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E. A. Fox and J. Altmann

Primate Families, Structure of

We often talk about animal ‘families’ when referring to the breeding units of animals. The word ‘family’ however, is derived from the Latin word for ‘household’ in which a man controls the resources of his wife and offspring. Such entities seem absent in non-human primates. In contrast, most female primates and their

dependent offspring forage largely independently of the males. Furthermore, mating and breeding occur in a large variety of ways. Biologists use the term ‘mating system’ to describe the patterns of behavior related to mate choice and reproduction. Such mating systems are intimately linked to the social system in which the animals live, but these systems are not identical. Mating partners include, but need not be restricted to, social partners. A key characteristic of female primates is their monthly ovulation. Breeding seasons do exist in many primates, but overall periods of female fertility are more frequent than in other mammals. Accordingly, sexual behavior is frequent and has acquired additional functions in many primates.

1. Diversity of Primates and Their Mating Systems

1.1 Types of Mating Systems

Primates include two hundred species ranging in size from mouse-sized prosimians and pigmy marmosets weighing less than 100g to orangutans and gorillas with males weighing over 200kg. Most primates are tree-dwelling but some, such as gorillas and baboons, are terrestrial. While some of the prosimians (a group of relatively ‘primitive’ primates such as galagos, pottos, lorises, and lemurs) are nocturnal and mostly solitary, the vast majority of primates are diurnal and extremely social. In fact sociality and sexuality are key primate adaptations. Primate mating systems represent a wide spectrum ranging from polyandry, where a single female mates with several males (South American tamarins), to monogamous pairs (owl monkeys, gibbons), to multi-male, multi-female groups (chimpanzees, spider monkeys, red colobus monkeys, and baboons) to harem type groups where a single male has exclusive reproductive access to multiple females (gorillas and langurs). Single-male groups can experience temporal visits by groups of bachelor males (Guenons) and solitary males and females can temporarily gather (orangutans). Size differences between males and females (called sexual dimorphism) seem to correlate with the degree to which males of a given species are polygamous. The males and females of the (serially) monogamous gibbons are the same size but males of the polygamous gorillas and mandrills can weigh more than twice as much as females. Primate mating systems are far more flexible and dynamic than previously thought. The same species may show different mating systems in different locations or at different times in the same location (Dunbar 1988). Changes in resource distribution or social changes can cause animals to alter the ways in which they find and choose mating partners.

1.2 Reproductive Costs for Male and Female Primates

Sexual reproduction refers to the process by which male and female germ cells fuse and produce individuals with unique combinations of genes. The germ cells carry half of the reshuffled genes that the parents inherited from the grandparents. Female germ cells (ova) are large and costly to produce whereas male germ cells (sperm) are tiny and much cheaper to produce. In animals with internal fertilization and gestation, this discrepancy in reproductive effort is exaggerated. Female mammals bear an even more disproportionate cost of reproduction because of lactation (the physiological cost of which is higher than gestation itself). Male investment often ends with successful insemination, after which males can look for further mates. The average number of offspring born to male and female species is roughly the same for both sexes, but the variance is much higher in males, where some highly successful males sire large numbers of offspring and many others none at all.

Biologists have repeatedly pointed at the imbalance between male and female reproductive costs to explain why males have a natural tendency to be promiscuous while females tend to be coy and choosier (Hrdy & Williams 1983). This caricature of male emphasis on quantity and female emphasis on quality is in part responsible for the fact that students of animal behavior have long overlooked the importance of female choice and multiple paternity (Gowaty 1992). Females, much rather than just being passive resources, for which males compete, are pursuing their own reproductive interests very actively. Their strategies are often less conspicuous and may involve long-term patterns, which explains why they have so often been overlooked.

Male primates can undoubtedly increase their lifetime reproductive success by maximizing the number of matings with fertile females. In primates, where mating often has more functions than simple fertilization, there may be strong advantages to multiple matings for females as well. Primates have long periods of development and infants are very dependent on parental assistance. Parental care is crucial to primate reproduction and is mostly the responsibility of mothers, though, in many cases males are also involved. The tamarins of the Amazon forest even have cooperative paternal care for twins born to the female. The young of many primates benefit from the protection and care from males with whom their mothers associate. Infant baboons and gibbons are often carried by males and chimpanzee males are known to adopt orphaned male youngsters. Wherever male help with the rearing of offspring is needed and there are several males present in the group, uncertainty of paternity can cause males to assist offspring that they did not sire, resulting in a strong motivation for females to mate with many different males. Too much

uncertainty about paternity is potentially dangerous, as males can be a threat to offspring that they perceive as not their own.

