Can male white-faced saki monkeys (*Pithecia pithecia*) detect female reproductive state?

C.L. Thompson[1,3)], **P.L. Whitten**[2)] **& M.A. Norconk**[1)]

([1] Department of Anthropology and School of Biomedical Sciences, Kent State University, Kent, OH, USA; [2] Department of Anthropology, Emory University, Atlanta, GA, USA)

(Accepted: 3 October 2011)

Summary

For mammalian males, copulating with females during ovulation is critical to reproductive success. However male knowledge of ovulation may not always be advantageous for females, as it could hinder mate choice or promote harassment. White-faced saki monkeys live in variably monogamous and polygamous social groups and hence females may have multiple motivations to conceal ovulatory timing. White-faced sakis further show no obvious physical or behavioral signs of ovulation, although they do use scent in a variety of contexts, including sexual behavior. We collected data on three wild groups of white-faced sakis at Brownsberg Naturepark, Suriname in order to assess whether male copulations are coordinated with female ovulatory timing. We recorded all occurrences of copulations and genital inspections, and collected fecal samples from females which were radioimmunoassayed to obtain estradiol and progesterone levels. We found that males copulated throughout the female reproductive cycle, although the association between copulation and reproductive state varied between dyads. Only one male–female dyad showed significantly more copulations than expected during ovulation. However four of five dyads copulated less than expected with pregnant females, suggesting that males may be able to differentiate cycling from non-cycling females. While genital inspections were distributed randomly with regard to female reproductive state, the decision to copulate was not: males were more likely to mate with both ovulating and cycling females than with non-cycling females after genital inspection. Regardless, males were not more likely to copulate with an ovulating vs. a cycling (non-ovulating) female. These data indicate that while males may receive olfactory information on female hormonal status, they do not make entirely accurate decisions with regard to copulation timing. This inaccuracy may be due to males' inability to detect ovulation, or alternately a lack of motivation to limit copulations solely to conceptive periods. Pair familiarity and sexual experience may also play a role in copulation accuracy.

[3)] Corresponding author's e-mail address: cthompson@neomed.edu

DOI:10.1163/000579511X605227

Behaviour 148, 1313-1331
Also available online - www.brill.nl/beh

Keywords: copulation, concealed ovulation, sexual experience, honest signals, estradiol, progesterone, primates.

1. Introduction

Since mammalian males and females utilize different strategies to maximize reproductive success (Trivers, 1972), traits that are beneficial for one sex may not be for the other. For males, copulating with females at (or near) the time of ovulation is critical to siring offspring. As such, there is presumably heavy selection on males to develop means of detecting female ovulation (Ostner et al., 2006). This information can be gained through behavioral, olfactory, pheromonal, visual, or auditory cues (Micheal & Keverne, 1968, 1970; Dixson, 1992; Ziegler et al., 1993; Converse et al., 1995; Rasmussen & Schulte, 1998; De Vleeschouwer et al., 2000; Ferris et al., 2001, 2004; Cerda-Molina et al., 2006; Heistermann et al., 2008; Higham et al., 2009; Charlton et al., 2010).

However, male ability to detect ovulation may not always benefit females. While females must inevitably conceive to gain reproductive success, concealing/obscuring ovulation from males can grant several advantages such as allowing females to more effectively exercise mate choice by decreasing male monopolization during ovulation (Kappeler & van Schaik, 2004), confusing paternity to reduce the risk of infanticide (Hrdy, 1977; Andelman, 1987; van Schaik et al., 1999; Heistermann et al., 2001), or enticing investment from males (Morris, 1967; Alexander & Noonan, 1979; Taub, 1980). Hence in certain cases, females may not be selected to provide honest indicators of their reproductive status. This ongoing battle between the sexes for females to hide/obscure ovulation and males to evolve mechanisms to detect it may result in males gaining partial, if not complete, knowledge of ovulatory timing. Evidence for such a phenomenon is emerging in some primate species (hanuman langurs, *Semnopithecus entellus*: Ostner et al., 2006; titi monkeys, *Callicebus moloch*: Reeder et al., 1998; pygmy marmosets, *Cebuella pygmaea*: Converse et al., 1995).

However, even if males are able to gain partial or full knowledge of ovulatory timing, both males and females may not be motivated to limit copulations solely to conceptive periods. It has been suggested that non-conceptive sex can serve an important function in reinforcing social bonds (Snowdon et

al., 2010), in which case individuals would benefit from engaging in copulations during all stages of female reproduction.

White-faced saki monkeys (*Pithecia pithecia*) are arboreal New World primates that live in small social groups with generally 1–3 adult males and 1–3 adult females (average group size 3.2 individuals) (Norconk, 2011). Groups occur variably in two-adult groups (a single male–female pair with offspring) and small multimale–multifemale groups with monogamous or polygamous mating (Lehman et al., 2001; Thompson, 2011). Thus, white-faced saki females may benefit from concealing ovulation through enticing male investment (for instance, to provide year-round territory defense, which is often associated with monogamous mating systems), as well as confusing paternity, which would be expected in polygamous mating systems. White-faced saki males, on the other hand, may face differing levels of selection to pinpoint ovulation, depending on their group's social structure and degree of mating competition.

White-faced sakis lack obvious physical or behavioral changes that signal the timing of ovulation (Savage et al., 1993, 1995; pers. obs.) and females have not been observed to actively solicit copulations from males. Yet they possess gular, sternal, and circumanal scent glands (Hill, 1960; Epple & Lorenz, 1967; Brumloop et al., 1994) and like many mammals, use scent in a variety of contexts including the marking of regular travel routes, marking during between-group encounters, identification of familiar/unfamiliar individuals, and genital inspections of group members (Dugmore, 1986; Setz & Gaspar, 1997; Gleason, 1998; Buzzell, 2006; pers. obs.). Given this prevalence, it is possible that olfactory or pheromonal cues could signal reproductive events in this species. Indeed, Setz & Gaspar (1997) proposed that scent marking may play some role in sexual communication, although this hypothesis has not been further investigated. White-faced saki females cycle regularly ($\sim$17 day cycles: Shideler et al., 1994; Savage et al., 1995; Norconk, 2006) between pregnancies (Shideler et al., 1994; Savage et al., 1995), but there is a trend toward birth seasonality with a peak from November through June in both captive and wild populations (Savage et al., 1995; Waters, 1995; Norconk, 2006).

