Male Competition and Paternity in Wild Chimpanzees of the Taï Forest

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ABSTRACT   In social animals, competition among males for mates affects individual reproductive success. The priority-of-access model attempts to account for the influence of demographic conditions within groups upon male reproductive success, but empirical data for testing this model are scarce. Our long-term study of chimpanzees in the Taï National Park, Côte d'Ivoire, encompasses a period of steady decrease in community size and fluctuating numbers of competing males and sexually receptive females. These demographic changes, in combination with genetic assessment of paternity for 48 offspring from three communities, allowed us to quantify the effects of varying levels of competition upon male reproductive success. On average, the highest-ranking male sired 50% of all analyzed offspring during a 14-year period from 1987–2000. Competition among males strongly decreased the relative reproductive success of the alpha male, such that the alpha male's rate of success decreased from 67% with few competitors to only 38% with four or more competitors. The increasing number of synchronously receptive females in large groups also reduced the proportion of paternities by the alpha male. Thus, patterns of paternity in Taï chimpanzees fit well the predictions of the priority-of-access model. We also found that despite the inability of dominants to monopolize reproduction, they achieved a higher reproductive rate in large multimale groups, because these have more females and a higher infant survival rate. Varied levels of male competition within communities seem to explain differences in the reproductive success of alpha males observed in different chimpanzee populations, and in other primate species. Am J Phys Anthropol 130:103–115, 2006.   © 2005 Wiley-Liss, Inc.

Large variance in reproductive success is predicted among males, as it is their ability to find mates that will determine the number of offspring a male produces, whereas in females, competition for mates determines mainly the quality of the offspring (Birkhead and Møller, 1992; Andersson, 1994; Eberhart, 1996). This sexual selection argument predicts that males who are more socially-dominant (i.e., higher-ranking) should be better at monopolizing mates and producing offspring. However, female choice was also shown to affect the ability of males to monopolize mates (Andersson, 1994; Eberhart, 1996). Finally, individuals face different competitive regimes during their lifetime that will influence their reproductive success. Therefore, the demographic conditions under which an individual happens to live influence its reproductive success (Dunbar, 1988; Stearns and Hoekstra, 2000). The "priority-of-access" model suggests that for animals living in social groups, male reproductive success should correlate not only with dominance rank, but also with two demographic factors: the number of other male competitors present in the group, and the number of simultaneously receptive females (Altmann, 1962; Dunbar, 1988). As either demographic parameter increases, the ability of the dominant male to maintain exclusive access to sexually receptive females is predicted to decrease, while reproductive access and success for lower-ranking individuals are expected to increase.

The study of variation in male reproductive success has been hampered by a lack of reliable measurement techniques. Indirect measures of reproductive success, such as mating frequency, have been widely used, but this is justified only if a representative sample of mating occurrences is observed, which is uncertain in wild animals, and if all matings have the same likelihood of lead-

ing to conception, which is not always the case (Baker and Bellis, 1993; Miller and Pitnick, 2002). In addition, factors such as the use of coalitions, the employment of alternative mating strategies by low-ranking males, and the varying importance of female choice may prevent the appearance of a simple positive correlation between male dominance status and reproductive success (Bercovitch, 1991; Cowlishaw and Dunbar, 1991; Harcourt and de Waal, 1992; Ellis, 1995). In recent years, paternity studies using genetic methods have revolutionized the study of reproductive success in wild animals, and now allow for analysis of the factors accounting for variation in male reproductive success (Gibbs and Weatherhead, 2001; Avise et al., 2002; Di Fiore, 2003). In addition, molecular genetic analyses revealed patterns of paternity unexpected by observers (Hoelzel et al., 1999; De-Woody et al., 2001; Vigilant et al., 2001). Some genetic studies of wild-living primates showed that dominant males tend to achieve higher reproductive success than subordinates, but to varying degrees (Altmann et al., 1996; Launhardt et al., 2001). However, only a few stud-

ies had large sample sizes, and even fewer encompassed different demographic conditions.

Chimpanzees offer an excellent opportunity to test theoretically relevant questions about male reproductive success, because of their unique social organization and mating system. They live in large multimale communities that exhibit a flexible fission-fusion grouping pattern (Goodall, 1986; Nishida, 1990; Boesch and Boesch-Achermann, 2000). Mature females give birth at about 5-year intervals. Females exhibit periodic sexual swellings associated with sexual receptivity (Boesch and Boesch-Achermann, 2000). Ovulation was shown to occur during the maximum swelling phase (Graham et al., 1973; Nadler et al., 1985). However, the timing of ovulation within the swelling period is variable (Deschner et al., 2003), and this finding, as well as the presence of swellings in pregnant females and in young females with newborn babies, indicates that the swelling might not be a reliable signal of fertility. Males remain all their lives in their natal community, while females leave their natal community at maturity. Males fight for dominance rank, and young males typically increase in rank as they age and achieve their highest position at about 25 years of age, with a gradual decrease in rank after around age 35 years (Goodall, 1986; Boesch and Boesch-Achermann, 2000).

Four different mating strategies have been described in chimpanzees: possessive mating, opportunistic mating, consortship, and extragroup mating (Tutin, 1979; Goodall, 1986; Hasegawa and Hiraiwa-Hasegawa, 1992; Watts, 1998; Vigilant et al. 2001). The possessive mating strategy involves the guarding of females by a male to prevent any other males within the group from mating with them. In contrast, in an opportunistic mating situation, most males have access to receptive females, and they do not obviously compete over females. An opportunistic situation may even occur prior to or a few hours subsequent to a possessive situation for a female nearing the beginning or end of her maximum swelling period. Female mate choice may play a role in the opportunistic mating strategy, particularly in social group situations, but it is difficult to distinguish this from male sexual preference. A consortship situation happens when a male and a female leave the group together for a period of days to a few months, a strategy that probably requires some cooperation by the female. Lastly, extragroup mating involves females mating with males from neighboring communities, and thus affords a potential opportunity for female mate choice (Goodall, 1986; Boesch and Boesch-Achermann, 2000). The possible combined use of these various mating strategies, combined with the extreme difficulty of observing all mating interactions, means that we could not evaluate the relative benefits to males of these strategies, and that only the use of genetic analysis can provide reliable paternity results.

Two early genetic studies of wild chimpanzee groups demonstrated the feasibility of using noninvasively collected samples, but findings regarding paternity were limited to four offspring in each (Sugiyama et al., 1993; Morin et al., 1994). Interestingly, the only adult male of the community at Bossou, Guinea, did not father one of the four offspring (Sugiyama et al., 1993). A larger study of a habituated community in Taï National Park, Côte d'Ivoire, found a high proportion of paternities (54%) that could not be attributed to males from within the community, and so inferred a significant role for female choice via extragroup mating (Gagneux et al., 1997). However, a subsequent study on the same and additional neighboring communities in the Taï forest found a much lower rate of extragroup paternity (7.1%) (Vigilant et al., 2001), and the difference between the two studies was attributed to a high error rate in the genetic analysis of Gagneux et al. (1997). Recent analyses of bonobos at Lomako and chimpanzees at Gombe found possessive mating to be successful only for dominant males (Gerloff et al., 1999; Constable et al., 2001). In Gombe chimpanzees, high-to-middle-ranking males successfully used an opportunistic strategy, while middle-to-low-ranking males achieved some reproductive success via consortship mating (Constable et al., 2001). Alpha males were credited with only 5 of 14 (35%) paternities. The bonobo study also found an association between high rank and reproductive success, although with a similarly limited number of offspring and some uncertainty in the paternity assignments (Gerloff et al., 1999).

