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Male-Male Competition, Synchronous Estrus, and Reproductive Skew in Multimale-Multifemale Primate Groups

Michelle Night Pipe

*Abstract: In recent years, paternity assessments utilizing DNA testing of primate populations have yielded valuable information regarding reproductive skew, male-male competition and synchronous estrus. In this paper, genetic data and demographic factors of multimale multifemale primate groups including West African chimpanzees (*Pan troglodytes verus*), bonobos (*Pan paniscus*), savannah baboons (*Papio cynocephalus*), mountain gorillas (*Gorilla beringei beringei*), and mandrills (*Mandrillus sphinx*) are examined and compared. The revealed patterns of paternity in multi-male groups are shown to support the priority-of-access model. The role of male-male competition in attracting females to the group is considered, as is the function of synchronous estrus in constraining reproductive skew. The importance of the interplay between male-male competition, female reproductive synchrony and dominance in hominid evolution is discussed.*

Introduction

An understanding of primate social systems, specifically primate mating systems, is a key factor in the consideration of human evolution. This is especially true in the case of multimale-multifemale primate groups, as it is generally assumed that hominid evolution occurred in this social context. In recent years, it has become apparent that observational data alone cannot capture the range of variation in the mating behavior of primates in multimale-multifemale communities. Not only is it impossible to observe all copulations by every individual in a population, but observation alone cannot reveal paternity when females mate with multiple males. As discussed by Charpentier et al, "Observed mating systems do not necessarily correlate with

reproductive systems and thus cannot provide reliable information about male reproductive success. This is especially true for primate species with a complex multimale-multifemale social organization" (Charpentier et al. 2005:614). The use of genetic paternity analysis in multimale primate groups has the potential to provide the highly-detailed information necessary to fully grasp the dynamics of complex primate reproductive systems.

Examining the genetic structure of primate communities can bring clarity to key areas of primate research, including the interplay between male-male competition, dominance, and reproductive success, as well as female mating strategies and the role of female reproductive synchrony in primate reproductive systems. With these themes in mind, this paper will review a number of studies utilizing DNA paternity analysis in multimale-multifemale primate groups, including West African chimpanzees (*Pan troglodytes verus*), bonobos (*Pan paniscus*), savannah baboons (*Papio cynocephalus*), mandrills (*Mandrillus sphinx*), and mountain gorillas (*Gorilla beringei beringei*). For ease of comparison, these primate groups will be divided into two categories: those characterized by male philopatry and female dispersal, and those characterized by female philopatry and male dispersal. The applicability of primate DNA paternity data in testing the predictions of reproductive skew models, including the priority of access model (Altmann 1962), will be illustrated and discussed.

Male Philopatry- Female Dispersal: Chimpanzees and Bonobos

As our nearest living primate relative, chimpanzees and their social organization are of particular interest. Unlike most primates, male chimpanzees are philopatric, staying in their natal community, with females dispersing at maturity (Boesch et al. 2006). According to Vigilant et al., "chimpanzee communities are primarily male bonded; that is, inclusive fitness and kin selection theory explain the high rate of occurrence of affiliative and cooperative actions among adult males" (2001:12890). It is this cooperation between males that sets chimpanzees apart from most primate species, and it is likely that "the social organization of the common ancestor of chimpanzees and humans was in all major respects like that of chimpanzees today and was characterized by female dispersal, male philopatry, and in particular the presence of male kin-based associations" (Vigilant et al. 2001:12890). Hominid evolution is thought to have occurred within this social and reproductive context.

It has always been assumed that chimpanzees mate primarily within their social group. Mating is promiscuous, with females typically mating one to four times an hour with up to thirteen or more males during their twelve

day fertile estrus period (Hrdy 1997). Despite this variety of partners, dominant males are thought have significantly higher reproductive success (Boesch et al. 2006). A review of three separate chimpanzee DNA paternity studies should provide clarification regarding these assumptions.