We assessed the relationship between physiological reproductive variables and sexual behavior in three free-ranging groups of white-faced saki monkeys at Brownsberg Naturepark, Suriname. Specifically, we asked: (1) do

white-faced sakis copulate during all phases of a female's reproductive cycle? (2) Do males make accurate copulation decisions in regard to female reproductive state (i.e., copulate only with ovulating females)? And (3) is this decision aided by olfactory information?

2. Methods

2.1. Study site and behavioral data collection

Data were collected on three groups (Junco, Mazaroni, Peach) of white-faced saki monkeys at Brownsberg Naturepark, Suriname (5°01′N, 55°34′W) from June 2008–October 2009. See De Dijn et al. (2007) and Lim et al. (2005) for a description of the study site. Groups varied in composition: Junco group (habituated in 2005) had 1 fully adult male (JM1), 1 old subadult male (JM2), 2 adult females (JF1, JF2), 1 young subadult female, 1 juvenile, and 1 infant born during the study; Mazaroni group (habituated in 2008) had 1 fully adult male (MM1), 1 old subadult male (MM2), 2 adult females (MF1, MF2), 1 young subadult male, and 1 infant born (and died) during the study; Peach group (habituated in 2003) had 1 adult male (PM), 1 adult female (PF), and 1 infant born during the study. JM2 and MM2 were old subadults at the start of this study, and would be better classified as full adults by the end. When birthdates were unknown, male age class was based on body size and fullness of the facial mask, a sexually dimorphic trait that is fully expressed by 3.5–4 years (Norconk, 2006). Female age classification was based on the hormonal data collected during the study period; females who consistently cycled were classified as adults, while subadult females began cycling during the study. Dates of birth and group history are provided in Thompson & Norconk (2011). Total observation hours with groups were: Junco 1295.5, Mazaroni 658.4 and Peach 860.1 h. All-day follows were conducted on groups in rotating four-day blocks by one to three observers. During follows, all occurrences of copulations and genital inspections (GI) were recorded, noting date, time and individuals involved.

2.2. Fecal hormone analysis

Fecal samples were collected opportunistically from all female study subjects. Samples could not always be regularly obtained due to rotating four-day group follows and the difficulties of acquiring and identifying the source

of the samples. A total of 157 fecal samples were collected from reproductive females (for each female: PF = 85; MF1 = 24; MF2 = 21; JF1 = 27). For Mazaroni group, it was difficult to collect samples early in the study as the group was recently habituated, and regular samples were not obtained until February (MF2) or April (MF1), 2009. The average number of samples per month for each female was: JF1 = 1.7, MF1 = 3.3, MF2 = 3.0, PF = 5.2. Collected samples were labeled with date, time, and individual, and were placed in a Gardenmaster® food dehydrator (Model UH 510825) set at 50°C until dry (approximately 10 days). Samples were then weighed and stored in sterile WhirlPak® bags.

Hormonal analyses were conducted at Emory University's Laboratory of Reproductive Ecology and Environmental Toxicology. Dried samples were ground with mortar and pestle; 0.1 g of dried feces was solubilized in 2 ml methanol/water (8:2) solution and vortexed. Particulate matter was filtered by centrifugation for 10 m (at 1500 × *g*) through a 0.2-μm Nylon centrifuge filter (Centrex MF® Disposable Microfilter, Whatman: Schleicher & Shuell, Florham Park, NJ, USA). The filtrate was then diluted with 2 ml water and vortexed. Finally, the filtrate was extracted into 3 ml methanol/water (8:2) solution with primed Sep-Pak VAC C18 cartridges (Waters, Milford, MA, USA) and frozen at −71°C.

Estradiol and progesterone levels were measured via radioimmunoassay using standards and reagents from MP Biomedicals (Orangeburg, NY, USA): [^{125}I]17β-Estradiol and [^{125}I]progesterone kits. For estradiol (E_2), aliquots of fecal extracts were evaporated under nitrogen and reconstituted 3:1 with 50 μl of 0 pg/ml standard. E_2 tracer (500 μl) and 500 μl E_2 antibody were added to samples, standards and controls. Samples, standards and controls were then vortexed and incubated for 90 min at 37°C. Then, 500 μl precipitant solution was added; thereafter, vials were vortexed and centrifuged at 1000 × *g* for 15 min at 8°C. The supernatant was decanted and radioactive precipitates determined via 1-min counts in a gamma counter. Similar procedures were followed for progesterone, except samples were reconstituted 1:1 in 250 μl of 0 pg/ml standard; 100 μl P_4 tracer and 500 μl P_4 antibody were added to samples, standards and controls, and samples were incubated for 60 min at 37°C. Precipitant, vortex, centrifuge, decanting and measuring procedures were the same as for estradiol. Inter-assay coefficients of variation for controls were 8.8% for P_4 assays and 17.6% for E_2. Average intra-assay CV was 7.7 ± 2.1% for E_2 and 5.1 ± 1.6% for P_4.

2.3. Data analysis

Estradiol and progesterone levels from the fecal hormone analysis were used to categorize females into one of the following reproductive categories:

(1) Ovulation: measured as ±3 days from an observed peak in fecal estradiol and/or progesterone. Peaks were defined as minimally >2 SD above baseline hormonal values (Ziegler et al., 2000). Baseline values were determined from (1) periods of postpartum amenorrhea immediately following births, or in cases in which females were not observed in postpartum amenorrhea, (2) from a 25% sample of that female's lowest hormonal values. Including ±3 days from the observed peak increases the chance of including the actual date(s) of impregnability. Error in finding the exact date of ovulation may be due to: (i) the fact that samples could not be collected every day and, hence, the highest peak in hormonal concentrations may have been missed, (ii) the delay in diffusion of hormones from the blood to feces, which may create a lag in dates of the real time hormonal profile (fecal samples have been shown to reflect the same reproductive events as urinary measurements in white-faced sakis (Shideler et al., 1994) and hence no delay function was included in our data), (iii) the fact that sperm may be able to persist in the vaginal tract and fertilize the egg for a period of time before/after ovulation (data on this length of time does not exist for this species, but see Parker, 1984; Johnson & Everitt, 1988). Lastly it is pertinent to note that since groups were followed in rotating 4-day blocks, the period of behavioral observations that occur in conjunction with ovulation are effectively a 4- rather than a 6-day period.

