

RESEARCH ARTICLE

Juggling Priorities: Female Mating Tactics in Phayre's Leaf Monkeys

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Extended sexual receptivity in primates is thought to facilitate paternity confusion, thus decreasing the risk of infanticide. However, females might also provide some indication of ovulation to attract preferred males during fertile periods. We examined female mate preferences across defined receptive periods ($N = 59$) in a group of wild Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) at Phu Khieo Wildlife Sanctuary (February–September 2006; 2,603 contact hours). The group contained seven cycling adult females and three reproductively active males (one adult and two adolescents). We predicted that females would prefer the adult male during periovulatory (POP) receptive periods, but the adolescent males during nonperiovulatory (NPOP) and postconceptive (PC) periods. We collected focal and ad libitum data on sexual and agonistic behaviors to determine female preferences and male awareness of female fertility. We also determined the degree of mating overlap to assess if males were capable of monopolizing females. Our results indicate that females were more frequently proceptive and receptive toward the adult male during POP. By contrast, females were more proceptive and receptive toward one of the adolescent males during PC periods, but rarely interacted with the other adolescent. Patterns of attractivity and agonism across receptive periods suggested that the adult male could detect fertility, while the preferred adolescent could not. Finally, we found a high degree of overlap in total receptive period days, but a low degree of overlap in POP receptive days, suggesting that the adult male might have monopolized females, especially since he seemed to be aware of female fertility. Although these results suggest that females provide some information on ovulation, they also suggest that females attempt to confuse paternity, perhaps capitalizing on male differences in the ability to detect fertility. *Am. J. Primatol.* 74:471–481, 2012. © 2012 Wiley Periodicals, Inc.

Key words: adolescent males; colobines; mate choice; postconceptive mating

INTRODUCTION

Among most mammals, female sexual behavior is confined to the period of “estrus,” when ovarian hormones simultaneously stimulate both ovulation and sexual behavior [Heape, 1900]. This tight coupling of reproductive function and behavior ensures that copulation occurs when conception is most likely [Wallen, 2001]. In contrast, most anthropoid primates are characterized by a more flexible mating pattern, with sexual receptivity (and in some species, tumescent sex skin swellings) also occurring outside of the periovulatory period (POP) [e.g., Brauch et al., 2007; Deschner et al., 2004; reviewed in Dixon, 1998; van Schaik et al., 2000]. In many primates, females even engage in sexual behavior during pregnancy, when conception is impossible [e.g., Borries et al., 2001; Engelhardt et al., 2007; Gust, 1994; Shelmidine et al., 2009]. These observations have led researchers to categorize anthropoid primates

as species with “concealed ovulation” [reviewed in Pawlowski, 1999; van Schaik et al., 2000]. Nevertheless, *rates* of female sexual behavior (as well as the size of swellings) often remain highest around ovulation [e.g., Carosi et al., 1999; Deschner et al., 2003; Engelhardt et al., 2005; Gesquiere et al., 2007;

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Higham et al., 2009; O'Neill et al., 2004; van Belle et al., 2009; reviewed in van Schaik et al., 2000], suggesting that fertility may honestly be advertised, at least some of the time.

At a functional level, females may benefit from employing a dual strategy of both "honest" and "dishonest" sexual behaviors, particularly in a promiscuous mating system [Nunn, 1999; Stumpf & Boesch, 2005] where male rank may influence the likelihood of mating with a receptive female. On the one hand, an extended period of receptivity decreases the likelihood of being monopolized by a single male [Hrdy, 2000]. By mating with several males, females may confuse paternity, thus reducing the incentive for males to commit infanticide [Hrdy, 1979]. Paternity confusion may also increase the likelihood that males will provide direct benefits to females or their offspring, such as infant carrying, tolerance during feeding, and protection from infanticide and/or predation [Borries et al., 1999; Crockett & Sekulic, 1984; Deag, 1980; van Schaik, 1994]. On the other hand, it may also be advantageous for females to advertise fertility when the likelihood of conception is high in order to increase the chances of mating and conceiving with the highest quality male [Clutton-Brock & McAuliffe, 2009; Maynard Smith, 1991]. Females might, therefore, be expected to prefer high-quality (which for primates is often equivalent to high-ranking) males around ovulation, but other males during nonfertile periods [Engelhardt et al., 2005; Stumpf & Boesch, 2005]. Indeed, in several primate species, females were found to direct proceptive and receptive behaviors more frequently toward high-ranking males during the POP, while showing no preference or favoring other males outside of the POP [Barelli et al., 2008; Knott et al., 2010; Stumpf & Boesch, 2005] and during pregnancy [Carnegie et al., 2004, 2005; Engelhardt et al., 2007; Gordon et al., 1991].

