetic structure of societies, which has sometimes been inferred from behavioral

data. In particular, the existence of matriarchies, defined as clusters of closely-related females, has been postulated or assumed without genetic data for several species by Waser and Jones (1983), Clark (1985), Bearder (1987), and Müller and Thalmann (2000), especially when several females form sleeping groups. However, genetic analyses of mitochondrial DNA variability demonstrated the existence of spatially discrete clusters of females sharing a particular mitotype in the absence of sleeping aggregations (*Mirza coquereli*: Kappeler, 1997b; Kappeler *et al.*, 2002) and of matriarchies that include many more females than the largest sleeping groups (*Microcebus murinus*: Schmid, 1998; Wimmer *et al.*, 2002). Future studies of solitary primates that combine behavioral and genetic data to explore diversity along this axis and the consequences of a particular social organization for dispersal, mating and social behavior should add exciting contributions to primate socioecology.

Finally, few studies have addressed the fundamental question about the adaptive bases of a solitary life style during the active period, so that only the most obvious and general determinants and correlates have been discussed (Bearder, 1987; Charles-Dominique, 1978, 1995; Kappeler, 1997a). First, nocturnal activity is strongly correlated with a solitary life style, perhaps because group cohesion and coordination would be difficult and might attract predators, but some nocturnal primates are not solitary and the only solitary anthropoid is diurnal (Gursky, 2000a; Wright, 1989). Second, Clutton-Brock and Harvey (1977) suggested that small body size is an important determinant of solitary activity, but it is not strictly associated with a particular social organization. Third, there is no dietary specialization that correctly predicts solitary activity. van Schaik and van Hooff (1983), Bearder (1987), and Gursky (2000b) suggested that heavy reliance on animal prey and gum, which typically occur in small patches that cannot be shared, favors solitary foraging, but there are too many exceptions in both directions to make this a general determinant. Fourth, van Schaik and van Hooff (1983) suggested that some primates may be solitary because there is no predation pressure on them, and a solitary social organization is the optimal response to other selection pressures, such as intense feeding competition. But recent studies demonstrated that some solitary primates are subject to intense predation risk (Goodman *et al.*, 1993; Rasoloarison *et al.*, 1995). Thus, the optimal response to predation risk may differ among species, with solitariness being the optimal response for nocturnal species. A solitary way of life is also not a response by relatively immobile animals to the high risk of predation (Terborgh and Janson, 1986; van Schaik and van Hooff, 1983) because most solitary primates are not cryptic (Bearder, 1987). Thus, in contrast to group-living primates (Janson, 2000), there is no satisfactory explanation for why some primates do not live in groups.

Primates in Pairs

Permanent association of one adult male and female defines pair-living species (Fuentes, 2000; van Schaik and Dunbar, 1990). Thus, there is not only coincidence of male and female ranges but also synchronized spatial association between the pair. Recognition of this category of social organization is difficult in cases in which intersexual spatial association is relatively loose. For example, in several nocturnal strepsirhines, such as *Galagoides zanzibaricus* (Harcourt and Nash, 1986), *Cheirogaleus medius* (Fietz, 1999; Müller, 1998), *Phaner furcifer* (Charles-Dominique and Petter, 1980; Schülke, 2003), *Lepilemur edwardsi* (Rasoloharijaona *et al.*, 2000; Thalmann, 2001) and *Lepilemur ruficaudatus* (Hilgartner *et al.*, unpublished data), male and female ranges overlap closely and are defended by both sexes against neighbors, but members of the pairs are neither consistently associated during the period of activity or necessarily always sleeping together in the same shelter. These species are interesting because they may represent examples of independent transitions from a solitary to a pair-living social organization (Kappeler, 1999c), as also evidenced by the occasional occurrence of social units consisting of one male and two females.

Phylogenetic models revealed that pair-living has evolved independently in all major primate radiations, but it is nevertheless the rarest type of social organization (Kappeler, 1999c; Kappeler and Heymann, 1996; van Schaik and Dunbar, 1990). The rarity of pair-living among primates (and other mammals) is not surprising, given our current understanding of sexual differences in potential reproductive rates and the resulting conflict of interest between the sexes. Males should seek to maximize their reproductive success by mating with as many females as possible, and the defining characters of mammalian reproduction provide them with the opportunity to do so. Hence, we must ask why some males opt to live permanently with a single female, especially in primates with relatively long interbirth intervals. This has been the traditional formulation of this question, focusing on the potential consequences of pair-living for the mating system.

Because these levels should be separated we should also seek explanations that account for pair-living as a form of social organization (Fuentes, 1999; van Schaik and Dunbar, 1990; Wright, 1986). Indeed, observations of extrapair copulations (EPC) in pair-living primates (Palombit, 1994; Reichard, 1995) and genetic evidence for the success of EPCs (Fietz *et al.*, 2000) indicate that mating activities of neither sex are principally constrained by living in pairs. Why some primate males permanently bond with a single female has been explained with two arguments that distinguish between two fundamental types of monogamy in primates: systems with obligate male care and ones without paternal care (Clutton-Brock, 1989a).

