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Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire

Abstract According to sexual selection theory, females should selectively mate with high-quality males to enhance offspring survival and maximize reproductive success. Yet, chimpanzee (*Pan troglodytes*) females are known to mate promiscuously. Although there is substantial rationale for a promiscuous mating strategy, there is also a strong expectation that females should be selective, and the question arises as to whether promiscuity precludes female choice. The aims of this study are to: (1) compare wild female chimpanzee sexual strategies throughout estrus, and (2) determine whether females exhibit mate preferences for particular males. Over 2,600 h of data were collected on two habituated chimpanzee (*Pan troglodytes verus*) communities in the Taï National Park, Côte d'Ivoire. Female mate preferences were measured by quantifying proceptivity and receptivity toward males. Results indicate that all females exhibited proceptivity and resistance to male solicitations, but that there was substantial variation in their magnitudes within and among females. Female proceptivity rates were lower and resistance rates were higher in the periovulatory period (POP) when conception is most likely. Females were more selective during POP, and more promiscuous outside of POP, suggesting that females may follow a mixed reproductive strategy, being selective when conception is likely and more promiscuous when conception is unlikely. Results from this study emphasize the importance of considering the fertility window when determining female mate preferences, and of examining female behavior in POP and non-POP phases separately when evaluating hypotheses for multi-male mating.

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Introduction

Among most mammals, male reproductive success is largely dependent on fertilizing as many females as possible, whereas female reproductive success is limited by fewer and larger gametes, lower reproductive potential, and considerably larger parental investment (Bateman 1948; Trivers 1972). Therefore, females are expected to maximize their reproductive success by selecting sires that will enhance their own and their offspring's survival and fitness (Andersson 1994). By being choosy, females may gain direct benefits, such as male protection or increased access to food and other resources (Kirkpatrick and Ryan 1991), or indirect benefits such as "good genes" for their offspring, who in turn would be more likely to survive and successfully compete for mates (Darwin 1871; Emlen and Oring 1977; Clutton-Brock 1988; Maynard Smith 1991).

Mate selectivity should be particularly important for female chimpanzees (*Pan troglodytes*), because of their extensive investment in offspring and limited reproductive potential. Chimpanzee inter-birth intervals average 4–6 years, infants have prolonged maternal dependence, and average female lifetime production of surviving offspring is below five (Tutin 1979; Goodall 1986; Nishida et al. 1990). However, contrary to this expectation, chimpanzee females do not seem particularly selective. Females mate with many males over the course of estrus, resulting in hundreds of copulations per conception (Tutin 1979; Hasegawa and Hiraiwa-Hasegawa 1990). Although promiscuity entails risks (Daly 1978), including decreased control over paternity, this strategy may benefit females by: (1) confusing paternity and discouraging infanticide (Hrdy 1979; Van Schaik et al. 2000); (2) providing high-

quality genes through enhanced male-male and sperm competition (Clutton-Brock and Harvey 1976; Cox and Le Boeuf 1977), and (3) ensuring fertilization (Milton 1985; Small 1990). Promiscuous mating may also reduce male aggression toward females (Lindburg 1971) and increase social support or protection from predators (Ransom and Ransom 1971; Goodall 1986; see Hunter et al. 1993 for review). Thus, while females may benefit from a promiscuous strategy, the expectation for choosiness remains, and the question arises as to whether promiscuous mating precludes female choice.

If females can influence paternity, then they should be most selective when they are most likely to conceive. In contrast to many primates and other mammals, female chimpanzees have an extended estrous period, accounting for 27–40% of the 36-day cycle (Butler 1974; Tutin and McGinnis 1981; Hrdy and Whitten 1987), and characterized by the presence of a pronounced perineal swelling. Estrus can be divided into a longer non-periovulatory phase (referred to here as Non-POP), during which conception is unlikely, and a 3- to 4-day periovulatory period (POP) during which conception most likely occurs (Elder and Yerkes 1936; Goodall 1986). Thus, female chimpanzees should mate more selectively during POP if they are to influence paternity, while mating more promiscuously during non-conceptive times of their reproductive cycle (Non-POP), to obtain the benefits of both selective and promiscuous strategies. More specifically, during POP, females should exhibit greater selectivity for preferred males and against non-preferred (eschewed) males than toward these males in Non-POP.

Females should prefer to mate with some males and to eschew or resist others. It is argued that females may prefer dominant males, since males able to achieve high rank may confer these characteristics onto their offspring (Darwin 1871; Trivers 1972). Additionally, dominant males may provide direct benefits to females through social and material gains such as increased protection, support in interactions with conspecifics, and resource access (Tutin 1979; Janson 1984). Male age is a second factor that may influence female preference. Older males may be preferred since prolonged survival attests to physical and/or social quality and confirms viability in the current environment (Trivers 1972; Manning 1985). Alternatively, older males may be less preferred since sperm may be less viable or sperm counts may be low (see Hansen and Price 1995; Brooks and Kemp 2001, for review).

Females may vary in their ability to express preferences. Higher-ranked female chimpanzees obtain greater reproductive success than lower-ranked females (Pusey et al. 1997). It is conceivable that variation in female ability to express preference in light of male coercion may contribute to this finding, and this ability may correlate with female age or rank. High-ranked and/or older chimpanzee females may show greater preference for high-ranked males (Takahata 1980; Hasegawa and Hiraiwa-Hasegawa 1990), whereas younger females may prefer subadult and/or subordinate males, possibly to avoid mating with their fathers (Pusey 1980; Smith 1987; Anderson and Beilert 1994). Determining female mate preference is challenging in light of existing and often conflicting male strategies, such as coercion of females and mate guarding (see Smuts and Smuts 1993). Particularly in long-lived, male dominant and highly social species such as chimpanzees, female responses to males may be influenced by past experience, such as aggression received. Thus, because female behavior may reflect interactions that occurred prior to the time of observation, the potential influence of male coercion is difficult to eliminate entirely in any study of female preferences. However, in light of the many evolutionary benefits to female mate selectivity, we expect that mating preferences will be manifested in female chimpanzee behavior, and that these behaviors are not conditioned responses to prior experience with males.

Thus, females should exhibit mate preferences and express them most intensely during POP, when conception is most likely to occur. In this study, we test: (1) whether females express mate preferences for particular males, and (2) if so, whether females are more mate selective at POP than Non-POP, (3) whether females differ inter-individually in their preferences, and (4) what factors influence female preferences.

Methods

Wild chimpanzees live in large, stable multi-male, multi-female communities. Males are dominant to females and philopatric, while females generally emigrate during adolescence and remain within their new community throughout their lifetime (Goodall 1986). Chimpanzees have a fission-fusion social system in which the community splits into smaller parties and rejoins throughout the course of the day. Three mating patterns have been described for chimpanzees. These include: opportunistic mating, when females mate consecutively with many males with little overt competition between males; possessive mating, when a dominant male actively attempts to prevent other males from copulating with a female; and consorts, when a female and male travel apart from the group for hours or days (Tutin 1979). (Additional information on chimpanzee social behavior and ecology can be found in Goodall 1986; Nishida 1990; Boesch and Boesch-Achermann 2000; and references therein).