In this study of male reproductive success in chimpanzees of the Taï National Park, Côte d'Ivoire, we consider a 14-year period between 1987–2000. During this time, community size diminished, and the number of adult males present decreased from 9 to 2, thus allowing an examination of the effect of demographic changes upon male reproductive success. This also represents the largest chimpanzee study to date, with paternity assignments made for 38 of 48 offspring analyzed. We address the following questions: Do dominant male chimpanzees sire more offspring than low-ranking ones? What is the role of age? Is the success of the alpha male influenced by the presence of male competitors? How well does the priority-of-access model explain the data on the Taï chimpanzees? What are the reproductive advantages of multimale groups in chimpanzees?

MATERIALS AND METHODS
Study site and subjects

Chimpanzees living in the Taï National Park, Côte d'Ivoire, have been subjects of long-term behavioral observation since 1979. The first study community habituated, the North group, included between 77–80 individuals, including 8–10 adult males, in the period 1982–1987 (Boesch and Boesch-Achermann, 2000). Since 1988, the community size decreased steadily, due to poaching, leopard predation, and different diseases, including ebola (Boesch, 1991; Le Guenno et al., 1995; Formenty et al., 1999; Boesch and Boesch-Achermann, 2000). The North community consisted of only about 25 individuals, including 2–3 males, by 1997–2000. Two additional neighboring communities, Middle and South, were habituated in 1998 and 1995, respectively (Herbinger et al., 2001). The average numbers of living members in 1999 for the Middle and South groups were 12 and 53, respectively. Young adult males were normally first observed as subadults, and age was determined in relation to the clear morphological changes associated with this age class (Goodall, 1986; Boesch and Boesch-Achermann, 2000). For older males, age estimates relied on comparisons with individuals of known age, and the error may have been larger because of individual variation in physical appearance (Boesch and Boesch-Achermann, 2000). Offspring considered in our analyses were born subsequent to the habituation of the communities, and their dates of birth were known to within weeks.

All three communities were followed on an almost daily basis, and demographic data on birth, death, migration, and sexual swellings were continuously col-

lected. Females were considered to be receptive during the maximal sexual swelling phase. In addition, continuous records of party composition and social interactions of focal chimpanzees, followed from nest to nest, were collected on check-sheets. Dominance ranking of males was determined by aggressive interactions and submissive pant-grunt greetings (Boesch and Boesch-Achermann, 2000). The directionality of pant-grunts is an unambiguous sign of dominance, and allowed us to follow dominance changes within males on a monthly basis. Because of the more recent habituation of the Middle and the South communities, social data were available only for recent years. Hence, sample sizes vary in some of the analyses presented below.

Genetic analysis

The collection of freshly produced fecal samples from individually recognized chimpanzees began in 1999. Samples were dried using silica gel, and DNA was extracted using the QIAmp DNA Stool Kit (Qiagen), as described previously (Bradley et al., 2000; Morin et al., 2001). Some individuals no longer alive in 1999 were genotyped using DNA extracted from either stored shed nest hair or skeletal material (Convention on International Trade in Endangered Species permit numbers E-1192/01, E-2110/00, E-0186/99, and E-1791/98) (Vigilant et al., 2001). The nine microsatellite loci used for genotyping (D2s1326, D2s1329, D5s1470, D7s817, D7s2204, D9s910, D11s2002, and vWF) were originally described in humans. Primer sequences and polymerase chain reaction (PCR) amplification conditions were as described by Bradley et al. (2000).

The accuracy of genotypes was controlled by multiple means. First, we guarded against inadvertent individual misidentification or sample mix-up by checking that the sex of the sample as ascertained by molecular analysis (Bradley et al., 2001) matched the expected sex of the individual. As a second means to check for sample mix-ups, we verified that genotypes from mother-offspring pairs shared an allele at every locus, as expected under normal Mendelian inheritance. For each locus, we also checked for discrepancies between mothers and offspring that might arise out of nonamplifying "null" alleles (Smith et al., 2000), and found none. For individuals who lacked known maternal relatives in the group, we compared the genotypes derived from two independent samples in order to confirm that both genotypes matched the supposed individual. Finally, because we necessarily relied on low-concentration DNA derived from noninvasive samples, it was necessary to guard against errors arising from allelic "dropout," the situation in which one of the two alleles at a heterozygous locus is not amplified and the genotype may be mistakenly recorded as a homozygote. Such errors may be avoided by replicating putatively homozygous results sufficient times to reach statistical confidence in the results. We previously described the relationship between DNA template concentration and incidence of allelic dropout in a study using DNA from these chimpanzees (Morin et al., 2001). We used the described 5' nuclease assay to estimate the concentration of amplifiable DNA present in each extract, and followed the guidelines regarding number of replications. Specifically, apparent homozygous results derived from amplifications containing fewer than 100 pg of DNA were replicated a total of seven times, while a minimum of four replications was completed from reactions containing more than 100 pg. We avoided using amplifi-

cations containing fewer than 25 pg of template DNA. Finally, all heterozygous genotypes were confirmed by detection of each allele at least twice. The rate of sporadic genotyping error in this study was quantified and estimated at less than 1% (Morin et al., 2001).

A number of offspring could not be analyzed in this study, as many died before reaching the minimum age (approximately 24 months) when a fecal sample could be obtained. In the North group between 1994–2001, 21% of infants died before reaching that age, while another 30% disappeared after that age but before we could obtain usable samples. In total, we examined the paternity of 48 offspring born into the three communities, including 24 of 49 infants born in the North community between 1987–2002.

Paternity determination

The genotype of the mother was available for all but one of the 48 offspring analyzed, allowing classification of the alleles seen in offspring as either maternally or paternally derived. In all cases, maternal relationships inferred from behavioral observations were confirmed. Paternity determination was done by exclusion, i.e., males assigned as fathers were required to be fully compatible with the paternal alleles of the offspring at all loci examined. Individual paternity exclusion probabilities were calculated as described in Morin et al. (1994). The exclusion method for paternity assignment was conservative, and for this study was more appropriate than likelihood-based methods, which are more useful in assigning paternity in studies with appreciable error rates (5% or more) and/or low resolution leading to the identification of multiple potential sires with genotypes compatible with those of the offspring (Slate et al., 2000). Nonetheless, we did conduct a second paternity analysis using the likelihood approach implemented in CERVUS (Slate et al., 2000), using the assumptions of 1% error rate and 90% complete sampling of sires.

Test of priority-of-access model

The priority-of-access model predicts that for each male, the number of competitors he faces at the time a female conceives, as well as the number of receptive females available during that time, will affect the likelihood of siring an offspring. We determined the exact dominance rankings of males at the time of each conception, with the exception of two infants in the Middle group, where, because of the recent habituation, we could not reliably judge the dominance relationship between the four males. Therefore, for each of 36 offspring with assigned paternity for whom we knew the dominance rank of the father, we determined the number of males aged 10 and older and the number of receptive females present at conception. We calculated conception dates by subtracting 229 days from birth dates (Martin, 1992). For each offspring, we then calculated the expected paternity likelihood for each male present in the group, as determined by the priority-of-access model. This calculation takes into account the number of males and receptive females present for each conception. For example, if three males were present with three receptive females at the probable conception time, the expected likelihood of becoming a father would be 0.33 for each male. If only two females were in estrus, it would be 0.50 for the two highest-ranking males, and 0 for the third male. This calculation assumes that males did not have preferences among different maximally

TABLE 1. Paternity assessments for 48 offspring in Taï chimpanzees born between 1987–2002[1]

