Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda

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Abstract Chimpanzees have complex and variable mating strategies, but most copulations occur when females with full sexual swellings are in parties with multiple males and mate with most or all of those males. Daily copulation rates for fully swollen females vary at different times of a female's cycle, among females, and across communities and populations. Variation in female age, parity, and cycle stage underlie some of this variation, but possible demographic effects on copulation rates have not been systematically investigated. Demographic variation can affect many aspects of behavior and ecology, including the frequency and success of different mating tactics. Analysis of data from the unusually large chimpanzee community at Ngogo produces two results that are consistent with the hypothesis that demographic variation 2affects female copulation rates. Copulation rates were high compared with those reported from other research sites, where females had fewer potential mates available. Daily copulation rates of fully swollen females were also positively related to the number of males with whom they associated. Ngogo data also re-confirm results from other studies, of both wild and captive populations, showing that female copulation rates increase during periovulatory periods. This is consistent with the hypothesis that sexual swellings and extended receptivity and proceptivity help to protect females against infanticide by helping to ensure they mate with all potential sires. As at some other sites, parous females at Ngogo copulated at higher rates than nulliparous females. Possible effects of demography on sexual behavior should be considered in assessments of

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differences between chimpanzees and bonobos and of variation across chimpanzee populations.

Introduction

Chimpanzees (*Pan troglodytes*) live in fission–fusion communities in which community members form temporary parties that vary in size, duration, and composition. Data from several sites show that variation in ripe fruit abundance and/or in the number of sexually receptive females can affect party size (Gombe: Stanford et al. 1994; Kanyawara: Chapman et al. 1995; Mahale: Matsumoto-Oda 1999a; Taï: Boesch 1996, Doran 1997; Budongo: Reynolds 2005). In particular, large parties with many males may form when adult females with full sexual swellings are present, irrespective of fruit availability (e.g. Ngogo: Mitani et al. 2002; Kalinzu: Hashimoto et al. 2001).

Reproductively mature female chimpanzees have menstrual cycles that last approximately 35 days; they develop sexual swellings that are maximally tumescent for approximately 12 days of each cycle (reviewed by Wrangham 1993; Morin 1993; Wallis 1997; Stanford 1998). Chimpanzee mating tactics are complex and variable (Tutin 1979; Tutin and McGinnis 1981; Hasegawa and Hiraiwa-Hasegawa 1983, 1990; Goodall 1986; Morin 1993; Takahata et al. 1996; Watts 1998; Matsumoto-Oda 1999b; Boesch and Boesch-Achermann 2000; Stumpf and Boesch 2005, 2006). Copulations occur mostly opportunistically, when maximally tumescent females in parties with multiple males mate with many or all of those males. Males are highly tolerant of each other's mating behavior, although adults disrupt some

mating attempts by adolescents and high-ranking adults disrupt some by subordinate adults, especially late in a female's fully swollen phase. Opportunistic mating carries high potential for sperm competition (Hasegawa and Hiraiwa-Hasegawa 1990). Alternatively, high-ranking males may try to mate exclusively in the presence of other males; mate guarding, most likely during presumed periovulatory periods (POPs), involves considerable aggression both to females and to other males. Finally, males sometimes persuade females to go on consorts, during which they avoid other males and mate exclusively with each other.

Data from several sites show that the rates at which both females and particular males copulate vary across the course of swelling cycles. Juvenile and adolescent males tend to copulate most often early in cycles, when interest from adult males is relatively low. Adult male interest increases as cycles progress (e.g. Gombe: Goodall 1986; Taï: Deschner et al. 2003; Kanyawara and Budongo: Emery Thompson 2005; Mahale: Takasaki 1985), and high-ranking males in particular may increase their mating effort during POPs even when females mate opportunistically (e.g. Mahale: Takasaki 1985; Matsumoto-Oda 1999b). Hormonal and behavioral data from Taï (Deschner et al. 2003) and from Sonso (Budongo) and Kanyawara (Kibale; Emery Thompson 2005) showed elevated copulation rates during POPs; females in Emery Thompson's sample also copulated at higher rates during conception cycles than during non-conception cycles (Table 1). Increased male interest in females and elevated copulation rates during POPs are consistent with the hypothesis that exaggerated sexual swellings provide reliable but imprecise information about ovulation (the ''graded signal'' hypothesis; Nunn 1999).

