Paternity and Social Rank in Wild Chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda

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ABSTRACT We analyzed patterns of paternity and male dominance rank in the Sonso community of wild East African chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. Our major objective was to determine whether and how social rank influenced paternity success. We successfully genotyped 52 individuals at up to nine microsatellite loci, using DNA extracted from fecal samples. Of 24 offspring analyzed, we identified sires for 21. Paternity success was significantly correlated with social rank, with alpha males siring a disproportionate number of offspring. However, both middle- and low-ranking males also fathered offspring, and the priority-of-access model provided a relatively poor prediction of which males would be successful and under what circumstances. The concentration of paternities among only seven males and the tendency for high-ranking males to sire offspring of multiparous females suggest that both individual variation in male quality and the resource value of particular females may be mediating factors. In comparison with other chimpanzee studies, our results support the hypothesis that larger male cohort size reduces the ability of the alpha male to monopolize females, though within our study, male number did not affect the success of the alpha. Successful sires were not necessarily those who achieved the highest mating success with the females whose offspring they sired, but were those who demonstrated higher investment by spending significantly more time in association with these females. Finally, we estimate extra-group paternity at 0–5%, supporting other evidence that the community serves as the primary reproductive unit in chimpanzees. Am J Phys Anthropol 142:417–428, 2010.

Male reproductive success is limited primarily by access to fertile mates (Trivers, 1972). Male–male aggressive competition is thought, therefore, to have a chief objective of increasing mating success: either directly, via access to individual copulation opportunities, or indirectly, via competition over social rank (Hausfater, 1975; Smuts, 1987). Among primates, however, there is considerable diversity in how male competition affects sexual access. In species with single-male mating systems, competitive success gives a male preferential, if not exclusive, long-term access to social and sexual partners (e.g., *Papio hamadryas*: Kummer, 1968; hylobatids: Leighton, 1987; *Leontopithecus rosalia:* Baker et al., 1993; *Gorilla gorilla* and *G. beringei*: Robbins et al., 2004). In multimale species, males with high-dominance rank typically earn a greater share of copulations, though the degree of skew varies considerably (e.g., Cowlishaw and Dunbar, 1991; Hager, 2003; Kutsukake and Nunn, 2006). The priority-of-access model (Altmann, 1962) presents a basic hypothesis for how both copulations and paternities should be distributed in such species if rank is the primary determinant of mating access. The expectation is that the alpha male can monopolize access to a single sexually receptive female, but that additional males, according to their rank, gain opportunities for sexual access when multiple estrous females are present.

The priority-of-access model proves to be a strong predictor of mating success in some species and contexts and an insufficient model in others. For example, male chacma baboons (*Papio ursinus*) pursue copulations in the context of lengthy dyadic spatial associations and the priority-of-access model closely fits observed mating patterns (Bulger, 1993; Weingrill et al., 2000). Departures from the model's predictions are still found, however, because, for a variety of reasons, high-ranking males often pursue less-persistent mating strategies and may not be able to effectively thwart mating attempts by competitors. A number of studies support the tug-of-war model, which predicts that a higher number of male competitors reduces the alpha male's ability to control mating behavior (*Macaca sylvanus*: Paul et al., 1993; *P. cynocephalus:* Alberts et al., 2003; *Pan troglodytes:* Watts, 1998; Boesch et al., 2006; interspecific comparisons: Cowlishaw and Dunbar, 1991; Kutsukake and Nunn, 2006). A larger cohort can make policing of

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competitors more costly or less comprehensive and may increase the success of alternative tactics, such as surreptitious and coalitionary mating behavior (e.g., *P. cynocephalus*: Noë and Sluijter, 1990; Alberts et al., 2003; *Macaca mulatta*: Berard, 1999; *P. troglodytes:* Constable et al., 2001). Tenure and rank stability are also implicated in altering male success relative to purely rank-based predictions (*Lemur catta*: Koyama, 1988; *P. cynocephalus*: Alberts et al., 2003, 2006). In some species, female choice can have important mitigating effects on male competition for sexual access (*L. catta:* Koyama, 1988; *M. mulatta*: Chapais, 1983; *Macaca fuscata:* Huffman, 1991, 1992; Takahata et al., 1999). Finally, some studies suggest that former or future alpha males have higher success than expected for their current rank, perhaps due to inherent competitive abilities or female preferences (*Macaca mulatta*: Smith, 1981 *Mandrillus sphinx*: Wickings et al., 1993; *P. troglodytes*: Boesch and Boesch-Achermann, 2000; *Pongo abelii:* Utami et al., 2002).

A second major issue for the priority-of-access model is that, in an absence of complete monopolization, mating success may not correlate with paternity success. In particular, variation in fecundity of both male and female partners can affect the value of particular matings. In a range of species, mating investment, particularly by high-ranking males, is more intense during the most fertile period of the cycle and during cycles of higher conceptive potential (*P. cynocephalus:* Bercovitch, 1989; Alberts et al., 2006; Gesquiere et al., 2007; *Macaca fascicularis*: Engelhardt et al., 2004; *Semnopithecus entellus*: Ostner et al., 2006; *Papio hamadryas anubis:* Higham et al., 2009; *P. troglodytes:* Deschner et al., 2004; Emery Thompson, 2005; Emery Thompson and Wrangham, 2008). High-ranking males may also bias mating investment toward particular females, usually older ones, who offer the highest probability of successful reproduction (*G. beringei:* Robbins, 1999; *P. troglodytes*: Tutin, 1979; Muller et al., 2006; review: Anderson, 1986). Finally, sperm competition or other postcopulatory mechanisms can affect the fertilization potential of males (Harvey and Harcourt, 1984; Small, 1988; Eberhard, 1998; Møller, 1998). It is perhaps for the above reasons that alpha males in some studies sire a greater proportion of offspring than would be expected based on their share of matings alone (*M. fascicularis:* de Ruiter et al. 1994; *Pan paniscus*: Gerloff et al., 1999).

Chimpanzees present a number of challenges for evaluating the importance of rank for male reproductive success: the existence of alternative mating tactics and complex coalitional behavior, within the context of a fission–fusion social system, violate some of the heuristic assumptions of the priority of access model. Females actively pursue a promiscuous strategy, spreading the probability of paternity over a typically large male cohort (Wrangham, 2002; Watts, 2007), but they also display varying levels of proceptivity and resistance to particular males (Stumpf and Boesch, 2005, 2006; Pieta, 2008). The fission–fusion social system, characterized by temporary associations of varying sizes, makes it difficult for males to continuously monitor the reproductive condition and mating behavior of females. Females usually cycle multiple times before conception and the period of sexual receptivity, marked by sexual swelling, extends for an average of 10–12 days (Wallis, 1997; O'Hara, 2005; Emery Thompson, 2005). Thus, complete monopolization of matings with a female is not feasible. Two or three males can form coalitions to guard females and share mating access, but even these efforts are not always successful (Watts, 1998). A male may instead attempt the high-risk strategy of luring a female away from other group members to retain exclusive sexual access ("consortship") for days or even weeks (Tutin, 1979; Goodall, 1986). Males may also use coercive aggression as a strategy to constrain female promiscuous behavior (Muller et al., 2007). However, social bonds among the males in a community seem to promote a degree of mating tolerance (Goodall, 1986), perhaps as a currency to garner agonistic support (Duffy et al., 2007). In fact, most mating contexts involve opportunistic copulations by multiple males (Hasegawa and Hiraiwa-Hasegawa, 1983; Goodall, 1986; Boesch and Boesch-Achermann, 2000), and the large testes size of males further suggests that sperm competition is a likely mediator of paternity success in this species (Harvey and Harcourt, 1984; Møller, 1988). Extra-group males also sire a small proportion of offspring, despite intense efforts by community males to exclude rivals (Boesch et al., 2006).