Over 2,600 h of data were collected on two habituated chimpanzee (*Pan troglodytes verus*) communities between September 1998 and December 2000 in the Taï National Park in Côte d'Ivoire (see Boesch and Boesch-Achermann 2000 for a more detailed site description). At the beginning of the study, the South and North communities included 62 and 32 individuals, respectively, with 25 and 11 adult females and 4 and 3 adult males, respectively. The adult sex ratio (M:F) for Taï chimpanzees is lower than for many other chimpanzee communities (see Doran et al. 2002). Detailed information on the history and changing demographics of these communities can be found in Boesch and Boesch-Achermann (2000) and Lehmann and Boesch (2004).

All-day focal follows (Altmann 1974) were conducted on a total of 14 parous, cycling, non-pregnant females of different ages and ranks (Table 1). The goal was to sample each female during early, middle, and late stages of her maximal swelling, which lasts an average of 10–12 days (Tutin and McGinnis 1981). Data from multiple estrous periods were collected for ten females. On 33% of estrous days, there was at least one other female in estrus.

Table 1 All females and males included in the study. Five categories of ranks are included: high, high-middle, middle, middle-low, low. Four categories of age classes are included: *1* estimated age 35+; *2* estimated age 25–34; *3* estimated age 15–24; and *4* estimated age 10–15. Total cycle count may differ from Non-POP and POP because not all phases were sampled from every cycle. One dyad (*SU* and *SA*) was related (mother-son)

	Individual			Cycles		
	Group	Rank	Age class	Total	Non-POP	POP
Female						
Duna (DU)	South	High	1	4	3	4
Sumatra (SU)	South	High	2	3	2	2
Tita (TI)	South	Middle-high	2	2	1	2
Zora (ZO)	South	Middle-high	1	1	1	1
Isha (IS)	South	Middle-high	2	1	1	0
Margot (MG)	South	Middle	3	3	3	3
Atra (AT)	South	Middle	3	4	3	2
Mandy (MN)	South	Middle-low	3	1	1	1
Coco (CO)	South	Middle-low	3	2	2	1
Yucca (YU)	South	Low	2	3	3	1
Wapi (WA)	South	Low	2	2	2	1
Mystere (MY)	North	High	2	2	2	2
Belle (BE)	North	Middle	3	1	1	1
Perla (PE)	North	Middle	3	3	3	2
Male						
Zyon (ZY)	South	Alpha	2			
Kaos (KA)	South	2nd	3			
Mkubwa (MK)	South	3rd	1			
Sagu (SA)	South	4th	4			
Macho (MA)	North	Alpha until 5/1999	1			
Marius (MR)	North	2nd; Alpha after 5/1999	3			
Nino (NI)	North	3rd	4			

Chimpanzee sexual interactions can be initiated by either males or females, and are generally marked by a clear behavioral solicitation (for a detailed description of chimpanzee courtship and copulatory behavior, see Tutin and McGrew 1973). We recorded all behaviors preceding, during, and after each sexual interaction between the target and a male, including the sexual initiator (male or female) and the response (resist or cooperate). The end of a sexual interaction sequence was marked by copulation, initiation of a different activity (such as feeding), or one of the two subjects leaving the party. Within the same dyad, we counted successive solicitations independently if they were separated by more than 10 min from the last solicitation, and by a clear, active behavioral change by the solicitor (such as eating, travelling, etc.), which could not be construed as continued solicitation.

Ranks of males and females were determined by the unidirectionality of pant-grunts, which are submissive vocalizations (Bygott 1979). Ranks in males were linear. Throughout the text, the name of the male is followed by his rank (in parentheses). Females were grouped into five rank categories, from high to low, based on all group females. When relative rank between two females could not be determined, they were regarded as occupying the same rank. Males and females were grouped into four age categories based on long-term data records (Table 1). Observations were recorded using a Psion Workabout handheld computer (Psion, London, UK), with Observer 3.0 software (Noldus, Wageningen, The Netherlands).

To accurately determine ovulation, urine was collected daily for hormonal analyses. We detected ovulation using Ovuquick test kits (Quidel, San Diego, Calif.), which reliably indicate reproductive status and timing of ovulation in apes (Czekala et al. 1987; Knott 1997). Ovulation was presumed to occur on the day the LH surge was detected. These tests were supplemented by laboratory hormonal analyses of urine samples for ovulation based on a sustained PdG rise (see Deschner et al. 2003). Hormonal detection of ovulation was conducted for 70% of cycles (*N*=23). Comparisons of presumed ovulatory days based on the use of both measures (*N*=12) were accurate to +/-1 day in 11 of 12 cycles (91.7%) and to within 2 days in 100% of cycles. The limited time period for a copulation to lead to conception is dependent upon sperm and extra-follicular egg viability (France 1981; Gomendio and Roldan 1993), and studies of fertility patterns in apes and humans suggest that most pregnancies result from copulations 1–3 days prior to and including

ovulation (Elder and Yerkes 1936; France et al. 1992; Wilcox et al. 1995). Based on this, the periovulatory period (POP) was defined in this study as 3 days prior to and including ovulation. When hormonal testing was not available (nine cycles), POP was defined as 5 days prior to the 1st day of detumescence (based on Elder and Yerkes 1936), as hormonal testing of our samples and concurrent detumescence was compatible with this criterion.

We devised operational measures for detecting female preference in wild chimpanzees that are based on a female's initial behavior in a sexual interaction. As a result, these measures are independent of the outcome of the interaction. We assessed female mate preference through two measures: (1) female proceptivity, as female-initiated sexual behavior toward a male, with no preceding male sexual invitation, and (2) female response to a male solicitation. Female chimpanzees can respond to male solicitations in two ways: by cooperating (rapidly approaching the soliciting male and presenting for copulation; Tutin 1979), or resisting a male (ignoring the solicitation, avoiding the male, screaming, or leaving). Female resistance does not imply that copulation did not occur. It only indicates the female's initial response to a male's solicitation. Because male coercion potentially may obscure the expression of female preference, additional controls were made in order to recognize whether this occurred (see below).

Information on how preference measures were determined is listed in Table 2. Proceptivity rates were calculated for each female-male dyad as the total number of unsolicited presentations by a female to a male, standardized by the dyadic association (presence in the party) time during estrus (in minutes). Resistance rates were calculated for each female-male dyad as the total number of female resistance events divided by the number of male solicitations.