(2) Cycling (non-ovulation): estradiol and progesterone increase and decrease in a manner consistent with regular ovulation. Times of ovulation were exclusive from these periods. Additionally, if observation/sample collection did not coincide with times of hormonal peaks (i.e., ovulations were 'missed' and hormonal levels were near baseline), but cycling was observed before and after, the period was classified as cycling.

(3) Pregnant (non-cycling): characterized by consistently elevated levels of progesterone and/or estradiol. However, in some cases an infant's date of birth was used to reconstruct periods of pregnancy, using Savage et al.'s (1995) average gestation length of 146.1 ± 5.2 days.

(4) Postpartum amenorrhea (non-cycling): characterized by flat-lined estradiol and progesterone profiles and in all cases were supported by observed births.

Female reproductive state was indeterminate when gaps in fecal samples were >15 days (i.e., long enough to miss an ovulatory cycle: Savage et al., 1995) and reproductive status could not be identified by other means (e.g., continuation of pregnancy after gap in data); these periods were excluded from data analysis. All sexually active adult females were included in the sample, totaling 11 observed ovulations, 15 months of pregnancy, and 15 months of postpartum amenorrhea. In order to illustrate the data, the hormonal profile and copulation data of female PF are presented in Figure 1. Note that resumption of cycling after postpartum amenorrhea was initially variable. These periods were excluded from the data set due to the ambiguous reproductive status.

We conducted Friedman's test in order to assess overall patterns of copulation frequency between reproductive states, among all dyads. Data during postpartum periods had to be excluded for this test, as not all females exhibited this phase. For all copulating dyads, a χ^2 single variable test was conducted to test whether copulations occurred randomly with regard to that female's reproductive state. For these tests, expected probabilities were determined using the percent of observation days that a female was known to be in each reproductive phase (e.g., number of observation days pregnant/total number of observation days female reproductive status was known). Since sample sizes for all the above χ^2 tests were low, which may lead to spurious results, a Monte Carlo simulation was utilized, with 10 000 iterations and a 95% confidence interval. For most tests, this bootstrapping did not appreciably change statistical results, and hence the original results are given, with bootstrapping values included only when it changed the level of significance. Also, for tests with low samples sizes we conducted a retrospective power analysis using Lenth's (2009) software in order to assess each test's power (although see Gerard et al. (1998) for a cautionary discussion on retrospective power analysis). A binomial test was also conducted for each dyad on the number of copulations solely during cycling and ovulating periods; expected values are likewise generated from the percentage of observations days in each reproductive phase. JM1 and JF1 were only observed copulating once (during early pregnancy; see Discussion) and, hence, the above statistical tests were not conducted for this dyad. No other individuals in Junco group were observed copulating.

In a typical copulation sequence, a male performs a GI on a female, and then may or may not proceed to copulate. GIs entailed sniffing the recipient's genital area and is often accompanied by tail lifting and urination by

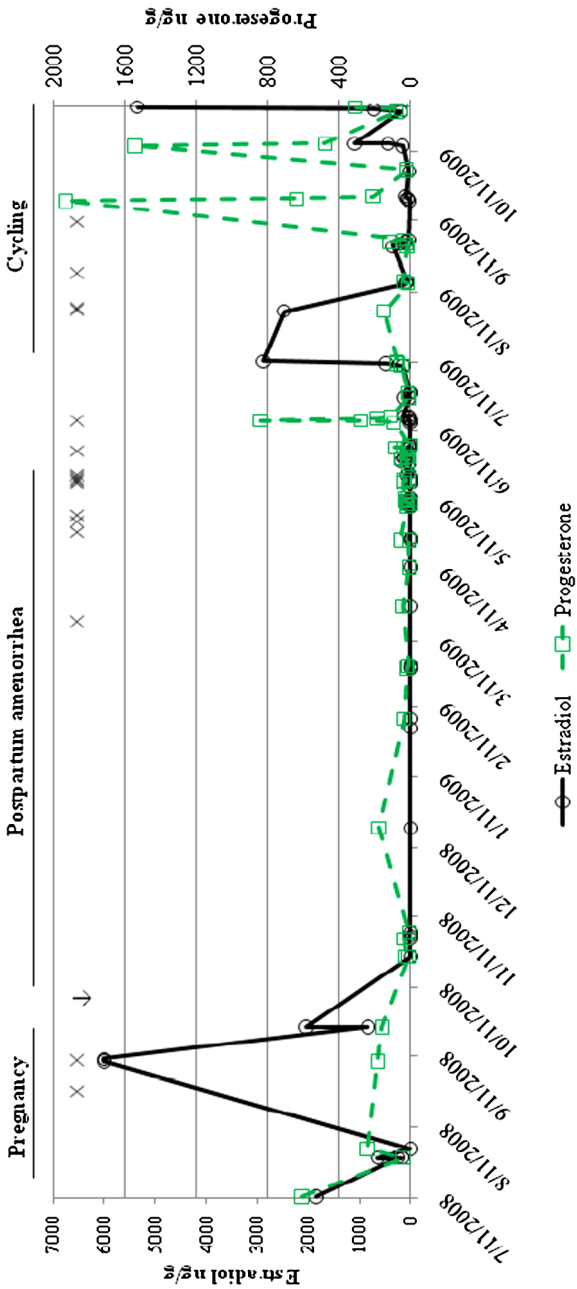

Figure 1. Hormonal profile for female PF. Crosses indicate a copulation, arrow indicates birth of an infant. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/beh

