RESEARCH ARTICLE

The Strategic Use of Sex in Wild Female Western Gorillas

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Human females, unlike most mammals, are sexually active outside of fertile periods. This decoupling of sexual behavior from its conceptional function has had an enormous impact on social relationships, and yet we know little about why there was selection for nonconceptive mating. Here we examine one form of nonconceptive mating, the mating that occurs during pregnancy or post-conceptive (PC) mating, in wild western gorillas (Gorilla gorilla). Using a near complete mating record for five females during gestation, we show that pregnant females varied in the timing and frequency of mating, and used PC mating conditionally, synchronizing copulations to occur on days when other females mated, and refraining from mating for lengthy periods when no other females mated. As pregnant females mated exclusively with the same male before and after conception, and mated in response to group female (and not male) behavior, we conclude that western gorillas used PC mating as a form of female competition, and not to confuse paternity or to obtain immediate benefits from the male, as suggested earlier. The male initiated copulations preferentially with females of high rank, rather than distinguishing between pregnant and cycling females. Therefore, PC mating appears to be a strategy by which high-ranking pregnant females attempt to minimize the interest of other females, while reinforcing their own status and potentially delaying conception in others. These findings indicate that female-mating competition is more important than considered earlier, and may be a factor in the evolution of nonconceptive mating in humans. Am. J. Primatol. 71:1–10, 2009. © 2009 Wiley-Liss, Inc.

Key words: post-conceptive mating; female reproductive competition; mating synchrony

INTRODUCTION

In most mammals, females mate primarily when conception is possible, or around the time of ovulation [Heape, 1900]. In humans, however, females also mate when conception is not possible: during gestation, lactation, and nonfertile periods of the menstrual cycle [Hrdy & Whitten, 1987; Miller, 1931]. This extreme decoupling of sexual behavior from conception is one of the defining features of human behavior [Lovejoy, 1981], and yet we know little about the evolutionary significance of nonconceptive mating [Hrdy & Whitten, 1987]. As many old world monkeys and apes also mate outside of conception periods [Dixon, 1968; Hrdy & Whitten, 1987], they provide an opportunity for assessing the function of nonconceptive mating, thereby illuminating the factors that may have shaped its evolution in humans.

The most common explanation for why nonhuman primate females engage in nonconceptive mating is that they gain benefits from males for themselves or their offspring. For example, pregnant females have been observed to mate with new males entering a group [Borries et al., 1995; Hrdy, 1974, 1979] or with males with whom they rarely mated before conception [Gordon et al., 1991], and it has been hypothesized that by mating with males other than the sire outside of conceptional periods, females attempt to confuse paternity and to thus reduce the risk of infanticide [Hrdy, 1979]. Although paternity confusion may explain why females mate preferentially with different males during conception and nonconceptive periods in multi-male groups [Stumpf & Boesch, 2005, 2006], it fails to explain nonconceptive mating when a female mates with the same male before and after conception.

Other hypotheses have been proposed to account for why females mate more frequently with the same male than is needed to insure fertilization [Hunter et al., 1993] or mate promiscuously for reasons other than paternity confusion, and these could also explain why females engage in nonconceptive mating.

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For example, it has been suggested that females mate repeatedly with the same male in exchange for immediate material benefits from the male such as food or protection [Hunter et al., 1993]. Supporting evidence comes from avian studies in which females copulate more frequently when courtship involves the transfer of food from male to female [Mougeot et al., 2002; Tasker & Mills, 1981]. Within primates, although there has long been the suggestion that the females trade sex for food [Stanford et al., 1984; Teleki, 1973, 1981] or grooming [Hemelrijk et al., 1992], supporting data based on explicit testing are rare [Gilby et al., 2006; Gumert, 2007].

Rarely considered is the hypothesis that nonconceptive mating may be a strategy by which females compete with each other rather than to obtain benefits from the male. In some birds and fish repeated mating with the same male is thought to be a form of female mate guarding, given that females mate to distract a male from other mating opportunities [Petrie, 1992], solicit copulations at a higher rate when the male begins courting a new female [Bens & Pinxten, 1996] or are more attentive to a preferred mate in the presence of a competing sex conspecific [Santangelo & Itzkowitz, 2004]. Although intriguing, these possibilities have rarely been considered as explanations for nonconceptive mating in primates. It has been speculated that nonconceptive mating may be a form of female reproductive competition used to delay or prevent conception in other females [Small, 1988; Sommer, 1989; Sommer et al., 1992]. It is hypothesized that pregnant females synchronize mating behavior to coincide with that of cycling females, in order to “sneak” sperm away from them as a strategy to delay or prevent conception. However, to date, no one has explicitly tested this hypothesis, in part because it requires complete mating records of pregnant and other group females, which have not been available.