A female's relative proceptivity (or resistance) index toward an individual male was quantified as the deviation of that dyadic proceptivity (or resistance) rate from the female's average proceptivity (or resistance rate) to all males (Fig. 1), such that for relative proceptivity rates:

$$RPR_a = \left(\frac{P_a}{T_a}\right) - \sum_1^N \left(\frac{P}{T}\right) * N^{-1}$$

where *RPR* is the relative proceptivity rate, *a* indicates a particular dyad, *P* is the number of proceptive attempts by the female of the

Table 2 Definitions of measures used in this study

| Measures	Definition
Proceptivity rate:	Count of unsolicited female presentations to a male divided by dyadic association time during Non-POP or POP
Resistance rate:	Count of female resistance divided by count of male solicitations
Relative proceptivity rate:	The deviation of a female's proceptivity rate toward one male from the female's average proceptivity rate toward all males
Relative resistance rate:	The deviation of a female's resistance rate toward one male from the female's average resistance rate toward all males
Preferred male:	Female proceptivity rate toward a male deviates more than 25% above (or for resistance rate, more than 25% below) her average for all males
Eschewed male:	Female proceptivity rate toward a male deviates more than 25% below (or for resistance rate, more than 25% above) her average for all males
Neutral male:	Female proceptivity or resistance rate toward a male ranges not more than 25% above or below her average for all males
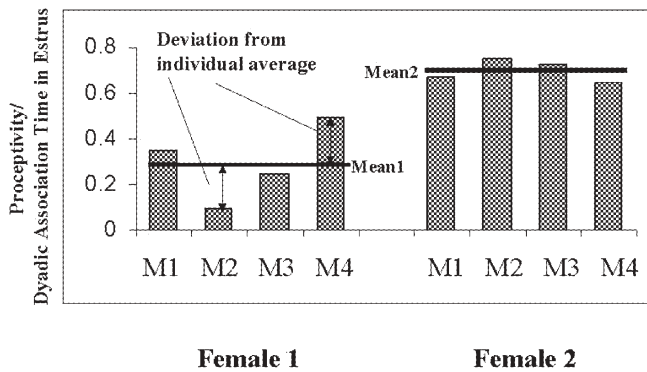
Fig. 1 Relative preference, measured as the deviation from a female's average. This figure illustrates the importance of relative versus absolute preference measures. Relative preference standardizes for variation among females. *Female 1* strongly favors M4 while eschewing M2, whereas *Female 2* has high absolute measures of preference for all males but little variation among males. Data are hypothetical.

dyad, T is the dyadic association time during estrus, and N is the number of adult males. Relative rates of preference are favorable because the standardization procedure adjusts for absolute measures of preference allowing preference measures to be compared between females. These relative preference measures were used in subsequent analyses that determine which male(s) is preferred by the females in their respective groups, and also to determine how female proceptive and resistance behaviors differ toward males throughout the female's estrous period (see below).

Individual males were categorized as *preferred*, *eschewed* or *neutral* for each female. A male was *preferred* by a female when the dyadic proceptivity rate was greater than 25% above (or the resistance rate was more than 25% below) that female's average proceptivity (or resistance rate) for all males. A male was *eschewed* when the dyadic proceptivity rate was more than 25% below (or the resistance rate was more than 25% above) the female's average for all males. Males were defined as *neutral* when they were neither preferred nor eschewed. These categories express the fact that female proceptivity or resistance behavior alone does not indicate that female's discrimination *between* males. The 25% threshold is arbitrary but one that is sufficiently high that it should indicate a clear difference in a female's behavior toward different males. Each female could prefer or eschew more than one male. For the majority of subsequent analyses, *preferred*, *neutral,* and *eschewed* males were categorized using proceptivity or resistance rates during POP, since this is when mate preference is expected to be strongest and have greatest evolutionary significance. An additional analysis was
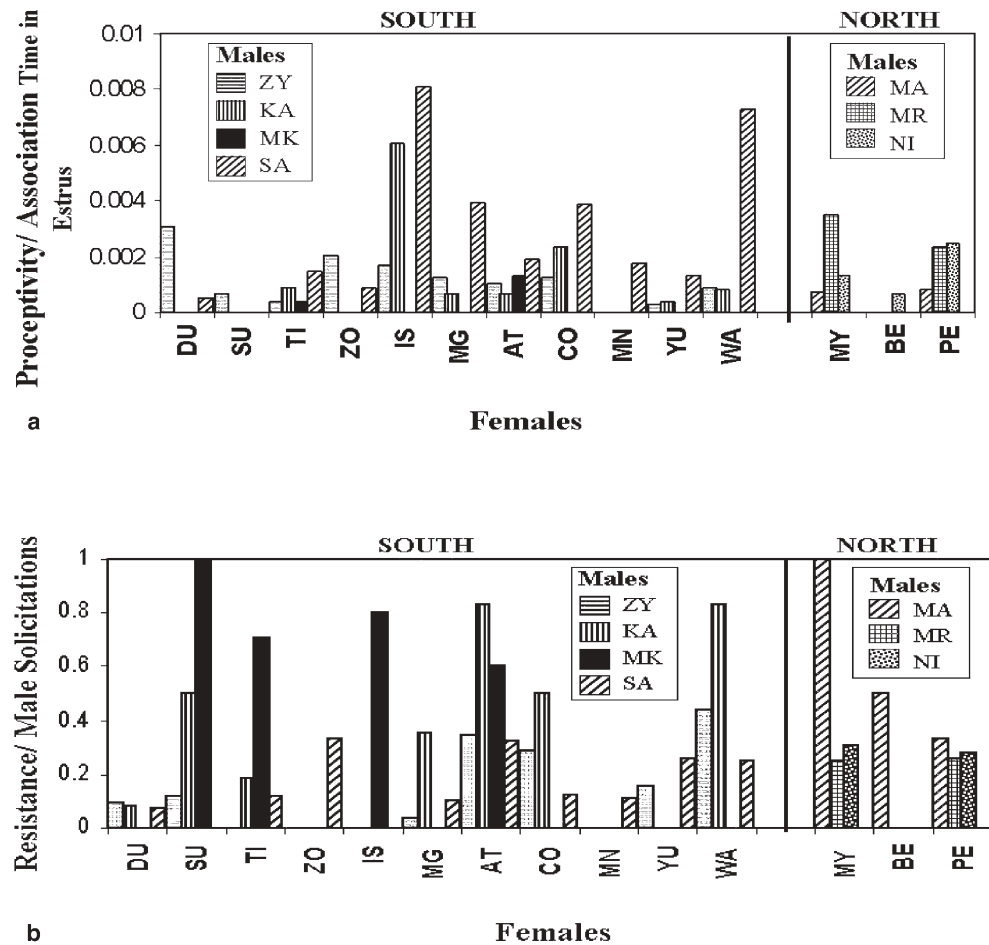
performed to determine which males were preferred during Non-POP, since females may also have non-reproductive preferences for particular males.

In order to determine whether all females express mating preferences, raw measures of preference (proceptivity and resistance rates) for each dyad are shown graphically for each female (Fig. 2). Spearman rank tests (r_s) were used to assess correlations between proceptivity and resistance rates and female rank and age. In order to account for the issue of replicated observations, sample sizes were based on the number of females (N_{adj}), not the number of dyads. This adjustment reduced the degrees of freedom for the analyses, raised the critical value (r_s) necessary to attain statistical significance, and made the test more conservative.

Differences in female selectivity (and male aggression and solicitation rates) between POP and Non-POP were assessed by using Wilcoxon Exact tests in two ways. First, because all dyads are not independent, to avoid pseudo-replication, comparisons were made between POP and Non-POP values for individual females. For these analyses, average proceptivity and resistance (and male aggression or solicitation) rates were calculated for each female for POP and Non-POP. These tests between individual females are more conservative because the smaller sample size requires larger critical values to attain statistical significance. Second, Wilcoxon Exact tests were used to determine if male-female dyads (sorted by preference) showed differences in proceptivity or resistance behaviors between POP and Non-POP. We are aware that matrix tests are a more applicable method for statistical analysis of multiple dyadic interactions (Hemelrijk et al. 1999). However, such analyses require more columns (i.e., males) than were present in either of the Taï chimpanzee groups, so matrix tests could not be performed on our data.