First, in species with male care, notably in the pair-living twinning calitrichids, Goldizen (1987a), Wright (1990), and Dunbar (1995a) invoked obligate paternal care via infant carrying as a crucial contribution of males to their own fitness. Interestingly, however, males that could not have fathered offspring also carry young (van Schaik and Paul, 1996). Pereira *et al.* (1987), Morland (1990), and Fietz (1999) suggested paternal care in the form of infant guarding as a mechanism to promote pair-living in some lemurs, but the empirical evidence for such an effect is weak and, in one case (Fietz *et al.*, 2000), a large proportion of males was cuckolded, making evolutionary scenarios based on paternal certainty unlikely.

Second, in species in which males provide no direct paternal care, notably most gibbons, there are two hypotheses for the permanent association between a male and a female. The first invokes limits of male monopolization potential (Emlen and Oring, 1977). Accordingly, males cannot successfully defend sexual access to >1 female because of the spatial distribution of females and their behavior (Brotherton *et al.*, 1997; Komers, 1996). According to the second hypothesis, permanent association as a pair is an evolved strategy that reduces the risk of infanticide by strange males (Palombit, 1999, 2000; van Schaik and Dunbar, 1990). Species with long interbirth intervals, long lactation in relation to gestation and infant carrying by the mother have a high risk of infanticide, which males can help to reduce via protecting their offspring (van Schaik, 2000a,b). The risk of infanticide and its general implications for primate social evolution have been recently examined (van Schaik *et al.*, 1999; Nunn and van Schaik, 2000; van Schaik, 2000a,b). This hypothesis can be generalized to include all forms of permanent male-female association, i.e., include single males with >1 female (van Schaik and Kappeler, 1997). Explanations for why some males opt to associate with only one female therefore require an additional factor.

The recognition that pair-living does not equate with a monogamous mating system raises questions about potential ecological causes for pair-living. Some obvious factors, such as range size, patch size and patch distribution have already been examined in some species (Robinson *et al.*, 1987; van Schaik and Dunbar, 1990; Wright, 1986), but, given the taxonomic and ecological diversity of pair-living primates, different explanations may apply to different taxa so this possibility should be examined more comprehensively. An additional approach could be to turn the question around and ask why the well-known benefits of group-living are apparently not realized in pair-living species. Increased benefits or reduced costs of predator detection and evasion or both factors, as well as resource defense, obviously have their largest *per capita* effects at small group sizes (Dunbar, 1988), which are clearly >2 . There may be specific ecological reasons favoring extremely small group size, such as facilitated coordinated movements at night and

improved hiding during the day in nocturnal pair-living species, but they are difficult to test *post hoc*. In brief, the adaptive bases for pair-living are far from being completely understood.

Group-Living Primates

The vast majority of primates lives in bisexual groups with ≥ 3 adults, which sets them apart from other mammals in which permanently bisexual groups are much less common (van Schaik and Kappeler, 1997). Moreover, an unusually large and detailed number of field studies of Primates versus other Mammalia, revealed an additional level of diversity with respect to the size, sex ratio and temporal stability of primate groups. The ratio of adult males and females provided the traditional criterion for further distinction among group-living species (Kappeler, 2000a). Accordingly, polyandrous, polygynous and multimale, multifemale groups have been distinguished (Clutton-Brock and Harvey, 1977; Crook and Gartlan, 1966; Eisenberg *et al.*, 1972). However, these labels also confuse social organization and mating systems. Variation in group cohesion has been used for yet finer distinctions among groups with multiple males and females. Their members can be either relatively cohesive or exhibit one of two types of temporal variation in group cohesion. In fission-fusion groups, subgroups of varying size and composition form temporarily (Nishida and Hiraiwa-Hasegawa, 1987; Rigamonti, 1993; Strier, 1992), whereas in multilevel societies, small social units, usually containing one male and several females, are also organized into higher-level sets (Stammback, 1987).

Variation in the number of adult males is the most striking feature of primate group composition with far-reaching consequences for many aspects of male and female behavior (Hamilton and Bulger, 1992; Preuschoft and Paul, 2000; van Hooff, 2000). The most basic dichotomy is that between single- and multimale groups. During the early years of primate socio-ecology, researchers sought ecological explanations for this dichotomy, such as habitat type or predation risk (Kappeler, 2000a). Today, this dichotomy is no longer recognized as an invariant species-specific traits, but instead as a flexible response to variation among groups in ecological and demographic factors (Robbins, 1995; Steenbeek *et al.*, 2000; Strier, 2000b; Struhsaker, 2000; Watts, 2000). Later analyses identified the number of females in a group and their degree of reproductive synchrony as important determinants of male monopolization potential, which is an important determinant of the outcome of the dichotomy (Altmann, 1990; Andelman, 1986; Ridley, 1986).