Thus far, paternity studies provide a mixed view of dominance and reproductive success in chimpanzees. As might be expected, while alpha males in the Gombe population of East African chimpanzees (*P. t. schweinfurthii*) sire a disproportionate share of offspring, alternative mating tactics granted lower-ranking males greater success than predicted by the priority-of-access model (Constable et al., 2001; Wroblewski et al., 2009). Similarly, among chimpanzee of M-group in Mahale, two alpha males sired five of the 10 offspring tested, with remaining paternity distributed across five other males—although only two of these were low ranking (Inoue et al., 2008). At Bossou, Guinea (*P. t. verus*), however, a single adult male was apparently not able to control reproductive access, although information on overlap in female's maximal swelling periods was not given (Sugiyama et al., 1993). In contrast to these findings, a direct test of the priority of access model using data from the Taï population of chimpanzees (*P. t. verus*) found that paternity success conformed to the model's predictions with an effect of male cohort size on alpha male success (Boesch et al., 2006).

Here, we present a new dataset on paternity in wild chimpanzees (*P. t. schweinfurthii*) in the Sonso community of Budongo Forest Reserve, Uganda. In light of these recent findings from Taï (Boesch et al., 2006), we examine the distribution of paternity with respect to male rank and the predictions of the priority-of-access model. Our analysis also considers male lifetime rank, size of the adult male cohort, and differential investment in parous versus nulliparous mates as potential causes for departures from the model. We additionally examine whether paternity success reflects relative mating investment, as reflected in copulation frequency and spatial association during conception periods.

METHODS

Study site and behavioral observations

We studied the Sonso community of chimpanzees in the Budongo Forest Reserve, 428 km^2 of moist semideciduous tropical forest in western Uganda (Eggeling, 1947). The Budongo Forest Project (BFP; now Budongo Conservation Field Station) has conducted ongoing observations of the Sonso community since 1990 (Reynolds, 2005). Behavioral observations for this study were conducted between 1994 and 2004, after identification and habituation of most study subjects and standardization of observation techniques. A mix of full (nest-to-nest) and partial-day follows of individuals and parties have been used throughout this period, totally at least 600–1300 hrs per year. Data were recorded collaboratively by observation parties typically consisting of two to three observers, drawn from two to four Ugandan field assistants and one to four students or senior scientists. Chimpanzees were located either at a known nest site, at fruiting trees or by following vocalizations or other signs. Party composition and female swelling stage (on a 0–4 scale) were recorded on first identification of each chimpanzee party, with subsequent changes in party membership and all sexual behaviors recorded *ad libitum*. Individual chimpanzees vary in their ranging habits and gregariousness (e.g., Pepper et al., 1999; Wrangham, 2000; Williams et al., 2002; Emery Thompson et al., 2007), and chimpanzee studies typically show a tendency for observation bias toward larger, noisier groups, and more centrally ranging individuals. This bias complements the purpose of this study, however, as female with maximal sexual swellings, and particularly those in conceptions cycles, typically associate with large numbers of males (e.g., Newton-Fisher, 2000; Emery Thompson and Wrangham, 2006, 2008). Male–female pairs forming exclusive consortships are difficult to locate, however, and so we lack data on any mating behavior that would have occurred in these contexts (although consortships do occur at Sonso: Newton-Fisher, personal observations; O'Hara, 2005; Reynolds, 2005).

Between 1994 and 2004, the Sonso community varied in size between 48 and 66 individuals (12–17 adult and adolescent males, 15–23 adult and subadult females, and 16–31 immature individuals). Ages of all community members were estimated using the appearance of the individual when first identified, together with the timing of subsequent developmental stages, changes in body size, behavioral characteristics, and signs of aging (particularly graying hair in males). Male chimpanzees were considered adolescents at the age of 10, based on morphological and social development, and this in combination with a report of a siring by a Taï chimpanzee at the estimated age of 10 years (Boesch et al., 2006) led us to test all males 9 years and older as potential sires.

Genotyping and paternity

Fresh fecal samples weighing ~5 g were collected in the field from chimpanzees of known identity and stored either in tubes containing silica gel desiccant, RNAlater (Ambion) solution, or ethanol and, subsequently, silica as previously described (Nsubuga et al., 2004). Extraction of DNA using the QIAamp DNA Stool kit (Qiagen) using either ~100 mg of dried feces or 2 mL of feces-RNAlater solution followed manufacturer's instructions. Quantitative PCR was performed on extracts as described by Morin et al. (2001) to estimate concentrations of amplifiable nuclear DNA. Extracts were genotyped at a total of nine microsatellite loci originally identified in humans following methods previously used in studies of chimpanzees (Bradley et al., 2000; Vigilant et al., 2001). To avoid mistyping caused by allelic dropout, contamination, or errors, all heterozygous genotypes were considered final only when each allele had been observed from a minimum of two independent PCRs. Homozygous genotypes were confirmed by replicating results according to the "multiple tubes" guidelines established previously (Morin et al., 2001). As samples might be misidentified, either in the field or subsequently, we required that the genotypes from known mother-offspring pairs be compatible with the allele-sharing pattern expected from normal Mendelian inheritance, and, in the case of any mismatches, we analyzed additional independently collected samples. For males or individuals without known relatives in the group, we required that genotypes from two independently collected samples agree.

Paternity assignment. Two candidate males (CH and MO) could not be genotyped due to a lack of sample material. CH was a low-ranking adult male who disappeared (presumed dead) in 1997, whereas MO was an adult, of unknown rank, who disappeared in early 1994. Paternity analysis was carried out for group members born between 1982 and 2002. As additional unknown males might have been present during that period, particularly in the 1980s–early 1990s, when using the CERVUS program for paternity assignment (see below) we conservatively used 90% as the proportion of males sampled.

Two complementary approaches were used to assign fathers to offspring. In the first, assignment by exclusion, the genotypes of offspring were first compared with those of their mothers (when available) to determine the alleles that must have been contributed by the fathers. The genotype of each candidate father was then examined to see whether he could have contributed the paternal alleles, or if he was excluded by one or more mismatches. We used the program CERVUS (Marshall et al., 1998) as a second method of paternity assessment. This program considers the frequencies of the alleles in the population when determining the male with the highest combined likelihood of providing the paternal alleles. However, because this program always indicates a best father from the candidates available for each offspring, some assignments may involve mismatches between a putative father and offspring. We combined the information from each paternity assessment approach so that for each offspring, the assigned father had both no mismatches to the offspring and had the highest paternity likelihood according to CERVUS analyses.

For each assignment, the paternity exclusion probability was calculated using allele frequencies from the entire population as is appropriate for a study including multiple generations and both unrelated and related individuals (Vigilant et al., 2001). This calculation provided a statistical measure of confidence in the assignment based upon the chance that a randomly chosen male from the population would be excluded as the father.

Behavioral data

The dominance rank of potential sires was determined using the frequencies and directionality of male aggression and "pant-grunt" vocalizations (data on frequencies of these interactions and the linearity of the hierarchy is reported elsewhere: Newton-Fisher, 2004, 2006; Emery Thompson et al., in preparation). Ranks were initially assessed for 1994–1995, the earliest period for which detailed interaction data were available (Newton-Fisher, 1997, 2004). Long-term BFP records (data collected under the direction of V. Reynolds) and the reports of research projects conducted since 1995 were inspected to determine changes in male rank from the 1994–1995 values (Fawcett, 2000; Arnold, 2001; Oliver, 2002; Notman, 2003; O'Hara, 2005; Newton-Fisher, unpublished data). These sources revealed small changes in the hierarchy, due primarily to the disappearance or known death of some individuals and the maturing of others. Small shifts near the top of the hierarchy were identified by the change in directionality of pant-grunt vocalizations. All ranks are ordinal and follow convention in assigning a rank of one to the alpha male.

Conception dates were determined from observed or estimated birth dates for all individuals born in 1993 or later. Birth dates were taken from BFP long-term records as determined by the date of first infant observation, size of the infant, and last date the mother was observed without an infant. These criteria provided a range encompassing all possible birth dates. We then calculated a probable conception window based on the average chimpanzee gestation period of 230 days (Yerkes and Elder, 1937; Yerkes, 1943; Martin et al., 1978; Shimizu et al., 2003). Periods of maximal sexual swelling [as defined by Dahl (1991)] nearest to or within the "conception window" dates were identified in the long-term records, and conception was assigned to the most recent of these periods. The maximal swelling period is the time during which the vast majority of chimpanzee copulations occur (Hasegawa and Hiraiwa-Hasegawa, 1983; Goodall, 1986), and endocrine data from wild individuals define conceptive windows almost exclusively within the maximal swelling period (Deschner et al., 2003; Emery Thompson, 2005). In a test of this method, we found that it consistently identified the correct conception cycles for the recent pregnancies for which endocrine analysis and pregnancy testing could provide independent verification of conception [as in Emery Thompson (2005); n.b. genetic data not yet available for these recent pregnancies].