Copulation rates can also vary with female age, parity, and residence status (Table 1). For example, Hasegawa and Hiraiwa-Hasegawa (1990) reported higher rates for prime adult females at Mahale than for both younger and older females, and higher rates for recent immigrants than for long-term residents.

Data on female copulation rates are relevant to understanding behavioral differences between chimpanzees and bonobos (*Pan paniscus*). Notable differences in sexual behavior clearly exist; for example, bonobo females are sexually active for much more of their adult lives than chimpanzee females (Wrangham 1993; Kano 1996; Stanford 1998), which may help to may reduce the potential benefits of male sexual coercion compared with those available to male chimpanzees (Smuts and Smuts 1993; Wrangham 1993; Parrish 1994). Whether females in these two species typically copulate at different rates has been the subject of some debate, however (summarized in Stanford 1998). In fact, reported values show considerable within-species variation (Table 1), and Wrangham (2002) has argued that instead of a simple bonobo–chimpanzee

difference, eastern chimpanzees females copulate at relatively high rates when maximally swollen whereas western chimpanzee females and bonobos copulate at lower rates.

Any comparative analysis of copulation rates should take demographic variation into account (Kano 1998; Hashimoto and Furuichi 2006). Demography can affect many aspects of social and reproductive behavior (Altmann and Altmann 1979; Dunbar 1988) and demographic effects are known in chimpanzees (Watts 1998; Mitani and Watts 1999; Watts and Mitani 2002; Mitani 2006). On the basis of comparative analysis of data from bonobos at Wamba and from several chimpanzee research sites, Furuichi and Hashimoto (2002) concluded that one reason copulation rates were lowest for bonobo females was that they had fewer potential mates available than did females at the chimpanzee sites. Likewise, Hashimoto and Furuichi (2006; cf. Table 1) argued that a major reason why female chimpanzees at Kalinzu copulated at high rates compared with female chimpanzees at sites like Mahale and Sonso (Table 1) was that the Kalinzu community had many more adult males (17–19) than those at the other sites.

Copulation rate data are also relevant to questions about the evolution of sexual swellings, of extended periods of sexual receptivity, and of high frequencies of non-conceptive sexual interactions between sexually mature males and females. These are characteristics of female chimpanzees and bonobos, who face physiological costs of maintaining and repairing injuries to sexual swellings and of dealing with male aggression, plus possible ecological costs of feeding competition that results from associating with many males (Wrangham 1993, 2002; Matsumoto-Oda 1999b). The potential for feeding competition and the costs of male harassment are lower for bonobos and vary among chimpanzee populations, but in both species sexual swellings, extended periods of receptivity, female proceptivity towards multiple males, and the high frequency of non-conceptive sex presumably confuse paternity and reduce the risk of male sexual coercion, particularly infanticide (Wrangham 1993, 2002). Infanticide is not known in bonobos, but is well documented both between and within communities in chimpanzees (Arcadi and Wrangham 1999).

Here, I use data from Ngogo, Kibale National Park, Uganda, to investigate the effect of the number of potential male mating partners, female parity, female cycle stage, and the simultaneous presence of multiple maximally swollen females on female copulation rates. Ngogo offers outstanding opportunities to investigate demographic effects on chimpanzee behavior because the chimpanzee community there is extremely large and has exceptionally many sexually mature males (Watts 1998; Mitani and Watts 1999; Watts and Mitani 2002). Results show that variation in the number of potential mates strongly affects copulation rates and is consistent both with the ''graded

Table 1 Hourly copulation rates for female chimpanzees and bonobos at different wild and captive research sites