To determine if changes in female behavior are influenced by male behavior (i.e., through corresponding differences in male solicitation effort, or through female responses to male aggression), it is necessary to address how male solicitation and aggression rates differ across female estrous stages and whether these male and female behaviors are correlated. More specifically, we test the following hypotheses: (1) differences between female behavior in POP and Non-POP are a product of corresponding differences in male solicitation or aggression rates, (2) increased male aggression is correlated with decreased female resistance or increased proceptivity, and (3) male solicitation rates are correlated with female resistance. Wilcoxon Exact tests were used to assess changes in male solicitation or aggression rates across the estrous phases. Spearman rank tests evaluated the effect of male solicitation and aggression rates on female resistance and proceptivity rates. Aggression rates were measured as the number of aggressive behaviors by a male directed at a female divided by the dyadic association time, and solicitation rates were measured as the number of solicitations by a male divided by the dyadic association time in estrus.

Fig. 2 a Individual variation in absolute rates of female proceptivity in the South (*left*) and North (*right*) groups (all data). Data are not standardized by each female's average proceptivity or resistance rate. Females are ranked from high to low, left to right, in their respective groups. Males are ranked from high to low in their respective groups. **b** Individual variation in absolute rates of female resistance in the South (*left*) and North (*right*) groups (all data).


Results

Do all females express proceptivity and resistance?

All females exhibited both proceptivity and resistance to males, though intra- and inter-individual variation in the degree of expression was found (Fig. 2). These differences were not significantly correlated with female rank or age (proceptivity by rank: $r_S=0.13$, $N=14$; $P=0.66$; resistance by rank: $r_S=-0.08$, $N=14$; $P=0.80$; proceptivity by age: $r_S=0.41$, $N=14$; $P=0.15$; resistance by age: $r_S=0.18$, $N=14$; $P=0.55$).

Do proceptivity and resistance rates change near ovulation?

We predicted that females would be more selective in POP than Non-POP. Female proceptivity rates were significantly lower in POP than in Non-POP (Wilcoxon exact test: $T=3$, $N_{females}=13$, $P=0.033$) (Fig. 3) and these results were confirmed on a dyadic level ($T=9$, $N_{dyads}=38$, $P=0.007$). However, resistance rates were significantly higher in POP than in Non-POP (Wilcoxon exact test: $T=0$, $N_{females}=13$, $P<0.001$) (Fig. 3). This also held true for all dyads ($T=6$, $N_{dyads}=29$, $P=0.003$). For the majority

To determine which males were preferred by the females of each group (North and South), relative proceptivity and resistance rates for each dyad were compared across males using a Friedman's analysis of variance (ANOVA). Some males neither associated with nor solicited some estrous females, preventing assessment of female resistance behavior for some dyads. In cases with missing values, a modified version of the Friedman ANOVA, using a permutation approach, was used (Mundry test; Mundry 1999). Following a significant result from a Friedman or Mundry analysis, post-hoc comparisons of males were conducted using Wilcoxon matched pairs or Mundry single comparison tests, respectively, to determine which males differed significantly (Siegel and Castellan 1988; Mundry 1999; Scheskin 2000).

There are many factors that could influence female proceptivity and resistance behavior toward males. Some of these factors include (but are not limited to) male and female rank, age, and group (North and South). The contribution of each of these listed factors (and their interactions) to explaining variation in rates of proceptivity and resistance during POP and Non-POP was assessed using Generalized Linear Model (GLM) analyses (Tabachnik and Fidell 2001). GLM analyses require parametric assumptions of homoscedasticity and normality. These parameters were assessed by a visual residual analysis of each model (Tabachnik and Fidell 2001). To control for multiple testing of the same females, we included female "identity" as a random factor in the model. Model selection was based on an adjusted r^2, the amount of which denoted the percentage of variance accounted for by the independent variables, while also accounting for sample size and the number of variables. All tests except Mundry were conducted using SPSS version 11.0 (SPSS, Chicago). The α-level of significance was 0.05 (two-tailed).

Fig. 3 Differences in average female resistance (**a**) and proceptivity (**b**) rates between the peri-ovulatory period (*POP*) and *Non-POP* phase for each female. Resistance rates are substantially higher in POP than in Non-POP. In contrast, proceptive behavior is higher in Non-POP than in POP for most males. Values for each female represent the average of all male-female dyadic interactions.
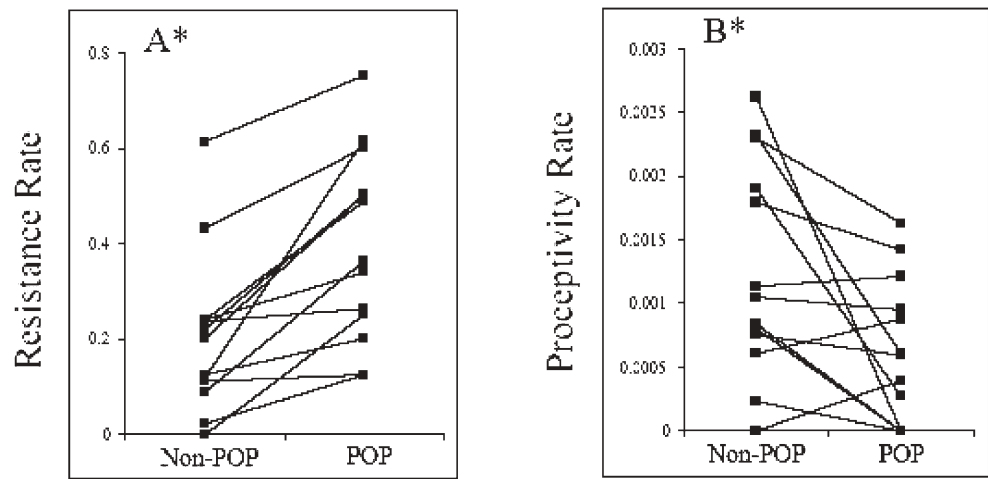
of dyads (29 of 38 dyads for proceptivity; 21 of 29 dyads for resistance), this change between POP and Non-POP was substantial (i.e., >25%), indicating that the differences between the phases are unlikely due to chance alone.

Is male behavior influencing this pattern?

Before concluding that the patterns observed above reflect female strategies, we tested for possible male influences on these relationships. First, higher female resistance rates in POP (than Non-POP) were not due to a corresponding difference between phases in male solicitations ($T=3$, $N_{males}=7$, $P=0.58$; $T=6$, $N_{females}=13$, $P=0.64$). In addition, no significant correlation was found between male solicitation rates and female resistance rates (Spearman test; $r_s=0.142$, $N_{adj}=13$; $P>0.05$). Male coercion has also been suggested to constrain female behavior, but no differences were found between male aggression rates toward females from Non-POP to POP ($T=3$, $N_{males}=7$, $P=0.58$; $T=4$, $N_{females}=12$, $P=0.68$), suggesting that the difference in female behavior between POP and Non-POP is not due to a difference in aggression. Furthermore, there was no significant correlation between male aggression rates and female resistance or proceptivity in POP (resistance: $r_s=0.153$, $N_{adj}=12$; $P>0.05$; or proceptivity: $r_s=0.123$, $N_{adj}=12$; $P>0.05$). While higher aggression was expected to decrease female resistance rates, the direction of the sign is not negative.