However, patterns of female sexual behavior may also reflect male reproductive tactics. Although proceptive behavior measures female initiative, receptive behavior such as copulation depends on both female and male initiative. In other words, high rates of receptive behavior toward a dominant male may indicate female preference for the male, the male's ability to monopolize particular females, or both. Moreover, the degree to which males are able to monopolize females might additionally be influenced by the degree of overlap in female receptivity [Ostner et al., 2008] and/or the ability of males to accurately detect ovulation [Gust, 1994]. Although a male's ability to detect ovulation has generally been assessed via rates of attractive behaviors (e.g., rates of male inspection and sexual solicitation), patterns of sex-related agonistic behaviors may also provide some information. Specifically, males may take on the risks associated with aggression only when the outcome (i.e., herding away a female or male from an

attempted copulation, or preventing a female from leaving) will increase his chances of siring offspring relative to other males. Therefore, if the frequency of male-directed agonism in the context of sex is greater during POPs relative to both non-POP (NPOP) and postconceptive (PC) periods, one can conclude that males are able to detect female fertility accurately.

In the current study, we use 8 months of behavioral and hormonal data from seven females to investigate mating patterns, female mate preferences, and male detection of ovulation in a wild group of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). Phayre's leaf monkeys live in groups containing 1–5 adult males and 3–12 adult females [Koenig & Borries, 2012], with mating patterns ranging from polygynous to promiscuous, depending on the composition of the group. Sexual swellings are absent, as might be expected for groups with variable or small numbers of adult males [Nunn, 1999]. Groups are generally cohesive, but individuals or subgroups may occasionally range >300 m apart. Menstrual cycles are 30 days long, on average [Lu et al., 2010]. Males are philopatric and begin mating with adult females as adolescents (defined by full descent of testes). Once adult, young males commonly outrank older adult males [Koenig & Borries, 2012].

Although studies of female mating tactics in primates have thus far focused on female mate choice in relation to *adult* males, examining mate choice in relation to both adult and adolescent males may provide an interesting comparison, particularly in cases where natal males remain in the group, eventually rise in rank, and become potential threats as adults. Furthermore, since adolescent males in Phayre's leaf monkeys are typically subordinate to and either the same size as or smaller than adult females, mating with an adolescent male should be a strong indicator of female choice (since adolescents cannot monopolize adult females). Our study therefore focuses on male–female sexual interactions in a group with one dominant adult male and two adolescent males.

We had three major objectives. First, we investigated female sexual behavior during potentially fertile (perioovulatory phase (POP)) and nonfertile (nonperioovulatory phase (NPOP) and PC) receptive periods to determine if ovulation is concealed. Second, we investigated whether and how the rate of proceptive and receptive behaviors differed across fertile and nonfertile receptive periods for each male, evaluating the hypothesis that females would prefer the adult male during fertile periods and the adolescent males during nonfertile periods. Finally, we assessed patterns of attractive behaviors, sex-related male agonism, and overlap in female receptivity to determine if males had any awareness of female fertility, and to determine if males could monopolize females. We predicted that if males could detect fertility accurately, they should be more attracted to females and be engaged in the highest proportion

of sex-related agonism during fertile receptive periods. More specifically, males should direct agonistic behavior toward other males or toward females when mating matters most (i.e., during POP).

METHODS

Subjects and Study Period

We collected data from a group of wild Phayre's leaf monkeys at Phu Khieo Wildlife Sanctuary, Thailand (16°5'–35'N, 101°20'–55'E, Chaiyaphum Province, elevation: 300–1,300 m above sea level). Our research was part of a long-term project (directed by A. Koenig and C. Borries) that began in October 2000. Between February and September 2006, we collected behavioral and hormonal data on one group, called PB. We habituated this group in 2004, and demographic data were available since June 2003 [Koenig and Borries, unpublished data]. All research complied with the protocols of the IACUC committee at Stony Brook University (IDs: 20041120–20061120) and adhered to the laws of Thailand and the American Society of Primatologists' Principles for the Ethical Care and Treatment of Nonhuman Primates.

During the study period, the PB group contained ten multiparous adult females, one adult male, two adolescent males, and 15–16 younger individuals. Based on the mean interbirth interval and observed mating patterns [Lu et al., 2010], we targeted seven cycling females for the collection of behavioral and hormonal data. All seven females cycled and conceived during the course of the study. Although absolute ages for females were unknown, relative estimates based on skin wrinkling, color of eye lens, and nipple length [Hrdy, 1977] indicated that most females ($N = 6$) were either young or prime adults, with only one female beyond prime age.

Fecal Hormone Collection and Analysis

We collected fecal samples at least every other day and often daily ($N = 24.1 \pm SE 0.6$ samples/female/month; 1,399 samples in total) from cycling females. Because conception for Phayre's leaf monkeys cannot be determined based on external cues, we continued this collection rate until the end of the study. We later confirmed the reproductive status of all females with ovarian hormone analyses [Lu et al., 2010]. We collected samples in 30 ml plastic vials, which were kept in a portable cooler in the field, and frozen (-20°C) upon return to the field station (within 2–13 hr). Upon conclusion of the study, we shipped all samples on ice to the center for Conservation and Research of Endangered Species (CRES, Zoological Society of San Diego, Escondido, CA). In San Diego, we lyophilized the samples, sifted them through mesh wire (16 \times 16 mesh), and transported them to the Core Assay Facility in the Department