the female recipient. In fewer instances, the male will briefly lick the genital area after the female has urinated, or touch the genital area with his fingers. In order to determine if males were more likely to engage in post-inspection copulations based on female reproductive status, a logistic regression was performed on all GIs by sexually active males toward females, with occurrence/non-occurrence of copulation as the dependent variable and female reproductive status as the predictor variable. In initial analyses, the comparison of pregnancy to postpartum amenorrhea did not affect copulations and, hence, these phases were pooled into one category (non-cycling) for the final analysis. Adding controls for individual identities increased the amount of variation explained by the model (Nagelkerke $R^2 = 0.264$; Cox & Snell $R^2 = 0.192$), but were not significant predictors of copulation (logistic regression; male ID: Wald's $\chi^2 = 0.16$, $p = 0.92$; female ID: Wald's $\chi^2 = 3.09$, $p = 0.54$) and, hence, were removed from the final regression model. These data were also analyzed via a binomial test for each reproductive state (ovulation, cycling, non-cycling) separately, with occurrence/non-occurrence of copulation as the outcome variable. A correlation between GI rate and copulation rate on a monthly basis was tested to determine whether GIs are temporally associated with copulations. Lastly, a χ^2 single variable test was performed on each female in order to determine if GIs were distributed randomly with respect to reproductive state. Expected values for this test were generated in the same manner as the copulation χ^2 tests above. All tests were non-directional with $\alpha = 0.05$.

3. Results

3.1. Copulation patterns and reproductive status

Copulations ($N = 81$) did not appear to be clandestine (e.g., Gibson, 2010) and even individuals in the least habituated group (Mazaroni) copulated in front of observers early in the habituation process. Mating occurred between a single dyad in both Peach and Junco groups, and between all possible adult dyads in Mazaroni group. Analyzing all dyads together did not generate significant differences in copulation rates by reproductive state (Friedman's test; $\chi^2 = 3.60$, $p = 0.165$), with average cycling and ovulating frequencies being roughly equal (0.263, 0.264 copulations/day) and higher than copulation frequency during pregnancy (0.101 copulations/day). However, this pattern

was largely driven by one dyad (MF2 and MM1) which copulated more frequently during ovulation than cycling (as indicated by frequency and significant chi-square and binomial tests, below). Analyzing the remaining four dyads separately did yield a significant association between reproductive state and copulation frequency (Friedman's test; $\chi^2 = 6.50$, $p = 0.039$), with copulations occurring more frequently with cycling females (0.308 copulations/day) than with ovulating (0.187) or pregnant (0.098) females.

The relationship between reproductive status and copulations varied between individual dyads (Figure 2). MM1 did not engage in copulations during any reproductive state more than expected by chance with MF1 (chi-square; $\chi^2 = 2.11$, $p = 0.35$, $N = 8$ copulations, power $= 0.24$), although copulations with MF2 were significantly more frequent than expected during ovulation and less than expected while cycling and pregnant (chi-square; $\chi^2 = 10.03$, $p = 0.007$, $N = 12$, power $= 0.82$). MM2 showed a trend toward a significant association between copulations and reproductive state with MF1 (chi-square; $\chi^2 = 5.15$, $p = 0.076$, $N = 8$, power $= 0.52$), which slightly improved with bootstrapping ($p = 0.065$, 95% CI: 0.060–0.070). MM2 displayed a similar pattern with MF2 (chi-square; $\chi^2 = 5.80$, $p = 0.055$, $N = 9$, power $= 0.82$, with bootstrap:

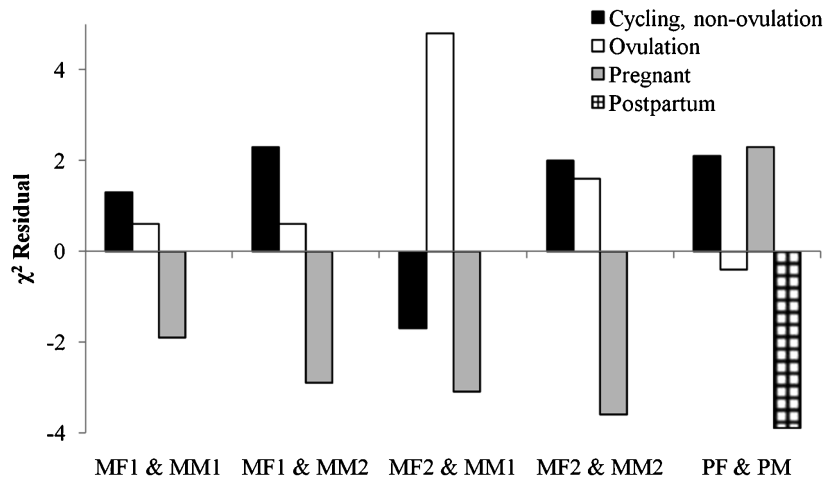

Figure 2. Copulations by dyad and female reproductive status. Reported values are residuals from the χ^2 test reported in the text, with sign added to denote the direction of deviation from expected values: negative residuals denote fewer observed copulations than expected, positive values reflect more copulations than expected. Mazaroni dyads did not have postpartum data. See text for p values and sample sizes.

$p = 0.046$, 95% CI: 0.042–0.050). However, for both dyads the significant values appear largely driven by fewer than expected copulations during pregnancy, although MM2 did copulate slightly more than expected by chance while females were cycling and ovulating (Figure 2). PM and PF also displayed significant differences in copulations by reproductive state (chi-square; $\chi^2 = 9.08$, $p = 0.028$, $N = 15$, power $= 0.72$), however this pair copulated less than expected during ovulation, and more than expected while the female was pregnant and cycling. It should be noted that all above chi-square tests had inadequate sample size (>20% cells had $E_i < 5$). When data are restricted to only analyzing copulations during cycling and ovulating periods, only MM1 and MF2 copulated significantly more than expected during ovulation (binomial test; $p = 0.029$).