1.3 Sex as a Social Tool

In bonobos, apes known for their frequent sexual interactions, sex is directly used to reduce tension in the group and is often exchanged for food. Chimpanzee females often exchange sex for meat that tends to be controlled by males, which do most of the hunting and use prey as a social currency. A female chimpanzee will copulate more than six thousand times with a very large number of males (10 to 30) while she can only produce a maximum of six surviving offspring. Similarly, the high frequency of same-sex sexual contact in bonobos plays important, entirely social roles. In fact, bonobos appear to be the one species of primates, where frequent female–female sex facilitates the existence of strong female alliances which are strong enough to keep male aggression in check.

1.4 Sexual Advertising in Multi-male Groups

Females in many species with multi-male groups exhibit conspicuous pink swellings of their genital area during several days around the time of their ovulation. These swellings are known as estrous swellings and they represent a formidable ‘tool’ for female primates. A female with a swelling becomes the focus of attention of all males in the group. Her social status increases and males will compete for access to her. Several females can have estrous swellings at the same time, thus making it virtually impossible for any given male to monopolize access to all of them. Estrous swellings appear to play an important role for species where females disperse and join new social groups after they become sexually mature. Swellings are a kind of ‘social passport’ which greatly facilitates a female’s acceptance by unfamiliar males. There is evidence for certain amounts of disconnect between the advertising of fertility and actual time of ovulation. Such a disconnect could work to the advantage of the female because she could escape the controlling efforts of certain males and exert a freer choice of paternity for her offspring. The topic of ‘concealed ovulation’ takes on considerable importance as many scientists have suggested that humans have attained a stage of perfectly concealed ovulation (concealed even from a large proportion of women themselves). To what degree the inability of human males to detect the moment of peak fertility in women has played a role in leading to the high frequency of (serial) monogamy in our species is a much-debated issue.

Some primates use vocalization as a way to attract mates. Notable cases are the orangutan, gibbons, and

siamangs. In the orangutan, an interesting case of multiple male mating strategy includes sexually mature but small males, that do not sing to attract females but rather rely on forced matings between several males and a very reluctant female. Female criteria for choosing their mates remain poorly understood. Females can certainly learn about future social partners through their yearlong interactions with males, but for detecting 'good genes' they must rely on indirect signs such as body symmetry and relative absence of disease and parasites.

2. Determinants of Sociality in Primates

2.1 The Need for Social Grouping

The distribution of resources and the presence of predators play key roles for the distribution of individuals across space. When resources are clumped, groups of animals can live around a particular cluster of resources and defend a certain territory. Such groups can form cohesive social units. When resources are few and very dispersed, no single cluster of resources can be defended even by large groups of animals. Such environments tend to harbor animals living in much smaller groups or as dispersed individuals. Even highly social populations of chimpanzees are known to scatter into much smaller sub-groups during periods of low food abundance. The solitary orangutans on the other hand can gather in large numbers during periods of plenty (mast fruiting).

There are many good reasons for living socially. More eyes can see better and more ears can hear better. Living socially facilitates the search for food and the detection of predators. Another advantage is the phenomenon of the 'selfish herd' where the presence of other individuals spreads the risk of predation, as any of the others is as likely to be preyed upon as oneself. Also, cooperation in anti-predator defense is only possible in groups. Obviously, social life facilitates finding mates, even if it will increase the competition for them. Animals in groups can cooperate in defending resources against competitors. Such cooperative resource defense, when done by males, may have the added benefit of attracting females to the group, which may represent unwelcome competition to the females already resident in the group. Finally, the presence of individuals possessing different capabilities (such as hunting, raiding beehives, remembering the time and place certain foods can be harvested) in a group will benefit all group members. Unique individual experience and history shape large-brained, long-lived organisms such as primates. The mating strategies within a social group can vary dramatically between individuals. Some males, for example, may not show any ambition with respect to the dominance hierarchy. They spend their

whole life as subordinate males. Their affiliative behavior and friendship with certain females in the group may in the end translate into numerous offspring. Certain females may be much more successful at forming social bonds with dominant males. Sheer force can allow a male to ascend in the dominance hierarchy, but the majority of animals in his group may not follow him. The cognitive capacities of primates appear to have coevolved with their tendency for sociality. Long-lasting relationships with many group members require good memory and social intelligence.