Gagneux, Woodruff, and Boesch (1997) conducted DNA genotyping of one community of wild chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Ivory Coast. The study utilized non-invasive methods and genotyped all 52 community members, including 13 infants. The researchers concluded that 7 of the 13 infants (over 50 percent) were sired by extra-group males (Gagneux et al. 1997; Gagneux et al. 1999). Further, they found that only two (15 percent) of the infants were sired by dominant males during their tenure (Gagneux et al. 1997). These findings ran contrary to everything primatologists believed about chimpanzee mating systems and had serious ramifications for the way male dominance, male-male competition and female choice in multimale-multifemale mating systems were viewed. Vigilant et al. discussed the effects of these unexpected findings, saying they "would seem to represent a hitherto unrecognized opportunity for female mate choice. Such a strategy by females would lessen the significance of male social ranking determining reproductive success, as well as result in a significant amount of gene flow among communities" (2001:12890).

In response to the Gagneux study, Vigilant, Hofreiter, Siedel and Boesch (2001) conducted a second DNA genotyping of the Taï National Park chimpanzees. However, this study genotyped 108 individuals, including 41 offspring, from all three Taï communities, resulting in a much larger and more rigorously controlled study (Vigilant et al. 2001). The findings were starkly different than those reported by Gagneux et al., with extra-group paternity (EGP) measured at 7 percent, as opposed to 50 percent. In addition, the two studies disagreed on the paternity assignment of 7 out of 11 offspring compared. The inconsistencies between the two studies are partially explained by allelic dropout, which is caused by "the amplification of only one of two alleles at a heterozygous locus, thus producing a falsely homozygous result" (Vigilant et al. 2001:12894). Other sources of error in the Gagneux et al. study could have resulted from sample mix-up or contamination. Vigilant et al. comment on the need for consistent criteria for reliability in DNA paternity analyses in primate populations, and caution that "critical evaluation of even published studies is necessary" (2001:12894).

The paternity data in the Vigilant et al. study was later used as a subset in a second DNA genotyping of the entire Taï chimpanzee population; however, this later study focused on dominance ranking and male reproductive success, as well as EGP, female reproductive synchrony and

male-male competition. Boesch et al. (2006) genotyped 115 individuals, including 48 offspring, and found an EGP of 10.5 percent. The rank of the father was known for 36 of 38 offspring, and of these 50 percent were sired by the alpha male within the community, illustrating that dominance status generally does predict reproductive skew (Boesch et al. 2006). Furthermore, it was shown that male-male competition constrained the ability of the alpha male to monopolize reproduction. With few competitors, alpha males sired 67 percent of offspring, but this was reduced to 38 percent when many competitors were present (Boesch et al. 2006). Interestingly, even though alpha males were less able to monopolize reproduction when many competitors were present, fathering a lower percentage of offspring, they actually produced four times more offspring in large groups. This, according to the researchers, is due to higher birth rates and increased survival of offspring, indicating that large multimale groups are advantageous for both high and low ranking males (Boesch et al. 2006).

While the effect of male-male competition on alpha male reproductive success is significant, it was not the most important factor decreasing alpha male reproductive skew. As predicted decades ago by the priority of access model (Altmann 1962), female reproductive synchrony had a profound effect upon the ability of the dominant male to monopolize reproduction. According to Boesch et al. "alpha males secured 88% of offspring when two or fewer estrous females were present within the community, and this decreased to 31% when more than two estrous females were present" (2006:110). The effects of female reproductive synchrony on reproductive skew will be discussed in greater detail below.

A DNA analysis of paternity on a group of wild bonobos (*Pan paniscus*) in the Lomako forest, Democratic Republic of Congo, has mirrored many of these chimpanzee findings. The community under consideration consisted of 41 individuals: 15 adult females, six adult males, and 20 subadults and infants (Gerloff et al. 1999). In addition to confirming the assumption that bonobos are characterized by male philopatry and female dispersal, there were some other interesting conclusions. Observational data indicated that all adult and adolescent males mated with group females, which is not surprising since bonobos, like chimpanzees, mate opportunistically and promiscuously. However, the highest ranking male did have a higher copulation rate than lower ranking males. Genetic data confirmed that 50 percent to 70 percent of infants were sired by the two most dominant males. The EGP rate was 10 percent, with only one of the ten infants being sired by an extra-group male (Gerloff et al. 1999). In sum, these results are remarkably similar to the chimpanzee data.