of Psychology at the University of Michigan for extraction and radioimmunoassay. Following protocols established by Wasser et al. [1994], we extracted a 0.1 g portion of each sample twice with ethanol. We then dried these extracts under nitrogen gas, reconstituted them in 1 ml of 100% ethanol, and stored them at -20°C until radioimmunoassay. We examined extracted samples for fecal estrogen (fE) and fecal progesterin (fP) metabolites following previously validated protocols [Lu et al., 2010]. Intra-assay CVs for high (20% binding) and low (80–85% binding) fecal pools were 2.8% and 7.2%, respectively, for progesterins and 6.2% and 1.7%, respectively, for estrogens. Interassay CVs for high and low fecal pools were 9.9% and 16.3%, respectively, for progesterins and 6.0% and 10.6%, respectively, for estrogens. Assay sensitivity was 6.25 ng/ml for progesterins and 5 pg/ml for estrogens.

Defining the POP

Because fP levels were subject to seasonal plant-induced fluctuations that obscured cycling patterns for a portion of the study period [Lu et al., 2011], we used daily means of fE levels to construct hormone profiles. We identified 20 fE peaks during this period. Based on the pattern of fE in relation to fP prior to the seasonal fP rise, we assumed that ovulation occurred within a day (mean = 0.55 days; range = 0–2 days) after the surge in estrogen. Herein we refer to the day of the fE peak as Day 0. Thus, 1 day before the fE peak is Day -1 , 1 day after the peak is Day 1, and so forth. All days were assigned post hoc once hormone data were available. Due to a 1-day lag between secretion and excretion of fecal hormones [Lu and Czekala, unpublished; variation in time across species is 0–2 days: Bahr et al., 2000; Wasser et al., 1994], we defined Day -1 as the ovulation date and conceptions as ovulations that were followed by a continuous rise in fE levels [Lu et al., 2010].

Studies on humans have found that ova rarely survive beyond 24 hr [France, 1981] and that most conceptions result from sperm that have been in the reproductive tract for no more than 3 days [Wilcox et al., 1995]. Hence, many studies have defined the POP as 5 days long [Deschner et al., 2003; Engelhardt et al., 2005; Higham et al., 2008a], encompassing the 3 days prior to ovulation, the day of ovulation, and the day following ovulation, although more conservative estimates are also common [e.g., 7 days; Carnegie et al., 2004; Harris & Monfort, 2006; van Belle et al., 2009]. Based on these studies, we defined the POP as a 6-day window surrounding ovulation, comprising the 3 days prior to ovulation, the day of ovulation, and the 2 days following ovulation. We included 2 days (as opposed to just 1 day) following ovulation because fecal ovarian hormones do not allow us to determine an exact day of ovulation, but rather a 2-day range. In this way, we conservatively

include all probable days of ovulation. Consequently, we defined the POP as Day -4 to Day $+1$ relative to the fE peak. Note that although fE peaks have previously been used as indicators of ovulation, a peak in fE may occasionally lead to an anovulatory cycle (no fP rise associated with ovulation and the formation of the corpus luteum). Therefore, some of our “POPs” may have been anovulatory.

Behavioral Data

We followed the study group for 220 of the total 240 days of the study period, resulting in 2,603 contact hours with the group. During observational periods, we collected focal and ad libitum data on sexual and agonistic behaviors. Focal data were collected continuously during 20-min periods, rotating through females in a predetermined order such that all females were sampled 14 times/month, with sampling periods for each female distributed evenly across the hours of the day. In total, we collected 4.67 hr of data/female/month (42.00 hr in total for each female). Ad libitum data were collected throughout the day by multiple observers (usually one individual at a time in addition to A. Lu). Most of the time, these observers were following females for the collection of fecal samples, simultaneously noting any instances of sexual behavior that they observed.

We recorded proceptive, receptive, and attractive behaviors [Beach, 1976]. Proceptive behavior included female presentation of the hindquarters, head shaking, and inviting (simultaneous presenting and headshaking) toward any adolescent or adult male. Receptive behavior included copulations (mount with intromission—visually determined by thrusting behavior) as well as attempted copulations (mounting only) [Sommer et al., 1992]. Finally, attractive behavior included male solicitations and inspections of female hindquarters (including visual, olfactory, and manual inspections). Male inspections were often, but not always, preceded by female proceptive behavior. For agonistic behaviors, we included displacements and any form of aggression (contact aggression, chase, etc.) [see Lu et al., 2008 for a complete list of the behaviors and their definitions] occurring within the context of mating. Within this definition, displacements ($N = 3$) consisted of two types of events: (1) a male displacing another male involved in a sexual encounter ($N = 2$), or (2) a male approaching a female directly following termination of mating and the female subsequently leaving, vocalizing in apparent distress ($N = 1$). No resources were involved in either situation, leading us to categorize these events as sex-related displacements.