In 3 recent comparative studies, researchers re-examined the proposed key determinants of the number of group males. A comparison among

arboreal folivores demonstrated that the presence of monkey-eating eagles tends to increase the number of males in howlers and colobus on average from one to two, whereas ecologically similar langurs (and some colobus), which are not exposed to such predators, tend to live in single-male groups (van Schaik and Hörstermann, 1994). Furthermore, Mitani *et al.* (1996a) found that the qualitative difference between single- and multimale groups is positively associated with the number of females, and not with temporal distribution of their receptive periods, but Nunn (1999a) demonstrated that temporal overlap of female receptive periods predicts the number of males after controlling for the number of females. A final assessment may therefore have to await the availability of additional data, in particular on group-living lemurs, which are characterized by the presence of several males, despite small female group size, and extremely short breeding seasons (Kappeler, 2000b).

Variation in group size is another striking aspect of diversity in the social organization of group-living primates. Across species, primate group sizes vary by 2 orders of magnitude (Kappeler and Heymann, 1996), and variation within some species is several-fold (Dunbar, 1988). Researchers have identified 4 main correlates, and hence possible determinants, of variation in primate group size. First, increasing foraging and travel costs set the upper limit of group size via increased intragroup feeding competition (Janson and Goldsmith, 1995; van Schaik, 1983). Second, living in larger groups is favored by decreasing predation risk and by intense intergroup feeding competition (van Schaik, 1983; van Schaik and van Hooff, 1983; Wrangham, 1980). Third, infanticide risk provides a selective force that reduces group size under certain conditions (Crockett and Janson, 2000; Steenbeek and van Schaik, 2001). Finally, neocortical size may constrain group size because it determines the ability to process complex information about social relationships (Dunbar, 1992, 1995b, 1998).

Birth and death rates are the most important proximate mechanisms regulating group size. Contrarily, immigration and emigration are constrained in effectiveness to modify group size by an inherent sexual bias in most species. Female philopatry is common among primates (Pusey and Packer, 1987), but female and bisexual group transfer also occur in various taxa (Goldizen and Terborgh, 1989; Isbell and van Vuren, 1996; Moore, 1984; Pope, 2000a; Sterck, 1998; Strier and Ziegler, 2000). Sexual biases in residency not only constrain the ability to adjust female group size but also have important consequences for the genetic structure of primate groups (Altmann *et al.*, 1997; de Ruiter and Geffen, 1998; Gerloff *et al.*, 1999; Melnick and Hoelzer, 1992; Pope, 1992, 1998), breeding patterns (Clutton-Brock, 1989b; Melnick *et al.*, 1984; Moore and Ali, 1984; Packer, 1985), breeding success (Pope, 2000b) and sex-specific life history strategies (Alberts and

Altmann, 1995a,b; Borries, 2000). Residency patterns also facilitate the formation of coalitions of same-sexed members of the resident sex through kin selection and structure other details of the social behavior of both sexes (Chapais *et al.*, 1997; Moore, 1992; Silk, 2002).

In sum, the social organization of group-living primates has been more intensely studied than that of other primates, so that variation in group size and composition, as well as the underlying mechanisms, are comparatively well-understood.

Mating Systems

The majority of mammalian mating systems that were characterized by Clutton-Brock (1989a) is found among primates. They include monogamy, in which males and females typically mate with only one member of the opposite sex and have roughly equal variances in reproductive success (MacKinnon and MacKinnon, 1980; Robinson *et al.*, 1987; Rutberg, 1983; Sommer and Reichard, 2000); polyandry, in which one female mates with several males and each male mates only with her (Garber, 1997; Goldizen, 1987b; Tardif and Garber, 1994); and various forms of polygyny and polygynandry. Spatial polygyny occurs among solitary species in which agonistically powerful males defend mating access to several females (Charles-Dominique, 1977). Scramble competition polygyny occurs when males roam widely in search of receptive females, which they desert soon after mating in search of additional mates, so that both sexes typically mate with several partners (Kappeler, 1997b). Moreover, several forms of female-defense polygyny exist among primates. In some species, coalitions of males defend a territory that contains several females with which most males mate (Gerloff *et al.*, 1999; Watts, 1998). In the remaining species, groups of females are defended directly by one or several males. Harem-polygyny occurs when a single male defends exclusive mating access to a group of females (Stammach, 1987), whereas promiscuous mating occurs when several males defend groups of females (Altmann *et al.*, 1997; Bercovitch, 1989; Brockman and Whitten, 1996; Paul *et al.*, 1993; Sauther, 1991), often with pronounced skew in male mating success as a function of dominance rank (Cowlshaw and Dunbar, 1991; Johnstone *et al.*, 1999; Paul, 1997). There is no case of lekking or resource-defense polygyny among primates.