Rank of sires. Paternal rank was determined for each conception. We tested two general predictions of the priority-of-access model: (1) that there should be a strong positive correlation between rank and number of offspring sired and (2) that there should be a negative correlation between the rank of sires and the number of females simultaneously showing maximal swellings, illustrating increased access for lower-ranking sires when the alpha male cannot monopolize all reproductive opportunities. We determined the number of females whose maximal swelling condition overlapped with that of the conceiving female, though we note that females' maximal swelling periods rarely overlapped completely.

In addition, we compared the observed distribution of paternities by rank to the expected distribution specifically generated from the priority-of-access model. We calculated expected values following Boesch et al. (2006). The number of maximally swollen females during each conception window determined the number of male competitors who were assigned a probability of expected paternity. This was assigned in strict rank order, but divided equally across qualifying males. Thus, when three females were maximally swollen, males of alpha, beta, and gamma ranks (1, 2, and 3 in the ordinal ranking) were each assigned an expected probability of paternity of 0.33; all other males were assigned a probability of 0.00. With only two receptive females, the alpha and beta males were each assigned a probability of 0.50, the gamma and lower ranked males receiving 0.00 (Boesch et al. 2006). These probabilities were summed across all conceptions for which we had paternity data to generate expected share of paternities according to rank. Following previous suggestions that alpha males are less effective at controlling reproductive access when they have more competitors (Boesch et al., 2006; Kutsukake and Nunn, 2006), we examined the correlation between competitor number and rank of sire.

It was possible to assign highest lifetime rank to all sires in the study, as they have subsequently died. Those who did not reach alpha status were either too young to have held higher rank prior to the study period, or, in the case of two beta males, were observed to move up the hierarchy to that rank, making it unlikely that they previously held the alpha rank. Thus, in addition to our consideration of current rank, we examined whether paternity success was related to the achievement of high rank during the male's lifetime.

Paternity, rank, and infant birth order. In chimpanzees, males show reduced sexual attraction to nulliparous females, which may be because these females experience many nonconceptive cycles (Tutin, 1979; O'Hara, 2005; Muller et al., 2006). Studies at Mahale also indicate that the use of possessive mating strategy is primarily restricted to parous females (Takasaki, 1985), suggesting that parity may affect the applicability of the priority-of-access model. To investigate whether the relationship between male rank and paternity was mediated by parity, we examined whether the paternity distribution differed for the offspring of primiparous versus multiparous mothers and recalculated the expected paternity distribution based on the conception periods and maximal swelling overlap of parous females only.

Relation of paternity to mating success and strategy. Tutin (1979) found that the amount of time individual chimpanzee males spent with maximally swollen females was correlated with their use of possessive mating tactics. Thus, we examined rates of association between males and maximally swollen females, where association is defined as membership of the same party [see Newton-Fisher (1999)], as a proxy for mating investment and probable mate-guarding effort. We determined the amount of time each male spent in association with the female during her conceptive sexual swelling phase as a percentage of the time she was observed during this phase. We had behavioral measures of association for 10 conceptions, and we used a Wilcoxon matched-pairs signed-rank test to compare, across conceptions, the association rate of the sire with the average association rate of other males during the conception window.

To determine whether copulation frequency was related to paternity, we totaled, for each female, the number of copulations with each adult or adolescent male during maximal swelling tumescence of her conception cycle. In the figures, this is standardized for the hours of observation of each female. We additionally determined the dyadic copulation rate, which was calculated by dividing the number of copulations by the number of hours that the target male spent in association with the female. Some chimpanzee females continue to display a maximal sexual swelling long after conception occurs (Wallis, 1982; Wallis and Goodall, 1993); in cases where the sexual swelling lasted longer than 2 weeks, copulation rates were calculated only until the last day of swelling on which a copulation was observed. We had copulation data for the conception periods of eight infants. The Wilcoxon matched-pairs test was used to compare the copulation rate of each sire with the average copulation rate of other males for the same conception window.

RESULTS

Genotyping and paternity assignment

A total of 52 individuals were successfully genotyped at up to nine microsatellite loci. One individual was genotyped at six loci, two at seven loci, and four at eight loci, so that the overall dataset was 97.6% complete.

Sires were assigned to 21 of the 24 offspring analyzed (Table 1). In the three unassigned cases, all tested males were excluded by two or more mismatches. In all but two assigned cases, the assigned male was the only tested individual without two or more mismatches to the offspring. For each of those two offspring (ZG and RE), CERVUS supported assignment of the paternities to one of two nonexcluded males with high (95%) confidence, and the other nonexcluded males each turned out to be paternal half-siblings of the two offspring in question. CERVUS confidence levels were 95% for all assignments but one (HW), which was supported at the "relaxed" level of 80%. The reduced confidence level in that case was due to the high-likelihood score assigned to the second-best candidate male (MA), despite the mismatches between the genotypes of MA and HW. The paternity exclusion probabilities were >0.99 for the 17 assigned offspring for which a mother's genotype was available. For the other four assigned offspring, paternal alleles could not be specified and so the paternity exclusion probabilities ranged from 0.91 to 0.98.

Extra-group paternity. Extra-group paternity did not appear to be a frequent occurrence at Sonso during the sampled period. Although paternity could not be assigned for three individuals, these were offspring from the early to mid-90s for which all possible Sonso fathers could not be tested and excluded. However, in one case (ZL), only one candidate sire was missing from the analysis. Although observed in Sonso parties from 1992 to the present, the mother of this infant is one of the least frequently encountered residents at Sonso, and it is therefore at least feasible that she may make contact with other groups. If this infant is the result of extra-group paternity, the rate of EGP is estimated at 4.5%.

Paternity and male social rank

Age and rank of sires. Seven males were collectively responsible for fathering 21 infants. With one possible exception, adolescents failed to father offspring: our independent age estimates of sire and offspring suggest that NJ may have fathered ZF at an age of 14. However, this birth occurred several years before the start of observations, and we assume an error of ±5 years for the age of NJ (±6 months for the age of ZF). On the other hand, old males did succeed in fathering offspring. In 2001, MA, clearly the eldest male in the group, fathered an offspring at an estimated age of 43 years (±5 years). A former alpha male, MG, fathered an offspring (ZG) while estimated to be at least in his late thirties, and it is notable that he was responsible for fathering offspring over a span of at least 15 years (1982–1997).

The father's rank at conception could be determined for 13 of the 14 offspring conceived from 1994 onward (the exception is ZL, whose sire could not be assigned). The alpha male sired four of these 13 infants (31%), while two were sired by a beta-ranked male (15%). Detailed dominance hierarchies were not available before 1994, although the male (MG) who was deposed from alpha rank in that year was the most successful sire (40%) in the earlier portion of our dataset (the 10 offspring conceived before 1994).

Due to the success of the alpha male, there was a significant relationship between higher dominance rank and the number of offspring sired between 1994 and 2002 ($r_s = 0.68$, $n = 12$ ranks, and $P = 0.02$; excluding alpha: $r_s = 0.57$, $n = 11$ ranks, and $P = 0.07$), but low-ranking males were successful at siring offspring (see Fig. 1).

Excluding one female who was not observed during her probable conception window, all female conception periods examined from 1994 to 2002 overlapped with the maximal swelling periods of at least two other females, raising the possibility that the spread in paternity was achieved under conditions when priority-of-access opened to a wider range of males. However, in contrast to the general prediction of the priority-of-access model, sire's rank at conception was not correlated with the number of maximally swollen females at that time ($r_s = 0.15$, $n = 12$, $P = 0.64$; number of max. swollen females: median = 4; range = 3–6; Fig. 2). Conceptions by the alpha male occurred at both the minimum number (three) and the maximum number (six) of overlapping maximally swollen females. Sire's rank was also unrelated to the number of male competitors ($r_s = -0.06$, $n = 13$, $P = 0.84$; number of competitors: median = 12; range = 8–14; Fig. 2).