3.2. Genital inspections and copulation

The majority of genital inspections (87%) were initiated by an adult male toward an adult female (in 3% of GIs a female inspected a male, 6% were intrasexual and 4% involved juveniles/infants). GI preceded 60% of copulations; however, of all intersexual GIs between adults only 33.3% were followed by copulation. Monthly GI frequency closely mirrored copulation frequency (Figure 3), and the two were significantly correlated (Pearson's correlation; $r = 0.51$, $p < 0.001$, $N = 17$), although GIs were performed even when copulation frequency was zero. These patterns held true when copulation and

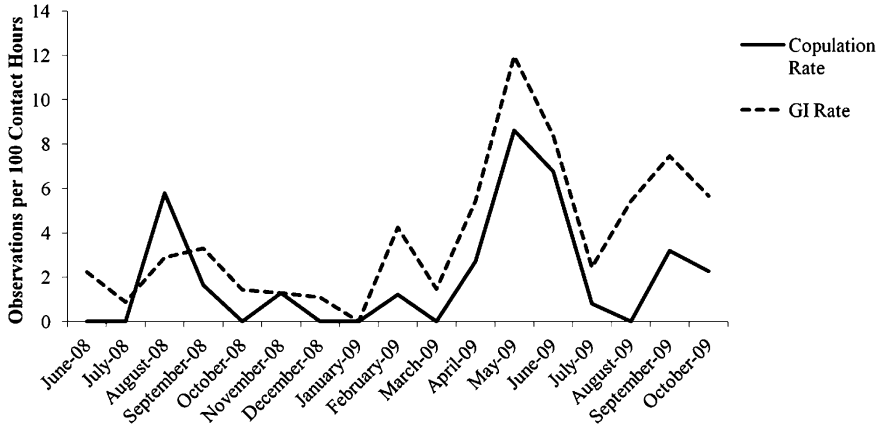

Figure 3. Genital inspection and copulation rates by month, all groups pooled.

GI frequency were analyzed separately by female. All females showed a significant positive relationship between GI and copulation frequency, except JF1 who had only one observed copulation (Pearson's correlation; $r = 0.03$, $p = 0.901$, $N = 17$).

GIs were distributed randomly with respect to reproductive state for all females (chi-square; PF: $\chi^2 = 0.15$, $p = 0.154$, $N = 33$; MF1: $\chi^2 = 1.74$, $p = 0.419$, $N = 30$, MF2: $\chi^2 = 4.24$, $p = 0.120$, $N = 22$, JF1: $\chi^2 = 0.01$, $p = 0.913$, $N = 10$). However, the logistic regression found that female reproductive status plays some, albeit small, role in a male's likelihood of copulating after performing a GI (Table 1, Figure 4). After a GI, males were 3.46-times more likely to copulate with a cycling female than a non-cycling female and 2.81-times more likely to copulate with an

Table 1. Logistic regression of the effect of female reproductive status on a male's decision to copulate following a genital inspection (GI).

Variable	β	SE	Wald's χ^2	df	p	Odds ratio
Constant	−1.15	0.31	13.93	1	$<0.001^{***}$	0.32
Female reproductive status			7.17	2	0.028^{*}	
Non-cycling vs. cycling	1.24	0.53	5.40	1	0.020^{*}	3.46
Non-cycling vs. ovulating	1.06	0.52	4.17	1	0.041^{*}	2.81
Cycling vs. ovulating	−0.18	0.60	0.09	1	0.763	0.83

$N = 102$; Nagelkerke $R^2 = 0.097$; Cox and Snell $R^2 = 0.07$; Hosmer and Lemeshow goodness-of-fit: $\chi^2 < 0.001$, $p = 1.0$; $^{*}p < 0.05$, $^{***}p < 0.001$.

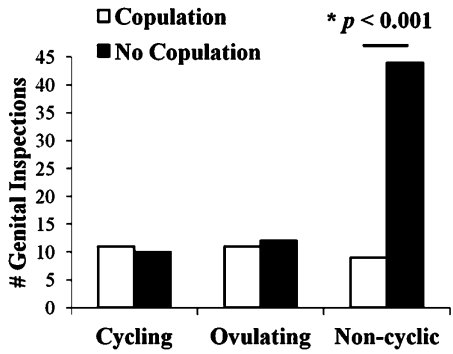

Figure 4. Male copulatory result after genital inspection (GI), by female reproductive state. All females in study population pooled. Line denotes categories with significant difference between occurrence/non-occurrence of copulation from binomial tests.

ovulating female over a non-cycling female. Despite this, males were not more likely to mate with an ovulating than a cycling female. Although the model passed the Hosmer and Lemeshow goodness-of-fit test, the estimated variance explained was low, suggesting other factors also play a heavy role in the decision to copulate. Analyzing reproductive states separately (Figure 4) also found no difference in the occurrence/non-occurrence of copulations for cycling (binomial test; $p = 0.67$) and ovulating (binomial test; $p = 0.5$) females, but copulations did occur less than expected with non-cycling females (binomial test; $p < 0.001$).

4. Discussion

Overall, the relationship between female reproductive state and copulations varied among dyads, with most dyads appearing unable to distinguish ovulation from other periods of the cycle. Yet, copulations were less frequent with non-cycling (pregnancy, postpartum amenorrhea) than cycling females, suggesting that white-faced saki males may be able to distinguish fertile from non-fertile females, even if they cannot pinpoint the exact timing of ovulation. This result adds to work on other species suggesting that male knowledge of ovulation is not an all-or-nothing phenomenon, but rather that males may be able to gain partial information on broad qualitative states of female reproduction (Reeder et al., 1998; Ostner et al., 2006).

In many species, GIs presumably provide males with olfactory and/or pheromonal information which they use to monitor female reproductive status (Epple, 1986). In this study, white-faced saki GI often preceded copulation and GI rate mimicked, but generally remained higher than, copulation rate. GIs were distributed randomly with respect to female reproductive state, suggesting that males do not have a priori knowledge of such information. Despite this, the occurrence of copulation after a GI was *not* distributed randomly: males were more likely to mate with cycling rather than non-cycling females. Taken in conjunction, these data suggest that white-faced saki males use GI to monitor female reproductive status and to inform copulation behavior.