Each of the above hypotheses assumes that females use nonconceptive mating strategically, mating at appropriate times to achieve their aims while refraining from mating at other times. However, to date, the degree to which females are flexible in nonconceptive mating is unclear, as published research examining the degree of individual variation in nonconceptive mating are not available. The hypotheses can be broadly divided into two categories, based on whether nonconceptive mating is viewed as resulting from intersexual conflict (paternity confusion or immediate material benefits) or intrasexual competition (female reproductive competition). One way to assess this basic separation is to determine the factors that elicit nonconceptive mating. Specifically, when nonconceptive mating is a form of intrasexual competition, it would be predicted that nonconceptive mating occurs in response to the behavior of other females, whereas when it results from intersexual conflict it should be in response to male behavior, and not vary as a result of female behavior. Here, we use a nearly complete mating record during 3.4 years of one group of wild western gorillas (Gorilla gorilla) to test whether nonconceptive mating varies based on the behavior of other group females.

Western gorillas typically live in small one-male, multi-female groups with an average of 3.7 females per group [Stokes et al., 2003]. As is typical for one-male mating systems where there is no need to confuse paternity [van Schaik et al., 1999], cycling female gorillas mate fairly infrequently, an average of 1–2 consecutive days per month [Watts, 1991] around the day of ovulation and coinciding with peak estrogen levels [Czekala & Sicotte, 2000; Nadler, 1980]. Female gorillas do not exhibit any external morphological indicators of ovulation or pregnancy [Czekala & Sicotte, 2000; Harcourt et al., 1980]. Rather, they are thought to advertise ovulation to the male by changes in behavior, by soliciting the male to copulate. Female gorillas are capable of mating throughout gestation, which typically averages 255 days [Watts, 1991], but in the wild they do not mate while nursing their young, a period of approximately 3.2 years in mountain gorillas [Watts, 1991]. Therefore, we focus specifically on postconceptive (PC) mating and provide evidence that PC mating in wild gorillas is used as a form of female-mating competition, building on our earlier presentation [Fernandez et al., 2007] and recently strengthened by evidence from Stoinski et al. [2009] corroborating findings in captive gorillas.

A first step in assessing the function of nonconceptive mating is to examine the degree of individual variation in nonconceptive mating behavior. We first examine the mating record during gestation for each of five western gorillas. PC mating occurs in several nonhuman primate taxa, but in most species it is more temporally proscribed compared to humans [Biedert et al., 1976; Borries et al., 2001; Engelhardt et al., 2007; Gust, 1994; Kuster & Paul, 1984; Nieuwenhuisen et al., 1986; Sommer et al., 1992; Wallis & Lemoon, 1986]. This has led to the suggestion that PC mating occurs as a byproduct of fluctuating hormone levels [Saayman, 1975]. If this is the case, then females should exhibit broadly similar patterns of mating during gestation. Conversely, if females differ in the frequency and timing of PC mating it would provide the flexibility for strategic use. Although there are anecdotal accounts of variation in PC mating within [Harcourt et al., 1981b; Kuster & Paul, 1984; Lindburg, 1983; Pazol, 2003] and between social groups [Barelli et al., 2007; Fujita et al., 2004; Inoue et al., 1993; Palombi personal communication], there are few studies which systematically examine the degree to which individuals vary in the frequency and timing of PC mating [but see Fernandez et al., 2007; Stoinski et al., 2009]. Thus, we first present evidence that females vary in the onset, frequency and extent of PC mating.

Next we consider what triggers mating in a pregnant female. Western gorilla females undergo routine natal and secondary dispersal [Bradley et al.,
2007; Stokes et al., 2003), presumably transferring to groups on the basis of male quality [Caïlaud et al., 2008], like dispersing females in other species that live in one-male units [Sterck et al., 1997]. As a result, gorilla female fitness is more likely to depend on male quality and services [Harcourt & Stewart, 2007] than on the enduring bonds formed with female kin as in female philopatric taxa [Silk et al., 2003]. As the single male present in the group is dominant to all other individuals, and dominant males may influence females’ access to resources [e.g. Janson, 1985], females could conceivably continue mating during pregnancy in exchange for food or grooming. However, in over five years of daily observation we never observed food-sharing or grooming between the adult male and females. Thus, we conclude that in wild western gorillas, as in most primates [van Noordwijk & van Schaik, 2000], mating (nonconceptive or otherwise) does not result in the accrual of any immediate material benefits to females.