	Setting	Site	Sample population	Rate	Number of males, adult/adolescent
Chimpanzees	Wild[1]	Kanyawara, Sonso	Parous, conception cycles	0.85 h^{-1}	11 (Kanyawara)[a]
			Parous, non-conception cycles	0.40 h^{-1}	14 (Sonso)[a]
			Nulliparous, conception cycles	1.16 h^{-1}	
			Nulliparous, non-conception cycles	0.40 h^{-1}	
			All, POPs, conception cycles	1.32 h^{-1} (0.98)[b]	
			All, POPs, non-conception cycles	0.50 h^{-1} (0.39)[b]	
	Wild[2]	Sonso	All swollen females	c. 0.03–0.55 h^{-1} [c]	15[a]
	Wild[3]	Mahale	Maximal swelling	0.79 h^{-1} (0.48–1.02)[d]	12[a]
	Wild[4]	Kalinzu	Maximal swelling	3.1 h^{-1}	17/1
				2.2 h^{-1}	19/2
				3.2 h^{-1}	18/2
	Wild[5]	Ngogo	Parous, POP	4.96 h^{-1}	22–26/13–15
			Parous, non-POP	3.68 h^{-1}	
			Nulliparous, POP	4.33 h^{-1}	
			Nulliparous, non-POP	2.90 h^{-1}	
			All	3.52 h^{-1} (2.51–4.85)[d]	
	Wild[2]	Gombe	All swollen females	0.5–3.5 h^{-1} [d]	12[a]
	Wild[6]	Gombe	Early morning	c. 5 h^{-1}	9/1
			Mid-morning	c. 2 h^{-1}	
			Late afternoon	c. 1 h^{-1}	
	Captive[7]	Arnhem	Maximal swelling	0.8 h^{-1}	4/2
Bonobos	Wild[8]	Wamba E$_1$	Females with 4–6y old infants	0.43 h^{-1} (0.33–0.67)[d]	7/3
	Wild[8]	Wamba E	Females with 4–6y old infants	0.08 h^{-1} (0–0.29)[d]	14/5
			No Infant	0.12 h^{-1} (0.05–0.39)[d]	
			All females	0.26 h^{-1}	
	Captive[9]	Stuttgart, Cologne	Maximal swelling	0.25 h^{-1}	1–2/0
	Captive[10]	San Diego	Adult males	0.18 h^{-1} [e]	1/2
			Adolescent males	0.45 h^{-1} [e]	

Sample population = females included in a given data set and timing of data collection; POP = periovulatory period; All = all females combined

[a] Published figures for Kanyawara, Sonso, and Mahale combined adult and older adolescent males

[b] Values in parentheses are for copulations with fully adult males only

[c] Values are for range of monthly values

[d] Values in parentheses are ranges for individuals

[e] Values are for all ''mounts'', without or without completed copulation

Sources: [1]Emery Thompson (2005); [2]Wallis 2002; [3]Takahata et al. (1996); [4]Hashimoto and Furuichi (2006); [5]this study; [6]Goodall (1986); [7]Klinkova et al. (2005); [8]Kano (1992), Takahata et al. (1996); [9]Reichert et al. (2002); [10]de Waal (1987)

signal'' hypothesis and with the argument that extended sexual receptivity and extensive non-conceptive mating help protect females against infanticide.

Methods

Study site and subjects

Ngogo is in the center of Kibale National Park, located in western Uganda between 0°13′ and 0°41′N and 30°19′ and 30°32′E. The study area is approximately 30 km^2 and consists mostly of mature and regenerating forest transitional between lowland and montane moist evergreen forest; it also includes smaller areas of other vegetation types, notably swamp forest dominated by the palm *Phoenix reclinata* and *Pennisetum purpureum* grassland (Butynski 1990; Struhsaker 1997; Lwanga et al. 2003). Mean annual rainfall is approximately 1,800 mm.

The Ngogo chimpanzee community, the largest ever identified, has been under continuous observation since mid-1995. It has had 140–150 members during that time,

including 22–28 adult males, 13–15 adolescent males, over 40 adult females, and up to 12 adolescent females. Data considered here come from 6,946 h of observation at Ngogo during six study periods between 1998 and 2004. In each period, I conducted focal samples on females with sexual swellings during which I recorded all observed copulations and noted the identities of the males involved. I also kept track of how many males associated with each swollen female on a daily basis (where "associated" means the male and female were known to be in visual contact and thus to have the opportunity to try to copulate) and on how many fully swollen females associated with each other. I sometimes sampled two fully swollen females on the same day. For analyses given below, I included only focal samples that lasted at least 3 h ($n = 304$). The sample population included 18 females, 14 parous and four nulliparous, each sampled on at least ten days on which she had a full swelling. Three nulliparous females were reproductively mature and conceived during or shortly after the relevant study periods. The fourth was cycling during February through July 1999. Her cycles were regular, but she might not yet have been fertile, given that she was again observed cycling in May through July 2000. She conceived during the 2000 study period. Two females each contributed data in two different study periods. Female CL was nulliparous in late 1998 and conceived in approximately March 1999. She was again observed fully swollen and mating in June 2004, after weaning her first infant. Parous female SI was cycling in June–August, 2000, then again in June–August, 2001. She conceived in 2001; whether she had conceived in 2000, but lost a fetus or a young infant, was unknown.