It has been argued that copulating outside of ovulation could entail selective disadvantages such as energy expenditure, loss of time for feeding, increased risk of predation and disease transmission, sperm depletion,

and potential aggression from competitors (Hunter et al., 1993; Westneat & Rambo, 2000; Stallmann & Harcourt, 2006). White-faced sakis' testes are small (Harcourt et al., 1995, estimated testicular mass (from measures of dimension in Hill, 1960) at <0.001% of body mass) and hence sperm could be depletable. In addition, male–male aggression in the context of copulations has been documented (Thompson, 2011). While these potential disadvantages may select for accuracy in copulatory timing, white-faced saki males in this study did not make entirely accurate decisions with regard to copulation timing. This imperfect fit between female impregnability and male behavior suggests that either (1) males may not be able to reliably detect female ovulation, (2) females are not providing 'honest indicators' of their reproductive status, (3) males are not motivated to copulate with females while ovulating, and/or (4) non-conceptive copulations may have a selective benefit (although low sample size of some tests may have also influenced this outcome). Wallen (1990) found that copulations in captive rhesus macaques were more closely linked to ovulatory timing when multiple males were present, suggesting that intrasexual competition or threat of retaliation motivates individuals to copulate only when most profitable (i.e., ovulation). As white-faced saki groups often have only one or two sexually active males, they may not have been motivated to limit copulations solely to ovulatory periods. Additionally, Snowdon et al. (2010) found that sexual behavior in tamarin monkeys was associated with levels of the pair-bonding hormone oxytocin, suggesting that non-conceptive copulations could function to promote the pair-bond. White-faced sakis indeed display strong social bonds between male–female pairs (Thompson & Norconk, 2011). However if reinforcing the pair-bond is of continual importance to white-faced sakis, then one would not expect to see the decreased copulation frequency with non-cycling females observed in this study.

Familiarity of the pair-bond and male sexual (in)experience may also play a role in how accurately a male can detect female reproductive status. The newly formed pair in this study (Peach group, with a nulliparous female and a young (and, thus, potentially sexually inexperienced) male) had the least accurate copulation record — with no statistically significant association between copulation timing and female reproductive status. On the other hand, Mazaroni group males performed better, engaging in more copulations with cycling than non-cycling females, and the oldest (and presumably most experienced) male showing more copulations than expected with ovulating

females. If correct, this hypothesis could explain the low number of copulations observed in Junco group: the core of Junco group is an established, long term, fecund pair with close social bonds (Thompson, 2011; Thompson & Norconk, 2011). If familiarity and experience with a specific female leads to more accurate decisions about copulation, JM1 may have replaced copulation frequency with accuracy. This hypothesis is supported by the observation that his mate (JF1) conceived quicker after postpartum amenorrhea than the other females in this study: time from resumption of cycling to subsequent conception was 1–3 months for JF1 vs. 5–6 months for MF1; PF cycled a minimum of 4 months, until the end of the study period, but the date of her next conception was unknown.

More data are needed to fully assess the effect of pair familiarly and sexual experience on mating efficacy in white-faced sakis, but such a phenomenon is not unjustified based on current research. Common marmosets (*Callithrix jacchus*) can be trained to associate arbitrary olfactory cues with female reproductive status (Snowdon et al., 2011). Similarly, newly housed pairs of this species show a relationship between intensity of social interactions and the likelihood of conception, regardless of copulation frequency (Silva & Sousa, 1997). In rhesus macaques, familiarity appears to play a role in male ability to identify female reproductive state from facial luminance (Higham et al., in press). The phenomenon has been demonstrated in birds as well, where both sexual experience and pair-bond duration have been shown to affect key factors of avian reproductive success (Bradley et al., 1990; Fowler, 1995).

In summary, this study shows that white-faced saki males consistently monitor females via genital inspection, and in turn males are likely gaining information on the general reproductive status of females. But despite whatever signals they are receiving, the poor association between copulations and ovulation suggests that males may have only limited knowledge of and/or interest in female ovulatory timing. Differences in male ability to detect ovulation may be due to male sexual experience and intensity of male–female social bonds, although more direct tests are needed to investigate this effect.

Acknowledgements

We would like to thank Joan Silk, Richard Meindl, C. Owen Lovejoy, and two anonymous reviewers for helpful comments on this manuscript. Field assistance was provided by Scott Dettloff, Chris and Freya Gordon, Rose Hores, Reshma Jankispersad, Guno Marjanom and Helen

Smith. This project was funded by the National Science Foundation (BSC No. 0925122), the International Primatological Society, Kent State Graduate Student Senate, The Explorer's Club, and STINASU. This research was approved by Kent State University's IACUC and complied with Suriname's legal requirements.

References

Alexander, R.D. & Noonan, K.N. (1979). Concealment of ovulation, parental care and human social evolution. — In: Evolutionary biology and human social behavior: an anthropological perspective (Chagnon, N.A. & Irons, W.G., eds). North Duxbury Press, North Scituate, MA, p. 436-452.

Andelman, S.J. (1987). Evolution of concealed ovulation in vervet monkeys (*Cercopithecus aethiops*). — Am. Nat. 129: 785-799.

Bradley, J.S., Wooller, R.D., Skira, I.J. & Serventy, D.L. (1990). The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. — J. Anim. Ecol. 59: 487-496.

Brumloop, A., Homburg, I., Peetz, A. & Riehl, R. (1994). Gular scent glands in adult female white-faced saki, *Pithecia pithecia pithecia*, and field observations on scent-marking behaviour. — Folia Primatol. 63: 212-215.

Buzzell, C. (2006). Strange and familiar scents: the role of scent marking in white-faced saki (*Pithecia pithecia*) social behavior. — MSc thesis, Kent State University, Kent, OH.

Cerda-Molina, A.L., Hernandez-Lopez, L., Rojas-Maya, S., Murcia-Mejia, C. & Mondragon-Ceballos, R. (2006). Male-induced sociosexual behavior by vaginal secretions in *Macaca arctoides*. — Int. J. Primatol. 27: 791-807.