Offspring	Date of birth	Father	Age of father	Rank of father	No. of males present	No. of estrous females present
North community						
Kana	5/6/87	Macho	22	3	9	–
Manon	10/9/87	–				
Sirène	11/87	Macho	23	2	8	4
Nino	2/3/88	Darwin	18	8	8	3
Bambou	6/2/89	Darwin	19	6	6	–
Mognié	31/7/90	Kendo	20	2	6	3
Hector	10/12/90	–				
Vanille	30/5/91	Kendo	21	1	7	–
Gargantua	21/9/91	Brutus	40	5	6	5
Lefkas	7/10/91	Kendo	22	1	6	8
Dorry	24/11/91	Kendo	22	1	6	7
Ovide	11/92	Kendo	23	2	6	5
Fédora	12/11/93	Fitz	18	1	6	–
Roxanne	28/8/94	Fitz	18	1	6	7
Pandora	2/9/95	Marius	12	3	3	4
Mozart[2]	18/11/95	Macho	31	1	3	1
Gisèle[2]	20/5/96	Macho	31	1	3	2
Noureyev[2]	23/4/97	Macho	32	1	3	2
Violetta[2]	22/8/97	Marius	15	3	3	2
Léonardo[2]	31/8/97	Macho	32	1	3	2
Faust[2]	10/1/99	Macho	34	1	2	2
Béyé[2]	20/12/99	Marius	17	2	2	4
Porthos[2]	1/10/00	Marius	17	1	2	1
Volta[2]	1/8/02	Marius	19	1	2	2
Middle community						
Nelly	89	–				
Koulo	91	–				
Noah[2]	95	Urs	27	Unclear	4	
Janin[2]	99	Urs	31	Unclear	4	
Kassiopée[2]	26/3/00	Léo	16	1	3	1
South community						
Max	95	Kaos	17	5	8	–
Mustapha	95	–				
Inousha	1/95	–				
Rébecca	3/95	–				
Alina	6/95	–				
Céline	11/95	Kaos	18	5	8	–
Yao	11/95	Zyon	31	2	8	–
Settut	3/96	Kaos	18	5	8	–
Huxel	10/96	Zyon	32	1	7	–
Endora	25/3/96	Mkubwa	36	5	7	–
Kuba	23/6/96	Zyon	31	1	7	–
Zita	7/96	Zyon	31	1	7	–
Lukas[2]	21/9/98	Kaos	20	3	4	–
Oreste[2]	12/98	–			4	4
Jacobo[2]	12/98	–			4	5
Romario[2]	1/99	Kaos	20	2	3	4
Voltaire[2]	8/99	Sagu	10	3	3	4
Athéna[2]	9/99	Zyon	35	1	3	3
Ibrahim[2]	1/00	Zyon	35	1	3	–

[1] – in father column indicates no assigned father, and for estrous females indicates that this information was unavailable.
[2] Offspring for which all potential within-community fathers were analyzed.

swollen females. These predictions were then compared with the observations.

Statistical analyses

We compared individual paternity successes with the null hypothesis in which males are expected to be successful in proportion to their demographic representation in the group at the time of each conception. The Spearman rank-order correlation coefficient was used to compare observations with the prediction. Because we consider four possible factors affecting male reproductive success (male rank, male age, number of competitors, and number of receptive females),

we favored a multivariate analysis to test for their respective influences and for possible interactions among them. However, the limited sample size in this study prevented us from doing a log-linear analysis, and therefore we had to perform a partial Pearson correlation coefficient test. This test was used because our sample size was large enough for the test ($N = 36$) and because of the robust power of the test. Statistical tests were performed with SPSS for Windows 9.0 (SPSS, Inc., 1998). We could not directly control for the fact that many males were fathers more than once (similar to repeated measurements). To evaluate the effect of individuality on our results, we did a qualitative analysis to see if individual males deviated from the overall tendency.
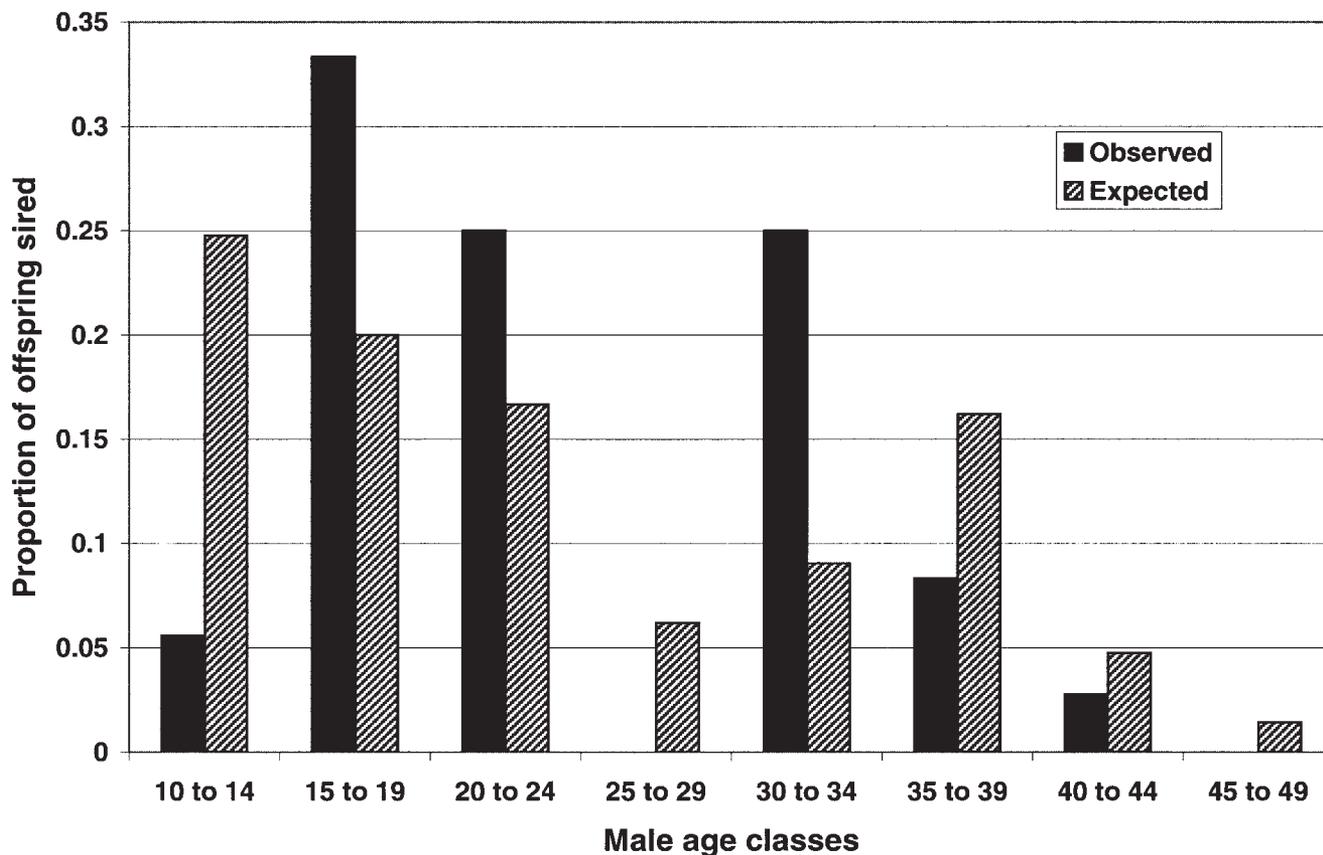
Fig. 1. Likelihood of paternity as function of age in Taï chimpanzees. Expected values are calculated assuming that paternity is distributed according to number of males in each age class at times of conception ($\chi^2 = 13.55$, df = 4, $P < 0.01$).