We defined receptive periods as a set of consecutive days (not interrupted by more than 2 days) during which sexual behavior occurred. Note that this definition is rather strict compared to defini-

TABLE I. Number of Receptive Periods per Female

Female	NPOP	POP	PC	Total
B2	3	2	4	9
B3	1	4	3	8
B5	4	2	6	12
B6	1	2	6	9
B7		3		3
B9	4	3	4	11
B12	5	1	1	7
Total	18	17	24	59

NPOP = nonperioovulatory receptive periods; POP = perioovulatory receptive periods; PC = postconceptive receptive periods.

tions used in previous studies [Borries et al., 2001; Shelmidine et al., 2009; Sommer et al., 1992]. Specifically, our definition of the receptive period included only days when we observed actual or attempted copulations and *not* days when we observed proceptive behavior only. A receptive period could be 1 day long only when at least one copulation was observed (copulation attempts were not sufficient). Based on hormonal profiles, we distinguished three types of receptive periods: (1) POP for cycling females; (2) NPOP for cycling females; and (3) PC for pregnant females (Table I). POP receptive periods were defined as periods that overlapped the hormonally defined 6-day period around ovulation. NPOP receptive periods were defined as receptive periods occurring within any other portion of the ovarian cycle, and PC receptive periods followed the contraceptive receptive period.

Data Analysis

We combined focal and ad libitum data to calculate hourly rates of proceptive, receptive, and attractive behaviors based on the number of contact hours with the group [Ostner et al., 2006]. Although some individuals may be overrepresented because of this, we chose to combine our data because mating behavior was so rare and difficult to see, particularly on a rotating focal schedule, that our analyses would not have been possible with focal data alone. Because we changed our position in the group routinely and systematically when switching between females (for collecting focal or fecal data), we minimized at least some of the bias that might have resulted from combining our data. Furthermore, because rates of behavior were most often compared *within* each female across receptive periods, we believe that the biases in our analyses were very small. Nevertheless, any comparison of the rates calculated from this study to focal rates from other studies should be carried out with caution.

All sexual and agonistic behaviors were considered as either occurring or not occurring within a receptive period as a whole, while synchrony in

receptive periods was calculated as a percentage of total receptive period *days* that overlapped *days* of at least one other receptive period. Because data were non-normally distributed, we used nonparametric statistical tests for all analyses. To compare differences between POP, NPOP, and PC receptive periods, we used the Friedman test. We calculated a mean hourly rate of behavior for each type of receptive period for each female (Table I). Of the seven total females, one was excluded because she was observed to mate only during POP receptive periods. Additionally, the mothers of the adolescent males were excluded from analyses involving adolescent males. Post-hoc tests for Friedman comparisons were conducted in SPSS 18 following suggestions by Conover [1980]. In all post-hoc comparisons, we were interested only in differences between (1) POP receptive periods and (2) NPOP or PC receptive periods.

Alpha level was set at 0.05. With the exception of comparisons of behavior involving the two adolescent males (where no clear prediction was made), all post-hoc tests were one tailed. Because multiple comparisons (N = 5) were made for several data sets, we corrected for the inflated Type I error rate by using the Benjamini & Hochberg [1995] correction. Benjamini & Hochberg corrections are less conservative than traditional Bonferroni adjustments [Holm, 1979] and are therefore less likely to inflate the Type II error rate [Perneger, 1998]. Nevertheless, sample sizes are small and should be interpreted with caution.

RESULTS

Proceptivity and Receptivity: Overall

We identified a total of 59 receptive periods, of which 17 were POP (Table I). We were, therefore, able to distinguish POP receptive periods for 85% (17 of 20) of all hormonally defined POPs (Fig. 1). On average, receptive periods were 4.27 (±SE 0.64)

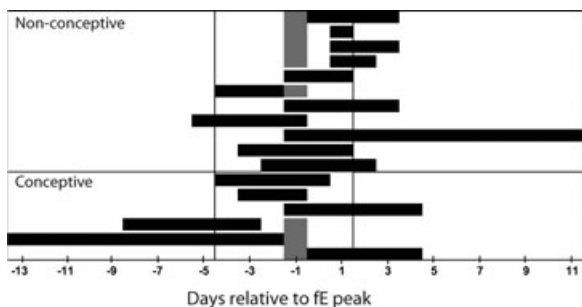


Fig. 1. Designated POP receptive periods (black horizontal bars) in relation to the hormonally defined periovulatory phase (bracketed by vertical lines). The estimated day of ovulation (Day -1) is indicated by the gray vertical bar, which is covered by the black horizontal bars when the receptive period overlaps that day.

days in length (median = 4.75, range = 2.78–7.33) with no differences between POP, NPOP, and PC receptive periods (Friedman test; N = 6; $\chi^2 = 1.33$, $df = 2$, $P = 0.513$). During receptive periods, females were proceptive toward males at a mean rate of 0.11 events/hr, and receptive at a rate of 0.20 events/hr (N = 6 females), although both rates were highly variable across females (proceptivity: 0.07–0.18 events/hr; receptivity: 0.11–0.34 events/hr). The rate of proceptivity differed across POP, NPOP, and PC receptive periods (Table II; Friedman test: N = 6, $\chi^2 = 8.33$, $df = 2$, $P = 0.016$) with significantly higher rates in POP compared to NPOP ($z_{adj} = -2.88$, $P = 0.006$), but not compared to PC receptive periods ($z_{adj} = 1.443$, $P = 0.223$). Similar results were found for receptive behavior (N = 6, $\chi^2 = 9.33$; $df = 2$, $P = 0.009$; POP–PC: $z_{adj} = -2.887$; $P = 0.006$), although differences between POP and PC receptive periods were also found ($z_{adj} = 2.31$, $P = 0.03$).