Do changes in proceptivity and resistance rates near ovulation depend on whether a male was preferred, neutral, or eschewed?

Females were more selective during POP than in Non-POP, and this difference between the phases depended upon the females' preference for the male. For example, most females were substantially (>25%) less proceptive to *eschewed* males during POP than in Non-POP (82% of

dyads), and all females were substantially more resistant to *eschewed* males during POP than in Non-POP (Wilcoxon Exact test: proceptivity, $T=1$, $N_{females}=9$, $P=0.039$; resistance, $T=0$, $N_{females}=8$, $P=0.008$) (Fig. 4). Similar results were obtained when comparisons were made between POP and Non-POP for each dyad (Wilcoxon Exact test: proceptivity, $T=3$, $N_{dyads}=17$, $P=0.017$; resistance, $T=0$, $N_{dyads}=9$, $P=0.004$). Thus, females resisted eschewed males substantially more in POP than in Non-POP. In contrast, females solicited these "non-preferred" males more during Non-POP. For preferred males, females in six of ten dyads were more proceptive (and females in nine of ten dyads were less resistant) toward preferred males in POP compared to Non-POP, but these differences were not significant (Wilcoxon Exact test: proceptivity: $T=4$, $N_{dyads}=10$, $P=1$; resistance: $T=4$, $N_{dyads}=13$, $P=0.56$). Results were similar when proceptivity and resistance rates for POP and Non-POP were compared for each female: (Wilcoxon Exact test: proceptivity, $T=4$, $N_{females}=9$, $P=1$; resistance, $T=4$, $N_{females}=9$, $P=1$) (Fig. 4).

For each female, the variance among males in resistance rates was significantly greater in POP than in Non-POP (Wilcoxon Exact test, $T=0$, $N_{females}=9$, $P<0.05$). This greater variation in resistance during POP implies that females may show greater resistance to some males and less resistance other males, allowing them to exercise selectivity for and against target males. Proceptivity rates did not show a similar pattern of variation between POP and Non-POP (Wilcoxon Exact test, $T=5$, $N_{females}=12$, $P=0.424$).

Which males are preferred?

Figure 5 illustrates differences in relative preference rates (i.e., deviations from female average proceptivity or resistance rate) for each of the males in the North and South groups. While the sample size of males is small, some interesting patterns in female preferences were observed over both phases. For the South group during POP

Fig. 4 Differences in average female resistance (**a**, **b**) and proceptivity (**c**,**d**) rates between the peri-ovulatory period (*POP*) and *Non-POP* phase for each female. Resistance rates for seven out of eight females are substantially (>25%) higher in POP than in Non-POP toward *eschewed* males (**a**), while females are not consistent in their pattern of resistance across phases for *preferred* males (**b**). In contrast, proceptive rates for six of nine females are substantially (>25%) higher in Non-POP than in POP toward *eschewed* males (**c**). Some females were more proceptive to *preferred* males (**d**) in POP, while others were more proceptive in Non-POP (* indicates a significant difference between the phases).
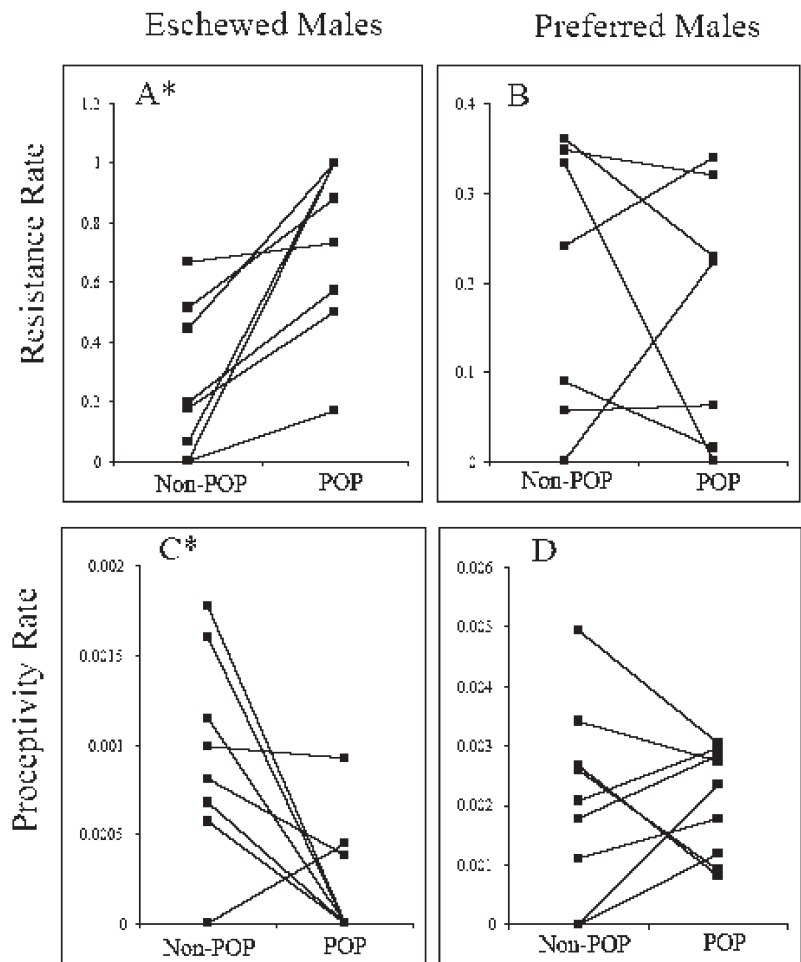
(Fig. 5a.ii, b.ii), the highest and lowest ranking males (ZY and SA, respectively) have significantly lower resistance rates (Fig. 5b.ii) and substantially higher proceptivity rates (Fig. 5a.ii) than the two middle-ranking males (Mundry test, resistance: $D_{4,22}=1.77$, $P<0.05$; Friedman test, proceptivity: $F_{r2,9}=5.04$, $P=0.08$). Post-hoc statistical comparisons support the former result for resistance (Zyon-Mkubwa; $N=5$; $P<0.05$; Sagu-Mkubwa; $N=5$, $P=0.05$; Zyon-Kaos; $N=9$, $P=0.068$; Sagu-Kaos; $N=9$, $P=0.068$). For proceptivity, only the comparison of KA (2) to SA (4) was significant (Fig. 5a.ii; Sagu-Kaos: $Z=-2.02$, $N=9$, $P<0.05$). During Non-POP, the lowest ranked male, SA, was the recipient of significantly more female proceptive behavior than any other male (Fig. 5a.i; Friedman test: $F_{r2,11}=6.54$, $P<0.05$; post-hoc test: Sagu-Kaos, $N=11$, $P<0.05$; Sagu-Mkubwa, $N=5$, $P<0.05$; Sagu-Zyon; $N=11$, $P=0.05$), while both ZY (1) and SA (4) encountered significantly less female resistance than other males during Non-POP (Fig. 5bi; Mundry Test: $D_{4,33}=1.24$, $P<0.05$; post-hoc test: Zyon-Mkubwa; $P<0.05$; Sagu-Mkubwa; $P<0.05$). These results imply that the dominant and lowest-ranking males were preferred by the majority of the 11 South group females, while middle-ranking males (MK, KA) were not.