RESULTS
Paternity assignments

In total, 115 individuals were characterized by genotyping at up to nine microsatellite loci. The table of genotypes for all individuals is available at www.eva.mpg.de/primat/files/data_sets.htm, or by request from C.B. Of 115 individuals, one was completed at only five loci, and four were done at only seven loci because a limited amount of DNA was available. The loci were highly variable, with an average of 9.11 alleles per locus, and a mean expected heterozygosity of 0.798. The genotype of the mother was available for all but one of the 48 offspring analyzed. In all cases, maternal relationships inferred from behavioral observations were confirmed by sharing between mother and offspring of one allele at every locus. Paternity determination was first done by exclusion, i.e., males assigned as fathers were required to share one allele with the offspring at all loci examined, and the mother-father-offspring trio was required to be fully compatible. Application of this procedure resulted in the exclusion of all but one male, who was therefore assigned as the father, for 38 of 48 offspring (Table 1). For the remaining 10 offspring, exclusion by mismatches at two or more loci of all tested males meant that no father could be assigned in these cases. All assigned fathers were members of the same communities as their offspring. It is reasonable to assume that the allele frequencies derived from the individuals in this study approximately reflect the allele frequencies in

neighboring populations, as gene flow mediated by female transfer among communities occurs. This means that we can calculate the probability that more than one male from the area could have a compatible genotype with an offspring, even though only one male could be the true father. We found that for each offspring, the paternity exclusion probability (Morin et al., 1994), a measure of the chance that the paternally derived alleles observed in the offspring were derived from the true father and not from another individual in the population, exceeded 0.99. We further confirmed this result by applying a likelihood approach as implemented in CERVUS (Slate et al., 2000), using the assumptions of a 1% error rate and 90% complete sampling of sires. This procedure resulted in assignment with high confidence of the same fathers for the 38 assigned offspring, and no paternity assignments with both high confidence and fewer than two mismatches for the remaining 10 unassigned offspring.

We analyzed all potential within-community fathers for 19 of the most recently born offspring, and could exclude all within-community fathers for two of these (Oreste and Jacobo). Thus, we inferred a rate of extragroup paternity of 2/19 or 10.5%, similar to the value of 7.1 % reported earlier from a subset of the data (Vigilant et al., 2001).

Male success as a function of age and rank

Wild male chimpanzees in the Taï forest have a potential reproductive lifespan of at least 30 years (Fig. 1).
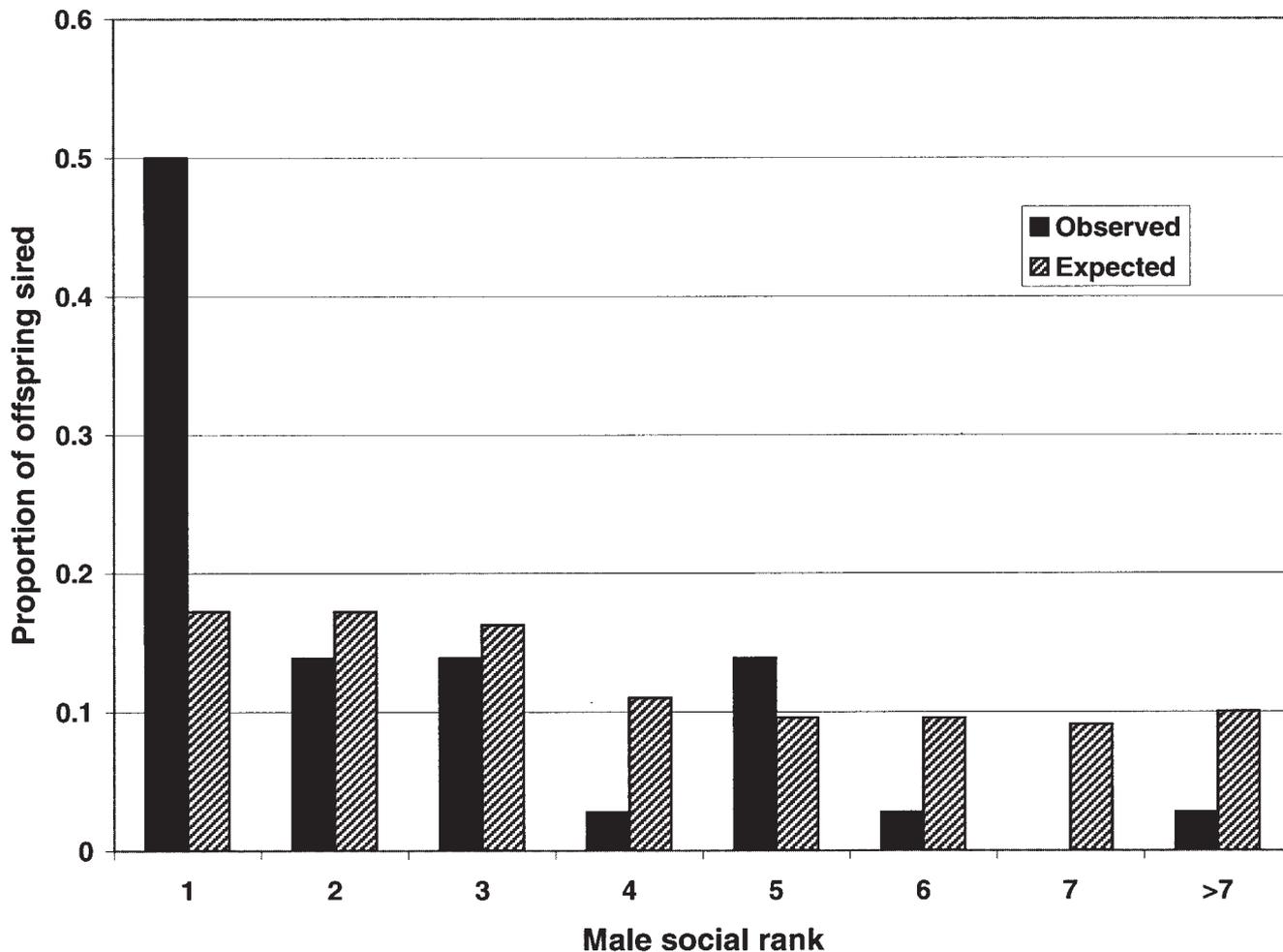
Fig. 2. Likelihood of paternity as function of rank in Taï male chimpanzees. Expected values are calculated by assuming equal probability of siring for any male present, regardless of rank ($\chi^2 = 31.19$, df = 4, $P < 0.001$).

The youngest confirmed father (Sagu) was 10 years old when he sired his first offspring, despite the presence in the community of three full-grown males. Marius, in the North group, was 12 years old when he sired his first offspring while competing with two full-grown males. Thus, adolescent males are fertile in the wild and successfully compete with adult males. The oldest known father, Brutus, was about 40 when he sired Gargantua. Age is not a good predictor of paternity, as younger males are much less successful than expected from their representation in the community (Fig. 1).

The rank of the father was known for 36 of 38 assigned offspring (Table 1). Rank is clearly an important determinant of reproductive success in Taï male chimpanzees, as 50% of the 36 infants assigned were sired by the alpha male within the community (Fig. 2). This proportion decreases slightly if we include the two offspring with no assigned paternity but for whom the alpha males were excluded. Specifically, Manon was not sired by Brutus, who was the alpha male at the time of her conception, and similarly, Hector was not sired by Kendo, who was the alpha male at the time. Hence, a figure of 18 of 38 infants (47%) attributed to the alpha male is more precise. The number of offspring produced seems to be directly dependent on rank, with higher-ranking males having more offspring than low-ranking males ($r_s = -0.88$, N = 10, $P < 0.001$). Age of fathers does not correlates linearly with rank (Table 2), but shows a tendency for a quadratic relation with rank ($P = 0.09$), as both younger and older males tend to be lower ranking than middle-aged males.