Female Philopatry- Male Dispersal: Savannah Baboons and Mandrills

Unlike chimpanzees and bonobos, most primate social systems are characterized by female philopatry, with males dispersing as they reach adulthood. In the case of wild savannah baboons (*Papio cynocephalus*), female philopatry allows for the development of matrilineal hierarchies, with females ranked in stable intergenerational hierarchies (Altmann et al. 1996). The dominance status of male baboons changes frequently, peaking for a few years in early adulthood, and thereafter declining rapidly. Savannah baboons live in multimale-multifemale groups and mating generally occurs within consortships, in which the male mate-guards during the highly fertile estrus period. A male can guard only one estrus female at a time (Altmann et al. 1996).

Altmann et al. (1996) conducted intensive DNA paternity analysis on a group of wild savannah baboons in Amboseli, Kenya, utilizing blood samples collected from 76 individuals after being immobilized by a blowpipe dart. In this "first quantitative test of the priority of access model among wild primates" significantly high reproductive skew of dominant males was supported (Altmann et al. 1996:5797). For the four year period between 1985-1988, the top-ranking male sired 81 percent of the 27 surviving offspring; however, this was an unusually long and stable tenure. In the years following 1988, no single male retained dominance for more than a year. In addition, none of the dominant males with less than a year-long tenure sired any surviving offspring. Overall, "the period over which any particular male experienced high success was a function of the length of time in which he was high-ranking" (Altmann et al. 1996: 5800). It was also noted that female reproductive synchrony affected the ability of the dominant male to monopolize paternity, and when two or more females were in estrus simultaneously, the second-ranking and lower-ranking males were also able to reproduce.

Mandrills (*Mandrillus sphinx*), like savannah baboons, are characterized by stable matrilineal hierarchies, female philopatry, and male dispersal (Charpentier et al. 2005). An analysis of the genetic structure of a semi-free-ranging mandrill colony at Centre International de Recherches Médicales de Franceville (CIRMF), Gabon, spanning twenty years and including 205 infants was conducted with the purpose of examining the factors affecting reproductive skew. The Charpentier et al. study (2005) is interesting because of its temporal depth and huge sample size, and produced many interesting findings. Out of 49 males capable of reproduction, only 17 (34.7 percent) sired offspring. Of these 17, nine dominant males sired 76.2 percent of

offspring during their tenure, as opposed to 23.8 percent sired by the eight subordinate males (Charpentier et al. 2005). Unusually, and contrary to the prediction of the priority of access model, male-male competition was *positively* associated with higher reproductive skew of the dominant male. In this mandrill population, higher numbers of male competitors led to higher reproductive success for the dominant male. Charpentier et al. suggest that this is due to an increase in intrasexual competition of subordinate males, which in turn deflects competition away from the dominant male (Charpentier et al. 2005).

Mixed Dispersal: Mountain Gorillas

The social organization and dispersal pattern of mountain gorillas (*Gorilla beringei beringei*) is not easily categorized. The majority live in unimale-multifemale groups, but 38 percent to 40 percent live in multimale-multifemale groups (Watts 1990, Bradley et al. 2005). Males usually disperse, but some stay in their natal group (Bradley et al. 2005), and can even inherit dominant status from their sires (Watts 1990). Females also usually disperse, but have also been known to remain in their natal groups. Breeding adult females may transfer groups several times throughout their reproductive careers (Watts 1990). As a result, neither sex can be said to be philopatric. Female mountain gorillas mate with dominant and subordinate males, yet it is believed that dominant males still sire most offspring. It has been shown that dominant males benefit from retaining subordinate males and forming multimale groups. According to Bradley *et al.* "multimale groups are more likely to attract and retain females, the females become fertile at an earlier age, and infants are less vulnerable to infanticide" (Bradley et al. 2005: 9418).