I collected data less systematically on several younger, adolescent females who were not yet reproductively mature and did not include these data in the multivariate analyses reported below. I also excluded data from two older, parous females who are apparently infertile (both have cycled regularly, without any evidence of conceptions, since they were first identified in 1998 and 1999, respectively), although I report data on their copulation rates for comparative purposes.

Although mate guarding by males has been documented at Ngogo (Watts 1998), all the data here come from estrus periods in which females mated opportunistically.

Data analysis

I analyzed variation in copulation rates with generalized linear models, which enable consideration of simultaneous effects of continuous and categorical independent variables on a continuous dependent variable. The dependent variable was the hourly copulation rate per female for a given day. Independent variables included three that were cate-

gorical: female parity (parous versus nulliparous), presence or absence of other swollen females on the same day, and whether the female was in her inferred periovulatory period on that day. I also used two continuous independent variables: the number of fully adult males who associated with the female and the combined number of adult and adolescent males who associated with her on each day. These two measures of mate availability were highly correlated ($r = 0.89$, $n = 305$, $P < 0.001$).

I constructed two models that both include each of the three categorical variables and interaction effects among them as independent variables. The first model also includes the number of adult males as a continuous predictor variable whereas the second model includes the number of adult plus adolescent males. Because each model uses the same data set, I used Bonferroni adjustments to set alpha levels at $P = 0.025$.

I did not collect endocrine data on females and so could not directly assess the timing of ovulation or conception. Pregnant female chimpanzees sometimes develop sexual swellings and show estrus-like behavior (Wallis and Lemmon 1986; Wallis and Goodall 1993), and male interest in mating may depend partly on whether a female is already pregnant. Wallis (1997) reported a mean gestation period of 225 days for female chimpanzees at Gombe. Parturition dates for the subsequent infants of females included in the sample here were known within a range of one day to one month. All cycles that I have included in data analyses were at least 200 days before these estimated dates, which should minimize the odds that females were already pregnant when I collected the behavioral data. I assumed that the four days before detumescence constituted the periovulatory period, based on endocrine data from Taï (Deschner et al. 2003). Any strictly chronological identification of POPs is tentative, however, because the Taï data and those from another site in Kibale (Kanyawara; Emery Thompson 2005) showed that ovulation can occur as early as six days before detumescence and Graham's (1981) data on captive chimpanzees indicated that it was most probably within a three-day window centered on the last day of maximum tumescence.

I used two sample t-tests to compare parous females with nulliparous females with regard to the variables copulation rates, the number of adult males with whom females associated per day, and the total number of males with whom females associated, after ascertaining that these were normally distributed and that variances were equal.

I used data on the identities of each female's copulatory partners to analyze the relationship between the total number of copulations per female and the total number of males with whom the female had mated.

Data on male copulation rates, which varied considerably across females, at different times in female cycles,

and, especially, in relation to male dominance rank, will be considered elsewhere.

Results

Females copulated at an overall mean daily rate of 3.52 times per hour (SD = 1.37; n = 304 days). Mean daily rates for individual females varied from 2.51 to 4.85 copulations per hour. The maximum number of copulations that I saw on a single day was 65 (with 17 different adult males and one adolescent), in 11 h of observation). Both models explained significant amounts of the variation in daily rates (Table 2). Copulation rates increased as the number of males with whom females associated increased, and the number of male associates had the strongest effect on copulation rates in both models (Table 2). The model that included total male number as a predictor explained slightly more of the variance in copulation rates (64%) than did the model that used the number of adult males only (59%; Table 2).

Parity also had significant effects in both models (Table 2). Parous females copulated at higher rates (mean = 4.05 h^{-1}; SD = 1.30; n = 222) than nulliparous females did

(mean = 3.32 h^{-1}; SD = 1.42; n = 82; t = 4.22, df = 302, P < 0.0001), although they did not associate with significantly more males. Parous females associated with a mean of 14.93 adult males per day (SD = 4.66) and nulliparous females associated with a mean of 14.18 (SD = 5.26; t = 1.20, P = 0.11). Parous females associated with a mean of 22.90 adult plus adolescent males per day (SD = 8.14); the corresponding value for nulliparous females was 22.21 (SD = 8.31; t = 0.66, P = 0.26).