Proceptivity and Receptivity: Comparing Different Males

Overall rates of proceptive and receptive behaviors differed across males (Friedman test; proceptivity: N = 4; $\chi^2 = 6.50$; $df = 2$; $P = 0.039$; receptivity: N = 4, $\chi^2 = 8.00$; $df = 2$, $P = 0.018$), with higher rates for the adult male compared to one of the adolescents (m6.1; proceptivity: $z_{adj} = 2.83$; $P = 0.013$; receptivity: $z_{adj} = 2.48$; $P = 0.020$), but not the other (m12.1; proceptivity: $z_{adj} = 0.71$; $P = 1.000$; receptivity: $z_{adj} = 1.41$; $P = 0.472$). No significant differences were found between the two adolescent males (proceptivity: $z_{adj} = 1.77$, $P = 0.231$; receptivity:

TABLE II. Rates of Sexual Behavior Involving Each Male Across Receptive Periods (Based on Averages of Females)

Behavior	Receptive period	Rate of sexual behavior (events/hour)		
		M5 (N = 6)	m12.1 (N = 5)	m6.1 (N = 5)
Proceptive	NPOP	0.05	0.01	0.00
	POP	0.31	0.03	0.01
	PC	0.04	0.13	0.00
Receptive	NPOP	0.13	0.01	0.00
	POP	0.35	0.02	0.00
	PC	0.04	0.12	0.00
Attractive	NPOP	0.06	0.01	0.01
	POP	0.27	0.02	0.02
	PC	0.04	0.05	0.00

Data from respective mothers excluded in calculations for adolescent males m12.1 and m6.1. NPOP = nonperiovulatory receptive periods; POP = periovulatory receptive periods; PC = postconceptive receptive periods; N = number of females included in the calculation.

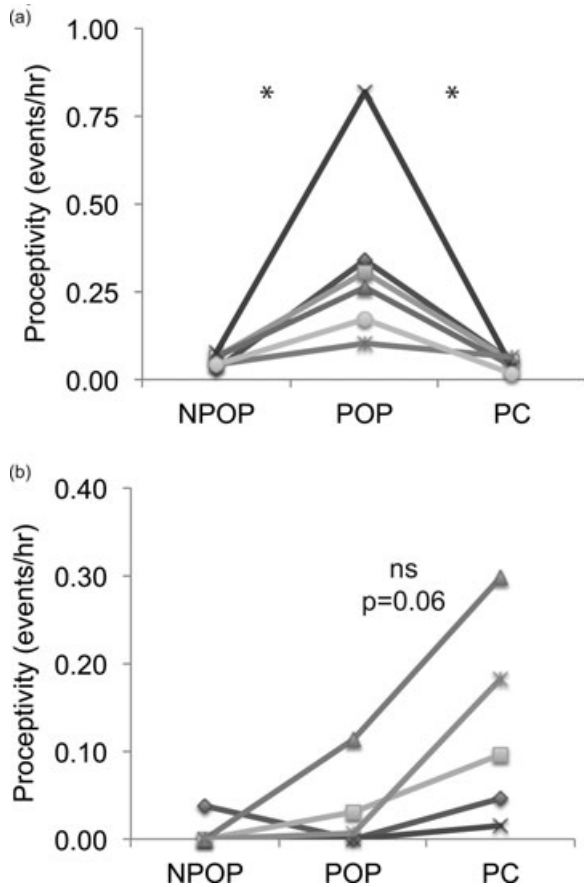


Fig. 2. Rates of proceptive behaviors during POP, NPOP, and PC receptive periods for the (a) adult male (M5) and the (b) preferred adolescent male (m12.1). Significant differences were found across receptive period types for each male (Friedman's test; M5: $N = 6$, $\chi^2 = 9.33$, $df = 2$, $P = 0.009$; m12.1: $N = 5$, $\chi^2 = 8.32$, $df = 2$, $P = 0.016$). Post-hoc differences were considered only between (1) the POP receptive and (2) the NPOP and PC receptive periods. Significant differences between receptive periods are indicated by asterisks ($\alpha = 0.05$). Each line represents a different female.

$z_{adj} = 1.41$, $P = 0.472$), although both behaviors were more often directed at m12.1 ("the preferred adolescent"; Table II).