We compared these results to the predictions of the priority-of-access model (see Fig. 3). Given the considerable overlap between females' maximal swelling periods, the alpha male's success at siring offspring was approximately as predicted by the model. However, other high-ranking males (beta, gamma) did less well than predicted (31 vs. 53%) and low-ranking males that were not predicted to gain any fertilization opportunities (ranks 7+) actually sired 3 of the 13 offspring (23%).

Paternity and maximum lifetime rank. We could determine highest achieved lifetime rank for all seven known fathers of the 21 offspring we genotyped, as all sires have subsequently died. The male who most recently held the alpha rank (DN) sired five offspring, including one conceived ~5 years before he reached that rank. A previous alpha male (MG) also sired five offspring, including one conceived ~2 years after he was deposed. Two males that reached beta rank (BK, MA) sired five total offspring. Thus, at least 71% of paternities were achieved by males who at one time held alpha or beta rank.

Nevertheless, some males with high current or lifetime rank appeared to have had relatively poor reproductive success. One male (VN) held alpha rank for <1 year and beta rank for 4 years but sired none of the offspring for which we have genetic data; the subsequent beta male (MA) sired only one of these offspring. In a previous report, VN had the lowest copulation rate of any adult male at Sonso (Newton-Fisher, 2004). Similarly, MA had lower copulation rates than expected for his rank (Emery Thompson, unpublished data). It is difficult to determine whether these males truly had lifetime reproductive success as low as suggested by this sample, because not all Sonso offspring have been genotyped and these males were old enough to have reproductive careers before the

TABLE 1. Paternity assignments of individuals in the Sonso community

YoB	ID	Sex	Mother	Pex	MG	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK	BB	GS	BO	MS
					born < 1958	*born* 1958	*born* 1960	*born* 1961	*born* 1965	*born* 1966	*born* 1968	*born* 1974	*born* 1976	*born* 1977	*born* 1978	*born* 1980	*born* 1982	*born* 1982	*born* 1982	*born* 1987	*born* 1987	*born* 1990	*born* 1991
1982	**ZF**	M	BN	0.9985	MG	MA	TK	VN	BY	DN	**$^{?}$NJ^{14}**												
1982	**NK**	M	RH	0.9984	**$^{?}$MG^{24}**	MA	TK	VN	BY	DN	NJ												
1987	**GS**	M	*	0.9497	MG	MA	TK	VN	BY	DN	**$^{?}$NJ^{19}**	BK	KK	MU	JM								
1987	**BB**	M	*	0.9646	**$^{?}$MG^{29}**	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM								
1990	**GZ**	F	ZM	0.9990	**$^{?}$MG^{32}**	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT							
1990	**SH**	F	BN	0.9990	MG	MA	TK	VN	BY	**$^{?}$DN^{24}**	NJ	BK	KK	MU	JM	ZT							
1990	BO	M	RD		MG	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT							
1991	**MS**	M	NB	0.9964	**$^{?}$MG^{33}**	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK				
1993	KT	M	KU		MG	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK				
1993	**HW**	M	(HT)	0.9775	MG	MA	TK	VN	BY	DN	NJ	BK	**$^{?}$KK^{17}**	MU	JM	ZT	ZF	AY	NK				
1994	**BH**	F	KL	0.9994	MG	MA	TK	VN	BY	DN	NJ	**^{4}BK^{20}**	KK	MU	JM	ZT	ZF	AY	NK				
1995	ZL	M	ZA		MG	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK				
1995	**KZ**	M	KW	0.9997	MG	MA	TK	VN	BY	DN	NJ	BK	KK	**^{12}MU^{17}**	JM	ZT	ZF	AY	NK				
1996	**NR**	F	NB	0.9962	MG	MA	TK	VN	BY	DN	NJ	**^{3}BK^{21}**	KK	MU	JM	ZT	ZF	AY	NK				
1997	**ZG**	M	ZM	0.9990	**^{5}MG^{38}**	MA	TK	VN	BY	DN	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK	BB	GS		
1997	**RE**	F	RD	0.9980	MG	MA	TK	VN	BY	DN	**^{10}NJ^{28}**	BK	KK	MU	JM	ZT	ZF	AY	NK	BB	GS		
1997	**RS**	F	RH	0.9988	MG	MA	TK	VN	BY	**^{1}DN^{31}**	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK	BB	GS		
1998	**KN**	F	KU	0.9987	MG	MA	TK	VN	BY	DN	NJ	**^{3}BK^{24}**	KK	MU	JM	ZT	ZF	AY	NK	BB	GS		
1998	**KE**	F	KG	0.9991	MG	MA	TK	VN	BY	**^{1}DN^{32}**	NJ	BK	KK	MU	JM	ZT	ZF	AY	NK	BB	GS		
1998	**KA**	F	KY	0.9997	MG	MA	TK	VN	BY	DN	NJ	BK	**^{7}KK^{22}**	MU	JM	ZT	ZF	AY	NK	BB	GS		
1999	**JT**	F	(JN)	0.9058	MG	MA	TK	VN	BY	**^{1}DN^{33}**	NJ	BK		MU	JM		ZF	AY	NK	BB	GS	BO	
2000	**KM**	F	KL	0.9993		MA	TK		BY	**^{1}DN^{34}**	NJ	BK		MU	JM		ZF	AY	NK	BB	GS	BO	
2001	**KR**	F	KW	0.9969		**^{2}MA^{43}**	TK		BY	DN	NJ	BK			JM		ZF		NK	BB	GS	BO	MS
2002	**CT**	M	CL	0.9992		MA	TK		BY	DN	NJ	**^{2}BK^{28}**			JM		ZF		NK	BB	GS	BO	MS

Each horizontal line contains the offspring's year of birth (YoB), name, mother, the paternity exclusion probability for the assigned father (Pex), and all candidate sires with the assigned father indicated by shading and bold text. Sire's rank and age at offspring conception are indicated by the prefixed and suffixed superscripts. Tenure for alpha and beta males is highlighted by the solid (alpha) and dashed (beta) outlines. Rank data are not available before 1994. Offspring names in bold indicate individuals with assigned fathers. Two male candidates (CH: born ca. 1967, died 1997; MO: born ca. 1970, died 1994) did not have samples for paternity analysis.

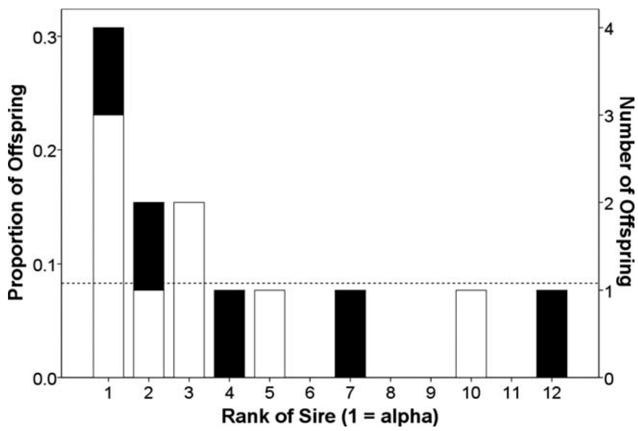

Fig. 1. Proportion of offspring sired as a function of male rank and female parity in Sonso chimpanzees. Black bars = females' first-born offspring, white bars = females' second or subsequent offspring.

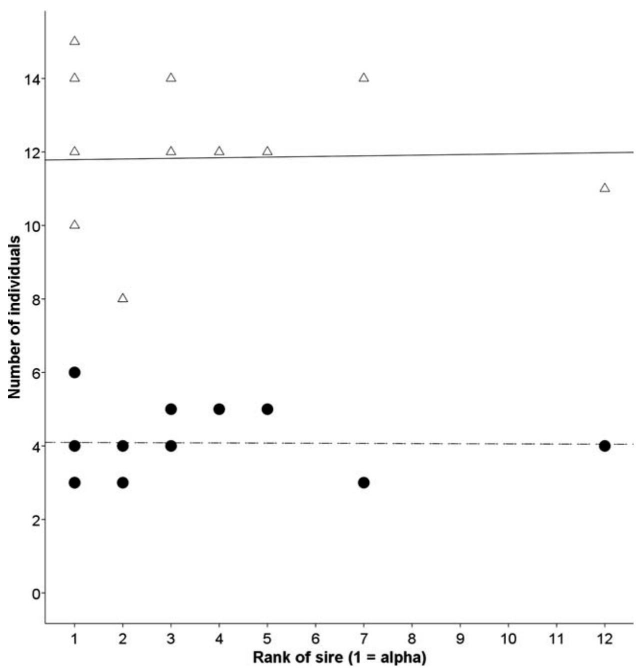

Fig. 2. Plot of sire's rank at conception against number of maximally swollen females (circles) and adult male competitors (triangles).