Charlton, B.D., Keating, J.L., Rengui, L., Huang, Y. & Swaisgood, R.R. (2010). Female giant panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase. — Proc. Roy. Soc. Lond. B: Biol. 277: 1101-1106.

Converse, L.J., Carlson, A.A., Ziegler, T.E. & Snowdon, C.T. (1995). Communication of ovulatory state to mates by female pygmy marmosets, *Cebuella-pygmaea*. — Anim. Behav. 49: 615-621.

De Dijn, B.P.E., Molgo, I.E., Norconk, M.A., Gregory, L.T., O'Shea, B., Marty, C., Luger, M., Ringler, M., Crothers, S., Noonan, B., Fitzgerald, K., Mitro, S., Vreedzaam, A. & Satyawan, D. (2007). The biodiversity of the Brownsberg. — CI RAP Bull. Biol. Assess. 43: 135-155.

De Vleeschouwer, K., Heistermann, M., Van Elsacker, L. & Verheyen, R.F. (2000). Signaling of reproductive status in captive female golden-headed lion tamarins (*Leontopithecus chrysomelas*). — Int. J. Primatol. 21: 445-465.

Dixson, A.F. (1992). Observations on postpartum changes in hormones and sexual behavior in callitrichid primates: do females exhibit postpartum "estrus"? — In: Topics in primatology, Vol. 2: behavior, ecology, and conservation (Sackett, G.P., Itoigawa, N. & Sugiyama, Y., eds). University of Tokyo Press, Tokyo, p. 141-149.

Dugmore, S.J. (1986). Behavioural observations on a pair of captive white-faced saki monkeys (*Pithecia pithecia*). — Folia Primatol. 46: 83-90.

Epple, G. (1986). Communication by chemical signals. — In: Comparative primate biology (Mitchell, G. & Erwin, J., eds). Alan R. Liss, New York, NY, p. 531-580.

Epple, G. & Lorenz, R. (1967). Vorkommen, Morphologie und Funktion der Sternaldruse bei den Platyrrhini. — Folia Primatol. 7: 98-126.

Ferris, C.F., Snowdon, C.T., King, J.A., Duong, T.Q., Ziegler, T.E., Ugurbil, K., Ludwig, R., Schultz-Darken, N., Wu, Z., Olson, D.P., Sullivan Jr., J.M., Tannenbaum, P.L. & Vaughn, J.T. (2001). Functional imaging of brain activity in conscious monkeys responding to sexually arousing cues. — NeuroReport 12: 2231-2236.

Ferris, C.F., Snowdon, C.T., King, J.A., Sullivan, J.M., Ziegler, T.E., Olson, D.P., Schultz-Darken, N.J., Tannenbaum, P.L., Ludwig, R., Wu, Z., Einspanier, A., Vaughan, J.T. & Duong, T.Q. (2004). Activation of neural pathways associated with sexual arousal in non-human primates. — J. Magn. Reson. Imaging 19: 168-175.

Fowler, G.S. (1995). Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. — Am. Zool. 35: 318-328.

Gerard, P.D., Smith, D.R. & Weerakkody, G. (1998). Limits of retrospective power analysis. — J. Wildl. Manage. 62: 801-807.

Gibson, K.N. (2010). Male mating tactics in spider monkeys: sneaking to compete. — Am. J. Primatol. 72: 794-804.

Gleason, T.M. (1998). The ecology of olfactory communication in Venezuelan white-faced sakis. — Am. J. Primatol. 45: 183.

Harcourt, A.H., Purvis, A. & Liles, L. (1995). Sperm competition: mating system, not breeding season, affects testes size of primates. — Funct. Ecol. 9: 468-476.

Heistermann, M., Brauch, K., Moehle, U., Pfefferle, D., Dittami, J. & Hodges, K. (2008). Female ovarian cycle phase affects the timing of male sexual activity in free-ranging barbary macaques (*Macaca sylvanus*) of Gibraltar. — Am. J. Primatol. 70: 44-53.

Heistermann, M., Ziegler, T., van Schaik, C.P., Launhardt, K., Winkler, P. & Hodges, J.K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging hanuman langurs. — Proc. Roy. Soc. Lond. B: Biol. 268: 2445-2451.

Higham, J.P., Hughes, K.D., Brent, L.J.N., Dubuc, C., Engelhardt, A., Heistermann, M., Maestriperi, D., Santos, L.R. & Stevens, M. (in press). Familiarity affects the assessment of female facial signals of fertility by free-ranging male rhesus macaques. — Proc. Roy. Soc. Lond. B: Biol. (doi: 10.1098/rspb.2011.0401).

Higham, J.P., Semple, S., MacLarnon, A., Heistermann, M. & Ross, C. (2009). Female reproductive signaling, and male mating behavior, in the olive baboon. — Horm. Behav. 55: 60-67.

Hill, W.C.O. (1960). Primates: comparative anatomy and taxonomy. Volume IV. Cebidae, part A. — Edinburgh University Press, Edinburgh.

Hrdy, S.B. (1977). The langurs of Abu: female and male strategies of reproduction. — Harvard University Press, Cambridge, MA.

Hunter, F.M., Petrie, M., Otronen, M., Birkhead, T. & Møller, A.P. (1993). Why do females copulate repeatedly with one male? — Trends. Ecol. Evol. 8: 21-26.

Johnson, M.H. & Everitt, B.J. (1988). Essential reproduction. — Blackwell Scientific, Oxford.

Kappeler, P.M. & van Schaik, C.P. (2004). Sexual selection in primates: review and selective preview. — In: Sexual selection in primates: new and comparative perspectives (Kappeler, P.M. & van Schaik, C.P., eds). Cambridge University Press, New York, NY, p. 3-23.

Lehman, S.M., Prince, W. & Mayor, M. (2001). Variations in group size in white-faced sakis (*Pithecia pithecia*): evidence for monogamy or seasonal congregations? — Neotrop. Primat. 9: 96-101.