Bradley et al. conducted a DNA paternity study which genotyped 92 mountain gorillas, including 48 offspring, from four multimale groups living in the Virunga Volcanoes region of Africa, comparing dominance status and reproductive success. They found that the dominant or second-ranking silverback sired all offspring, with the dominant male siring 85 percent of offspring, and the second-ranking male siring 15 percent of offspring (Bradley et al. 2005). In no case was the second-ranking male the offspring of the dominant male, although two out of the five dominant-subordinate male pairs could have been half-siblings. There were no instances of extra-group paternity, which is predictable as extra-group copulations in mountain gorilla groups are extremely rare. Simultaneous estrus is rare in mountain gorilla groups and is not likely a factor in second-ranking male reproductive success (Bradley et al. 2005).

Priority of Access Model: Dominance Predicts Reproductive Success

The priority of access model predicts that for animals living in social groups, male reproductive success should correlate with each male's dominance rank, but will be also be affected by two demographic factors: the number of male competitors in the group and the number of simultaneously receptive females present (Altmann 1962; Boesch et al. 2006; Wroblewski et al. 2009). Advancements in techniques of molecular genetic analysis have, in recent years, allowed for direct testing of this model. The vast majority of genetic analyses conducted on multimale-multifemale primate groups have confirmed the priority of access of dominant males, including the studies reviewed here. Table 1 summarizes these results.

SPECIES	DOMINANT percent OFFSPRING	2ND RANKING percent OFFSPRING	LOWER RANKING percent OFFSPRING	EGP	SAMPLE SIZE	#OF OFFSPRING
Chimpanzees Boesch et al.	50%	13%	37%	10.5%	115	48
Bonobos Gerloff et al.	50- 70%	20% -40%	0%	10%	41	10
Savannah Baboons Altmann et al.	81%	N/A	19%	N/A	76	27
Mandrills Charpentier et al.	76.2%	N/A	23.8%	N/A	N/A	205
Mountain Gorillas Bradley et al.	85%	15%	0%	0%	92	48

TABLE 1 RELATIONSHIP BETWEEN RANK AND REPRODUCTIVE SKEW IN 5 PRIMATE SPECIES LIVING IN MULTIMALE-MULTIFEMALE GROUPS

It is clear that there is a strong correlation between male dominance rank, reproductive skew, and reproductive success. The priority of access model has also been confirmed by a multivariate and phylogenetically controlled analysis of 27 primate populations from 19 species in 11 genera conducted by Ostner, Nunn, and Schulke (2008). All populations lived in multimale-multifemale groups. The study found an average alpha male paternity rate of 60 percent, with a range from 20 percent to 100 percent (Ostner et al. 2008). This wide range of dominant male reproductive success between species is accounted for by the priority of access model because the

number of male competitors in the group and the number of simultaneously receptive females present will affect the degree of reproductive skew; however, it is clear that rank must remain the key indicator of male reproductive success in multimale-multifemale primate groups.

Male-Male Competition and Reproductive Skew

It is important to understand the effect of male-male competition on the ability of alpha males to control reproduction. The Boesch et al. (2006) study of the three Taï chimpanzee groups is useful in this regard because the population under investigation experienced a steady decrease in community size over the course of the study due to poaching, predation, and disease. As a result, the researchers were able to compare reproductive skew in high competition communities (5-9 males) and low competition communities (2-3 males). As discussed earlier, in low competition communities alpha males sired 67 percent of offspring, but this was reduced to 38 percent in high competition communities (Boesch et al. 2006). However, reproductive skew only measures the degree to which alpha males monopolize paternity; counterintuitively, this does not always mean higher individual reproductive success. In the larger high competition communities, alpha males sired an average of 2.48 offspring per year, whereas in smaller low competition communities this fell to 0.69. According to Boesch et al., "alpha males produced four times more offspring in large groups, due to both a higher birth rate and increased survival of offspring" (2006:110). While large group size leads to increased male-male competition, it also attracts more females with which to reproduce. Therefore, even though the alpha male in a large chimpanzee group has to share reproduction with subordinates, evident in lower levels of reproductive skew, he can still win by siring many times more offspring.

In the population of mandrills at CIRMF, male-male competition was *positively* associated with higher reproductive skew of the dominant male (Charpentier et al. 2005). In this mandrill group, higher numbers of male competitors led to higher reproductive success for the dominant male. As noted earlier, Charpentier et al. (2005) suggest that this is due to an increase in intrasexual competition of subordinate males, which in turn deflects competition away from the dominant male.