The ability of individual males to defend successfully exclusive mating access to females is probably the major determinant of primate mating systems. When females are clumped in space and/or when their receptive periods are not synchronized, male monopolization is much greater than when females are solitary and/or when they have synchronized receptive

periods (Dunbar, 2000; Emlen and Oring, 1977). However, females are not mere passive objects of male mating strategies. Their reproductive interests can be used to modify their spatial distribution and especially the degree of estrous synchrony (e.g., Zinner and Deschner, 2000; Zinner *et al.*, 1994). Additional mechanisms, such as female choice, sexual swellings and modifications of the fertile period of the cycle assure that sexual coercion of females is minimized and that females largely determine the identity and number of their mates (Nunn, 1999b; van Noordwijk and van Schaik, 2000; van Schaik *et al.*, 1999; Zinner and Deschner, 2000). Many reproductive strategies of female primates appear to be aimed at confusing paternal certainty, thereby reducing the risk of infanticide (van Noordwijk and van Schaik, 2000). Finally, because of the physiological constraints of gestation and lactation, most primates (and other mammals) are characterized by virtually exclusive female parental care, so that, compared to birds, polygynous mating systems are overwhelmingly common.

With few puzzling exceptions among lemurs (Kappeler, 1993a), morphological correlates of different mating systems correspond well to theoretical predictions and patterns that occur among other mammals (Clutton-Brock *et al.*, 1977; Harcourt, 1997; Harvey *et al.*, 1978; Kay *et al.*, 1988; Mitani *et al.*, 1996b; Plavcan and van Schaik, 1992). Accordingly, males of species in which females typically mate with several males have, on average, larger testes in relation to body mass than males of monandrously mating females. Similarly, variation in male mate monopolization potential and intensity of direct male mating competition covaries positively with the degree of sexual dimorphism in body and canine size.

Characterizations of primate mating systems continue to be importantly influenced by characteristics of social organization because observations of mating patterns, and, most importantly, genetic analyses of reproductive success are lacking for the majority of species. There is, of course, a rough correspondance between the social organization and mating system of a society or taxon but several facts argue against simple equation of them. Foremost, promiscuity outside the social unit appears to be widespread, as evidenced by copulations outside the pair-bond, the group or community (Cords, 2000; Digby, 1999; Launhardt *et al.*, 2001; Richard, 1985; Sommer and Reichard, 2000). Intensified genetic sampling in the future may reveal that such discrepancies between social and mating partners are even more widespread than currently known. Moreover, temporal instability of social organization during the mating season contributes to a mismatch with mating systems (Borries, 2000; Cords, 2000). Finally, there is variation within species, and sometimes even within populations, in social organization and mating patterns, or both (Heymann, 2000; Steenbeek *et al.*, 2000; Struhsaker, 2000). Therefore, ultimately analyses of individual female mating decisions may be

more illuminating than those of system characteristics (Pereira and Weiss, 1989).

Social Structure

Relationships among individuals reflect behavioral strategies that have been selected because they maximize inclusive fitness (van Schaik, 1989). Differences in the patterning and nature of social interactions give rise to particular social relationships between pairs of individuals, and consistent features of dyadic relationships can be used to characterize social structure (Hinde, 1976). Variation among relationships is brought about by differences in the nature, frequency and intensity of affiliative, affiliative and agonistic interactions (de Waal, 1986, 1989). Sex is a major organizing principle in the analysis of social structure, with both ecological and social factors as ultimate determinants of the observed variation in social relationships. However, the relative importance attributed to these determinants or their components is still unresolved (Dunbar, 1988; Sterck *et al.*, 1997; van Schaik, 1996; Wrangham, 1987).

Interfemale Relationships

Socioecological models of female social relationships are focussed on causes and consequences of feeding competition (Sterck *et al.*, 1997; Koenig, 2002), primarily in Old World monkeys and apes. The nature of feeding competition is shaped by the distribution of resources and can occur within and between groups. When food patches are clumped, monopolizable, and of intermediate size relative to group size, contest competition among females is expected, whereas scramble competition predominates over other types of patches (van Schaik, 1989). Whether related females form coalitions to defend access to preferred food sources against other such coalitions (Wrangham, 1980) or intergroup feeding competition predominates because groups form in response to predation risk (van Schaik and van Hooff, 1983), each female in a group-living species will experience a mix of contest and scramble competition within and between groups (Koenig, 2002).

The consequences of a given competitive regime for social relationships with other females can be summarized by 4 interrelated variables: philopatry, nepotism, tolerance and despotism, according to which there are 4 main categories of female relationships (Sterck *et al.*, 1997). Among them, 2 categories are most common. In resident-nepotistic groups, females

are philopatric and establish stable, linear and nepotistic hierarchies with despotic dominance relations. Contrarily, in dispersal-egalitarian groups, females regularly transfer between groups, forming neither stable linear hierarchies nor coalitions. The basic difference between them is the strength of intragroup contest competition, as confirmed by empirical field studies (Barton *et al.*, 1996; Koenig *et al.*, 1998; Mitchell *et al.*, 1991). There are other forms of female social structure. In resident-nepotistic-tolerant groups female philopatry is combined with decided relationships within a stable hierarchy—regular coalitions—and pronounced tolerance by dominants. The functional interpretation of this kind of social structure is that subordinates have enough leverage over dominants to reduce the extent to which they actually reap the benefits of dominance, though the course of the leverage is unidentified. It need not be ecological because, social factors, especially mating conflict, may also affect female-female social relationships (Preuschoft and van Schaik, 2001). An important goal for future research is to integrate the still poorly characterized competitive regimes of callitrichids and lemurs into the existing framework (Kappeler, 1999b; Pereira and Kappeler, 1997).