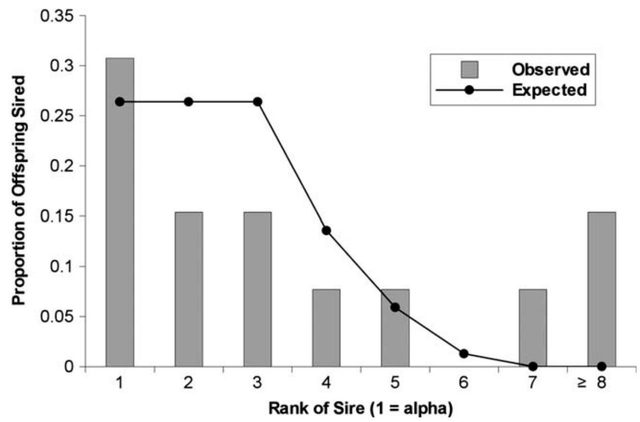

Fig. 3. Plot of predicted proportion of paternity achieved from the priority-of-access model against observed male success for the Budongo (Sonso) community. Males ranked eight or lower are grouped together based on an expectation of no paternity. Gray bars, observed distribution; solid circles, expected distribution. Expected values are calculated as detailed in the Methods section: Rank of Sires, and follow Boesch et al. (2006).

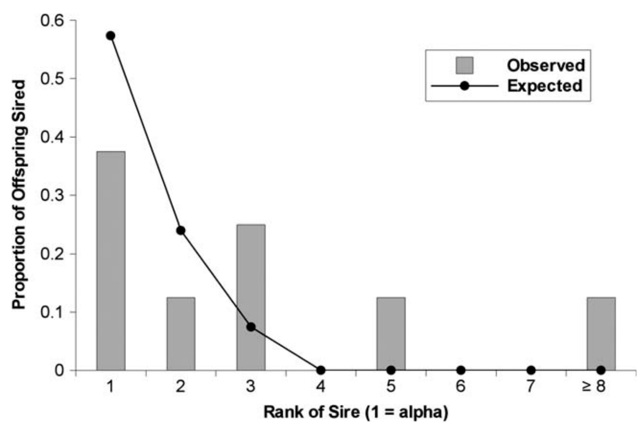

Fig. 4. Comparison of the observed paternity distribution in relation to the priority-of-access model if only births to multiparous mothers, and the number of simultaneously receptive parous females, are considered. Gray bars, observed distribution; solid circles, expected distribution. Expected values are calculated as detailed in the Methods section: Rank of Sires and follow Boesch et al. (2006).

onset of study at Sonso. It is interesting, however, that during the period 1995–2002, when VN and MA successively held beta rank and the majority (59%) of all offspring were genotyped, only one offspring could be assigned to the beta male.

Paternity, rank, and infant birth order. Of the 13 offspring sired by a Sonso male between 1994 and 2002, five were first births for the mother. Only two (25%) of these were sired by high-ranking males, one by the alpha male and one by a beta male (mean ± S.E. rank of sire = 5.2 ± 2.0). In contrast, of the eight offspring born to parous females, six (75%) were fathered by high-ranking males, including three by the alpha male and one by a beta male (mean rank = 3.3 ± 1.1, Fig. 1). This trend suggests that high-ranking males may focus greater mating investment in parous females, allowing lower-ranking males to gain reproductive opportunities with nulliparous females. However, at this sample size, the distribution of paternities with respect to male rank (alpha, beta, and gamma vs. other) and female parity (primiparous vs. multiparous) was not statistically distinguishable from chance (Fisher's exact test, $P = 0.29$). Controlling for parity did not improve the applicability of the priority-of-access model. When we considered only multiparous mothers and overlapping parous maximally swollen females in a modified priority-of-access model, alpha and beta males were less successful, and mid- and low-ranking males more successful than expected (see Fig. 4).

Behavior and conception success. Relative mating success was not a strong predictor of which male sired the offspring. Sires did not copulate at higher rates with conceiving females, per hour of time spent together dur-

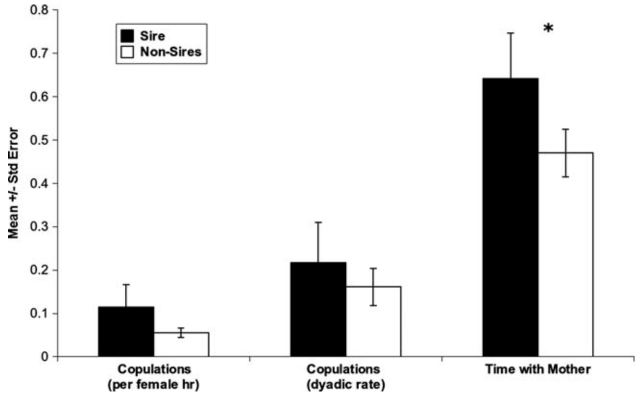

Fig. 5. Association with maximally swollen females, but not copulation rates, predicted conception success in Sonso chimpanzees: comparison of copulation rates and time spent with mother (% of females' total observation time during conception maximal swelling phase) by sires (black bars) and non-sire (white bars) adult males.

ing the conception period, than did other males (dyadic copulation rate: Wilcoxon matched-pairs test: $z = -0.56$, $N1 = N2 = 8$, $P = 0.58$ vs. nonsire adult males; $z = -0.70$, $P = 0.48$ vs. nonsire adults and adolescents). However, sires did spend significantly more time in the same party with mothers during their conception periods than did the other males ($z = -2.31$, $N1 = N2 = 9$, $P = 0.02$ vs. adult males; $z = -2.07$, $P = 0.04$ vs. adults and adolescents, Fig. 5); in those cases, when the alpha male succeeded in siring offspring, his rates of association with conceptive females were particularly high (see Fig. 6) although subsamples were too small to test for significant differences in strategy between alpha and non-alpha males.

If sires did not copulate at higher rates per hour of association, they may have spent more time in association as a means to gain absolutely more copulations than other males. However, we did not find that sires copulated more frequently than nonsires overall (Wilcoxon matched-pairs test: $z = -1.18$, $N1 = N2 = 8$, $P = 0.24$ vs. adult males, $z = -1.40$, $P = 0.16$ vs. adults and adolescents, Fig. 5). In only two of eight cases did the male who was observed to copulate the most sire the infant; this is unremarkable because in both cases this was the alpha male, who copulated significantly more than other males generally ($z = -1.96$, $N1 = N2 = 8$, $P = 0.05$, vs. adult males; $z = -2.10$, $P = 0.04$ vs. adults and adolescents, Fig. 6).

In three cases, females were not observed with maximal swellings during their probable conception windows, suggesting the possibility that conceptions occurred in the context of exclusive consortships. However, we were not able to definitively assign any fertilization to the consortship context, because female absence coincided with low-observation frequencies for males other than the sire or because the female's own observation rate was very low, even during the probable conception period.

