1 • Primate males: history and theory

PETER M. KAPPELER

INTRODUCTION

The integration of behavioral and ecological studies that generate and test hypotheses about the adaptive bases of diversity in animal social systems is a major goal of socioecology. Studies of primates continue to provide important contributions to this discipline because our comparatively well studied closest relatives exhibit a stunning diversity of grouping patterns and complex social behavior that continue to inspire the interest of numerous zoologists, anthropologists and psychologists.

Across groups, populations and species, the number of adult males per group is the most variable aspect of the social system of those primates that live in permanent groups of more than two adults. This volume features a combination of case studies and synthetic reviews that examine questions revolving around causes of variation in male numbers and its consequences for male and female social behavior. In this introductory chapter, I will review salient earlier studies with the goal of sketching a theoretical framework for the other contributions to this volume.

CAUSES OF VARIATION IN THE NUMBER OF MALES PER GROUP

Single and multi-male primate groups have been recognized as fundamental types of reproductive units since the earliest comparative analyses of primate social systems (Crook & Gartlan, 1966; Eisenberg *et al.*, 1972). These influential studies used the number of males as a variable to organize the rapidly growing information about primate social systems. The resulting categories or grades were used to examine correlations with ecological variables, an approach that had been successfully applied earlier to birds (Crook, 1968), and later to other mammals (Jarman, 1974). These categories were, at least implicitly, treated as adaptive, species-specific traits.

The first of these attempts by Crook & Gartlan (1966) to order information about primate social systems was structured after Crook's thesis (1964), in which he successfully correlated the diversity in social organization and behavior of more than 90 species of weaver birds with broad characteristics of their habitat. As in the earlier study, group characteristics were considered as a target of selection. A new element was introduced to the analysis of primate social systems by postulating a progressive shift between grades that culminated in the presumed condition of early humans. Males played the prominent role in this discussion of different grades. One-male groups characterized the members of the highest grade, which all live in open grassland and savannah habitats. Under these harsh ecological conditions, 'the presence of several large males, only functional in mating and playing no part in rearing young, results in the consumption of much food not used in maintaining the species' (Crook & Gartlan, 1966). The occurrence of predominantly multi-male groups in the next lower grade was attributed to an apparently increased predation risk, even though many of these species also live in open country. Here, 'the increased size and aggressive nature of males are considered to have been pre-adaptive to their role in troop defence', however (Crook & Gartlan, 1966).

Sexual selection theory was also implicated in explanations of both types of groups. Increased competition among males was recognized as an inevitable consequence of a multi-male structure, due to excellent visibility, group cohesion and the seasonality of mating: 'The exclusive possession of a harem probably increases inter-male competition for females further and the occurrence of all-male population units indicates a considerable degree of exclusion of potential reproductives from breeding'.

Subsequently, Crook (1970) acknowledged the existence of intraspecific variation in social organization and discussed the then-available information on baboons, langurs and vervets. He continued to link social systems, in particular one-male and multi-male groups, to ecological factors, such as diet, food dispersion and predation. Gartlan (1968), in a later analysis of social dominance, continued to view the group as 'an adaptive unit, the actual form of which is determined by ecological pressures', but he conceded 'that there is no evidence of simple, linear social evolution from the arboreal Lemuriformes to the anthropoid apes'.

Thus, cause and effect of variation in the number of males were not yet clearly identified, and different questionable functional explanations for species in very similar habitats were provided by this first analysis. In retrospect, these analyses were tremendously important for two reasons. First, they clearly indicated that ecology and behavior are intricately linked. Second, they stimulated a new wave of primate field studies, which continue to provide a valuable basis for our current knowledge of primate behavior and ecology (Terborgh & Janson, 1986).

An important paper by Eisenberg *et al.* (1972) refined and broadened the general approach initiated by Crook and Gartlan. They refined the classification of multi-male species by introducing the category of age-graded male troops, which are defined by the absence of fully adult males of equivalent age. Functionally, age-graded male groups were considered 'a variation on the uni-male theme,' brought about by intermediate levels of tolerance by adult males toward several younger males, which were allowed to mature longer in their natal group. Multi-male groups, in contrast, were characterized by the presence of several adult males of equivalent age, which, presumably as a result of their increased tolerance, show affiliative and cooperative behavior among each other. Importantly, these authors stressed that such permanently bisexual groups with several males are unusual among mammals. Eisenberg *et al.* not only differentiated between different types of groups with variable numbers of functionally adult males, they also suggested that there may be a greater range of causes underlying this variability than the antipredator benefit of multi-male groups and the adaptation to extreme environments of uni-male groups.