Females were more often proceptive toward the adult male during POP relative to both NPOP and PC receptive periods (Friedman test: $N = 6$, $\chi^2 = 9.33$, $df = 2$, $P = 0.009$; see also Fig. 2 for significant post-hoc tests). However, rates of receptivity toward the adult male were higher during POP compared to PC receptive periods only, and not to NPOP receptive periods (Friedman test: $N = 6$, $\chi^2 = 12.00$, $df = 2$, $P = 0.002$; post-hoc: POP-PC, $z_{adj} = 2.00$, $P = 0.001$; POP-NPOP, $z_{adj} = 1.732$, $P = 0.13$). Rates of proceptive and receptive behaviors toward the preferred adolescent male (m12.1) also differed across receptive periods ($N = 5$, proceptivity: $\chi^2 = 8.32$, $df = 2$, $P = 0.016$; receptivity: $\chi^2 = 8.44$, $df = 2$, $P = 0.015$). In contrast to the adult male, however, females directed proceptive and receptive behaviors more

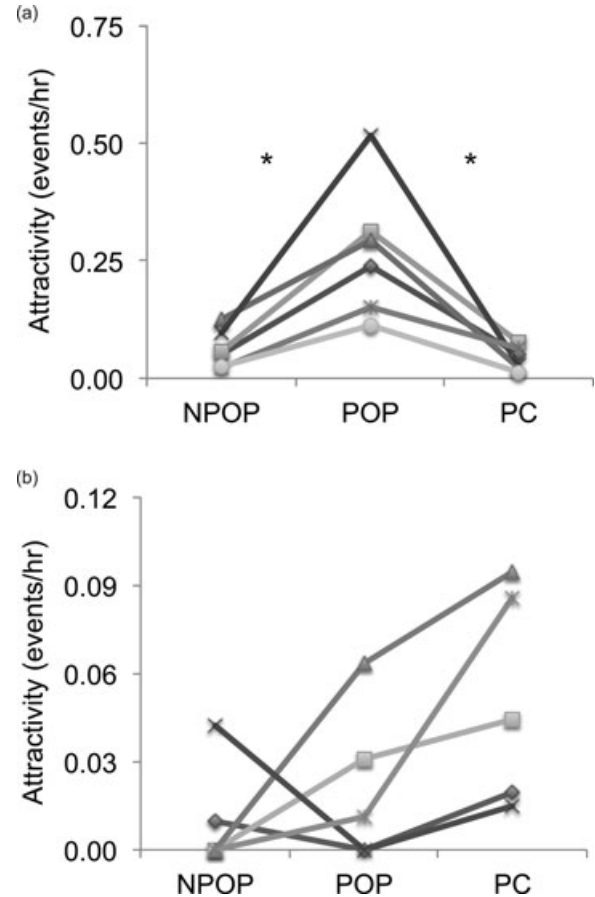


Fig. 3. Rates of attractive behaviors during POP, NPOP, and PC receptive periods for the (a) adult male (M5) and the (b) preferred adolescent male (m12.1). Significant differences were found across receptive period types for the adult male (Friedman's test; M5: $N = 6$, $\chi^2 = 9.00$, $df = 2$, $P = 0.011$), but not the preferred adolescent male (m12.1: $N = 5$, $\chi^2 = 4.80$, $df = 2$, $P = 0.091$). Post-hoc differences were considered only between (1) the POP receptive and (2) the NPOP and PC receptive periods. Significant differences between receptive periods for the adult male are indicated by asterisks ($\alpha = 0.05$). Each line represents a different female.

frequently toward m12.1 during PC periods compared to POP receptive periods (proceptivity: $z_{adj} = -2.69$, $P = 0.06$, ns trend; receptivity: $z_{adj} = 2.21$; $P = 0.04$; Fig. 2 for proceptivity). There were no significant differences across receptive periods in the rate at which females directed sexual behaviors toward the nonpreferred adolescent (m6.1; Friedman test; proceptivity: $\chi^2 = 5.143$, $df = 2$, $P = 0.076$; receptivity: $\chi^2 = 4.00$, $df = 2$, $P = 0.135$).

Attractivity

Similar to rates of proceptive and receptive behaviors, males were attracted to females at different rates across receptive periods, with the pattern again differing for each male. Specifically, the adult male was more attracted to females during POP relative to both NPOP and PC receptive periods (Fig. 3a;

TABLE III. Number of Agonistic Interactions Between Sexually Active Males and Adult Females Across Different Receptive Periods

Actor to recipient	NPOP	POP	PC	Totals
Male to male	0	9 (9) ^a	1	10
Male to female	0	9 (8)	1	10
Female to male	0	8 (1)	0	8
Female to female	0	0	2	2
Other	2	4	1	7
Total	2	30	5	37

^aInteractions involving the adult male are indicated in parentheses. NPOP = nonperioovulatory receptive periods; POP = perioovulatory receptive periods; PC = postconceptive receptive periods.

Friedman test: $N = 6$; $\chi^2 = 9.00$, $df = 2$, $P = 0.011$; post-hoc POP-PC: $z_{adj} = -2.60$, $P = 0.014$; POP-NPOP: $z_{adj} = -2.60$, $P = 0.014$). However, there were no significant differences in the rates at which the preferred (Fig. 3b; $N = 5$, $\chi^2 = 4.80$, $df = 2$, $P = 0.091$) or the nonpreferred ($N = 5$, $\chi^2 = 0.29$, $df = 2$, $P = 0.867$) adolescent male was attracted to females across receptive periods.