Presence of competitors

Does the intensity of competition among males affect an individual's ability to sire offspring? We divided the competition level into two categories: "high competition" when 5–9 males were present in a community, and "low competition" when 2–3 males were present (in our study period, no offspring when the male dominance rank was known were sired when four males were present). Figure 3 reveals a detrimental effect of male competition on the alpha male's ability to monopolize reproduction: the proportion of offspring sired decreased from 67% with few competitors to 38% with many competitors (alpha vs. other rank success, $\chi^2 = 2.86$, $P = 0.09$; Table 2). The increase in success by lower-ranking males in a high-competition situation could occur from an increase in consortship success or from opportunistic matings. Of 18 consortships we observed, only two led to a conception

TABLE 2. Results of analysis of four factors predicted to affect reproductive success in Taï male chimpanzees[1]

Pearson correlation coefficient	Father's rank	Father's age	Number of competitors	Number of receptive females
Father rank				
Coefficient	1	−0.222	**0.419**	0.078
P value		0.193	0.011	0.731
N		36.0	36.0	22.0
Father age				
Coefficient		1.0	0.024	−0.124
P value			0.89	0.582
N			36.0	22.0
Competitors				
Coefficient			1.0	**0.582**
P value				0.004
N				22.0

Partial Pearson correlation coefficient, controlling for	Correlation	Coefficient	P-value	N
Number of receptive females	Rank/competition	**0.502**	0.021	19
Number of competitors	Rank/female	−0.255	0.264	19

[1] For 14 conceptions, no data were available for number of receptive female present in group. Significant results are presented in bold.
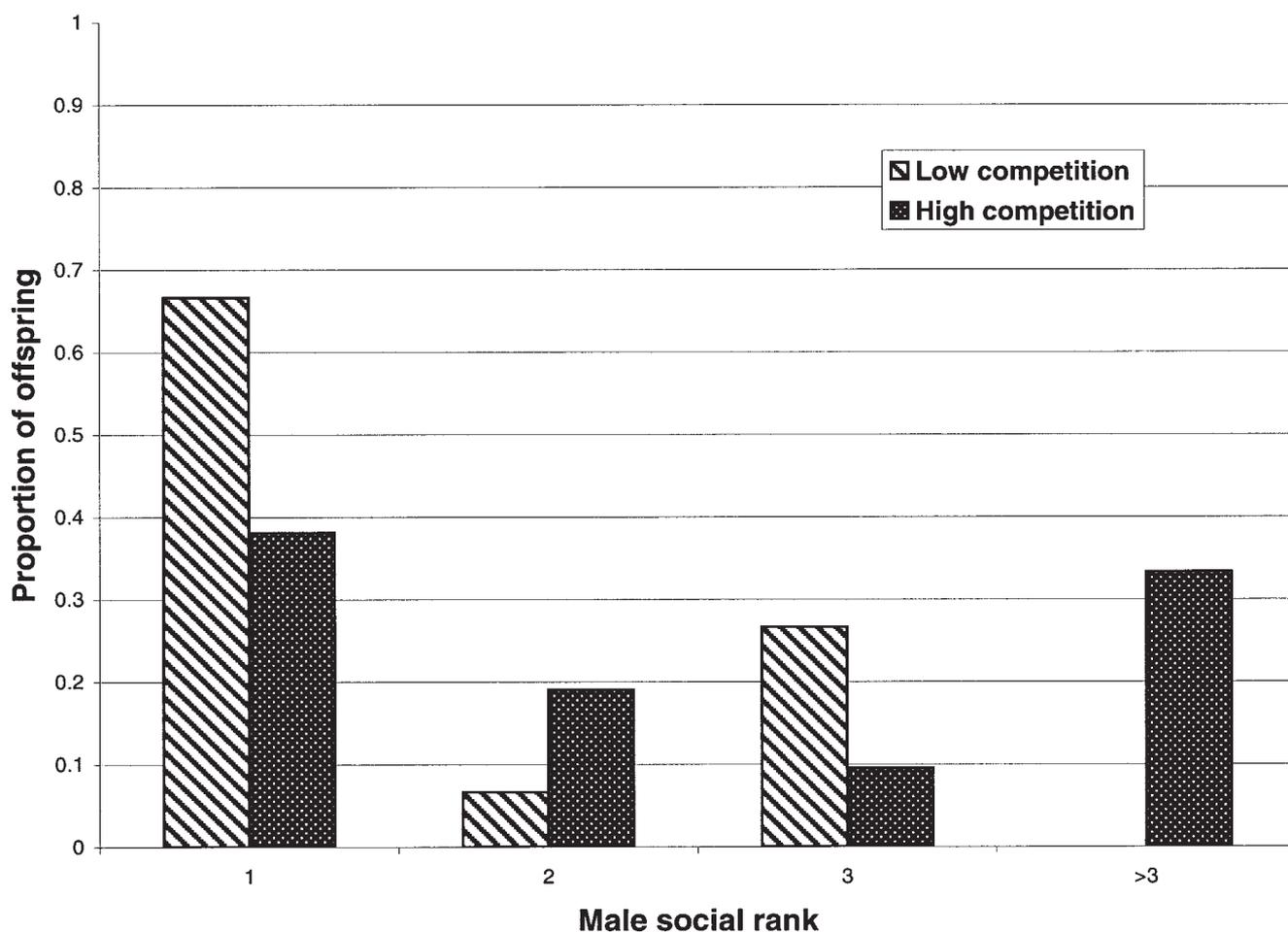

Fig. 3. Male reproductive success as function of dominance rank and number of competitors. Low-competition situation is one in which two or three males are present, and in high-competition situation, five or more males are present.

(once by the second-ranking and once by the third-ranking male). Thus, increased success by low-ranking males in a high-competition situation apparently occurred largely as a consequence of opportunistic matings.

Effect of synchronously receptive females

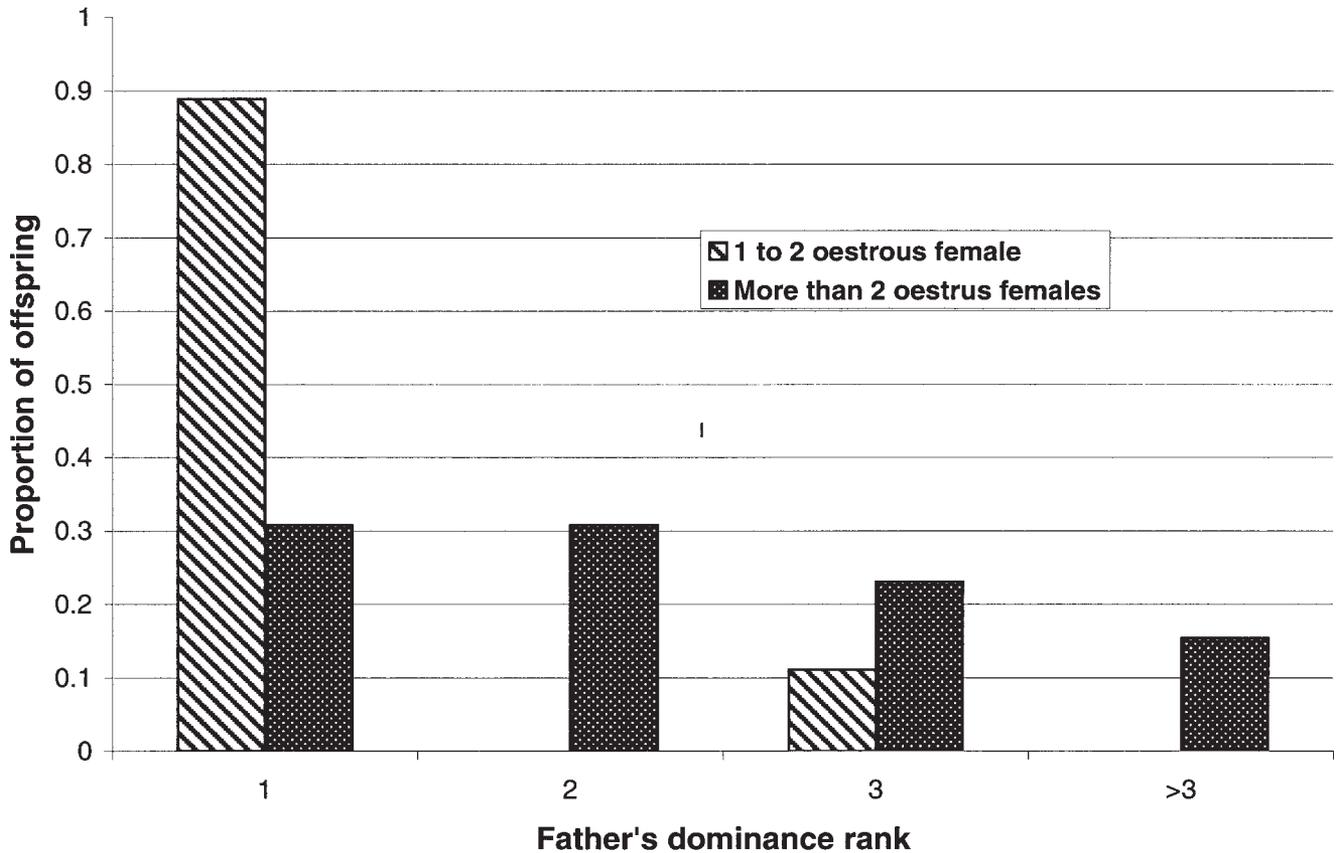Does the number of concurrently receptive females affect male reproductive success? As shown in Figure 4,