Next, we consider whether nonconceptive mating is more likely to be a form of intra- or intersexual competition. If PC mating is primarily a form of female–female competition, i.e. if its function is to either distract a male from other mating opportunities [Eens & Pintxen, 1996; Petrie, 1992] or delay conception in other females [Small, 1988], then we predict that the females engage in PC mating more often on days when other females mated. Furthermore, if PC mating is a tactic specifically used to delay or prevent conception in other females [Small, 1988; Sommer, 1989; Sommer et al., 1992], then pregnant females should mate when cycling, but not pregnant, females mate. If PC mating is a form of intersexual competition, although the pattern of mating could take many forms, it should be independent of the behavior of other females. Finally, as a successful strategy should increase the relative reproductive success of those that enact them [Hrdy, 1984], we consider whether there are consequences to mating overlap that could be costly to the targets and beneficial to the actors.

**METHODS**

We recorded all copulations in one group of western gorillas at the Mondika Research Center, Republic of Congo and Central African Republic during 93% (1,147 of 1,255) of days between September 6, 2003, and January 18, 2007. From September 6, 2003, through November 5, 2005, we conducted all or half day focal follows of the group male, adult females or simultaneous follows of both (mean length of focal follow was 579 min, SD = 89.9, n = 673 focal follows). From November 6, 2005, through January 18, 2007, focal follows were no longer conducted but the group was followed on a near daily basis (n = 474 days). For each copulation, we recorded the (1) copulation duration (in seconds) from intromission to ejaculation or withdrawal, (2) the identity of the female involved, (3) whether the male or the female initiated the copulation, and (4) whether the copulation was harassed by other group members. During focal follows it is unlikely that we missed copulations because (1) they were conspicuous events, with both males and females emitting copulations calls that attracted the attention of other group members, (2) the silverback was the subject of focal follows during 96% of observation days and observers were within 10 m, and (3) neither genetic nor behavioral evidence indicates that group females mate with males other than the group silverback [Bradley et al., 2004, 2007]. This research adhered to the American Society of Primatologists’ principles for the ethical treatment of nonhuman primates, received IACUC approval from Stony Brook University, and complied with the laws of the country in which the research took place.

**Data Analysis and Statistics**

In the absence of hormonal data, we define reproductive parameters on the basis of female-mating behavior, as in earlier studies [Harcourt et al., 1980, 1981b; Watts, 1990, 1991]. We measured the “mating period” as the number of consecutive days with mating, not interrupted by more than one day without mating. We measured the number of days between two consecutive mating periods for both cycling and pregnant females, comparable to measures of “cycle length” in earlier studies [Watts, 1991]. This averaged 32 (±6) days for cycling females, but was shorter and/or more irregular in pregnant females (unpublished data), as in earlier studies [Harcourt et al., 1980]. We could therefore identify the mating period in which conception occurred for each of five pregnancies based on changes in cycle length, with the first mating period after conception occurring sooner (<24 days) or later (>44 days) than is typical for cycling females. In one case where there were two potential conception mating periods, we eliminated one because it would have led to a gestation length outside all known reported values for gorillas [Dixon, 1981]. After identifying the conception mating period, we categorized all the earlier and subsequent mating periods (and copulations therein) as “cycling” (nompregnant) or “pregnant,” respectively. We then compiled a daily record of all mating activity, including the total number of copulations per female and male per day along with the reproductive state (cycling or pregnant) of each female. Female rank, which did not change during the study period, was assessed using David’s scores [De Vries et al., 2006] based on direction of pig grunt vocalizations.