The effects of cycle stage also were significant for both models (Table 2). Females copulated a mean of 4.79 times per hour (SD = 1.19) during POPs and 3.44 times per hour (SD = 1.23) outside POPs. Mean copulation rates for parous females were 4.96 per hour (SD = 1.17) during POPs, significantly higher than the mean rate of 3.68 per hour (SD = 1.20) outside POPs (t = 53.33, df = 220, P < 0.0001; Fig. 1). Nulliparous females copulated a mean of 4.33 times per hour (SD = 1.32) during POPs, significantly higher than the mean rate of 2.90 times per hour (SD = 1.12) outside POPs (t = 13.97, df = 80, P < 0.0001; Fig. 1). Parous females copulated at higher rates than nulliparous females both during POPs (t = 7.02, df = 91, P < 0.001; Fig. 1) and outside POPs (t = 30.51, df = 209, P < 0.0001; Fig. 1).

Table 2 Results of generalized linear models analyzing variation in daily copulation rates

Effect	SS	DF	MS	F	P
Model 1					
Intercept	39.08	1	39.08	51.14	<0.0001
Adult males	191.90	1	191.91	251.12	<0.0001
PAR	5.07	1	5.07	6.63	0.0105
POP	39.53	1	39.53	51.72	<0.0001
FEM	0.93	1	0.93	1.21	0.27
PAR * POP	2.13	1	2.13	2.79	0.10
PAR * FEM	0.26	1	0.26	0.34	0.56
POP * FEM	1.69	1	1.69	2.21	0.14
PAR * POP * FEM	1.48	1	1.48	1.93	0.17
Error	225.43	295	0.76		
Model	341.47	304	341.47	55.85	<0.0001
Model 2					
Intercept	48.10	1	48.10	68.70	<0.0001
All males	210.78	1	210.78	301.03	<0.0001
PAR	9.14	1	9.14	13.05	0.0004
POP	34.23	1	34.23	49.02	<0.0001
FEM	4.15	1	4.15	5.93	0.0155
PAR * POP	0.49	1	0.49	0.70	0.40
PAR * FEM	0.09	1	0.09	0.13	0.72
POP * FEM	0.35	1	0.35	0.50	0.48
PAR * POP * FEM	0.51	1	0.51	0.73	0.39
Error	206.56	295	0.70		
Model	360.34	8	45.04	64.33	<0.0001

The number of adult males who associated with a female was included as an independent variable in Model 1; the total number of adults plus adolescents males who associated with the female was included as a dependent variable in Model 2.
POP = periovulatory period; PAR = parity; FEM = other fully swollen female present.
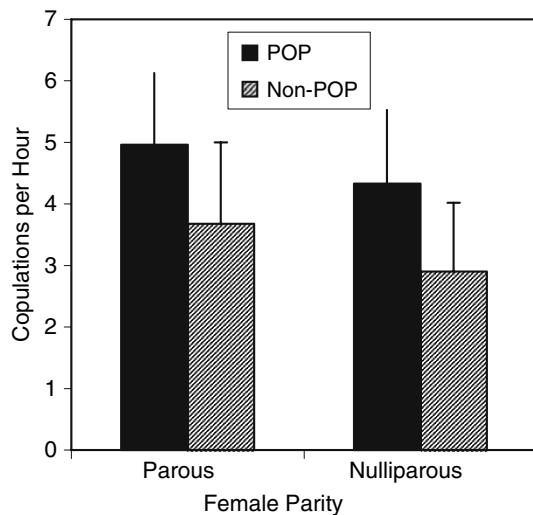Adjusted r^2 = 0.59 (Model 1), 0.64 (Model 2)

Fig. 1 Daily copulation rates (copulations per hour) for parous and nulliparous females. *POP* inferred periovulatory periods (those four days before the day of detumescence); *non-POP* outside presumed periovulatory periods. *Vertical bars* show one standard deviation

The presence or absence of other swollen females had a significant effect in the model that included the total number of adult and adolescent males, but not in the model that included only adult males (Table 2). Nulliparous females copulated at slightly lower rates when other swollen females were present (3.21 h^{-1}, SD = 1.60; n = 38) than when no other swollen females were present (3.41 h^{-1}, SD = 1.21; n = 44; t = 1.90, df = 80, P < 0.01); this was specifically true during POPs (4.08 h^{-1} vs. 4.70 h^{-1}, respectively). In contrast, parous females copulated a mean of 4.15 times per hour (SD = 1.31; n = 120) when other swollen females were present, but at slightly lower rates (3.95 h^{-1}; SD = 1.28; n = 102) when no other swollen females were present, although this difference was not significant (t = 1.10, df = 220, P = 0.16). Per capita rates for parous females might not have dropped on days when they associated with one or more other fully swollen females, because they had more potential mates available on these days (adult males: mean = 16.26, SD = 4.52; adults plus adolescents: mean = 25.75, SD = 8.01) than on days when no other females had swellings (adult males: mean = 13.77, SD = 4.46; adults plus adolescents: mean = 20.48, SD = 7.47). These differences were significant (two-sample *t*-tests with equal variances: t = 4.11, df = 220, P < 0.0001 for adult males; t = 5.08, df = 220, P < 0.0001 for all males).