Fig. 4. Effect of number of synchronously receptive females on male reproductive success.

the relative success of the alpha male diminished as the number of simultaneously estrous females present at time of conception increased. The effect seems even stronger than that of number of competitors, as 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 (alpha vs. other rank success, Fisher's exact test, $P = 0.011$) (Table 2). The result of the partial correlation shows that after controlling for the effect of number of receptive females, the correlation between rank and number of competitors remains significant, while the opposite is not true (Table 2). However, Table 2 also shows that the number of receptive females correlated strongly with the number of competitors. A closer look at the data reveals that males were confronted with the situation of few synchronous females only when in small groups, while the situation with many estrous females may occur in both small and large groups. In other words, the effect of the number of females is only seen in large groups. This explains why the partial correlation suggests a larger role for number of males over number of females, despite the fact that the latter effect taken alone is stronger than number of males.

These results could be influenced by the fact that a few males fathered multiple offspring and thereby affected the result. To evaluate this, reproductive success for each male who sired two or more offspring was plotted against rank (Fig. 5). For all but one of the males, the same pattern of decreasing reproductive success with

decreasing rank was observed. Thus, the results do not appear to be unduly biased by a few highly successful males.

Test of the priority-of-access model

The priority-of-access model predicts male reproductive success to be a function of rank and of the number of competing males, as well as the number of receptive females present in the community at time of conception. Figure 6 shows that male success in Taï chimpanzees conformed closely to the predictions of the model ($r_s = 0.81$, N = 10, $P < 0.005$). In addition, the model accurately predicted the success of males both when they faced low competition (2–3 males present) and when they faced high competition (more than six males) (high competition, $r_s = 0.748$, N = 10, $P = 0.012$; Fig. 7).

Reproductive advantages of multimale groups

Why do alpha males tolerate so many competitors if they lose reproductive opportunities in large groups? To look for possible benefits, we compared the reproductive success of alpha males in large vs. small communities containing many or few competitors, respectively (Table 3). We found that in large groups, alpha males sired an average of 2.48 offspring per year surviving to age 5, whereas in small groups, the comparable number was 0.69. Thus, alpha males produced four times more offspring in large groups, due to both a higher birth rate and increased survival of offspring. Even with equal sur-
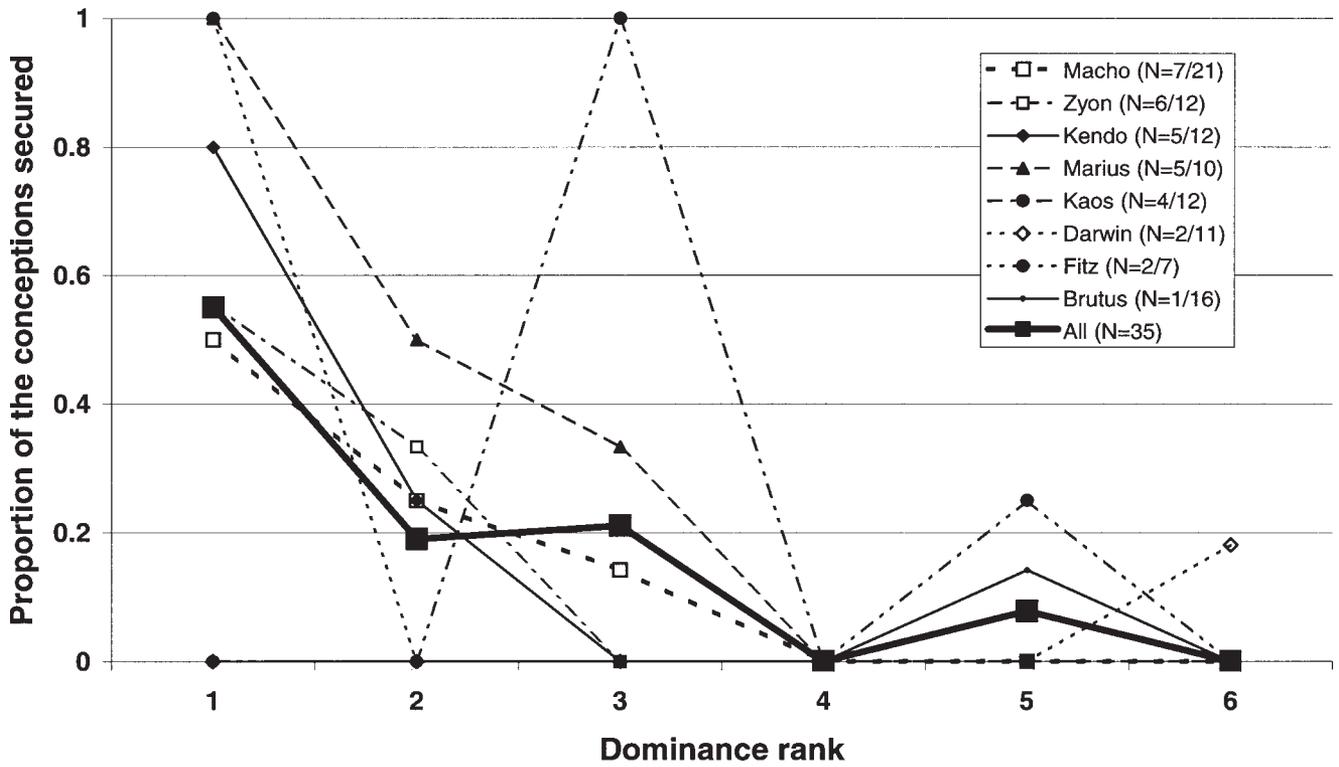
Fig. 5. Reproductive success of individual males as function of dominance rank. Proportion of conceptions was calculated by dividing number of conceptions secured by total possible number of conceptions that could have been secured.
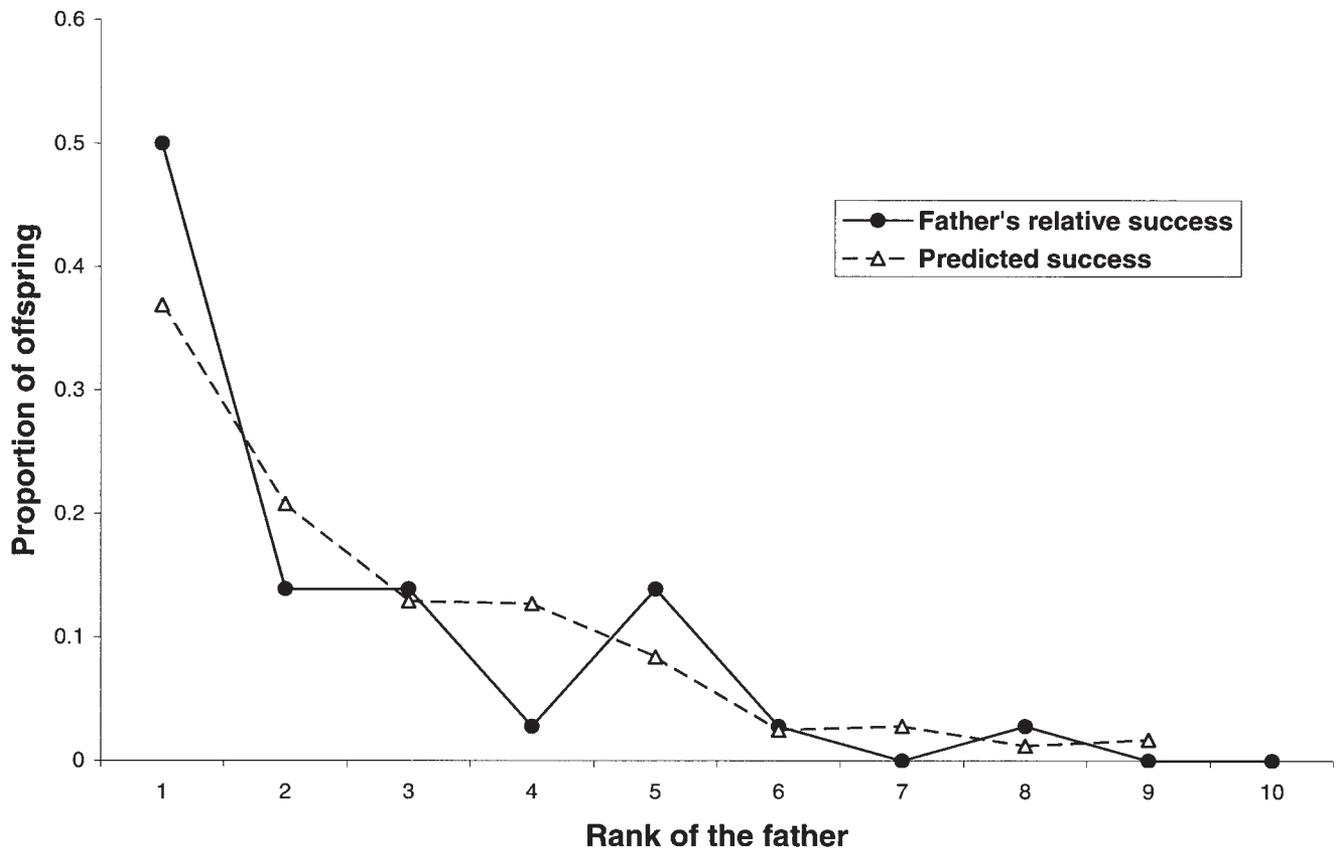