To test whether a pregnant female mated more frequently on days when another female mated (i.e. mating overlap) than expected by chance, we determined for each of five pregnancies (1) the total number of days during gestation when at least one other female in the group was cycling or pregnant and could therefore in principle mate, i.e. “potentially strategic” days, (2) the number of days during gestation on which
at least one other female mated, thereby providing
occasions on which a pregnant female could mate
strategically, i.e., "strategic" days, (3) the number of
days on which the pregnant female mated, and (4) the
number of days on which the pregnant female and at
least one other group female mated. We calculated the
expected probability of mating overlap, i.e., the prob-
ability of mating overlap if pregnant females mated
randomly relative to other females, as (2) divided by
(1), and observed mating overlap as (4) divided by
(3). Differences between observed and expected
mating overlap were tested using the binomial test
[Lehner, 1998]. To test which females were targeted by
pregnant females for mating overlap, we calculated
observed and expected mating overlap separately for
cycling, pregnant and all females. As female mating
periods are so short, we repeated all analyses for
mating period (rather than mating day) overlap, but
discuss these results only when they differ.

RESULTS
Female mating during pregnancy was highly
variable across individuals (Fig. 1). All five

![Image](image_url)

Fig. 1. All days on which pregnant females (MK, UG, MA, BE, and VI) mated (vertical bars) between conception (con) and birth of
offspring (B) relative to days on which any other group female mated (indicated by crosses). Horizontal gray bar indicates period when
no other female in the group could potentially mate. Data are not available beyond day 210 and 178 of gestation for females UG and BE,
respectively. Gestations of females BE and UG largely coincide with each other and no other females. BE conceived 32 days after UG.

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females copulated during pregnancy, but females differed in (1) how quickly they resumed mating after conception, ranging from 13 to 97 days, (2) how regularly they mated during pregnancy (i.e. there was significant variation in the mean number of days between mating periods, ranging from 12 to 53 days; Kruskal-Wallis test: $\chi^2 = 11.6$, df = 4, $P = 0.021$), and (3) how late into gestation they continued to mate, in some cases mating until the day before birth (Table I). All the females mated more often than expected on days when other females mated, significantly so for four of five pregnancies (Table II: observed mating overlap for all the females). This effect was even stronger when overlapping mating periods, rather than days, were considered (Table II). When each of the five females first began mating after conception, at least one cycling or pregnant female was present in the group. As soon as only lactating females (who do not mate) were present, one of the two pregnant females ceased mating. This is illustrated in the contrasting mating patterns during two pregnancies (Fig. 1: MK and UG). After conception, MK mated regularly for three “cycles,” overlapping in each case with another female (EB). When EB emigrated and only lactating females remained, MK ceased mating for 114 days. She resumed mating again one day after another female began mating following the death of her infant. In contrast, UG mated at frequent intervals throughout her entire pregnancy, with almost all copulations coinciding with those of another female. Contrary to the prediction for reproductive interference, mating overlap occurred more often than expected by chance with both pregnant and cycling females, indicating that pregnant females did not specifically target cycling females for mating overlap (Table II). To further investigate, we considered whether females were capable of distinguishing the reproductive state of other females because without this ability pregnant females would

### TABLE I. Timing of Mating During Pregnancy for Five Western Gorilla Females

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>MA</th>
<th>MK</th>
<th>VI</th>
<th>UG</th>
<th>BE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Days to 1st mating after conception</strong> [SD, N = † of pregnancies]</td>
<td>49 (34.7, 5)</td>
<td>97</td>
<td>43</td>
<td>70</td>
<td>13</td>
<td>22</td>
</tr>
<tr>
<td><strong>Mean † days between mating periods (range), [SD, N]</strong></td>
<td>18.9 (8-117)</td>
<td>22.9 (9-98)</td>
<td>52.5 (20-117)</td>
<td>19.5 (8-71)</td>
<td>12.2 (8-17)</td>
<td>13.6 (9-23)</td>
</tr>
<tr>
<td><strong>Days between last mating and birth</strong> [SD, N = † of pregnancies]</td>
<td>18 (19.9, 57)</td>
<td>16 (26.5, 11)</td>
<td>38 (44.3, 4)</td>
<td>14 (17.1, 12)</td>
<td>0 (2.4, 17)</td>
<td>22 (3.7, 13)</td>
</tr>
</tbody>
</table>

### TABLE II. Pregnant Western Gorilla Female Observed (OBS.) and Expected (EXP.) Mating Overlap (OVL.P.) Towards All (ALL), Cycling (CYCLE), or Pregnant (PREG) Females. Results, Sample Sizes and Significance are Reported for Analysis Overlapping Days (days with mating) and Mating Periods