2.2 Costs of Living Socially

There are multiple costs to sociality. Competition between males can create social instability and conflict. Such conflict is often violent and can lead to harm to bystanders or even infanticide by males hoping to remove the offspring of competitors and gain rapid access to fertile females (the loss of an infant causes lactating females to resume ovulatory cycles). Competition occurs not only between males for access to females, but also between females for access to males, access that may lead to support (shared resources) and male protection during social conflicts. Competition between female may be the factor that precludes the formation of strong female coalitions against males in many species. Infanticide perpetuated by females has been observed in some wild primate groups and may represent the darkest side of female-female competition for resources. The study of female dominance hierarchies in natural primate populations is still in its infancy. Such hierarchies tend to be more subtle, nevertheless, female social rank can play an important role for reproductive success and change the way females invest in sons or daughters. Finally, higher risk of infection by pathogens and parasites is an important cost to sociality.

2.3 Most Primate Groups are Female Bound

In most primates, females and their female relatives remain in their native groups while most males disperse to other groups when they reach sexual maturity. Some notable exceptions to female residence are found in colobus and spider monkeys and in our closest living relatives, chimpanzees and bonobos, where females disperse upon reaching sexual maturity and males remain in their natal communities. The driving force behind dispersal is thought to be inbreeding avoidance and/or competition with animals of the same sex (Moore & Rauf 1984). Sexual mimicry in white-cheeked gibbons, where adolescent females look like males, and in red colobus, where young males have pseudo-swellings, indicates that same-sex competition is important in those species. The mechanisms

underlying inbreeding avoidance are poorly understood. Whether primates are able to recognize their paternal kin by features inherited from the father or whether they simply avoid mating with individuals from the same age cohort is still unclear (Alberts 1999). In humans, close proximity at an early age seems to be the crucial mechanism that triggers avoidance as sexual partners.

2.4 Do Males Follow Female Spacing?

The way females deploy themselves across time and space tends to determine how males can space themselves around females. Only if the ecosystem is capable of feeding a large number of females with enough tolerance for each other can males attempt to control such groups, either as the solitary reproductive male in a harem or as a group of males cooperating in female and territory defense and sharing the reproductive access to those females. All multi-female groups create the potential for female–female competition over access to resources and access to males and the support they may provide. Competition between potential mates may create the opportunity to enhance the visibility of positive traits or weaknesses. Because competition involves stress and stress is known to impact an animal's immune system, competition can exaggerate the visible differences in male quality. If female choice incites increased male competition, then female choice may indirectly lead to an increased size difference between males and females. Because strong and assertive males can be more successful at guarding resources that they share with females, females may favor the evolution of such males. Females need male protection from unwanted attention of other males, including, in the extreme case, forced copulation, as well as against the threat of male infanticide; both are part of male mating strategy in many primate species (Smuts 1993). Strong and protective males by the same token will be more successful at restricting the independence of females.

3. The Importance of Genes

3.1 The Benefit of Multiple Paternity to Females

Mating with multiple males can be advantageous for a female in various ways. As mentioned above, confusing paternity of her offspring can effectively protect them from male infanticide. She may gain support from her mating partners, both in terms of social support during conflicts with other group members and in terms of material support in the form of shared resources. More recently, the possibility of a genetic benefit has been proposed and some evidence is starting to accumulate (Zeh & Zeh 1996, 1997).