Interactions of parity, fertility, and presence of other swollen females did not have significant effects in either model (Table 2).

Three young adolescent females sampled for at least 3 h on a combined total of 16 days copulated at a pooled mean rate of 2.65 times per hour, lower than the mean for older nulliparous females. One of these three was a presumed natal female who later disappeared (possibly because she emigrated). The other two were presumed recent immigrants who have since given birth, but were still having typical adolescent cycles, characterized by swellings larger than those of fully adult females and short periods of detumescence between maximum swellings (Goodall 1986; Wallis 1997). Two adult females who are apparently parous (both were accompanied by juveniles when first identified) but who have cycled repeatedly without known conceptions since 2001 were sampled for at least three hours on eight and 14 days, respectively. They copulated at mean rates of 2.56 and 2.67 times per hour, respectively. These values are lower than the mean for fertile parous females outside POPs (above).

The number of different males with whom individual females were seen to copulate while maximally tumescent varied from 28 to 38. No female was seen to copulate with all males who were sexually mature at the time of her swelling cycles. Although failure to see copulations with some males might have resulted from sampling error, occasionally one or more males apparently did not associate with an estrous female. For example, three adult males and several adolescents who belonged to the western subgroup of males (Mitani and Amsler 2003) apparently did not associate with parous female SI, an east-central female, during two cycles in 2001, and beta male HO was not seen to associate with either BL or CL (both parous females) during their cycles in 2004. Females typically associated and copulated with many males during the first few days of maximum swelling, which meant the number of mating partners initially increased steeply with the number of observed copulations (Fig. 2). Females subsequently added new partners at a decreasing rate as they encountered new males (Fig. 2). The number of partners was exponentially related to the total number of copulations and described by the equation:

Number of partners

$$= [6.41(\ln(\text{number of copulations})] - 4.29.$$

Females could, presumably, defend their infants against young adolescent males. Assuming, however, that all adult males and at least older adolescents, who are as large as females, potentially pose an infanticide risk, females in the sample considered here would have needed to copulate with at least 30 males to gain whatever insurance against infanticide that copulation provides. On the basis of the regression equation above, the average Ngogo female would need 218 copulations to include at least one with 30 males, and many of these would fall outside the temporal window when she is most likely to conceive. High copulation rates at Ngogo meant females there routinely
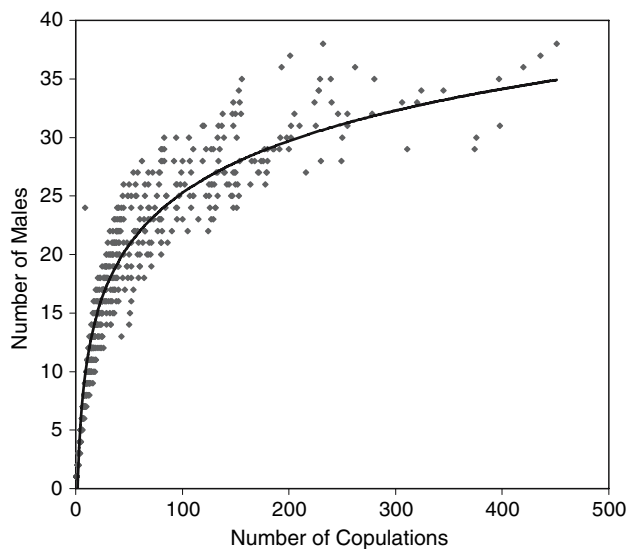
Fig. 2 Cumulative number of copulations by individual females per number of individual males with whom they copulated. Each point represents the observed sequential copulation in a given swelling period in which a female mated with a new partner, with partners numbered consecutively. The variables are exponentially related by the equation: number of partners = [6.41 × ln (number of copulations)] – 4.29; $r^2 = 0.92$

copulated more often than this per cycle. The maximum number of copulations I saw during one estrus was 439. Fifteen estrus periods for which the days of swelling onset and of detumescence were known give a mean 13.93 days (SD = 1.33 days) for the duration of maximum tumescence. With a mean rate of 3.5 copulations per hour and assuming a 13-hour activity period, the average female would have copulated 542 times per cycle.