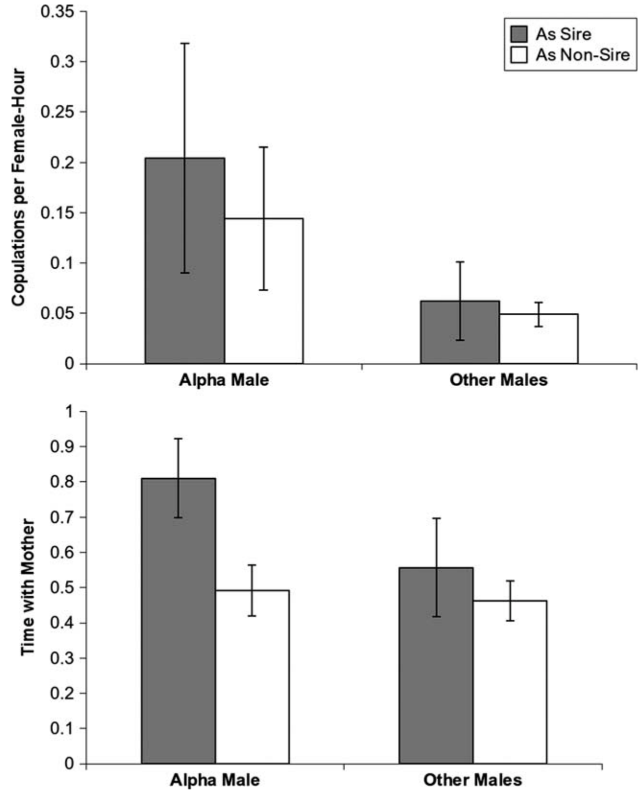

Fig. 6. Comparison of alpha and non-alpha male behavior when they were successful sires (gray bars) or non-sires (white bars).

DISCUSSION

Dominance rank is expected be crucial to male reproductive success among wild chimpanzees given the frequency of dominance interactions and the influence of relative rank on priority of mating access to females (Nishida, 1997; Muller, 2002; Newton-Fisher, 2004). Our results from the Sonso chimpanzees of the Budongo Forest indicate that dominance rank confers a significant reproductive advantage for males, but that the distribution of paternity does not conform readily to the expectations of the priority-of-access model. It is likely that the mating context of chimpanzees is more complex and varied than the assumptions of this model allow.

In our sample, alpha males fathered the largest share of infants. Studies at Gombe suggest that alpha males were the only males successful in implementing the possessive mating strategies assumed by the priority-of-access model (Tutin, 1979; Constable et al., 2001). In accordance with that observation, the alpha male's share of paternity in our study was close to that predicted from the model, whereas the remaining paternities were distributed much more widely than expected. The rank distribution of paternity in Sonso chimpanzees was similar to that found at Gombe (Constable et al., 2001; Wroblewski et al., 2009), but unlike that at Taï, where the priority-of-access model had high predictive value (Boesch et al., 2006). Our data also failed to support the more specific prediction that the rank of the sire should be related to the number of maximally swollen females available during that particular conception period. In addition, three offspring in our study were sired by males whose rank should never have granted them reproductive access under the queuing conditions assumed by the model. More complex models are needed to describe the acquisition of paternity in this species, particularly to explain paternity outcomes among males other than the alpha.

In interspecific comparisons of multimale mating, the number of male competitors exerts a significant impact on the degree of reproductive skew (Kutsukake and Nunn, 2006). Despite this, we did not find a relationship between the number of competitors at the time of conception and the rank of the sire. Our group was relatively stable in size, however, so it is possible that this may be an important effect across larger scales of variation, like that seen between chimpanzee communities. There is general conformity to this prediction: with the largest number of potential sires (12–17 males aged 10 and older), the Sonso alpha males had slightly lower success (31% of offspring sired) than Gombe alpha males (36%) with slightly fewer competitors (10–14 potential sires, Constable et al., 2001). Taï alpha males had only marginally better success (38%) under conditions with five to nine males and considerably higher success (67%) under conditions with only two to three males (Boesch et al., 2006). More studies under a broader range of demographic conditions would allow for a better test of this effect and rule out the influence of particularly successful or unsuccessful individuals.

We were able to assign paternities to 21 offspring born over a period of 21 years. It was therefore surprising that only seven males out of more than 19 potential sires fathered these offspring. In particular, it was notable that alpha males were successful at siring offspring both before and after holding high rank, which accords with reports from other studies of chimpanzee (Constable et al., 2001; Vigilant et al., 2001; Wroblewski et al., 2009). In contrast, some males that rose to very high rank had little or no evidence of paternity success despite being potential sires to most offspring in the dataset. It is feasible, therefore, that in addition to the influences of current rank, individual male success may be related to long-term factors such as variation in sperm quantity and quality (Møller, 1988; Anderson and Dixson, 2002; Snook, 2005), female-preferred traits (Small, 1993), aptitude at alliance formation (Duffy et al., 2007), or the ability to successfully implement mating tactics with females of high fecundity (Emery Thompson and Wrangham, 2008); some of these traits may correlate with male competitive success.

On average, the sires of first-born infants in our study were lower-ranking than those of later-born infants. Although a larger dataset is needed to confirm that this distribution differs from chance, this trend conforms to observations that male-mating investment is relatively more intense and more restrictive with older females (Tutin, 1979; Takasaki, 1985; Wrangham, 2002; Muller et al., 2006), who have prior maternal experience, are higher-ranking (Nishida, 1989; Pusey et al., 1997; Wittig and Boesch, 2003; Kahlenberg et al., 2008a,b), and experience fewer cycles to conception (Wallis, 1997; Deschner and Boesch, 2007). If male-mating effort is stratified in relation to female quality, male chimpanzees may experience "tiered" competition, wherein multiple high-ranking males compete for access to the most desirable female(s), leaving lower-ranking males increased opportunities for fertile mating with less desirable females. This would represent a critical violation of the main assumption of the priority-of-access model, which may then be restricted to the competition between high-ranking males; findings from Gombe (Constable et al., 2001; Wroblewski et al., 2009) suggest low-ranking males can achieve paternity through nonpossessive strategies such as consortship.

How did males achieve paternity at Sonso? We first examined the influence of mating frequency, as rank is often correlated with copulation frequency chimpanzee populations (Matsumoto-Oda, 1999; Duffy et al., 2007). We found no significant difference in either the absolute frequency or the rate (per hour of association) with which sires and nonsires were observed to copulate with mother during their conception window. Only alpha-male sires achieved paternity by securing the largest share of copulations. A number of studies of primates and other mammals also report that mating success is not necessarily a good predictor of paternity outcomes (e.g., *Cervus elephus:* Pemberton et al., 1992; *Helichoerus gryphus:* Amos et al., 1993; *Macaca fuscata*: Inoue et al., 1993; *M. sylvanus*: Paul et al., 1993; *M. fascicularis*: de Ruiter et al., 1994).

We found instead that sires spent significantly more time in association with the mothers during the maximal swelling period of their conception cycles than did nonsires. Prior findings in chimpanzees indicate that increased association is correlated with the use of possessive mating tactics (Tutin, 1979). This fits with our finding of particularly high rates of association between the alpha male and females whose offspring he successfully sired. Close association with maximally swollen females could have a number of other potential advantages, which are not possible to distinguish in the scope of this study. Males in close association may have better access to information about timing of ovulation [as suggested by Emery Thompson and Wrangham (2008)], find opportunities to copulate covertly, engage in social investment [e.g., grooming (Tutin, 1975)] to increase female cooperation in mating, gain her tolerance through persistence, or exert coercive control over her mating behavior via aggression or intimidation (Muller et al., 2007).

Finally, our data do not support a prominent role for extra-group paternity in Sonso chimpanzees. This is consistent with the absence of extra-group mating observations in this population and with the low rates of confirmed EGP at other chimpanzee sites. There is no genetic evidence for EGP at Gombe, even though low rates of female transfer increase the risk of inbreeding when mating within the community (Constable et al., 2001; Wroblewski et al., 2009). At Taï, EGPs accounted for 7.1 and 10.5% of conceptions (Vigilant et al., 2001; Boesch et al., 2006). Female chimpanzees may have little to gain and much to risk by seeking extra-group copulations. Male territorial behavior influences this in two ways: first, community males can aggressively exclude rival males from access to females within the territory, particularly when they have a numerical advantage (Watts and Mitani, 2001; Wilson et al., 2001), which, in turn, may increase females' search costs; second, females, particularly those with dependent infants, may risk injury or infanticide from aggressive males when entering another territory to seek extra-group mating (Goodall, 1986; Wilson and Wrangham, 2003; but see Emery Thompson et al., 2006; Boesch et al., 2008). Our genetic findings support the general expectation that the community functions as the reproductive unit in chimpanzees, indicating that cooperative territoriality functions at least in part as an effective reproductive strategy for male chimpanzees. Furthermore, our data indicate that, while reproduction is skewed towards high-ranking individuals, lower-ranking males have realistic opportunities for direct reproductive benefits that may promote their participation in territorial behavior [as suggested by Watts and Mitani (2001)].