Because the primate fetus develops inside the mother, the female and the fetus need to achieve a type of 'immunological détente.' That is, the fetus must not be rejected by the mother's powerful immune system but, at the same time, the demands of the fetus must be kept in check, not allowing it to exact too high a toll on maternal resources. Multiple paternity will produce more diverse offspring. Such diversity may have much to do with defense against disease. The vertebrate immune system is an immensely sophisticated and very costly system, in order to allow long-lived organisms such as primates to survive in a world in which very short-lived, rapidly evolving parasites and pathogens (ranging from worms and protozoa to bacteria and viruses) are a constant threat.

The immune system relies on genetic variation present in all populations, as well as generated anew in each individual in order to produce a flexible repertoire of molecular probes (antibodies and T-cell receptors) which detect specific intruding pathogens. It seems critical that each fetus inherits genes coding for two rather different immunological 'tool kits' in order for the offspring to be well equipped for its countless future encounters with pathogens. Conceiving offspring with different fathers would allow females to produce sets of offspring with more variation in their immune repertoires, strongly reducing the risk of losing all or most offspring to the same disease. The same obviously applies to males as well. Furthermore, paternal and maternal genes have to work in harmony in order to produce healthy offspring. Some combinations may simply fail to work and yet others may work but put the offspring at a disadvantage from the beginning. The detection of embryos with strongly limited immune repertoires (i.e., two almost identical sets of multi-histocompatibility complex or 'MHC' alleles) inherited from both parents, can cause spontaneous abortions in many mammal species including our own. Because of the importance of compatibility between genomes, the most promising genes for each female are found in different males. Finally, multiple paternity may allow females to reduce inbreeding where females cannot recognize close kin.

3.2 Molecules and Behavior

Ova and sperm engage in intense molecular dialogue, a process which is important for creating reproductive barriers between species but which is also suspected to involve an additional level of (post-mating) female choice. Female primates are known to produce a large quantity of antibodies against sperm in their genital tracts, a process which strongly favors diversity in paternity as the antibodies would be formed against the sperm of the 'usual' mating partner leaving sperm from unknown males at an advantage. The role of chemoreception (pheromones) in regulating some primate behavior remains very poorly understood.

The fact that primates may be able to smell important immune molecules (MHC) points towards potentially important roles of such molecules and their detection in mate choice and sexual behavior (Wedekind & Fürti 1997).

3.3 Post-mating Female Choice and Sperm Competition

Certain sperm may be more likely to be taken up by the egg as they approach it. Such cryptic female choice would represent a choice of individual sperm, possibly based on the genes carried by that sperm. Certain genes of crucial importance in early embryonic development are known to be expressed on the surface of sperm. Males can compete for fertilization of females via a process called 'sperm competition.' When females mate with many males within a short period of time, the sperm of different males will be available for fertilizing her egg. This exerts pressure on males to produce larger quantities of sperm in order to succeed in preference to other males. In chimpanzees, where multiple matings with many males give rise to strong sperm competition, males have conspicuously large testicles and produce large amounts of sperm. They even produce 'copulatory plugs,' a gelatinous mass blocking the entry to the uterus. In gorillas, on the other hand, where silver back males face very little competition in their harems, males have very small testicles. Female-female competition may take place via the depletion of sperm supply for other females.

3.4 Genomic Conflicts

Because different males can sire subsequent offspring, a conflict of interest can arise between the paternal and the maternal genes. A female will spread her total reproductive efforts across all her subsequent offspring. Males are likely to have sired offspring with other females and thus are spreading their reproductive effort across several females. Paternal genes in the embryo are likely to cause each embryo to be over-demanding from the point of view of the mother. Such paternal genes will increase the male's reproductive success at a detriment to each female, who will have invested too much in that particular offspring. It is this conflict which seems to be at the root of a phenomenon called 'imprinting.' Imprinting occurs when, among the two variants of each gene present in the embryo (the paternal and maternal alleles), only one of the two is expressed. Often, only the allele inherited from the mother is expressed, while the paternal allele appears to be silenced. Imprinting may have several functions but one of them may be female control of over-demanding genes from the father (Mochizuki et al. 1996, Spencer et al. 1998).

Primate mating systems represent the outcome of a delicate balance between various constantly changing forces. These include:

(a) ecological factors such as the distribution of resources and pressure by predators;

(b) female foraging and mating strategies, including the need to find multiple fathers of high genetic quality and good genetic compatibility and one or more supportive social partners;

(c) male mating strategies that may entail the access to the largest number of fertile females often in severe competition with other males; and,

(d) the need for parental care of infants and juveniles.