Fig. 6. Test of priority-of-access model against observed male success, considering individual male rank, number of males, and number of estrous females.
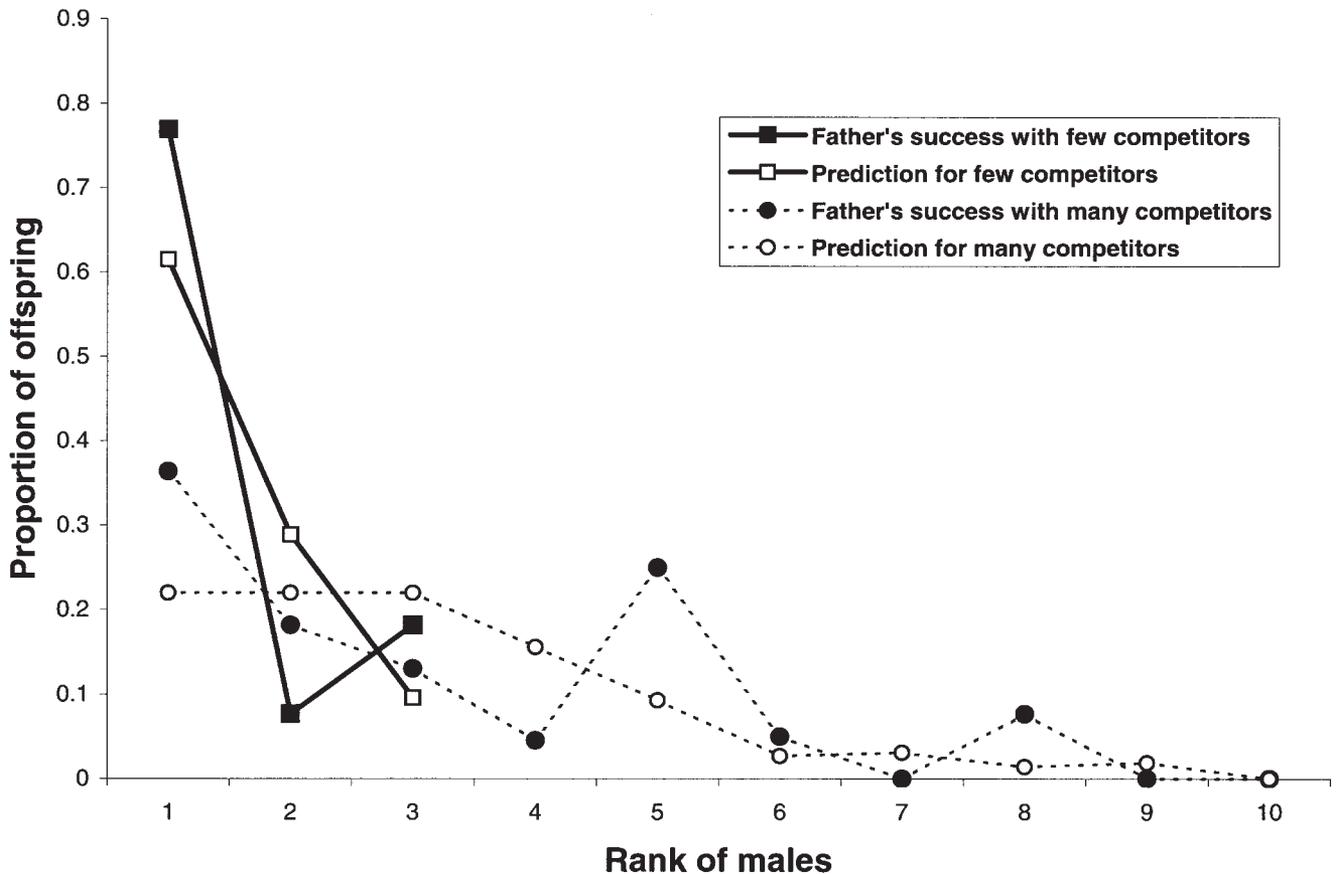
Fig. 7. Test of priority-of-access model with few and many competitors present in group. Total of two or three males is defined as few competitors, while total of five or more males represents situation with many competitors.

vival rates for different community sizes, this result would still emerge due to a higher birthrate in large groups (alpha males still produce 64% more offspring in large groups). The trend is the same for second- and third-ranking males. Therefore, under the conditions of the Taï forest, living in a large community with many male competitors is, on average, beneficial for high-ranking males.

DISCUSSION

The reproductive lifespan of wild male chimpanzees is relatively long, as we found them to start reproducing as early as 10 years of age and continue until death, with no apparent decrease of fertility with age (Fig. 1). Sperm production in wild chimpanzees was observed to start around 9 years of age, with fertility proposed to be achieved only some years later, based on inferences from humans (Goodall, 1986; Nishida, 1997). Among Taï chimpanzees, sperm production and fertility seem to be achieved fairly concomitantly, and this corresponds quite well with the timing found with some captive male chimpanzees (Marson et al., 1991). Additional observations from other sites are needed to determine the average age of male chimpanzee sexual maturity in the wild.