<table>
<thead>
<tr>
<th>Females</th>
<th>EXP. OVL.P.</th>
<th>OBS. OVL.P.</th>
<th>n</th>
<th>$P$</th>
<th>OBS. OVL.P.</th>
<th>n</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ALL</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ma</td>
<td>0.14</td>
<td>0.38</td>
<td>24</td>
<td>0.003*</td>
<td>0.55</td>
<td>11</td>
<td>0.002*</td>
</tr>
<tr>
<td>Me</td>
<td>0.11</td>
<td>0.78</td>
<td>09</td>
<td>0.000*</td>
<td>1.00</td>
<td>4</td>
<td>0.000*</td>
</tr>
<tr>
<td>Vi</td>
<td>0.09</td>
<td>0.11</td>
<td>18</td>
<td>0.509</td>
<td>0.25</td>
<td>12</td>
<td>0.094*</td>
</tr>
<tr>
<td>Ug</td>
<td>0.13</td>
<td>0.47</td>
<td>32</td>
<td>0.000*</td>
<td>0.65</td>
<td>17</td>
<td>0.000*</td>
</tr>
<tr>
<td>Be</td>
<td>0.15</td>
<td>0.65</td>
<td>23</td>
<td>0.000*</td>
<td>0.85</td>
<td>13</td>
<td>0.000*</td>
</tr>
<tr>
<td><strong>CYCLE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ma</td>
<td>0.15</td>
<td>0.38</td>
<td>24</td>
<td>0.005*</td>
<td>0.46</td>
<td>11</td>
<td>0.015*</td>
</tr>
<tr>
<td>Me</td>
<td>0.12</td>
<td>0.78</td>
<td>9</td>
<td>0.000*</td>
<td>1.00</td>
<td>4</td>
<td>0.000*</td>
</tr>
<tr>
<td>Vi</td>
<td>0.09</td>
<td>0.18</td>
<td>11</td>
<td>0.273</td>
<td>0.29</td>
<td>7</td>
<td>0.201</td>
</tr>
<tr>
<td>Ug</td>
<td>0.16</td>
<td>0.15</td>
<td>15</td>
<td>–</td>
<td>0</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td>Be</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>PREG</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ma</td>
<td>0.08</td>
<td>0.18</td>
<td>11</td>
<td>0.21</td>
<td>0.75</td>
<td>4</td>
<td>0.002*</td>
</tr>
<tr>
<td>Me</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vi</td>
<td>0.08</td>
<td>0.17</td>
<td>12</td>
<td>0.24</td>
<td>0.83</td>
<td>9</td>
<td>0.028*</td>
</tr>
<tr>
<td>Ug</td>
<td>0.13</td>
<td>0.56</td>
<td>27</td>
<td>0.000*</td>
<td>0.73</td>
<td>15</td>
<td>0.000*</td>
</tr>
<tr>
<td>Be</td>
<td>0.15</td>
<td>0.65</td>
<td>23</td>
<td>0.000*</td>
<td>0.85</td>
<td>13</td>
<td>0.000*</td>
</tr>
</tbody>
</table>

Significant (*) or trends toward significance (†) results are from binomial testing

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TABLE III. Sexual Behavior of Cycling and Pregnant Females

<table>
<thead>
<tr>
<th></th>
<th>Cycling</th>
<th>Pregnant</th>
<th>Difference?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean copulation duration (sec)</td>
<td>51.2</td>
<td>55.3</td>
<td>ANOVA</td>
</tr>
<tr>
<td>(SD, range, N) of copulations</td>
<td>[23.6, 12–158, 94]</td>
<td>[32.0, 8–330, 192]</td>
<td>$F (1,284) = 1.25$</td>
</tr>
<tr>
<td>Mean ° copulations/day</td>
<td>2.4</td>
<td>2.2</td>
<td>ANOVA</td>
</tr>
<tr>
<td>(SD, range, N) of copulations</td>
<td>[1.4, 1–7, 44]</td>
<td>[1.5, 1–8, 106]</td>
<td>$F (1,148) = 0.82$</td>
</tr>
<tr>
<td>Mean duration (days) of mating period</td>
<td>1.85</td>
<td>1.9</td>
<td>ANOVA</td>
</tr>
<tr>
<td>(SD, range, N) of receptive periods</td>
<td>[0.61, 1–3, 26]</td>
<td>[0.87, 1–4, 58]</td>
<td>$F (1,82) = 0.07$</td>
</tr>
<tr>
<td>% of copulations initiated by male</td>
<td>46%</td>
<td>48%</td>
<td>$\chi^2 = 0.68$, $P = 0.41$, ns</td>
</tr>
<tr>
<td>[N = 290 copulations]</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