A genetic analysis of paternity in a group of chimpanzees (*Pan troglodytes schweinfurthii*) from Gombe in Tanzania by Wroblewski et al. (2009) found a lower than expected rate of reproductive skew. The authors attributed this to a fission-fusion grouping pattern and explained that the priority of access model may apply to chimpanzees, but only on a within-

party basis. In this scenario, males who are lower-ranking in a large group become relatively higher-ranking in a small party, allowing access to females (Wroblewski et al. 2009). This illustrates how male-male competition and rank can be context-specific.

In the case of mountain gorillas, male-male competition had the effect of decreasing reproductive skew, but only by 15 percent. Yet, according to Bradley et al., "multimale groups are more likely to attract and retain females, the females become fertile at an earlier age, and infants are less vulnerable to infanticide" (2005: 9418). As was the case with alpha male chimpanzees in large groups, male silverbacks in multimale groups may trade-off lower reproductive skew with higher overall reproductive success, by virtue of attracting more females to the group.

The Ostner, Nunn, and Schulke (2008) analysis of paternity data from 27 multimale primate groups across 19 species looked at the effects of male-male competition, EGP and estrus synchrony on reproductive skew. Surprisingly, in the "phylogenetically controlled multivariate analysis, the number of males in the group had no independent explanatory value. Thus, reproductive skew was solely explained by estrus synchrony" (Ostner et al. 2008:1155). This point is reinforced when they say "synchrony is the main factor driving male monopolization potential. The number of males per group less consistently predicted the degree of skew, and EGP was not an independent predictor of reproductive skew" (Ostner et al. 2008:1156).

As illustrated, the relationship between male-male competition and reproductive skew may be less straightforward and more complicated than previously thought. Rather than decreasing reproductive skew, male-male competition has been shown to occasionally increase both reproductive skew and reproductive success in at least two of the five multimale species reviewed here. Further research in this area might provide some answers to the question of why dominant males (willingly or unwillingly) share reproduction with subordinate males. It seems that rather than constraining the alpha male's monopolization of paternity, under some circumstances male-male competition can increase reproductive skew and reproductive success of dominant males in multimale primate groups.

Synchronous Estrus and Reproductive Skew

When females in multimale-multifemale primate groups are in estrus simultaneously, the dominant male cannot effectively mate-guard more than one female at once. This allows for the second-ranking and subordinate males to reproduce. In this review of paternity analysis and reproductive skew, reproductive synchrony was shown to reduce skew in chimpanzees,

savannah baboons and mandrills (Altmann et al. 1996; Boesch et al. 2006; Charpentier et al. 2005).

In the study of genetic structure of three Taï National Park chimpanzee groups, Boesch et al. were able to compare reproductive skew with levels of reproductive synchrony. They found that "alpha males secured 88% of offspring when two or fewer estrous females were present within the community, and this decreased to 31% when more than two estrous females were present" (Boesch et al. 2006:110). Synchronous estrus had a more significant effect on reproductive skew than did male-male competition.

As discussed, the Ostner et al. (2008) study of 27 multimale groups found female reproductive synchrony to be the main factor driving reproductive skew. In this study, female synchrony ranges from total asynchrony (0 percent) to total synchrony (100 percent), with a mean of 47 percent. High synchronous estrus showed a strong negative correlation with reproductive skew. Figure 1 summarizes the results.

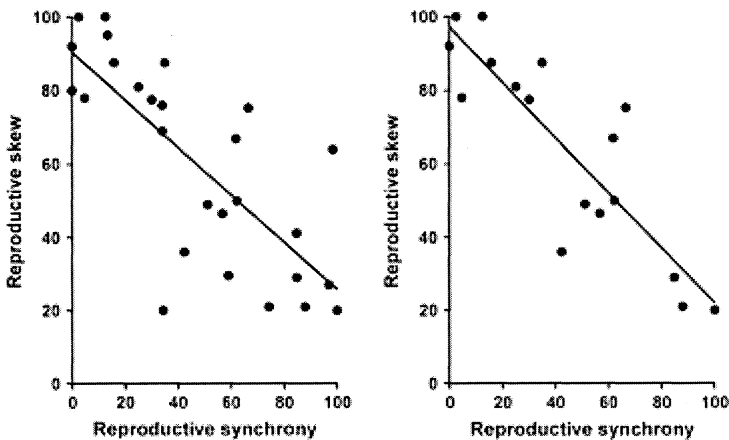


Figure 1. MALE REPRODUCTIVE SKEW REGRESSED ON female synchrony in 27 Populations (left) and in a subset of 17 Populations with EGP Data (right). Reprinted from Ostner et al. 2008:1154.