In conclusion, our results are consistent with other genetic studies in chimpanzees and in multimale groups of primates more generally, in demonstrating a significant influence of rank on the reproductive success of males. Our results suggest that alpha rank, in particular, may function to increase paternity success via priority-of-access to fertile females (Altmann, 1962), but that the priority-of-access model is not adequate to explain the distribution of paternities across males, with neither the number of maximally swollen females (Altmann, 1962) nor the number of male competitors (Cowlishaw and Dunbar, 1991; Kutsukake and Nunn, 2006) a significant predictor of the sire's rank. Our data lend initial credence to the role of individualistic male traits, as well as variation in the mate quality of particular females, as mediating factors in the relationship of rank to reproductive success and suggest that high-investment mating strategies may produce the highest fitness rewards.

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LITERATURE CITED

Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Anim Behav 72:1177–1196.

Alberts SC, Watts HE, Altmann J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. Anim Behav 65:821–840.

Altmann SA. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Ann NY Acad Sci 102:338–435.

Anderson CM. 1986. Female age: male preference and reproductive success in primates. Int J Primatol 7:305–325.

Anderson MJ, Dixson AF. 2002. Sperm competition: motility and the midpiece in primates. Nature 416:496.

Arnold K. 2001. Affiliation, aggression and reconciliation in male chimpanzees of the Budongo Forest, Uganda, Ph.D. dissertation, University of St. Andrews, St. Andrews.

Baker AJ, Dietz JM, Kleiman DG. 1993. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. Anim Behav 46:1091–1103.

Berard J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). Primates 40:159–175.

Bercovitch FB. 1989. Body size, sperm competition, and determinants of reproductive success in male savanna baboons. Evolution 43:1507–1521.

Boesch C, Boesch-Achermann H. 2000. The Chimpanzees of the Taï Forest: behavioural ecology and evolution. Oxford: Oxford University Press.

Boesch C, Crockford C, Herbinger I, Wittig R, Moebius Y, Normand E. 2008. Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. Am J Primatol 70:519–532.

Boesch C, Kohou G, Nene H, Vigilant L. 2006. Male competition and paternity in wild chimpanzees of the Taï Forest. Am J Phys Anthropol 130:103–115.

Bradley BJ, Boesch C, Vigilant L. 2000. Identification and redesign of human microsatellite markers for genotyping wild chimpanzee (*Pan troglodytes verus*) and gorilla (*Gorilla gorilla gorilla*) DNA from faeces. Conserv Genet 1:289–292.

Bulger J. 1993. Dominance rank and access to estrous females in male savanna baboons. Behaviour 127:67–103.

Chapais B. 1983. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. Behav Ecol Sociobiol 12:215–228.

Constable JL, Ashley MV, Goodall J, Pusey AE. 2001. Noninvasive paternity assignment in Gombe chimpanzees. Mol Ecol 10:1279–1300.

Cowlishaw G, Dunbar RIM. 1991. Dominance rank and mating success in male primates. Anim Behav 41:1045–1056.

Dahl JF, Nadler RD, Collins DC. 1991. Monitoring the ovarian cycles of *Pan troglodytes* and *P. paniscus*: a comparative approach. Am J Primatol 24:195–209.

de Ruiter JR, van Hooff JARAM, Scheffrahn W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). Behaviour 129:203–224.

Deschner T, Boesch C. 2007. Can the patterns of sexual swelling cycles in female Taï chimpanzees by explained by the cost-of-sexual-attractiveness hypothesis? Int J Primatol 28:389–406.

Deschner T, Heistermann M, Hodges K, Boesch C. 2003. Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes* verus. Anim Behav 66:551–560.

Deschner T, Heistermann M, Hodges K, Boesch C. 2004. Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. Horm Behav 46:204–215.

Duffy KG, Wrangham RW, Silk JB. 2007. Male chimpanzees exchange political support for mating opportunities. Curr Biol 17:586–587.

Eberhard WG. 1998. Female roles in sperm competition. In: Birkhead TR, Møller AP, editors. Sperm competition and sexual selection. New York: Academic Press. p 91–115.

Eggeling W. 1947. Observations on the ecology of the Budongo rain forest, Uganda. J Ecol 19:179–197.

Emery Thompson M. 2005. Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. Am J Primatol 67:137–158.

Emery Thompson M, Kahlenberg SM, Gilby IC, Wrangham RW. 2007. Core area quality is associated with variance in reproductive success among female chimpanzees at Kanyawara, Kibale National Park, Uganda. Anim Behav 73:501–512.

Emery Thompson M, Newton-Fisher NE, Reynolds V. 2006. Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda. Int J Primatol 27:1601–1617.

Emery Thompson M, Wrangham RW. 2006. Comparison of sex differences in gregariousness in fission-fusion species: reducing bias by standardizing for party size. In: Newton-Fisher NE, Notman H, Reynolds V, Paterson J, editors. Primates of Western Uganda. New York: Springer. p 209–226.

Emery Thompson M, Wrangham RW. 2008. Male mating interest varies with female fecundity in *Pan troglodytes* of Kanyawara, Kibale National Park. Int J Primatol 29:885–905.

Engelhardt A, Pfiefer J, Heistermann M, Niemitz C, van Hooff JA, Hodges JK. 2004. Assessment of female reproductive status by male longtailed macaques, *Macaca fascicularis*, under natural conditions. Anim Behav 67:915–924.

Fawcett K. 2000. Female relationships and food availability in a forest community of chimpanzees, Ph.D. dissertation, University of Edinburgh, Edinburgh.

Gerloff U, Hartung B, Fruth B, Hohman G, Tautz D. 1999. Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. Proc Natl Acad Sci USA 266:1189–1195.

Gesquiere LR, Wango EO, Alberts SC, Altmann J. 2007. Mechanisms of sexual selection: sexual swellings and estrogen con-