Agonistic Behavior

Of 3,949 agonistic events observed during the study period, only 37 (<1%) occurred in the context of sexual behavior, with the majority ($N = 30$) taking place between adults. Of these 30 events, 87% took place during POP receptive periods, with the same trend characterizing male-to-male aggression, male-to-female aggression, as well as female-to-male aggression (Table III). Notably, the adult male was the aggressor in 100% of male-to-male (100% of POP) and 80% of male-to-female encounters (89% of POP). In contrast, adolescent males, specifically m12.1, was very rarely the aggressor in either type of encounter (0% of male-to-male, 20% of male-to-female), with only one encounter each occurring during POP and PC receptive periods. Finally, of the eight encounters involving female-to-male agonism, 88% involved refusal of mating with the adolescent male m12.1.

Receptive Period Overlap

We observed 53% (78 of 146) of receptive period days during which two or more females were simultaneously receptive and 26% (38 of 146) during which three or more females were simultaneously receptive. In theory, males could still monopolize females if there was less overlap in receptive period days during POP receptive periods. When we considered all types of receptive periods, we did not find this pattern; POP receptive period days overlapped with those of another receptive period 63% of the time, compared to 70% for NPOP and 55% for PC receptive period days. However, if only POP receptive periods were considered, then 19% (9 of 48) of POP receptive period days overlapped with other POP re-

ceptive period days. Hence, a male could have easily monopolized females during their POP receptive periods if he were able to distinguish potentially fertile from nonfertile periods.

DISCUSSION

Consistent with the studies on a variety of other primates [e.g., Borries et al., 2001; Brauch et al., 2007; Carnegie et al., 2004, 2005; Engelhardt et al., 2005, 2007; Heistermann et al., 2001; Pazol, 2003; reviewed in van Schaik et al., 2000], female leaf monkeys were receptive during both fertile and nonfertile periods. However, proceptive and receptive behaviors were significantly more frequent during fertile (POP) relative to nonfertile NPOP receptive periods, but not necessarily relative to nonfertile PC receptive periods. Much of the discrepancy between the two categories of nonfertile receptive periods can be accounted for by different patterns of mating with respect to each male. Specifically, females exhibited more “interest” in the dominant male during POP, while interest in the preferred adolescent male peaked during the PC period. This interest was reflected in both higher rates of advertisement (proceptivity) and higher rates of mating (receptivity). Although our sample size was small, these results support the hypothesis that females preferred the adult male during POP.

Patterns of agonistic data also support this hypothesis. Mainly, female-to-male aggression resulted from females refusing to mate with one of the adolescent males (m12.1) during POP receptive periods. These results are consistent with studies on chimpanzees and orangutans [Knott et al., 2010; Stumpf & Boesch, 2005], where females more often rejected lower-quality males while accepting the advances of higher-quality males.

In general, patterns of attractive behavior mirrored those of proceptive and receptive behaviors. This was particularly the case for the adult male, who was more attracted to females during POP relative to both NPOP and PC receptive periods (Fig. 3). The adult male was also involved in the highest proportion of agonistic encounters, particularly during POP relative to other receptive periods. These patterns certainly suggest that the adult male could detect female fertility accurately. They may also suggest that the reproductive strategies of adult females and the adult male worked in concert with one another.

However, Muller et al. [2011] have recently argued that if higher rates of male interest and female proceptivity during POP truly reflect shared strategies, male aggression toward females should be low during POP. In other words, if females are “cooperating,” male aggression should be unnecessary. In our study, we found that both male-to-male and male-to-female aggression rates were actually

highest during POP. Hence, based on the agonistic data, we cannot rule out the alternative hypothesis that higher rates of sexual behavior involving the adult male during POP were a general result of male coercion rather than female choice [Muller et al., 2007].

Our data on the monopolizability of females also fail to resolve this issue. On the one hand, the majority of receptive period days in this study were synchronous with the receptive period days of at least one other female, suggesting that males were unlikely to monopolize or monitor all receptive females simultaneously. However, when we examined synchrony among fertile receptive periods only, we found that the level of synchrony was much lower, suggesting that one male could easily have monopolized all fertile females, if he, indeed, had the ability to discriminate female fertility.

Our results—a higher rate of proceptivity and receptivity during fertile periods coupled with the ability of the adult male to monopolize females—are, therefore, consistent with two possibilities: either male and female strategies worked in concert or the adult male coerced females into mating with him during POP. Note, however, that during POP periods, females were aggressive toward the adolescent male even if the adult male was nowhere in sight. Furthermore, several of the male-to-female aggressive events occurred in the context of mating interference by an immature (often the female's infant). Hence, many of the aggressive events cannot be interpreted as attempts by the dominant male to guard females from other males. We, therefore, believe that female choice is a more likely explanation for our results.