It is clear that synchronous estrus constrains the ability of dominant males to monopolize reproduction, but the question remains whether or not it is an evolved female strategy. According to Nunn (1999) it is: "in many cases female synchrony probably allows females to break the monopoly of a single male; hence, synchrony may encourage the formation of multimale social groups if this reduces the risk of infanticide or predation" (1999:9).

Nunn goes on to say that pheromonal or social mechanisms allow for synchronous estrus beyond levels expected by chance.

However, if this female counter-strategy was effective, how is the dominant male still able to achieve such high levels of reproductive skew in multimale groups? It is actually quite remarkable that reproductive skew remains such a consistent feature, considering the degree to which females mate with multiple males, as well as the degree to which synchronous estrus prevents the mate guarding of multiple females by alpha males. One explanation for this is that dominant males have the ability to distinguish between conceptive and non-conceptive cycles and can identify the most fertile days within the estrus cycle, competing for access only at the most opportune time for fertilization (Wroblewski et al. 2009; Boesch et al. 2006). An alternate explanation is that dominant males compete better at the level of the sperm. Sperm competition, as expressed by testes size, can be viewed as an indicator of levels of male-male competition within a species.

Hrdy (1997) offers a compelling explanation. She suggests that promiscuous female primates are, in a sense, gaming the system. On one hand, they are mating with multiple males in order to confuse paternity, reaping rewards in terms of protection from infanticide, occasional provisioning (in the case of chimpanzees and meat sharing), and other benefits. On the other hand, they are mating with dominant males at the time when they are most likely to conceive in order to gain the best genetic contribution for their offspring. When it comes to females mating with dominant males, according to Hrdy, "the interests of dominant males and females coincide" and "there might not exist much incentive for females to strive to escape an advantageous status quo" (1997:16-17). In other words, females may ultimately want to reproduce with alpha males while simultaneously ceding mating access to subordinate males as a means to draw them to the group for protection. For dominant males, allowing subordinate males into the group attracts more females, which may positively affect reproductive success in spite of lowering reproductive skew. For subordinate males, any chance of mating is a positive. In this volley of strategies, counterstrategies, and counter-counter strategies, it seems that females, dominant males, and subordinate males in multimale-multifemale

groups have found a win-win-win equilibrium.

Primate Sexuality and Hominid Evolution

It is interesting to look at the dynamics of multimale primate reproductive systems in the context of hominid evolution. For instance, how did the transformation from unimale harem primate groups to multimale pair-bonded hominid groups take place? Based on the data reviewed here, a few generalizations can be made. Male-bonded and male-philopatric groups most likely allowed for a loosening of reproductive control by dominant males. Reproductive synchrony and male-male competition further limited the ability of alpha males to control reproduction, allowing subordinate males access to the mating game. Subordinate males, unable to compete directly with dominant males, came up with alternative mating strategies like consortships and meat provisioning in order to attract females. Eventually, as early hominids began to rely on hunting more exclusively, meat sharing consortships may have lead to pair-bonding and the eventual erosion of dominant male status.

Summary

This paper has reviewed genetic paternity analyses from five multimale-multifemale species, looking at reproductive skew, male-male competition, and female reproductive synchrony. In all five species, significant reproductive skew was illustrated. Consistent with the predictions of the priority of access model, dominant males in multimale groups were found to monopolize reproduction to a large degree. Synchronous estrus was found to constrain reproductive skew, while male-male competition was found to either increase or decrease skew, depending on situation specific factors. When male-male competition led to higher reproductive success for dominant males, it was because the presence of multiple males attracted more females to the group or deflected competition away from the dominant male. The impact of these dynamics of multimale-multifemale primate sexuality on hominid evolution was discussed.

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