Female preferences in the North group were more difficult to interpret because the small sample size of both males (3) and females (3) precluded statistical analysis. However, all three females were the least proceptive and most resisting to the transitory alpha male (MA), particularly during POP, and most proceptive and least resisting to MR (who became alpha during the study), and NI (3) (Fig. 5a.iv, b.iv). Both of these results imply that females did not prefer the departing dominant male (MA).

Do male and female age and rank influence female preference in POP and Non-POP?

Contrary to expectation, higher-ranked and/or older females did not express greater POP proceptivity and resistance rates than lower-ranked or younger females (female rank and proceptivity, $r_S=0.248$, $N_{adj}=14$, $P=0.133$; female age and proceptivity, $r_S=0.158$, $N_{adj}=14$, $P=0.345$; female rank and resistance, $r_S=-0.135$, $N_{adj}=14$, $P=0.468$; female age and resistance, $r_S=-0.073$, $N_{adj}=14$, $P=0.697$).

The influences of male and female rank and age (and their interaction effects) on proceptivity and refusal rates in POP and Non-POP were assessed using GLM analyses. Combinations of factors that explained the greatest

Fig. 5 a Boxplots of median upper and lower quartiles showing variation in relative female proceptivity rates in Non-POP versus POP in the South and North groups. The *two-letter codes* represent individual males. Males are ranked from high to low, left to right, in their respective groups. Values above 0 indicate that, relative to the other males, females have higher proceptivity (or resistance) rates to the male in question. The opposite holds for values below 0. *Bars* represent maximums and minimums. **b** Boxplots of median upper and lower quartiles showing variation in relative female resistance rates in Non-POP versus POP in the South and North groups.

a

b
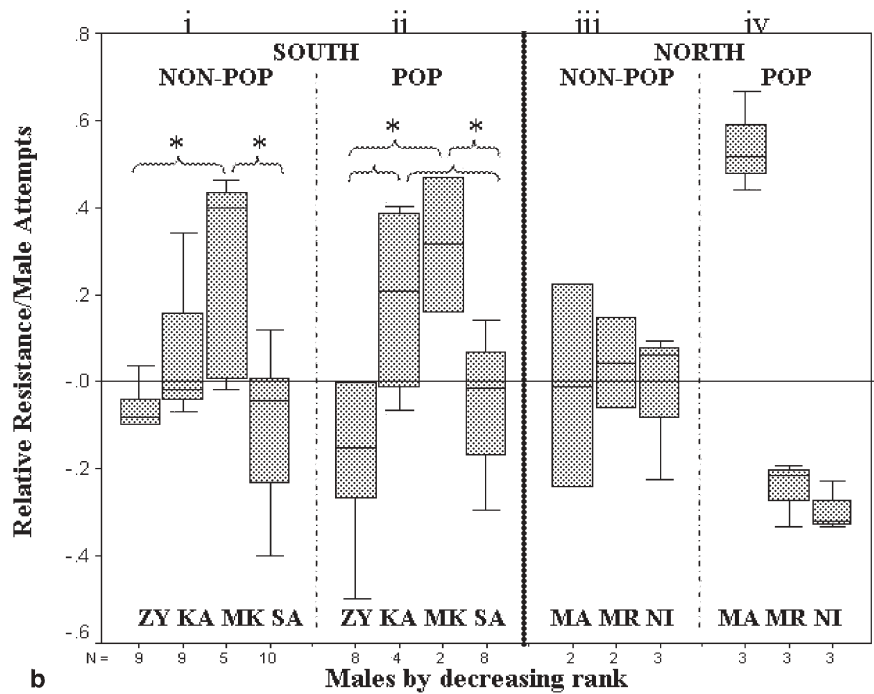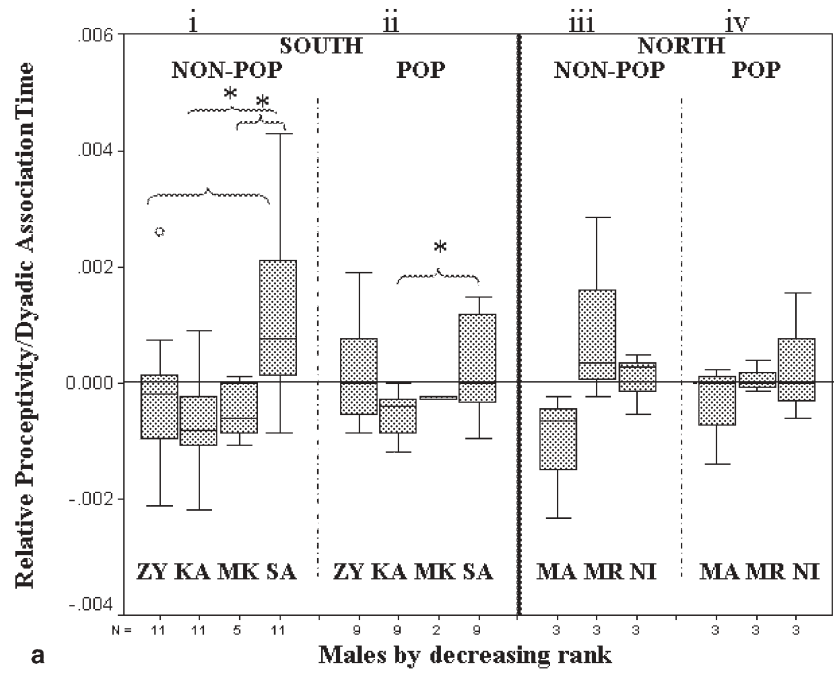
amount of variation in each dependent variable are listed in Table 3. None of the models (or factors) explained a significant amount of the variation in proceptivity rates during POP. However, during Non-POP, three factors contributed to the best model which explained 25% of the variation in female proceptivity: male and female rank, and the interaction between male and female rank. The results suggest that lower-ranking females were more proceptive to lower-ranking males and higher-ranking females were more proceptive to higher-ranking males.

Male age, group, and the interaction between group and male age were the most significant predictors of female resistance rates during POP (Table 3), which appears to result from high female resistance rates toward older males, particularly for the North group. When the influence of group was removed, the variable male age was a lesser but significant factor positively influencing resistance rates during POP (Adjusted R^2=11.2%). Male age appears to be the most significant factor influencing resistance rates in Non-POP, as older males experience higher resistance rates than younger males.