Intermale Relationships

Relationships among male primates in intra- and intergroup competition are also highly variable across species (Kappeler, 1999a). They are primarily shaped by female distribution and the resulting nature of intrasexual selection. Because the contested fitness-limiting resource—fertilizations—cannot be shared, male relationships are typically characterized by competition, intolerance and clear dominance relations (Bercovitch, 1991; Cowlshaw and Dunbar, 1991; van Hooff, 2000; van Hooff and van Schaik, 1994). Therefore, agonistic interactions are common among males, while affiliative behavior and alliances are mainly observed when large numbers of males find themselves within a single group (Noë and Sluiter, 1990; Plavcan and van Schaik, 1992; van Hooff and van Schaik, 1992). Contrarily, in a few species with male philopatry, grooming bonds and coalitionary behavior among males are well-developed (Strier, 1994; van Hooff, 2000; van Hooff and van Schaik, 1992, 1994).

Intersexual Relationships

Male-female relationships are ultimately shaped by sexual selection and sexual conflict (Smuts, 1987; Smuts and Smuts, 1993; van Schaik, 1996). Intersexual relations among primates are highly variable, both within and among species. They are influenced, among other things, by the duration of

male residence in a group, the respective rank in the same-sex dominance hierarchy, the degree of paternal certainty, the risk of infanticide and the degree of sexual dimorphism (Hamilton and Bulger, 1992; Kappeler, 1999c; Manson, 1994; Paul *et al.*, 2000; Perry, 1997; Sicotte, 1994; Takahata, 1982; van Noordwijk and van Schaik, 1988; Watts, 1992; Weingrill, 2000). If males and females form affiliative bonds, females often provide most of the grooming, whereas males provide agonistic protection for the female and her infants and additional vigilance against predators (de Ruiter, 1986; Hemelrijk and Ek, 1991; Kappeler, 1993c; Koenig, 1998; Noë and Hammerstein, 1994a,b; Palombit *et al.*, 1997; Smuts, 1985). Except for most lemurs (Kappeler, 1993b; Pereira and McGlynn, 1997; Richard, 1987), adult primate males dominate females in dyadic interactions.

Interrelationships

The 3 elements of a social system are discrete, interrelated entities. The links may be of 3 possible kinds: (i) causal—one aspect imposes a direct constraining effect on the values of the other; for instance, when social organization determines which animals are available for relationships; (ii) evolutionary—adaptive values of one aspect have led over time to a particular range of values in another aspect, such as when the benefits of the formation of particular kinds of alliances has led to a particular social organization; and (iii) correlational—the values of the 2 elements reflect the effects of another factor, for instance sex-biased dispersal, without strongly affecting each other. However, it is often impossible to say which relationships actually hold in a particular example, especially since they are usually not exclusive. Moreover, there is a remarkable degree of freedom for each element to vary independently, which is the *raison d'être* for distinguishing the separate elements in the first place.

The most pronounced relationships exist between social organization on the one hand, and mating system and social structure, on the other. First, in many cases the spatial dispersion of individuals, and, in the case of females, their number and reproductive synchrony, impose a direct constraint on the mating system. Thus, polyandrous mating by females is less likely and indeed less common in single-male groups (pairs or female groups) than in multimale groups, though many exceptions occur to this rule. However, it is difficult or impossible to model the polarity of the evolutionary relationships between the 2 aspects. For instance, did multimale, multifemale groups form for ecological reasons after which promiscuous mating developed by default, or did selection for polyandrous mating by females, e.g., to reduce the risk of infanticide (Hrdy, 1979), lead to the formation of multimale groups? Thus,

at the proximate level, social organization determines the mating system in some cases, rather than *vice versa*, but the relationship is neither strict nor predictable, and the evolutionary relationships are difficult to disentangle.

Second, social organization and social structure are trivially linked at the proximate level in that certain demographic conditions must exist for the occurrence of particular classes of relationships; for example, female social relationships cannot develop in pair-living species. However, demography may also have more direct effects on social options (Strier, 2000b). Whether social organization is a given and social relationships develop within these constraints (van Schaik, 1996) or social organization emerged as a byproduct of the establishment of particular social relationships (Wrangham, 1980) is unresolved. The diversity of female social relationships among group-living species (Sterck *et al.*, 1997) argues against the notion that a particular kind of social organization predisposes for a particular social structure. For example, demographically similar groups of gelada and hamadryas baboons are characterized by very different social structures (Stammback, 1987). Thus, the two aspects of a social system are relatively free to vary independently of one another, both synchronically and evolutionarily.