Eisenberg *et al.* (1972) also rejected the notion of species-specific social structures. Instead, they emphasized intraspecific variation and recommended using modal categories for interspecific comparisons. They continued to define grades, based on group composition, feeding ecology and habitat use, but they emphasized parallel evolution, rather than linear increase of social complexity. Correlations between social system and ecological parameters continued to be stressed, however. Exceptional populations or species were explained with a new factor: phylogenetic inertia (see also DiFiore & Rendall, 1994), even though this undermined the socioecological approach focusing on adaptations.

A number of different male roles in various societies were discussed, such as leadership, defense against neighboring groups and protection against predators, but females and their reproductive strategies were still largely neglected. Females were discussed in detail only in connection with their role in infant care. In addition, they were assigned an important function in modifying social structure: 'In an evolutionary sense, the number of males in a given troop will depend on what advantage the males are to the reproducing females.' What the exact nature of these determinants of social systems beyond ecological ones and their underlying mechanisms were, was not clearly identified, however.

This early phase of primate socioecology characterized by collecting and classifying information was followed by a set of quantitative comparative studies (Terborgh & Janson, 1986). Following Jorde & Spuhler (1974), Clutton-Brock, Harvey and their collaborators (Clutton-Brock, 1974; Clutton-Brock & Harvey, 1977a, 1977b; Clutton-Brock *et al.*, 1977; Harvey *et al.*, 1978) used the distinction between single-male and multi-male species successfully to explain variation in life history and sexually selected traits, but there were no breakthroughs on the question of the adaptive origins of the social systems *per se*.

Using a much larger data base from the increasing number of field studies, Clutton-Brock & Harvey (1977a) recognized that social organization is not entirely independent of taxonomic affiliation. In contrast to previous analyses, they studied not merely group composition, but also group size and other population parameters, an approach that further emphasized the continuous nature of the observed variation. Single-male and multi-male groups could still be associated with habitat type, but no longer with particular diets. Clutton-Brock & Harvey (1977a) also clearly identified the individual as the appropriate level of analysis, as exemplified by their cost/benefit analysis of adding an extra male to an initially single-male group. In further contrast to previous studies, they concluded that reproductive costs and benefits are more important than energetic ones, and that different factors are probably involved in different species in determining the number of males.

Despite, or perhaps because of, growing dissatisfaction with these largely correlational studies, most researchers moved on to other questions. Following important papers by Wrangham (1979, 1980) and van Schaik (1983; van Schaik & van Hooff, 1983), the focus began to shift toward questions about female behavior in the early 1980s, partly because it is more closely linked to ecological conditions, and perhaps also because females were largely ignored by the first socioecological studies. Nevertheless, some studies from that

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period contributed important arguments to the discussion about the number of males. Predation risk as the ultimate cause of multi-male groups had been questioned before (Eisenberg *et al.*, 1972), but van Schaik & van Hooff (1983) showed that cooperative defense could only be a consequence of the presence of multiple males and not a cause of it. More importantly, monopolization of females was clearly identified as the key factor responsible for the distinction between single-male and multi-male groups (Clutton-Brock & Harvey, 1977a; Wrangham, 1979; van Schaik & van Hooff, 1983). Genetic relatedness among males and the costs of being solitary were also identified as important potential determinants of male behavior (van Schaik & van Hooff, 1983).

Important papers revisited the issue of variation in the number of males per group in the late 1980s. First, Ridley (1986) refined the key concept of male monopolization potential by examining the effects of the length of the breeding season on group composition. The important idea, which goes back to Trivers (1972), was that 'In a species with a short breeding season, in which several females may become sexually receptive at the same time, a single male may not be able to monopolize and mate with them all.' As a result, a male has little to gain from excluding other males, and a multi-male system results. Conversely, a single strong, powerful male might be able to monopolize each female of a group in species with a long breeding season. Using a new method that controls for evolutionary dependence among species values, Ridley (1986) showed in a comparative test that the number of males and the length of the breeding season are not independent of each other and that they are correlated in the predicted direction. Ridley argued that the relationship is a causal one and that the length of the breeding season may be partly under female control.

In the same year, Andelman (1986) presented an analysis which identified female numbers and dispersion as important determinants of male monopolization potential. Among Cercopithecines, groups with up to five females are single-male, whereas those with ten or more females are generally multi-male. In groups with intermediate numbers of females (six to ten), both social systems occur. In the latter groups, several factors, such as group cohesion, predation risk and male coalitions, which vary in their relative importance, are responsible for variation within and between species with very similar female group sizes (see also Rowell, 1988a). In contrast to Ridley's study, Andelman found no evidence for a relationship between birth synchrony and social system among the Cercopithecines. A second important result of this analysis was the observation that adult sex ratios among multi-male Cercopithecines were relatively invariant, which argued against the long-held notion that multi-male groups present an adaptation to high predation pressure. This result also reinforced the general argument that the number of males, beyond the single-male/multi-male dichotomy, strongly depends on female group size.