Table 3 Multiple regression analyses of factors influencing female proceptivity and resistance rates in POP and Non-POP. In **bold type** are F, P and adjusted R^2 scores for the multiple regression. Non-bold scores refer to the influence of the individual factor in a simple regression (* parameter estimates indicate this factor is significant in the multiple regression)

Preference measure (phase)	Best model	Direction of effect[a]	F, P and adjusted R^2: for model and individual factor in a simple regression
Proceptivity rate (POP)	None	N/A	N/A
Proceptive rate (Non-POP)			**$F(3,43)=6.12$; $P<0.05$, $R^2=25.0\%$**
	*Female Rank×Male Rank	+	$F(1,45)=2.30$, $P=0.14$, $R^2=2.7\%$
	Female Rank	-	$F(1,45)=5.29$, $P<0.05$, $R^2=8.5\%$
	Male Rank	-	$F(1,45)=14.51$, $P<0.05$, $R^2=22.7\%$
Resistance rate (POP)			**$F(3,27)=4.69$; $P<0.05$, $R^2=26.9\%$**
	*Male Age	+	$F(1,29)=4.79$; $P<0.05$, $R^2=11.2\%$
	*Group	+	$F(1,29)=0.51$; $P=0.48$, $R^2=-0.02\%$
	*Male Age×Group	+	$F(1,29)=2.41$; $P=0.11$, $R^2=8.6\%$
Resistance rate (Non-POP)	*Male Age	+	**$F(1,39)=4.60$; $P<0.05$, $R^2=8.30\%$**

[a] t-statistics in a simple regression: proceptivity in Non-POP: Female Rank×Male Rank: $t=3.81$; Female Rank: $t=-1.52$; Male Rank: $t=-2.30$; resistance in POP: Male Age: $t=2.19$; Group: $t=0.71$; Male Age×Group: $t=1.99$; resistance in Non-POP: Male Age: $t=1.94$.

Discussion

The results of this study indicate that, despite a male-dominant social system, all Taï chimpanzee females express proceptivity and resistance behaviors in sexual interactions with males. Females are more selective when they are most fertile (POP) and less selective when they are least likely to conceive.

Female sexual strategies

Females exhibit proceptive behavior, actively soliciting copulations from some males. Females also actively resist solicitations from males and attempt to avoid copulating with them. While the expression of these behaviors varies widely between individual females, most females use these behaviors in predictable ways in POP and Non-POP. Females are more resisting of male solicitations during POP, particularly to unwanted male solicitations (Figs. 3a, 4a); see also Pereira and McGlynn 1997). This is consistent with a female strategy to deflect solicitations of non-preferred males when females are most fertile (see also Soltis et al. 1999). In contrast, during Non-POP, many females are more proceptive and will actively solicit particular males (some preferring different males than in POP), even though they are not likely to be fertilized by these males. High proceptivity during Non-POP allows females to increase matings with all (particularly eschewed) males (Figs. 3b, 4c). Such a strategy allows females to mate promiscuously during Non-POP for non-reproductive reasons (such as paternity confusion) without much risk of conception. Other direct benefits, such as potential support, grooming and increased access to food may also be attained. Alternatively, proceptivity in Non-POP may also be a strategy to increase male competition. Female use of proceptive behavior early in the follicular cycle to get males interested and stimulate male-male competition may lead to the male most able to deter other competitors copulating during POP, thereby increasing a

female's chances of mating with a superior male (Clutton-Brock and Harvey 1976; Cox and Le Boeuf 1977), such that the reproductive interests of females and these males coincide (Hrdy 1997). The differences in female behavior between POP and Non-POP are unlikely to result from corresponding differences in female libidinousness because female proceptivity does not decrease and resistance does not increase toward preferred males in POP compared to Non-POP (Fig. 4b,d).

The combination of the POP and Non-POP strategies suggest that female chimpanzees may use a mixed strategy of promiscuity and selectivity, and may attempt to influence which males sire their offspring (see also van Schaik et al. 2000). In a similar vein, the graded-signal hypothesis (Nunn 1999) suggests that exaggerated sexual swellings in old-world primates such as chimpanzees, are probabilistic signals of ovulation, which allow females to manipulate male behavior across the cycle in order to both confuse and concentrate paternity. Recent studies on human hypothetical mate preferences also suggest variation in female strategies across the estrous cycle (Gangestad and Thornhill 1998; Penton-Voak and Perrett 2000).

In this study, we assayed female preferences by variation in (1) initial female responses to male solicitations, and (2) female solicitations of males. In this way, we have tried to distinguish female-based behavior from male influence. It is difficult to fully eliminate the possibility of male coercion, as aggressive or persistent behavior may influence females and confound the clear expression of mating preferences. While male coercion could affect some of our results, these effects appear limited for several reasons. Most generally, the fission-fusion social system, the ease of furtive mating and the rarity of forced copulations in chimpanzees (Goodall 1986) may allow females some freedom of association and mate choice, and could limit the influence of coercion. More specifically, while we might expect that females would be less likely to resist aggressive males, male aggression (and solicitation) rates were not correlated with female resis-

tance (or proceptivity). In addition, all Taï females attempted to resist solicitations by males of any rank. Females were consistently and highly resistant to one of the most aggressive males (MK), despite the expectation that aggression and coercion should decrease female resistance. Moreover, males that were highly resisted (eschewed) in Non-POP were also highly resisted in POP (Fig. 5b; also for proceptivity, Fig. 5a), suggesting that females were consistent in their aversion to these males (and similarly consistent for preferred males), despite potential variation in male behavior across the phases. Furthermore, one of the least resisted (and most solicited) males during Non-POP and POP was the lowest-ranking male SA (Fig. 5a,b). It is unlikely that SA needed additional female encouragement because male solicitation rates did not differ between males (Stumpf 2004).

Because males often closely guard females during the later stages of their maximal swellings, female proceptivity or acceptance of male solicitations during POP may result in aggression from higher-ranked bystanding males (Chapais 1983; Estep et al. 1986). However, females in this study were often proceptive to lower-ranked males in both swelling phases, even in close proximity to the alpha (Stumpf 2004). It is unlikely that higher female resistance (and lower proceptivity) in POP is a strategy to avoid aggression from bystanding males because female resistance rates were not uniformly higher (and proceptivity rates were not lower) toward all subordinate males in POP (or Non-POP, see Fig. 5a,b). Thus, females appear to express proceptivity and resistance behaviors toward males despite the potential for male coercion.

While no differences were found between male aggression and solicitation rates across estrus, non-parametric statistics have limited power to detect significant differences. Although results suggest that coercion or increased male interest are not affecting the findings of this study, the possibility cannot be entirely ruled out, and the potential influence of male coercion on the expression of female preferences deserves explicit testing in subsequent studies. Based on our observations, we recommend controlling for pre-solicitation and post-solicitation male aggression rates in future studies.

Which males are preferred and when?

Female proceptivity and resistance rates were not consistent toward all males, but varied substantially depending on the particular dyad, suggesting that females prefer particular males. Despite variation within individual females toward particular males, all South group females preferred ZY(1) or SA(4) while KA(2) and MK(4) were not preferred by any female. Previous data have suggested that male dominance rank is an important factor influencing female mate preference (humans: Alexander and Noonan 1979; capuchins: Janson 1984; baboons: Smuts 1985; Bercovitch 1991; chimpanzees: Wrangham 1986; Matsumoto-Oda 1999). Relative preference toward the South group alpha, ZY, in particular

increased during POP and this preference may help to explain ZY's greater siring success relative to subordinate males during his tenure as alpha (Vigilant et al. 2001; see also Constable et al. 2001). Infanticide is reported at all long-term chimpanzee sites (Goodall 1986; Hamai et al. 1992; Arcadi and Wrangham 1999; Boesch and Boesch-Achermann 2000; Watts and Mitani 2000), and data from Mahale suggest alpha males were mainly responsible for within-group infanticides, and that in these cases, mothers had mated predominantly with younger, subordinate males during the likely conceptive period (Hamai et al. 1992).