The link between social structure and mating system is clearly more variable. However, social relationships can affect mating relations when male-female friendships exist (Smuts, 1985), which could lead to the formation of multiple pairs within larger groups (Pereira and McGlynn, 1997; van Schaik and Kappeler, 1993). Similarly, mating history predicts male-female and male-infant relations in some species (Palombit *et al.*, 1997; Paul *et al.*, 2000). Male-female association may have evolved as a result of paternity defense (Palombit, 1999, 2000) or to reduce risk of infanticide (van Schaik and Kappeler, 1997). Unlike most birds, in most primates obligate paternal care is absent, so that parental care has presumably played only a minor role in shaping primate social structure evolutionarily.

Dispersal pattern may determine social organization and structure, which would be correlated due to this effect. Thus, female philopatry produces clusters of females, which also happen to be relatives, facilitating cooperative behavior among them (Moore, 1992; Waser and Jones, 1983). However, although female philopatry may historically have been the pathway to gregariousness, group-living is adaptive in itself and no longer necessarily linked with female philopatry. Likewise, given that female dispersal occurs where the need for female cooperation is reduced, the benefits of cooperation with relatives may have selected for female philopatry (van Schaik, 1989; Wrangham, 1980), which suggests that the dispersal pattern is the evolutionary product of social processes rather than its evolutionary cause. In other cases, too, it is plausible to regard dispersal as the evolutionary product of social processes. Eviction of particular targets or group fission occur

in groups that exceed a particular size (Henzi *et al.*, 1997; Vick and Pereira, 1989). In brief, whether dispersal is the evolutionary cause or consequence of particular social processes is unresolved.

DETERMINANTS AND MECHANISMS

For each of the three components of social systems, we have already summarized important ultimate determinants of inter- and intra-specific variability, as well as the mechanisms that implement them, in previous sections. An important remaining question is whether all important factors have already been identified. Might we have identified and quantified factors that are easy to measure at the expense of more important ones that are more difficult to measure?

a priori Measures

Recent progress in understanding the difference between predation rate and risk provide an illustrative example of the problem. The fact that predation risk exerts a major influence on primate behavior is uncontested (Stanford, 2002). Previous researchers who examined specific predictions about the effects of predation on primate social systems used predation rates to operationalize this independent variable (Anderson, 1986; Boinski and Chapman, 1995; Cheney and Wrangham, 1987). However, now there is consensus that predation rate is not suitable for such analyses because it ignores the effects of various countermeasures already in place to reduce the risk (Hill and Dunbar, 1998a; Hill and Lee, 1998; Janson, 1998). Realistic estimates of the underlying predation risk are much more difficult to obtain, so definitive tests are difficult (Janson, 1998).

The same logic may explain why some authors refuse to acknowledge the importance of the threat of male infanticide in the evolution of (primate) social systems (Bartlett *et al.*, 1993; Dagg, 1999; Sussman *et al.*, 1995). For them, rates of male infanticide appear too low to qualify as a major force in social evolution, but the rates may be low precisely because effective countermeasures are already in place to minimize the risk: the white knight rejoinder (van Schaik, 2000a). The same problem may apply to studies of feeding competition and its social consequences (Koenig, 2002). Ideally we need independent *a priori* measures of risk, such as the ratio of lactation and gestation length for risk of infanticide (van Schaik, 2000b; van Schaik and Kappeler, 1997), and longevity (Janson, 2003) or predator assemblages (Nunn and van Schaik, 2001) for intrinsic predation risk. Such logically and independently derived variables can provide much more powerful explanations than *post hoc* arguments, which are often difficult to falsify.

Genetic Aspects

Social behavior also has a genetic basis, which has received little attention in recent socioecological analyses. Studies of hybrids and controlled experiments help to illuminate the relative importance of genetic predispositions for a particular social organization, social structure or mating system. First, some sister taxa with radically different social systems produce hybrids under natural conditions. For example, hybrids between hamadryas and anubis baboons express certain taxon-typical traits of their respective parental specific social system, such as male herding of females (Colmenares, 1992; Nagel, 1973; Sugawara, 1988), indicating a genetic basis for the behavior. Studies of the behavior of other hybrids could help to define the nature and extent of genetic predispositions for other aspects of social behavior.

Second, several experimental approaches have been successfully used to determine social reaction norms of individual species. Demographic manipulations, such as captive housing under different social conditions, can reveal limits of plasticity in social organization. A classic example, which is well understood in retrospect (Kummer, 1968), concerns the formation of a large multimale multifemale group of hamadryas baboons at London Zoo, followed by an immediate violent response of adult males (Zuckerman, 1932). A similar approach was used by Mendoza and Manson (1986), Harrison and Tardif (1989), and French *et al.* (1995) to test the strength of pair bonds in captive callitrichids by presenting strange adults of both sexes to them. Understanding the limits of social plasticity also has obvious practical applications for captive housing and propagation (Berger, 1996; Tilson, 1986).

The flexibility of some aspects of the social structure can also be studied experimentally. For example, de Waal and Johanowicz (1993) showed that juvenile rhesus macaques housed for several months with juvenile stump-tailed macaques subsequently showed elevated levels of reconciliation, but not of affiliative and grooming behavior. Thus, some components of the species-specific social structure (de Waal and Luttrell, 1989) are apparently more flexible than others. Additional cross-fostering studies would clearly be of great interest in this context.