Discussion

Variation in the number of males with whom females with sexual swellings associated strongly affected variation in daily copulation rates at Ngogo, where the community has enough males to have effects of demographic variation at the level of the size and composition of mating parties. This result supports Kano's (1998) suggestions that demographic variation explains some of the variation in copulation rates in chimpanzees and bonobos (cf. Hashimoto and Furuichi 2006) and that we should look for demographic effects before concluding there are fundamental biological differences between these taxa. Copulation rates for females at Ngogo were higher than those reported for chimpanzee communities at several other study sites where females had fewer potential mating partners (Gombe: Goodall 1986; Mahale: Hasegawa and Hiraiwa-Hasegawa 1990; Matsumoto-Oda 1999b; Kanyawara and Sonso: Emery Thompson 2005). Female

copulation rates at Kalinzu, where the number of adult males was also unusually high, were closer to those for Ngogo (Furuichi and Hashimoto 2002, Hashimoto and Furuichi 2006; Table 1). The positive relationship between the number of males in mating parties and female copulation rates is one of multiple demographic effects on behavior at Ngogo. Others include the relationships between the large number of males and the high success rate of red colobus hunts (Mitani and Watts 1999) and the high frequency of boundary patrols (Watts and Mitani 2002) and the unique substructuring of male social networks and use of the community's range (Mitani and Amsler 2003).

Inter-site contrasts in observation conditions and degree of habituation may also explain some of the variation among sites in reported copulation rates, all of which are underestimates because of limited visibility (Wrangham 1993). More importantly, the number of potential mates is only one of many variables that can affect the rate at which female chimpanzees copulate in situations where mating is opportunistic. Others include female age, parity, residence status, and cycle stage (Goodall 1986; Takasaki 1985; Hasegawa 1989; Hasegawa and Hiraiwa-Hasegawa 1990; Matsumoto-Oda 1999b; Emery Thompson 2005; Klinkova et al. 2005; Stumpf and Boesch 2005). For example, Hasegawa (1989) found that adult females who immigrated to Mahale M Group after the dissolution of K Group copulated at higher rates than cycling adult females who were long-term M Group residents. Competition among males can also affect copulation rates. In particular, rates may be lower when males mate guard females—i.e. when mating is restrictive—because females then mate with fewer males than are available and male copulation rates limit those of females. I did not see mate guarding during the study periods considered here, but it happened during at least some of the other studies that have provided data on copulation rates. For example, Hasegawa (1989) reported that 15% of copulations by long-term resident females in Mahale M Group occurred in restrictive situations, and Hasegawa and Hiraiwa-Hasegawa (1983) found that restrictive mating was more common during POPs than earlier in cycles. Wrangham (2002) found mate guarding to be common at Kanyawara also, although only for parous females.

Copulation rates of Ngogo females increased during presumed periovulatory periods. Studies at other sites in the wild (Gombe: Wallis 1992; Mahale: Matsumoto-Oda 1999b; Taï: Stumpf and Boesch 2005, 2006; Kanyawara and Sonso: Emery Thompson 2005) and in captivity (Klinkova et al. 2005) have documented similar increases. The rate increase during POPs was independent of female parity and was partly because of increases in female attractiveness to adult males, especially high-ranking adults (Watts 1998; unpublished data). Studies at Gombe (Tutin

1979; Goodall 1986), Mahale (Hasegawa and Hiraiwa-Hasegawa 1990; Matsumoto-Oda 1999b), Kanyawara and Sonso (Emery Thompson 2005), and Arnhem Zoo (Klinkova et al. 2005) gave similar results.

Parous females at Ngogo copulated at higher rates than older, reproductively mature nulliparous females. Young, reproductively immature nullipares copulated at even lower rates. Comparative data on rates of copulation by parous and nulliparous females vary. Ngogo data are consistent with those from Gombe (Tutin 1979; Goodall 1986) and from Wrangham's (2002) study at Kanyawara. In contrast, nulliparous females copulated at higher rates than parous females at Mahale (Hasegawa and Hiraiwa-Hasegawa 1990), at Sonso (Emery Thompson 2005), and during another study period at Kanyawara (Emery Thompson 2005), although the differences were small. Comparisons of relative copulation rates for parous and nulliparous females have typically involved only a few nullipares per site (e.g. four at Ngogo). Inter-site contrasts between the results might simply be artifacts of these small sample sizes, although Wrangham (2002) noted that parous Kanyawara females were more attractive to males, induced more male–male contest competition, and copulated more often with high-ranking males, whereas nulliparous females copulated more often with low ranking-males (similar differences exist at Ngogo; Watts, unpublished data). The overall parity-related difference in rates was small and did not reflect these differences between male tactics.