Interactions Between Females and Adolescents

In relation to the adolescents, females seemed to show a clear preference for one male (m12.1) over the other (m6.1). Although m12.1 was the higher ranking of the two, both were of similar age and size. Furthermore, both males were subordinate to and either the same size as or smaller than adult females [adult females varied in body size; Koenig and Borries, unpublished data], suggesting that m12.1 could not have mated without the cooperation of the female.

Female preference for specific subordinates and/or adolescents has previously been documented in chimpanzees [Stumpf and Boesch, 2005], where preferred subordinates were generally those rising in dominance rank. Female leaf monkeys may have had a similar basis for their preference of m12.1 because he became the alpha male 9 months later [the other male, m6.1, dispersed; Koenig and Borries, unpublished data]. Although these events suggest that females may have had some awareness of male

“potential,” the causality is uncertain. In other words, we cannot be certain that female preference did not influence male rank acquisition.

Interestingly, patterns of attractivity involving the preferred adolescent male suggest that, unlike the adult male, the adolescent male's ability to detect female fertility was poor. Specifically, the rate at which he was attracted to adult females showed no differences across types of receptive periods. However, despite the fact that females initiated copulations more frequently with the preferred adolescent during PC receptive periods (Figs. 2 and 3), he was not more attracted to females during PC receptive periods relative to other periods. Although these results suggest that the adolescent male was unable to distinguish fertile from nonfertile periods, they also suggest that the attractiveness of females was not influenced solely by female initiative.

The most likely explanation for these results is that males are assessing female fertility using multiple cues [Engelhardt et al., 2004; Higham et al., 2008b]. It has long been known that males attend to both behavioral [e.g., proceptive behaviors: Carosi et al., 1999; Engelhardt et al., 2005; e.g., copulatory calls: Engelhardt et al., 2004] and visual signals [e.g., color and size of sexual swellings: Dahl, 1986; Higham et al., 2008b; reviewed in Nunn, 1999 and Pagel, 1994; facial coloration: Dubuc et al., 2009] when assessing female fertility. Recent studies have also suggested that male primates, including humans, use olfactory cues [Cerdeña-Molina et al., 2006; Clarke et al., 2009; Miller & Maner, 2010] to assess the reproductive potential of females. Because olfactory cues, as chemical signals, might be more difficult to “fake” and thus a better indicator of a female's physiological state [Hasson, 1994], males may attend more strongly to olfactory cues rather than behavioral ones.

PC Mating

Perhaps the most puzzling result of this study was that females preferred to mate with the adolescent male during PC, but not during NPOP receptive periods. Presumably, if females are seeking to confuse paternity, they should mate with less preferred males during *all* nonfertile periods. One possible explanation is that because PC receptive periods occurred predominantly in the latter half of the study period (while the adolescent male was maturing), the greater degree of female interest in this male during the PC period may simply be a by-product of his age. As this male grew older, females became more receptive to him, and this just happened to coincide with most females' PC periods.

Although PC mating has been documented in several species of colobines [Borries et al., 2001; Harris & Monfort, 2006; Li & Zhao, 2007; Sheldidine et al., 2009; Sommer et al., 1992] and occurs in

59% (36 of 61) of primate species investigated [van Noordwijk & van Schaik, 2000], its systematic occurrence across one-male and multi-male groups and its stereotyped occurrence during specific periods of pregnancy have suggested that PC mating is nothing more than a hormonal by-product [Saayman, 1975; reviewed in Engelhardt et al., 2007] and cannot be an effective female strategy for paternity confusion [Sommer, 1994].

However, hormonally induced PC mating may facilitate paternity confusion if males use previous mating experiences as a simple “rule of thumb” for assessing paternity. Whether this is indeed the case is debatable. In Hanuman langurs, males that mated only with pregnant females never defended the resultant offspring and most attacked them [Borries et al., 1999], suggesting that males were aware that pregnant females were unable to conceive even if they were sexually receptive. However, several studies have suggested that males have differential abilities in detecting female fertility [Engelhardt et al., 2007; Gust, 1994], suggesting that PC mating may confuse paternity effectively for at least some males. This may be particularly true if males require experience to detect fertility from nonbehavioral signals (e.g., olfactory or visual cues). In support of this hypothesis, a recent experimental study on macaques has shown that males are more likely to discriminate between fertile and nonfertile females based on facial coloration (an indicator of fertility in this species) if the female was a familiar social partner [Higham et al., 2011]. Familiarity in this case was defined as whether or not a male had spent the last two mating seasons in the same group as the female. Young, inexperienced males may have less success in distinguishing fertile from nonfertile periods simply because they have spent less time associating with receptive females. Because an increasing number of studies have demonstrated that PC mating primarily involves subordinate males [e.g., Carnegie et al., 2005; Engelhardt et al., 2007; Gust, 1994], additional experimental studies (e.g., preference tests) are needed to determine whether young males differ from older males in their ability to discriminate female fertility, and whether this difference is due, in part, to experience. These assessments will be crucial for determining whether PC mating is actually an adaptive strategy for females.

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