Using a different experimental approach, Gore (1993) manipulated food distribution of captive rhesus macaques and hamadryas baboons with the goal of changing the quality of female social relationships. The food manipulations had no detectable effect, which demonstrates that the degree of female bonding is inert to short-term fluctuations in the selective force that is thought to have generated it. Gore's experiment serves as an important reminder that immediate and evolutionary levels of responses should not be confused.

Finally, the study of intraspecific variation in aspects of social systems can help to identify the breadth and limits of social reaction norms. Variation among subspecies or populations in social organization, social structure or mating systems can be used to separate relative contributions of genetic and ecological determinants, but this information is available for only a few primate species in sufficient detail (Barton *et al.*, 1996; Castles *et al.*, 1996). Therefore, there are results from few carefully controlled studies of the exact nature and causes of intraspecific social variation (Barton, 2000; Srivastava and Dunbar, 1996; Sterck, 1999).

A logically separate issue is the degree of phylogenetic inertia in aspects of societies. Clearly, closely related taxa tend to share more similarities in their social systems than more distantly related ones do. This holds not only for sister species but also at higher taxonomic levels. For example, Old World cercopithecoids tend to live in multimale multifemale groups with female philopatry and very similar social structures (di Fiore and Rendall, 1994) and female dominance is limited to lemuriformes (Richard, 1987). Obviously, such phylogenetic inertia does not necessarily imply the presence of genetic constraints on social evolution: related taxa tend to have similar life histories and ecologies, and the similarities may therefore be adaptive (Pagel and Harvey, 1991). In support of the adaptive interpretation, the same traits that are phylogenetically conserved in one taxon can be highly variable within another equivalent higher-order taxon. For example, hominoids have extremely diverse social organizations (McGrew *et al.*, 1996), and dispersal among ceboids is not limited to one particular sex (Pope, 2000a).

What Have We Learned So Far?

The first four decades of primate socioecology have greatly advanced our understanding of variation in primate social systems and the underlying determinants and mechanisms. Following the first phase, characterized mainly by descriptive inventories, and a second phase dominated by correlational approaches, the ongoing hypothetico-deductive approach towards analyzing primate social systems has been by far the most productive and successful. Thus, there is no need to refrain from formulating and testing specific predictions, simply because not all the basic natural history data from all species are available yet (Rodman, 1993; Sussman, 1999). After all, hypotheses are erected to be tested with empirical data; if the relevant data do not exist yet, hypotheses provide focal points for field researchers to collect the relevant data (e.g., van Schaik and Kappeler, 1996; Wright, 1999). The result is always at least more pertinent information about the natural history of focal species.

More specifically, much current research and many insights have been dominated by a cercopithecentric perspective, portraying semiterrestrial cercopithecines as typical primates (Strier, 1994). Yet, much of the interesting variation in social systems is among New World primates and prosimians. They exhibit interesting similarities in social organization to one another, and idiosyncracies in social structure and mating systems that differ from the more familiar pattern of the few better-known Old World primates (Garber, 1997; Jolly, 1966, 1998; Kappeler, 1997a, 2000b; Kinzey and Cunningham, 1994; Pereira, 1995; Pereira and Kappeler, 1997; Strier, 1996; Wright, 1997, 1999). Accordingly, intensified study of platyrrhine and prosimian species and integration of the resulting insights into existing models is an important task for the next generation of field primatologists.

PRIMATES AND EVOLUTIONARY BIOLOGY

One goal of this special issue, and this paper in particular, is to link primatological research with the important developments in behavioral ecology and evolutionary biology. Hauser (1993) and Harcourt (1998), noted that primate and nonprimate socioecologists have largely ignored each other, so it is not surprising that most behavioral ecologists and evolutionary biologists are familiar with only a few, mostly out-dated, primate studies (Krebs and Davies, 1992). Apart from the common mutual taxonomic ignorance of both primatologists and non-primatologists and the fact that researchers studying other taxa, especially other mammals, have fewer taxonomically specialized journals at their disposal, there may also be biological reasons for this isolation.

Mainstream behavioral ecology has traditionally been dominated by students of birds and invertebrates. Many new questions and trends have originated via studies on them (Lack, 1947; Wilson, 1975). During the last decade, topics dealing with various aspects of sexual selection have dominated the main journals of behavioral ecology. Research addressing causes and mechanisms of noncontest aspects of sexual selection, such as female choice, reproductive skew and sperm competition, has reached new levels of detail and theoretical sophistication (Gibson and Langen, 1996; Johnstone, 1995, 2000). Questions dealing with the relevant costs of signalling, such as the genetic quality of mates and their phenotypic indicators, particularly fluctuating asymmetry, have received more attention from behavioral ecologists than any other topic (Møller, 1997; Watson and Thornhill, 1994; Widemo and Saether, 1999). Interestingly, relevant work on primates, with the possible exception of humans, is conspicuously absent from these areas of research (Manning, 1995; Manning and Chamberlain, 1993; Thornhill *et al.*, 1995). Conservation biology and studies of the evolution of cooperation are the

only examples of modern integrative disciplines in which information about social systems and other aspects of behavioral ecology are relevant and in which primates are not underrepresented (Jernvall and Wright, 1998; Noë and Hammerstein, 1995).