be unable to specifically target cycling females. We reasoned that if any individual should be capable of detecting female reproductive state it should be the male, as male fitness is dependent on mating with fertile females, and in some [Gust, 1984; Ostner et al., 2006; Watts, 1991], but not all [Heistermann et al., 2001; Yan & Jiang, 2006] species, males have been shown to mate preferentially with cycling vs. pregnant females. However, we found no evidence that the male distinguished between cycling and pregnant females. He did not mate more often or for longer durations or initiate copulations more frequently with cycling vs. pregnant females (Table III). Rather, he initiated copulations on the basis of rank, initiating a greater proportion of copulations with two high-ranking females (% copulations initiated by male towards high-ranking females: MA, 66% of 59 copulations; VI, 67% of 60 copulations; $\chi^2 = 1.7$, df = 1, $P = 0.19$; VI = 6.7, df = 1, $P = 0.001$) and a lower proportion with the two lowest ranking females (% copulations initiated by male: UG, 35% of 63 copulations; BE, 22% of 67 copulations; $\chi^2 = 9.7$, df = 1, $P = 0.001$; Be = 20.4, df = 1, $P < 0.001$), compared with his overall rate of initiation (47.6% of 290 copulations).

Last we considered potential costs to mating overlap. Females did not mate less often on days with mating overlap (days with mating overlap: mean number of copulations per day = 2.35 ± 1.7; N = 60 days; days with no overlap: mean number of copulations per day = 2.2 ± 1.3; N = 90 days; t-test: $t = -0.58$, df = 148, $P = 0.56$, ns). Accordingly, the male copulated more than twice as often on days with mating overlap (4.9, SD = 2.5, N = 38 days) compared with days when only a single female mated (2.2, SD = 1.2, N = 112 days; t-test: $t = -6.5$, df = 43, $P < 0.001$).

DISCUSSION

Western gorilla females varied in the timing and frequency of mating during pregnancy, rather than exhibiting the stereotypic pattern described in several other primate species [Bielert et al., 1976; Engelhardt et al., 2007; Gust, 1994; Kuster & Paul, 1984; Nieuwenhuijse et al., 1986; Sommer et al., 1992; Wallis & Lemmon, 1986]. This flexibility permitted individuals to engage in conditional sexual behavior, and pregnant females mated more often on days when other females were mating and often discontinued mating altogether when no other group females were available (i.e. cycling or pregnant) to mate. Thus, as female PC mating was in response to other females’ behavior we conclude that PC mating in western gorillas is a tactic used against other females in female-female competition. Although limited sample size may raise questions as to how generalizable these results are to gorillas in general, Stoinski et al. [2009] recently tested this hypothesis, and found a strikingly similar pattern of PC mating overlap in captive gorillas, strengthening the likelihood that PC mating may routinely serve as a form of female competition in gorillas.

But what are females competing for? One possibility is that PC mating reduces sperm available to other females, thereby delaying or preventing conception in cycling females [Small, 1988; Sommer, 1989; Sommer et al., 1992]. Consistent with this hypothesis, we found that the male mated more than twice as often on days with mating overlap compared with days with no mating overlap. It is known that in multi-group populations, increased male mating frequency is linked to sperm depletion [Marson et al., 1989; Synnott et al., 1981] with higher mating frequency ultimately reducing the likelihood of fertilization [Danielsson, 2001; Preston et al., 2001; Warner et al., 2002]. In groups with a single breeding male, the effects of sperm depletion should be even stronger because relative testes size, which correlates with daily sperm production rates and the number of sperm per ejaculate [Moller, 1989], is smaller [Harcourt et al., 1981a]. This is particularly true in western gorillas where relative testes size is among the smallest of all the primates [Harcourt & Stewart, 2007]. Evidence from studies of other primate species with one-male mating systems found a reduced likelihood of conception associated with
mating overlap [Dunbar, 1980; Sommer et al., 1992; Zinner et al., 1994] and, thus, it is possible that sperm might become a limited resource over which western gorilla females compete. However, although plausible, it seems unlikely that the observed increase in male mating frequency was sufficient to routinely prevent fertilization, as two of five conceptions occurred on days of mating overlap. Furthermore, we did not find that pregnant females specifically targeted cycling females for mating overlap as predicted by the sperm depletion hypothesis, although we could not rule out that this was because females were unable to distinguish cycling from pregnant females.