Males at Ngogo were less interested in two parous Ngogo females who cycled repeatedly for several years without known conceptions than in other parous females, and copulation rates for these females were relatively low. This difference may reflect a male response to cues about fertility. The increase in male interest and mating effort during those parts of cycles in which females were statistically most likely to ovulate (POPs), which has also been consistently documented at other sites (above), is presumably such a response. Analysis of behavioral and endocrine data from captive chimpanzees at Arnhem Zoo (Klinkova et al. 2005) and wild chimpanzees at Taï (Deschner et al. 2004) show, however, that although male behavior tracks the state of sexual swellings, these give imprecise information about the timing of ovulation. Swelling stage affected male mating behavior at Arnhem, but the exact timing of ovulation did not (Klinkova et al. 2005; cf. Reichert et al. 2002 for captive bonobos). These findings, plus increases in copulation rates during presumed POPs at Ngogo and elsewhere, support the ''graded signal'' hypothesis for the function of sexual swellings (Nunn 1999).

Females at Ngogo copulate many more times per day and at much higher total frequencies over the course of swelling cycles than reported for females at several other sites. Wrangham (2002) used his data from Kanyawara and published data from Mahale and Taï to estimate that parous females at those sites copulated approximately 400–700 times per conception, although his estimate for Gombe was 3,000. Matsumoto-Oda (1999b) obtained an estimate of 577 copulations from her own Mahale data, and noted that females there typically need 7.4 cycles to conceive. Few data on the number of cycles to conception are available for Ngogo, but with 600 or more copulations per menstrual cycle females may typically copulate several thousand times per conception.

Why female copulation rates vary is partly a different issue from that of whether non-conceptive mating and exaggerated sexual swellings protect females against male coercion, including infanticide. The main reason why copulation rates were high at Ngogo was that estrous females were often accompanied by many males, who initiated most copulations. Females might, however, still need many days and multiple cycles before they encounter all males who could pose a threat of infanticide and copulate with them sufficiently often to gain whatever protection copulation provides against infanticide. Wrangham (2002) calculated that the probability that females at Kanyawara would copulate with all twelve adult males in their community exceeded 99% after only 60 copulations; this is much lower than the corresponding value for Ngogo. He added that we do not know whether a single copulation can inhibit infanticide, and that females often remain proceptive to males with whom they have already mated. The issue of infanticide avoidance is also relevant to investigating the possible function of sexual swellings and pseudo-estrous behavior during pregnancy, which is common in chimpanzees (Wallis and Goodall 1993); this topic merits further research at Ngogo and elsewhere.

Female behavior can affect copulation rates in several ways. Female chimpanzees can exercise mate choice by means such as associating preferentially with some males and by being differently receptive or proceptive to individual males, especially during POPs (Matsumoto-Oda 1999b; Stumpf and Boesch, 2005, 2006). They need to balance attempted mate choice against the incentive to copulate with all males, however, even at the cost of aggression from some, and thereby to gain protection against coercion (Wrangham 1993, 2002; Stumpf and Boesch 2005). Even the high copulation frequencies at Ngogo are not absolute guarantees against within-community infanticide. A case occurred in 2005 during an attack by many males on a female and her neonate, and gang attacks by males have led indirectly to the death of at least one, and possibly two, other neonates (Watts and Mitani, unpublished data). Variation in infanticide risk and in other forms of male coercion seems to explain some of the variation documented across chimpanzee populations

and between chimpanzees and bonobos in copulation rates, copulation frequencies, and other aspects of non-conceptive sex (Furuichi and Hashimoto 2002; Wrangham 2002). For a given number of potential mates, female eastern chimpanzees may need to initiate more copulations and to copulate at higher rates than females in at least some populations of western chimpanzees (e.g. Taï) and than female bonobos, because they are more vulnerable to male sexual coercion, including infanticide (Furuichi and Hashimoto 2002; Wrangham 2002).

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