Why, then, is primatology not in the mainstream of evolutionary biology? We suggest the following 3 main reasons. First, the main topics of sexual selection dealing with aspects of female choice are by-and-large not applicable to primates. Striking ornaments of males with a potential function in mate choice are widespread among primates (Dixson, 1998), but the few existing studies have only suggested a function in intrasexual competition (Gerald, 2001; Setchell and Dixson, 2001a,b; Wickings and Dixson, 1992). This does not imply that primate females do not choose their mates (Manson, 1995; Paul, 2002; Small, 1989). We propose instead that mate selection based on arbitrary phenotypic traits is usually not as important to female primates because they know their potential mates from regular interactions as a result of and sometimes years of association.

Second, the required experimental approach for conclusive studies of problems in sexual selection or other central topics in behavioral ecology is rarely, if ever, possible with primates. Both ethical and practical problems, having to do with slow reproductive rates or small sample size, explain this limitation (Janson, 2000). In addition, it is possible that the important ultimate factors under investigation are hidden behind counterstrategies, so that theoretically major perturbations of the system are required to elicit meaningful responses experimentally. For example, adaptations against infanticide may be so effective that it rarely occurs under normal conditions, or female primates may opt to mate polyandrously to confuse paternity, rather than to chose a particular best male.

Finally, the natural history of an organism typically guides the kinds of questions that can be asked meaningfully. Because big differences in natural histories are typically related to qualitative differences in key life-history traits, e.g., internal vs. external fertilization, ovipary vs. vivipary (Clutton-Brock, 1991), asking all of the same questions about all organisms does not make sense. Questions dealing with paternal care and quality are much more pertinent to understand female birds than female mammals. Similarly, primates may not always be the best or even an appropriate taxon to address some specific hypotheses in behavioral ecology (Harcourt, 1998). Thus, aspects of primate natural and life-histories may underly and explain our limitations.

The Future of Primate Socioecology

Now that primatologists have at least begun to study the rarest primates in the most remote places, often for several years, the amount of detailed

information about primate natural history, social systems, and ecology is unparalleled among vertebrate orders, with possible exceptions of some avian taxa. However, this does not signal the near end of socioecological research. Instead, the situation provides a unique opportunity to launch research offensives that explore several new frontiers which could have impact on future developments in behavioral ecology (Janson, 2000).

First, the availability of large comparative data bases provide opportunities to test predictions of the socioecological model via comparative tests to demonstrate correlated evolution between pairs of traits, such as predation risk and group size, or group size and home range size (Hill and Lee, 1998; Nunn and Barton, 2000). The development of ever more refined comparative tests and more detailed phylogenies in recent years alone (Gittleman and Luh, 1992; Harvey and Pagel, 1991; Nunn and Barton, 2001; Purvis, 1995) provided an underused tool box for primatologists. Using a broad comparative approach holds the potential to identify and to measure the actual selective forces, and not merely their outcomes (Nunn and Barton, 2001).

Second, the link between behavior and life-history is a key pillar in the evolution of social systems. Exploring their many causal and integrative interactions could provide a new frontier for primate socioecology. The slow life-histories of primates may have consequences for all 3 components of their social systems (Kappeler *et al.*, 2003). The slow rates of growth and reproduction, in particular, make more conservative behavioral strategies, including a safer life in permanent groups, adaptive (Janson and van Schaik, 1993). Residence in stable groups over many years results in increased social complexity and perhaps cognitive abilities. Moreover, slow life-histories may also affect mating strategies and systems because they affect the operational sex ratio and the risk of infanticide (Kvarnemo and Ahnesjö, 1996; Mitani *et al.*, 1996a; Willson and Pianka, 1963).

Third, extended periods of juvenility are defining features of slow life-histories, but the various developmental trajectories of juvenile primates and their integration into adult social systems remain virtually unstudied (Altmann, 1998; Pereira and Fairbanks, 1993; Pereira and Leigh, 2002). Exploration of these and many other potential links has only begun and provides great potential for future research.

Finally, potential main determinants of some aspects of social systems, as well as some important consequences, remain virtually unexplored. There are few studies on diseases of natural primate populations, and their effects on behavior (Freeland, 1976; Davies *et al.*, 1991; Heymann, 1999; Nunn *et al.*, 2000). Similarly, the consequences of variation in social systems for conservation and captive management need to be understood in much greater detail to implement effective strategies quickly (Dobson and Lyles, 1989; Ganzhorn, 1987; Gursky, 1998). Fortunately, both primates and primatologists already

have prominent roles in international conservation programs (Jernvall and Wright, 1998; Myers *et al.*, 2000).

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