Lenth, R.V. (2009). Java applets for power and sample size. — Available online at http://www.stat.uiowa.edu/~rlenth/Power

Lim, B.K., Engstrom, M.D., Genoways, H.H., Catzeflis, F.M., Peters, S.L., Djostero, M., Brandon, S. & Mitro, S. (2005). Results of the Alcoa Foundation-Suriname expeditions. XIV. Mammals of Brownsberg Nature Park, Suriname. — Ann. Carnegie Mus. 74: 225-274.

Michael, R.P. & Keverne, E.B. (1968). Pheromones in the communication of sexual status in primates. — Nature 218: 746-749.

Michael, R.P. & Keverne, E.B. (1970). Primate sex pheromones of vaginal origin. — Nature 225: 84-85.

Morris, D. (1967). Primate ethology. — Weidenfeld and Nicholson, London.

Norconk, M.A. (2006). Long-term study of group dynamics and female reproduction in Venezuelan *Pithecia pithecia*. — Int. J. Primatol. 27: 653-674.

Norconk, M.A. (2011). Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed predators. — In: Primates in perspective (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K. & Stumpf, R.M., eds). Oxford University Press, New York, NY, p. 122-139.

Ostner, J., Chalise, M.K., Koenig, A., Launhardt, K., Nikolei, J., Podzuweit, D. & Borries, C. (2006). What hanuman langur males know about female reproductive status. — Am. J. Primatol. 68: 701-712.

Parker, G.A. (1984). Sperm competition and the evolution of animal mating strategies. — In: Sperm competition and the evolution of animal mating systems (Smith, R.L., ed.). Academic Press, San Diego, CA, p. 2-60.

Rasmussen, L.E.L. & Schulte, B.A. (1998). Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. — Anim. Reprod. Sci. 53: 19-34.

Reeder, D.M., Mendoza, S.P. & Mason, W.A. (1998). Social behavior and sexual motivation across the reproductive cycle in titi monkeys (*Callicebus moloch*): concealment or communication of ovulation? — Am. J. Primatol. 45: 202-203.

Savage, A., Lasley, B.L., Vecchio, A.J., Miller, A.E. & Shideler, S.E. (1995). Selected aspects of female white-faced saki (*Pithecia pithecia*) reproductive biology in captivity. — Zoo Biol. 14: 441-452.

Savage, A., Shideler, S. & Lasley, B. (1993). A preliminary report on the behavior and reproductive patterns of captive white-faced sakis (*Pithecia pithecia*). — In: North American regional studbook for the white-faced saki (*Pithecia pithecia*) (Miller, A., ed.). Roger Williams Park Zoo, Providence, RI, p. 3-7.

Setz, E.Z.F. & Gaspar, D.A. (1997). Scent-marking behaviour in free-ranging golden-faced saki monkeys, *Pithecia pithecia chrysocephala*: sex differences and context. — J. Zool. Lond. 241: 603-611.

Shideler, S.E., Savage, A., Ortuno, A.M., Moorman, E.A. & Lasley, B.L. (1994). Monitoring female reproductive function by measurement of fecal estrogen and progesterone metabolites in the white-faced saki (*Pithecia pithecia*). — Am. J. Primatol. 32: 95-108.

Silva, H.P.A. & Sousa, M.B.C. (1997). The pair-bond formation and its role in the stimulation of reproductive function in female common marmosets (*Callithrix jacchus*). — Int. J. Primatol. 18: 387-400.

Snowdon, C.T., Pieper, B.A., Boe, C.Y., Cronin, K.A., Kurian, A.V. & Ziegler, T.E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. — Horm. Behav. 58: 614-618.

Snowdon, C.T., Tannenbaum, P.L., Schultz-Darken, N.J., Ziegler, T.E. & Ferris, C.F. (2011). Conditioned sexual arousal in a nonhuman primate. — Horm. Behav. 59: 696-701.

Stallmann, R.R. & Harcourt, A.H. (2006). Size matters: the (negative) allometry of copulatory duration in mammals. — Biol. J. Linn. Soc. 87: 185-193.

Taub, D.M. (1980). Female choice and mating strategies among wild barbary macaques (*Macaca sylvanus*). — In: The macaques: studies in ecology, behavior and evolution (Lindburgh, D.G., ed.). Van Nostrand Reinhold, New York, NY, p. 287-344.

Thompson, C.L. (2011). Sex, aggression, and affiliation: the social system of white-faced saki monkeys (*Pithecia pithecia*). — PhD thesis. Kent State University, Kent, OH.

Thompson, C.L. & Norconk, M.A. (2011). Within-group social bonds in white-faced saki monkeys (*Pithecia pithecia*) display male–female pair preference. — Am. J. Primatol. 73: 1051-1061.

Trivers, R.L. (1972). Parental investment and sexual selection. — In: Sexual selection and the descent of man 1871–1971 (Campbell, B., ed.). Aldine, Chicago, IL, p. 136-179.

van Schaik, C.P., van Noordwijk, M.A. & Nunn, C.L. (1999). Sex and social evolution in primates. — In: Comparative primate socioecology (Lee, P.C., ed.). Cambridge University Press, Cambridge, p. 204-231.

Wallen, K. (1990). Desire and ability: hormones and the regulation of female sexual-behavior. — Neurosci. Biobehav. Rev. 14: 233-241.

Waters, S.S. (1995). A review of social parameters which influence breeding in white-faced saki (*Pithecia pithecia*) in captivity. — Int. Zool. Yb. 34: 147-153.

Westneat, D.F. & Rambo, T.B. (2000). Copulation exposes female red-winged blackbirds to bacteria in male semen. — J. Avian Biol. 31: 1-7.

Ziegler, T., Hodges, K., Winkler, P. & Heistermann, M. (2000). Hormonal correlates of reproductive seasonality in wild female hanuman langurs (*Presbytis entellus*). — Am. J. Primatol. 51: 119-134.

Ziegler, T.E., Epple, G., Snowdon, C.T., Porter, T.A., Belcher, A.M. & Kuderling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. — Anim. Behav. 45: 313-322.