This argument was forcefully repeated in a critique of Ridley's (1986) analysis. Jeanne Altmann (1990) identified several methodological flaws in Ridley's study, most of them concerned with the reliability and classification of individual observations. More importantly, she extended Andelman's (1986) argument about the importance of female group size for the number of males to all primates. She also stressed the importance of considering long-term advantages and population sex ratios in studies of male reproductive strategies. In extending Ridley's suggestion about female control of reproductive synchrony, Altmann proposed that females may synchronize their reproduction in order to increase the likelihood of the presence of several males, which in turn would reduce their risk of infanticide and the intensity of reproductive competition with other females.

Since then, three studies examined the proposed key determinants of the number of males in sophisticated quantitative analyses. First, a carefully controlled comparative study demonstrated that predation risk may increase the number of adult males (van Schaik & Hörstermann, 1994). Controlling for the number of females per group, it could be shown that the presence of monkey-eating eagles tends to increase the number of males in howler and colobus monkeys on average from one to two, whereas ecologically similar langurs, which are not exposed to such predators, tend to live in single-male groups. This result is especially interesting because these taxa represent the majority of primates with intermediate numbers of females, where variation in the number of males is most pronounced (Andelman, 1986).

Finally, two recent comparative studies re-examined the relative importance of spatial and temporal distribution of females on male monopolization potential, using methods that control for phylogenetic dependencies of social systems among taxa (DiFiore & Rendall, 1994; Kappeler, 1999a). Mitani *et al.* (1996a) found that the number of males in primate groups, in particular the qualitative difference between single-male and multi-male groups, is positively associated with the number of females, and not with temporal distribution of their receptive periods. They noted

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several exceptions of species in which a small number of females is associated with several males and suggested that males may gain benefits in these species that offset the potential costs incurred through increased male–male competition. Using the same data set, Nunn (1999) confirmed the effect of female group size, but he also demonstrated that temporal overlap of female receptive periods predicts the number of males after controlling for the number of females. A complete assessment may therefore have to await the availability of additional data, in particular on group-living lemurs, which are characterized by small group size, the presence of several males and extremely short breeding seasons (Kappeler, 1997a).

CONSEQUENCES OF VARIATION IN THE NUMBER OF MALES PER GROUP

Variation in the number of males is also interesting because it has important consequences for social behavior at several levels. For example, the switch from single-male to multi-male groups has profound consequences for the resulting mating system, as well as the associated reproductive strategies of both sexes. It also affects social relationships, in particular the organization of male co-residence in multi-male groups and male–female relations.

Relationships among males are dominated by reproductive competition. Males are inherently less tolerant of each other than females because their reproductive success is limited by access to a nonshareable resource: fertile females. Whenever possible, they should therefore attempt to monopolize access to this resource (Trivers, 1972). Superior size, strength, weaponry and aggressiveness promote this endeavor, and stunning sexual dimorphism in these traits is one consequence of these selective pressures (Clutton-Brock *et al.*, 1977; Clutton-Brock, 1985; Plavcan & van Schaik, 1992). Whenever monopolization of females is not possible, behavioral and physiological mechanisms that promote reproductive skew have apparently evolved to facilitate male coexistence (Bercovitch, 1991; Dixson, 1997). Formalized dominance relationships are of paramount importance in this context (Bernstein, 1976; de Waal, 1986, 1989a). Delayed maturity, group transfers and alternative reproductive strategies are important mechanisms available to subordinate males to alleviate the consequences of their disadvantaged position (Cowlishaw & Dunbar, 1991; Dunbar & Cowlishaw, 1992; Alberts & Altmann, 1995a, 1995b).