Dominance rank is a key determinant of male reproductive success in Taï chimpanzees, with an average of 50% of offspring being sired by the alpha male. However, this success varies significantly as a function of the demographic situation of the group, specifically the number

of competitors, and the situation appears to be similar in other populations of chimpanzees (Table 4). For example, the relatively low success of alpha males in Gombe chimpanzees could be explained by the larger number of males living in the group at the time of the study, as 10–14 males over 10 years of age were present (Table 1 in Constable et al., 2001). Thus, the 27% success rate experienced by alpha males in Gombe, recalculated by applying the same paternity attribution criteria as in the present study, is very similar to the value from the high-competition situation observed in Taï (31%). Likewise, the high success of the alpha male in Bossou chimpanzees, who sired 3 out of 4 infants, is easily explained by the fact that there was only one adult male living in the community (Sugiyama et al., 1993), which corresponds to the low-competition situation in Taï (75%). Thus, in chimpanzees, the available studies indicate that male competition is an important component of male reproductive success, and that the priority-of-access model may be of general value.

Genetic studies of paternity in other wild primate species also revealed that alpha males living in multimale groups enjoy a reproductive advantage (Table 4). Among savanna baboons in Amboseli, the success of high-ranking males diminished strongly in periods where a large number of males were present, or where large age differences existed between males (Alberts et al., 2003). A similar effect was described in long-tailed macaques (De Ruiter et al., 1992). Results from Hanuman langurs highlight the point that monopolization of females needs

TABLE 3. Comparative reproductive success of male chimpanzees in different demographic conditions[1]

	Births per year	Survival to 5 years	Male's paternal probability	No. of infants sired by male per year	No. of infants surviving to 5 years by male
Alpha male					
Large group	7.67	0.89	0.364	2.79	2.48
Small group	2.33	0.39	0.769	1.79	1.09
Beta male					
Large group	7.67	0.89	0.182	1.39	1.24
Small group	2.33	0.39	0.077	0.18	0.07
Delta male					
Large group	7.67	0.89	0.091	0.69	0.62
Small group	2.33	0.39	0.182	0.42	0.16

[1] Two alternative demographic conditions were taken from North group in Taï forest. Large group (between 1982–1987), 67.8 individuals including 9.0 adult males and 23.7 adult females. Small group (between 1994–2000), 32.2 individuals including 2.28 adult males and 11.5 adult females.

TABLE 4. Male reproductive success in wild multimale primate groups[1]

	Alpha male reproductive success	Male competition effect on alpha male reproductive success	EGP
Papio cynocephalus	81%	Decrease	
Alouatta seniculus	100%		
Erythrocebus patas	81%		50%
Macaca fuscata	29%		29%
Macaca mulatta	36%		36%
Macaca fascicularis	65–70%	Decrease	0%
Semnopithecus entellus	57%	U[2]	22%
Pan troglodytes			
Taï	50%	Decrease	12%
Gombe[3]	27%		8%
Bossou	75%		25%
Pan paniscus	50%		9%

[1] Success of alpha male is presented as well as, when available, effect of higher male competition. Extragroup paternity (EGP) is rate of paternity by extragroup males. Savanna baboons (*Papio cynocephalus*), Altmann et al., 1996; Alberts et al., 2003. Howler monkeys (*Alouatta seniculus*), Pope, 1990. Patas (*Erythrocebus patas*), Oshawa et al., 1993. Japanese macaques (*Macaca fuscata*), Takahata et al., 1999. Pigtailed macaques (*Macaca mulatta*), Berard et al., 1993. Long-tailed macaques (*Macaca fascicularis*), De Ruiter et al., 1992. Hanuman langurs (*Semnopithecus entellus*), Launhardt et al., 2001. Chimpanzees (*Pan troglodytes*), Taï National Park, this study; Gombe National Park, Constable et al., 2001; Bossou, Sugiyama et al., 1993; bonobos (*Pan paniscus*), Gerloff et al., 1999.
[2] U means that alpha male's success starts high, diminishes with increasing number of competitors, and finally increases again.
[3] Constable et al. (2001) allowed mismatches when assigning paternity. Here we amended results using exclusion criteria, whereby the proposed paternities were not accepted because of one mismatch between offspring and putative father, combined with low exclusion probability (<0.95). One of these three was proposed alpha male paternity, and a second became a case of extragroup paternity (N = 1/12).

to be considered both within and outside the immediate social unit. In that species, alpha males sired more infants when the number of males exceeded three or four (Launhardt et al., 2001). This counterintuitive result was explained by the fact that extragroup paternity did not occur once four or more males were present within the group, which benefited the reproductive success of the alpha male. The occurrence of extragroup paternities, which were confirmed genetically in different primate species (Table 4), might contribute to lower-than-expected reproductive success in high-ranking males.

Our results raise questions about the benefits to male chimpanzees of living in multimale communities. Do alpha males tolerate other males mating with receptive females, or are they unable to exclude them from doing so? The close fit of the data presented here to the predictions of the priority-of-access model suggests that in chimpanzees, dominant males are simply not able to control lower-ranking males and are forced to share paternity. An alternative theoretical framework for explaining the distribution of reproduction, the concession model,

suggests that dominant males have full control over reproduction of other males, but as the presence of subordinates increases the fitness of the dominants, the latter tolerate breeding by subordinates in order to retain them in the group (Vehrencamp, 1983; Reeve et al., 1998; Clutton-Brock, 1998). In lions, larger groups of males control a pride of females for longer period of times, thereby substantially increasing the survival of their offspring (Packer et al., 1991). In this situation, the fact that dominant males have to share paternity to some extent is balanced by gains in terms of offspring survival. A similar argument was given for howler monkeys, where larger coalitions of males are able to control females for longer than smaller groups of males (Pope, 1990). Do dominant male chimpanzees profit from the presence of subordinates? Table 3 clearly shows that the dominant male's fitness increased fourfold when sharing paternity with many competitors. Contrary to lions, chimpanzee adult males have only rarely been observed to leave their groups, and therefore one key assumption of the concession model is not fulfilled (Clutton-Brock,

1998). Theoretically, dominant males would fare better in groups with many females and no other male. However, we observed that in the Taï forest, dispersing females only join communities containing six or more males (Boesch and Boesch-Achermann, 2000), and therefore this theoretical situation does not exist. Dominant males benefit from the presence of subordinate males, as their presence makes the community attractive to immigrant females.

It might appear that low-ranking subordinates should prefer to be in smaller multimale communities. However, in chimpanzees, competition between males occurs not only within the community but also between communities (Goodall et al., 1979; Manson and Wrangham, 1991; Boesch and Boesch-Achermann, 2000; Wilson and Wrangham, 2003). Subordinate males do not have the option to change groups due to the tremendously aggressive behavior of males to neighboring males (Goodall, 1986; Wrangham and Peterson, 1996; Boesch and Boesch-Achermann, 2000). Therefore, dispersal is very costly for males, and has only been observed in the context of fission of large communities (Goodall, 1986).

It is also important to point out that stochastic events may have important effects on individual life histories. For example, Macho was a small male who reached the alpha position when he was 25 years old, only to lose it some 18 months later to a stronger team of maternal brothers. Following his loss of the top position, he produced no known offspring for 8 years. After an ebola outbreak killed many males in 1994, Macho regained the alpha position and produced five offspring, before once more losing the top position. In other words, the success of staying a subordinate in the group may pay, depending on future stochastic demographic events, and under some circumstances, waiting might pay.

CONCLUSIONS

Dominance proved to be an important predictor of male success in chimpanzees and other primates. The "priority-of-access" model that integrates the demographic effects of male competition and mate availability predicts the reproductive success of male Taï chimpanzees quite precisely. Including demographic parameters (e.g., birthrate and infant mortality) in the calculation showed that dominant males have higher reproductive success in large groups, despite the fact they have to share more paternity with subordinate males. The importance of demographic factors has to be integrated in our reflections about reproductive strategies, as they can be responsible for large variations in reproductive success.

ACKNOWLEDGMENTS

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