A second possibility is that female gorillas use PC mating as a form of mate guarding to outrace other females for male attention. We occasionally observed females harassing, interrupting, and replacing lower-ranking females during copulations, which would be consistent with this hypothesis. But why should pregnant females use mating as a tactic to compete against other females? Western gorilla females compete with each other in several arenas. For example, females compete over access to food and have clear and stable rank differences, which are partially dependent upon male support [Lodwick & Doran-Sheehy, unpublished data]. If maintaining high rank depends, to some degree, on coalitionary support from the male, then PC mating may be an effective spiteful strategy [Trivers, 1985; Vervaecke et al., 2003], used to deflect the male’s attention away from other females, thereby enhancing one’s own status with the male while minimizing male interest in and support of other females.

We found that the male mated preferentially with females on the basis of rank rather than reproductive state. This is a surprising finding given that mating with cycling, but not pregnant, females should increase male fitness, and males have been shown to mate preferentially with cycling females in mountain gorillas and some other taxa [Gust, 1994; Ostner et al., 2006; Watts, 1991]. Why then are western gorilla males, in contrast to closely related mountain gorillas, unable to distinguish between cycling and pregnant females? One possibility may be that pregnant females effectively mimic the behavior of cycling females. Given the absence of conspicuous sexual swellings, cycling female gorillas typically indicate ovulation to the male through changes in sexual activity during brief mating periods, in response to hormonal stimuli [Czekala & Sciotte, 2000]. For pregnant females although such monthly hormonal stimuli are absent [Chapeau et al., 1993; Smith et al., 1999], they continue to exhibit short mating periods of 1–2 days and mate with the same frequency and duration as cycling females. As a result, the mating of pregnant females appears indistinguishable from that of cycling females, except in the flexibility of when the mating periods occur. Thus, if the male relies primarily on visual cues of female reproductive state, pregnant females may successfully manipulate the male into choosing to mate with them.

Anecdotal evidence suggests some significant outcomes may result from female competition, both involving low-ranking females. In the first case, the lowest-ranking female took 11 months to conceive following the death of her offspring, although two higher-ranking females conceived 30 and 50 days following the death of similarly aged or older offspring. This is consistent with the hypothesis that female harassment during mating and in other contexts may delay conception and slow down reproduction as suggested earlier [Dunbar, 1980; Sommer, 1989; Wasser & Starling, 1988]. In a second case, a female emigrated from the group after ten months of cycling following the death of her infant, supporting the possibility that females compete both directly and indirectly through male preference, for group membership.

In sum, female western gorillas used PC mating strategically, synchronizing copulations to occur on days when other females mated, and refraining from mating for lengthy periods when no other females mated. Thus, in western gorillas nonconceptive mating is likely used to compete against other females, and not to confuse paternity or to obtain immediate benefits from the male, as suggested earlier. This strategy, which may be effective because males fail to distinguish between cycling and pregnant females, may serve to reinforce a female’s status and potentially delay conception in other females. Although our sample size is limited (based on a single group), the recent finding that pregnant captive western gorillas females also engaged in targeted mating overlap [Stoinski et al., 2009] further strengthens the possibility that PC mating may serve as a form of female competition in gorillas. Exactly how common the use of strategic nonconceptive mating as a form of female competition is across taxa, we cannot say, given the nearly complete lack of data on individual variation in female nonconceptive mating. However, we can speculate that nonconceptive mating during pregnancy may be an equally important strategy in other species with one-male groups and female-dispersal, when females do not have any morphological indicators of ovulation or pregnancy. We would assume that PC mating would be an ineffective tactic in primates where females have exaggerated sexual swellings, as swelling type and size typically differ in cycling and pregnant females, thus, allowing males to distinguish pregnant from cycling females. In these taxa, other forms of nonconceptive mating such as mating during nonfertile portions of the cycle could conceivably serve a similar function. Although extended mating periods in cycling females is typically viewed
as a means to confuse paternity, it may also provide the opportunity for females to compete with each other if females use nonconceptive periods to target mating overlap toward other females. To assess the extent to which nonconceptive mating is used in female–female competition and elucidating its competitive outcome will require long-term studies documenting individual variation in female nonconceptive mating, the factors that influence it, and its impact on life-history and demography across a wide variety of taxa. At present, our findings indicate that in gorillas, female-mating competition is potentially more important than previously considered. If proven more generally true, female–female competition should be considered a potential factor in the evolution of nonconceptive mating in humans.

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