Although ZY (1) was most preferred in POP, the results of the current study do not support clear female preference for dominant males. In the South group, the lowest-ranking male SA received significantly higher proceptivity rates than other males during Non-POP, and SA (4) rivaled ZY (1) for experiencing low female resistance during POP. Similarly, in the North group, the dominant male MA was clearly eschewed by all females during POP (although this result cannot be supported statistically, the magnitude of the difference between MA and the other males is strongly suggestive of this interpretation; Fig. 5biv). Thus, on the surface, these results suggest there is no simple linear relationship between male rank and female preference. However, upon more detailed examination, in the North group MR (2), who was little resisted by females during POP, displaced alpha male MA early during the course of this study. Similarly, in the South group, while ZY remained undisputed alpha throughout this study, the lowest ranking and adolescent male, SA, increased the frequency of his challenges to the alpha, sired offspring shortly after maturity, had the continued support of his high-ranking mother (a factor important for attaining high rank in chimpanzees; Boesch and Boesch-Achermann 2000), and became alpha 1.5 years after this study ended.

Thus, in both study groups, females preferred subordinate males who, in turn, quickly ascended in dominance. Other primate studies have shown that females mate preferentially with males that eventually obtained high dominance rank (macaques: Duvall et al. 1976; Takahata 1982; Curie-Cohen et al. 1983; Kuester and Paul 1992; chimpanzees: Takahata et al. 1996), and paternity data suggest that up-and-coming dominant males have high reproductive success (Smith 1994; Utami et al. 2002). The observation that females' preference for subordinate males preceded each male's assumption of dominance provides support that females may anticipate which male will become alpha or may influence their rank ascension. However these data are only suggestive and more data are clearly needed before the relationship between female behavior and male rank can be properly assessed.

The link between male dominance and mating success, while generally supported, has proved equivocal in many primate studies (see Cowlishaw and Dunbar 1991 for review). Many reasons may exist for such findings. Studies such as this suggest that female preference for

(and thus increased mating opportunities for) subordinate males likely diminish this relationship (see also Soltis et al. 1997). In addition, the lack of consistent relationship between male rank and mating success may be due to the practice of grouping both POP and Non-POP phases together, which may produce a result quite different from that of either phase. Group dynamics and demographics are also important. Female preference for subordinates may be most apparent when hierarchies are less stable, and may predict a hierarchy change (see also Utami et al. 2002). In addition, group structure such as the lower male:female ratio and the greater female-female cohesiveness of the Taï population may allow females more opportunity to express mate preferences than in communities where males are more abundant and females are more isolated, as is found in most eastern chimpanzee communities (*Pan troglodytes schweinfurthii*).

Other factors affecting preference: female rank and age

During Non-POP, low-ranking females were more proceptive to low-ranking males, and higher-ranked females were more proceptive to higher-ranked males. Evidence has been found in other multi-male primates that copulatory partners sort by age and dominance rank (Takahata 1982; Hasegawa and Hiraiwa-Hasegawa 1990; Strier 1997; but see Small and Smith 1982; Manson 1997). This may be influenced by female proceptivity toward males of similar ranks and age, and driven by avoidance of mating with fathers, lack of access to older, higher-ranked males, or potential long-term social benefits from younger males. In this study, male age was an important factor influencing female resistance rates (Table 3), since females generally resisted older males more than younger males. Nishida (1997) also found higher resistance rates to older, non-alpha males, and hypothesized that this may be because older males have lower-quality sperm (see also Hansen and Price 1995). Older, never-alpha males may also be less preferred because: (1) they do not carry qualities important for potential dominance, (2) sexually transmitted infections likely correlate positively with age (C. Nunn, personal communication), and (3) offspring from older sires would be unlikely to benefit directly from these males for very long.

That male age, male rank and female rank only partly explain the variance in female preference indicates that, although these factors are important, there are other influences. Other factors may include male aggression and affiliation, other cycling females, and individual preferences. Another possibility that was not tested is the probability of conception, since this likely varies substantially from one cycle to the other, and may account for some variation in the expression of female preference towards particular males.

Evaluating hypotheses for multi-male mating and mate choice

Promiscuous mating occurs in many species, including chimpanzees, and several hypotheses have been proposed to explain why females mate with multiple males. The results of this study may be used to evaluate female-based hypotheses for the evolution of multi-male mating. One hypothesis, ensuring fertilization (Milton 1985; Hoogland 1998), is not supported by these behavioral data in chimpanzees. If sperm were in short supply and females had difficulty in finding mates, one would expect increased proceptivity and lower resistance rates toward all males in POP. Results from this study indicate that this pattern is not observed. Other hypotheses suggest that promiscuity may allow females to obtain genes from successful sperm competitors (Harvey and Bennett 1985; Keller 1985) or to exploit post-copulatory cryptic choice for genetically compatible sperm (Hurst et al.1996; Zeh and Zeh 1996; Jennions 1997). Under each of these scenarios, female promiscuity should be greater during the fertile phase, POP, compared to Non-POP, in order to attain the specified benefit. In contrast to this expectation, chimpanzee female sexual behavior limits sexual opportunities during POP since females are less proceptive and more resisting to males during POP than Non-POP. Thus, although chimpanzee females are promiscuous, this strategy does not promote sperm competition among males or genetic compatibility. Rather, these data lend support to Hrdy's (1997) arguments that, "to the extent that genes affect offspring quality, females should fare better under a 'priority of access' system (distinguishing between individual males) than under a system emphasizing priority of fertilization (distinguishing between sperm)".

One model that is supported by the data in this study is that females mate promiscuously to confuse paternity in the non-periovulatory phase, but not the periovulatory phase. Further studies that separately and comparatively assess female behavior during conceptive and non-conceptive periods may provide more insight into the evolution of multi-male mating.

In conclusion, in multi-male groups, the reproductive interests of males and females are often in conflict. Females have two possibilities: they may relinquish control over paternity to the males, or they may actively attempt to influence which males father their offspring. Results from this study indicate that females show preferences for particular males through variation in proceptivity and resistance behaviors. Greater proceptivity and less resistance during Non-POP than POP may help females to confuse paternity. Females are more selective (i.e., less proceptive and more resisting) during POP, suggesting that females do not mate indiscriminately, but try to influence paternity when most likely to conceive. Female reproductive success depends not only on offspring paternity, but also on offspring survival and fitness. Consequently, a strategy of promiscuity during Non-POP and selectivity during POP may provide females with the dual

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benefits of concentrating and confusing paternity. One implication of females' use of a mixed reproductive strategy is that female proceptivity and resistance during Non-POP may not accurately reflect their mate preference. Consideration of a female's mate preference during the constrained periovulatory period may provide the clearest insight into what females look for in potential sires and the strategies they use to promote fertilization by preferred males.

We expect such a mixed strategy of promiscuity and selectivity in many primates and other multi-male, multi-female species characterized by female multi-male mating and long non-conceptive estrous phases. Based on this expectation, we predict that female chimpanzees at other sites (i.e., Gombe, Mahale, and Kibale) use a similar mixed sexual strategy. Whether females are able to attain their preferences and influence mating frequencies, and ultimately affect which male sires her offspring, remains to be documented for this (and other) species.

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