Compromises between male and female strategies seem to occur at every level, from gene expression to behavior. The existence of life-long friendships between adult primates of both sexes introduces an additional dimension, that of emotional attachment and trust between individuals.

4. Future Directions

Long-term field studies of primates in their natural habitat are being complemented by powerful molecular methods of analysis. Genetic analyses are providing detailed information on pedigrees and kinship, while hormone studies can provide knowledge of female reproductive state. Studies of hormones, such as oxytocin and vasopressin and their receptors, which seem to have dramatic effects on male social attachment behavior, are likely to produce new insights (Young et al. 1999). The study of genomic conflicts and imprinting is in its infancy. Similarly, further insight into the determinants of genetic compatibility and the maximizing of immune repertoires will produce much badly needed knowledge. The large number of longitudinal studies of natural primate communities under way is bound to reveal additional ways in which males and female primates strike compromises and successfully reproduce in ever-changing environments. Understanding mating systems is not only essential if one wants to understand evolution, because many primates are facing extinction, such an understanding is also crucial for conservation efforts in the wild and in captivity.

See also: Group Processes, Social Psychology of; Primate Behavior: Significance for Understanding Humans; Primates, Social Behavior of

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P. Gagneux

Primate Socioecology

Sociality is the primary behavioral adaptation of the anthropoid primates, the monkeys and apes. All of the anthropoid primates, except orangutans, spend most of their lives in stable groups of familiar individuals. However, the social organization among the anthropoid primates encompasses great diversity, ranging from the pair-bonded groups of gibbons and owl monkeys, to the polyandrous groups of tamarins; one-male groups of howlers and blue monkeys; multimale, multifemale groups of cebus monkeys and baboons; and fission-fusion communities of chimpanzees and spider monkeys. This great diversity in social organization shapes the behavioral options available to males and females and profoundly influences the evolution of social behavior and reproductive strategies in both sexes.

1. The Evolution of Social Organization

The great diversity in primate social organization has prompted researchers to ask a number of related

questions: Why do primates live in groups? How should groups be structured? How big should groups be? These questions were first raised in the 1960s and 1970s by primatologists who conducted comparative analyses searching for broad ecological correlates of social organization (reviewed by Janson 2000). These comparative efforts yielded some consistent associations between diet, home range size, group size, body weight, and group composition. But the analyses were unsatisfying because they could not account for much of the observed variation in social organization among primates. Moreover, while these studies revealed a number of robust associations among various ecological variables, they did not produce much insight about the causal processes underlying these correlations. Finally, these comparative studies did not consider the possibility that some of the similarities between species were the result of common phylogenetic history, not independent adaptations to ecological conditions, a problem that has become a central methodological concern in comparative studies in behavioral ecology.

In the 1980s researchers returned to these questions, equipped with the theoretical and methodological tools of contemporary behavioral ecology (Krebs and Davies 1993). Behavioral ecologists try to explain how evolutionary processes shape behavior in particular ecological contexts. Sociality is presumed to reflect a dynamic balance between the advantages and disadvantages of living in close proximity to conspecifics. Sociality is beneficial because animals who live in social groups are better able to acquire and control resources or less vulnerable to predators. On the other hand, sociality is disadvantageous because group-living animals may face more competition over access to food, become more vulnerable to disease, and become more susceptible to cuckoldry, infanticide, and cannibalism. The size and demographic composition of the groups that we see in nature reflects a compromise between the costs and benefits of sociality for individuals who occupy particular ecological niches.

1.1 Why do Primates Live in Groups?

For primates, the primary advantages of sociality are thought to be enhanced access to resources, reduced vulnerability to predation, or some combination of both these factors. Many primates feed on foods, such as fruit, that occur in patches large enough to feed several individuals at the same time. Taking note of this fact, Wrangham (1980) suggested that primates aggregate because groups are more successful in defending access to resources than lone individuals, an argument that has also been applied in other taxa. Thus, the potential for between-group competition over resources favors sociality.

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