Cooperation among males is primarily expected when they live with relatives, so that they can accrue inclusive fitness benefits (van Hooff & van Schaik, 1994). Communal defense of groups of females or their ranges and male bonding are indeed observed in species with male philopatry (van Hooff & van Schaik, 1994), sometimes even within groups (Watts, 1998a). Mutual or reciprocal benefits can also promote short-term cooperation between unrelated males (Noë & Sluijter, 1990). However, affiliative behavior between non-relatives is also commonly observed, but still poorly understood (Rowell, 1988a). Several of these topics have been studied in some detail (de Ruiter & van Hooff, 1993; van Hooff & van Schaik, 1994), but long-term studies of all aspects of male relationships are still scarce (see, for example, Altmann *et al.*, 1997), so that a number of questions remain unanswered. For example, do age-specific patterns of male mortality differ among single-male and multi-male species? What are the maturational and sexual strategies employed by adolescent males? Why do some males stay in their natal groups whereas others leave and join established groups or found new ones? Why are all-male bands so rare among primates, and what are the relationships among their residents? How common are solitary males and how do they try to optimize their survival and reproductive success?

Variation in the number of resident males also has far-reaching consequences for intersexual relationships. Questions about the female perspective are particularly relevant here (Smuts & Smuts, 1993), i.e., which social costs and benefits can females expect in single-male and multi-male groups? Female choice of mates is constrained by definition in stable single-male groups. Females in single-male groups also experience a high potential risk of infanticide in the case of group takeovers (Watts, 1989; Sommer, 1994). On the other hand, the risk or intensity of other forms of sexual coercion may be reduced, compared to multi-male groups (Smuts & Smuts, 1993). Females in multi-male groups have potentially more male assistance in rearing young (Wright, 1990) and have opportunities to establish friendships with individual males that support them in conflicts (e.g., Smuts, 1985). Thus, females are clearly not just passive bystanders that, depending on male competitiveness or tolerance, happen to end up in single-male or multi-male groups, but rather have fundamental interests of their own at stake.

Several recent studies indicate that female primates are very sensitive to the risk of infanticide and that they adjust

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their behavior and even physiology accordingly (Sterck, 1997, 1998; Steenbeek *et al.*, 1999), and females in other species may form alliances in response to this sort of conspecific threat (Treves & Chapman, 1996). In general, females can reduce this risk in multi-male groups, which they should prefer, if given a choice (Altmann, 1990). Females may also benefit through increased opportunities for mate choice in a multi-male group. Why females in some multi-male groups also engage in copulations with extra-group males remains to be studied in detail, however.

Males and females are therefore likely to have a conflict of interest over the number of males in a group. Which mechanisms do females have at their disposal to win this evolutionary battle? Resource characteristics permitting, they could form such large groups that defensibility by a single male becomes impossible. Critical female group size with respect to defensibility may also vary according to visibility (Rowell, 1988a) and group cohesion (van Schaik & van Hooff, 1983). Synchronization of fertile periods within groups is another theoretically possible way to reduce male monopolization potential (Ims, 1990). Variation in other aspects of female reproductive behavior and physiology suggests that females can modify them to make matings with several males possible. Sexual swellings and mating calls are common among multi-male species, which also tend to have longer follicular phases (van Schaik *et al.*, 1999). Finally, in species in which females are free to migrate, they can transfer into groups with the optimal number of males (Sterck, 1997). Thus, females could take an active role in influencing basic aspects of group composition, but these questions have only begun to be studied in detail (van Schaik, 1996; Sterck *et al.*, 1997).

CONCLUSIONS

Thus, the causes and consequences of variation in the number of males per group are far from completely understood. Much progress has been made in the past 30 years toward understanding the selective factors that determine the composition of primate groups. The focus has shifted from group to individual adaptations, from concentrating exclusively on males to considering reproductive strategies of both sexes, and from looking for only ecological correlates to acknowledging the importance of social factors and sex-specific interests in structuring group composition. Similarly, the list of known or suspected mechanisms underlying variation in group size and composition has grown in parallel.

It was not until recently, however, that new questions, e.g., about mechanisms of sperm competition and aspects of sexual coercion (Dixson, 1991; Smuts & Smuts, 1993; Harcourt & Gardiner, 1994; Harcourt, 1995), new methods, such as DNA-fingerprinting and comparative phylogenetic analyses (Cheverud *et al.*, 1986; Ely & Kurland, 1989; Martin *et al.*, 1992; Sillén-Tullberg & Møller, 1993; de Ruiter *et al.*, 1994; Garber, 1994; Purvis, 1995; Goldberg & Wrangham, 1997) and new data on variability in social organization within and among species (Gautier-Hion *et al.*, 1988; Kappeler & Ganzhorn, 1993; Davies & Oates, 1994; McGrew *et al.*, 1996; Norconk *et al.*, 1996), permitted each contributor to this volume to take a fresh look at a particular taxon or a specific question in this context based on the developments outlined in this chapter. The final chapter attempts to summarize and evaluate their new results, conclusions and questions about primate males (see also Pereira, 1998; Kappeler, 1999c).