centrations as fertility indicators and cues for male consort decisions in wild baboons. Horm Behav 51:114–125.
Goodall J. 1986. The Chimpanzees of Gombe: patterns of behavior. Cambridge, MA: Belknap.
Hager R. 2003. Reproductive skew models applied to primates. In: Jones C, editor. Sexual selection and reproductive competition in primates: new perspectives and directions. Norman, OK: American Society of Primatologists. p 65–101.
Harvey N, Harcourt AH. 1984. Sperm competition, testes size, and breeding systems in primates. In: Smith R, editor. Sperm competition and the evolution of animal mating systems. New York: Academic Press. p 589–600.
Hasegawa T, Hiraiwa-Hasegawa M. 1983. Opportunistic and restrictive matings among wild chimpanzees in the Mahale Mountains, Tanzania. J Ethol 1:75–85.
Hausfater G. 1975. Dominance and reproduction in Baboons (*Papio cynocephalus*). Basel: Karger.
Higham JP, Semple S, MacLarnon A, Heistermann M, Ross C. 2009. Female reproductive signaling, and male mating behavior, in the olive baboon. Horm Behav 55:60–67.
Huffman MA. 1991. Mate selection and partner preferences in female Japanese macaques. In: Fedigan LM, Asquith PJ, editors. The monkeys of Arashiyama: thirty-five years of research in Japan and the West. New York: SUNY. p 101–122.
Huffman MA. 1992. Influences of female partner preference on potential reproductive outcome in Japanese macaques. Folia Primatol 59:77–88.
Inoue E, Inoue-Murayama M, Vigilant L, Takenaka O, Nishida T. 2008. Relatedness in wild Chimpanzees: influence of paternity, male philopatry, and demographic factors. Am J Phys Anthropol 137:256–262.
Kahlenberg SM, Emery Thompson M, Muller MN, Wrangham RW. 2008b. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Anim Behav 76:1497–1509.
Kahlenberg SM, Emery Thompson M, Wrangham RW. 2008a. Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. Int J Primatol 29:931–947.
Koyama N. 1988. Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. Primates 29:163–175.
Kummer H. 1968. Social organization of Hamadryas Baboons. Chicago: University of Chicago Press.
Kutsukake N, Nunn CL. 2006. Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. Behav Ecol Sociobiol 60:695–706.
Leighton DR. 1987. Gibbons: territoriality and monogamy. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 135–145.
Marshall T, Slate J, Kruuk L, Pemberton J. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655.
Martin D, Graham CE, Gould KG. 1978. Successful artificial insemination in the chimpanzee. Symp Zool Soc Lond 43:249–260.
Matsumoto-Oda A. 1999. Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. Behav Ecol Sociobiol 46:258–266.
Møller AP. 1988. Ejaculate quality, testes size and sperm competition in primates. J Hum Evol 17:479:488.
Møller AP. 1998. Sperm competition and sexual selection. In: Birkhead TR, Møller AP, editors. Sperm competition and sexual selection. New York: Academic Press. p 55–90.
Morin PA, Chambers K, Boesch C, Vigilant L. 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Mol Ecol 10:1835–1844.
Muller MN. 2002. Agonistic relations among Kanyawara chimpanzees. In: Boesch C, Hohmann G, Marchant LF, editors. Behavioural diversity in Chimpanzees and Bonobos. Cambridge: Cambridge University Press. p 112–124.
Muller MN, Emery Thompson M, Wrangham RW. 2006. Male chimpanzees prefer mating with old females. Curr Biol 16: 2234–2238.
Muller MN, Kahlenberg SM, Emery Thompson M, Wrangham RW. 2007. Male coercion and the costs of promiscuous mating for female chimpanzees. Proc Roy Sci Lond B 274:1009–1014.
Newton-Fisher NE. 1997. Tactical behaviour and decision making in wild chimpanzees, Ph.D. dissertation, University of Cambridge, Cambridge.
Newton-Fisher NE. 1999. Association by male chimpanzees: a social tactic? Behaviour 136:705–730.
Newton-Fisher NE. 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii*): party size in the Budongo Forest Reserve, Uganda. Int J Primatol 21:613–628.
Newton-Fisher NE. 2004. Hierarchy and social status in Budongo chimpanzees. Primates 45:81–87.
Newton-Fisher NE. 2006. Female coalitions against male aggression in wild chimpanzees of the Budongo forest. Int J Primatol 27:1589–1599.
Nishida T. 1989. Social interactions between resident and immigrant female chimpanzees. In: Heltne PG, Marquardt LA, editors. Understanding Chimpanzees. Cambridge, MA: Harvard University Press. p 68–89.
Nishida T. 1997. Sexual behavior of adult male chimpanzees of the Mahale Mountains National Park, Tanzania. Primates 4:379–398.
Noë R, Sluijter AA. 1990. Reproductive tactics of male savanna baboons. Behaviour 113:117–169.
Notman H. 2003. The meaning, structure, and function of chimpanzee pant hoots from the Budongo Forest, Uganda, Ph.D. dissertation, University of Calgary, Calgary.
Nsubuga A, Robbins MM, Roeder A, Morin PA, Boesch C, Vigilant L. 2004. Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. Mol Ecol 13:2089–2094.
O'Hara SJ. 2005. Female sexuality and male violence in wild Chimpanzees, Ph.D. dissertation, University of Cambridge, Cambridge.
Oliver L. 2002. Female mating patterns in the Budongo community of chimpanzees (*Pan troglodytes schweinfurthii*), M.Sc. thesis, Bucknell University, Lewisburg, PA.
Ostner J, Chalise MK, Koenig A, Launhardt K, Nikolei J, Podzuweit D, Borries C. 2006. What hanuman langur males know about female reproductive status. Am J Primatol 68:701–712.
Paul A, Küster J, Timme A, Amemann J. 1993. The association between rank, mating effort, and reproductive success in male barbary macaques (*Macaca sylvanus*). Primates 34:491–502.
Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20:613–632.
Pieta K. 2008. Female mate preferences among chimpanzees (*Pan troglodytes schweinfurthii*) of Kanyawara, Kibale National Park. Int J Primatol 29:845–864.
Pusey AE, Williams J, Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828–831.
Reynolds V. 2005. The Chimpanzees of Budongo Forest. Oxford: Oxford University Press.
Robbins MM. 1999. Male mating patterns in wild multimale mountain gorilla groups. Anim Behav 57:1013–1020.
Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes EJ. 2004. Social structure and life-history patterns in Western gorillas. Am J Primatol 64:145–159.
Shimizu K, Douke C, Fujita S, Matsuzawa T, Tomonaga M, Tanaka M, Matsubayashi K, Hayashi M. 2003. Urinary steroids, FSH and CG measurements for monitoring the ovarian cycle and pregnancy in the chimpanzee. J Med Primatol 32:15–22.
Small MF. 1988. Female primate sexual behavior and conception: are there really sperm to spare? Curr Anthropol 29:81–95.
Small MF. 1993. Female choices: sexual behavior of female primates. Ithaca: Cornell University Press. 245 pp.
Smith DG. 1981. The association between rank and reproductive success of male rhesus monkeys. Am J Primatol 1:83–90.

Smuts B. 1987. Sexual competition and mate choice. In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 385–399.

Snook RR. 2005. Sperm in competition: not playing by the numbers. TREE 20:46–53.

Stumpf RM, Boesch C. 2005. Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. Behav Ecol Sociobiol 57:511–524.

Stumpf RM, Boesch C. 2006. The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. Behav Ecol Sociobiol 60:749–765.

Sugiyama Y, Kawamoto S, Takenaka O, Kumazaki K, Miwa N. 1993. Paternity discrimination and intergroup relationships of chimpanzees at Bossou. Primates 34:545–552.

Takahata Y, Huffman MA, Suzuki S, Koyama N, Yamagiwa J. 1999. Why dominants do not consistently attain high mating and reproductive success: a review of longitudinal Japanese macaque studies. Primates 40:143–158.

Takasaki H. 1985. Female life history and mating patterns among the M group chimpanzees of the Mahale National Park, Tanzania. Primates 26:121–129.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man 1871–1971. Chicago: Aldine. p 136–179.

Tutin CE. 1975. Sexual behavior and mating patterns in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*), Ph.D. dissertation, University of Edinburgh, Edinburgh.

Tutin CE. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6:29–38.

Utami S, Goossens B, Bruford MW, de Ruiter JR, van Hooff JARAM. 2002. Male bimaturism and reproductive success in *Sumatran orangutans*. Behav Ecol 13:643–652.

Vigilant L, Hofreiter M, Siedel H, Boesch C. 2001. Paternity and relatedness in wild chimpanzee communities. Proc Natl Acad Sci USA 98:12890–12895.

Wallis J. 1982. Sexual behavior of captive chimpanzees (*Pan troglodytes*): pregnant versus cycling females. Am J Primatol 3:77–88.

Wallis J. 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. J Reprod Fertil 109:297–307.

Wallis J, Goodall J. 1993. Anogenital swelling in pregnant chimpanzees of Gombe National Park. Am J Primatol 31:89–98.

Watts DP. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. Behav Ecol Sociobiol 44:43–55.

Watts DP. 2007. Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. Primates 48:222–231.

Watts DP, Mitani JC. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299–327.

Weingrill T, Lycett JE, Henzi SP. 2000. Consortship and mating success in chacma baboons (*Papio cynocephalus ursinus*). Ethology 106:1033–1044.

Wickings E, Bossi T, Dixson AF. 1993. Reproductive success in the mandrill, Mandrillus sphinx: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. J Zool (Lond) 231:563–574.

Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J. 2002. Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Anim Behav 63:347–360.

Wilson ML, Wrangham RW. 2003. Intergroup relations in chimpanzees. Ann Rev Anthropol 32:363–392.

Wittig RM, Boesch C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. Int J Primatol 24:847–867.

Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler PM, editor. Primate males: causes and consequences of variation in group composition. Cambridge: Cambridge University Press. p 248–258.

Wrangham RW. 2002. The cost of sexual attraction: is there a trade-off in female *Pan* between sex appeal and received coercion? In: Boesch C, Hohmann G, Marchant LF, editors. Behavioural diversity in Chimpanzees and Bonobos. Cambridge: Cambridge University Press. p 204–215.

Wroblewski EE, Murray CM, Keele BF, Schumacher-Stankey JC, Hahn BH, Pusey AE. 2009. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. Anim Behav 77:873–885

Yerkes RM. 1943. Chimpanzees: a laboratory colony. New Haven: Yale University Press.

Yerkes RM, Elder JH. 1937. Concerning reproduction in the chimpanzee. Yale J Biol Med 10:41–48.