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Can the Patterns of Sexual Swelling Cycles in Female Taï Chimpanzees be Explained by the Cost-of-Sexual-Attraction Hypothesis?

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Abstract Chimpanzee females of East and West African populations differ in the average number of cycles per interbirth interval. Whereas females in Gombe, Mahale, and Kibale (eastern chimpanzees, *Pan troglodytes schweinfurthii*) average <9 cycles before they conceive, females at Taï (western chimpanzees; *Pan troglodytes verus*) average 29 cycles. We examined data from 2 different study groups (North and South) at Taï. By showing that Taï females interrupt cyclic activity for, on average, 7.4 mo between the end of the postpartum amenorrhea period (PPA) and the subsequent conception, and by calculating the number of cycles to conception based on a probability distribution of cycles over the interbirth interval, we show that Taï females average 19.4 cycles (North Group) and 11.7 cycles (South Group) to conception; therefore, the earlier calculation of 29 cycles was an overestimate. Further, at Taï young parous females have a significantly shorter PPA than those of older females, but the number of cycles to conception does not differ significantly between primiparous and nulliparous females. Some of our results are therefore not in line with the predictions of the cost-of-sexual-attraction hypothesis, which proposes that the factor ultimately responsible for the intensity of female sexual attractiveness is female intragroup scramble competition. We discuss an alternative hypothesis—the social passport hypothesis—which is compatible with the results of the study.

Keywords chimpanzee · postpartum amenorrhea period · reproduction · sexual swellings

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Introduction

Among eutherian mammals, Primates are unique in that a high number of species have extended mating periods (Hayssen *et al.* 1993). Whereas in most mammalian orders mating is restricted to relatively short periods and sometimes even just a few hours, e.g. Alpine marmot, *Marmota marmota* (Goossens *et al.* 1998); or bison, *Bison bison* (Berger and Cunningham 1994), primates often mate throughout the complete female ovarian cycle (Hrdy and Whitten 1987; Loy 1987). It is assumed that species-specific mating patterns are an adaptation to socioecological selection pressures (Crews and Moore 1986; Steklis and Whiteman 1989). Researchers have recently given increased attention to the influence of infanticide risk on mating patterns across mammal taxa (van Noordwijk and van Schaik 2000; van Schaik *et al.* 1999; Wolf and MacDonald 2004). By extending the period of estrus, and thus increasing the chance of overlapping with other estrous females, a female might reduce the possibility of being monopolized by the dominant male and thereby allow other males to copulate. Assuming that males are not able to detect when ovulation occurs, i.e., ovulation is concealed, by mating over an extended period the female might be able to confuse paternity (Heistermann *et al.* 2001). Though infanticide risk is an especially good explanation of the distribution of mating patterns in primates, other factors, including cryptic female choice, best genes, or more direct benefits for the female, e.g., male infant care, might be important in certain species (van Noordwijk and van Schaik 2000; Wolf and MacDonald 2004).

However, extended mating periods are not restricted to intracycle periods. By having a series of nonconceptive cycles before conceiving, a female might as well be able to mate with several males (van Noordwijk and van Schaik 2000); e.g., after the takeover of their pride by new males, female lions mate frequently but show reduced fecundity in the first 3 mo (Pusey and Packer 1994). Similarly, researchers explain an extended period of nonconceptive postpartum attractiveness in female bottlenose dolphins as a female strategy to avoid male harassment (Connor *et al.* 1996).

In chimpanzees, each conception is also preceded by a series of nonconceptive cycles (Boesch and Boesch-Achermann 2000) but, interestingly, chimpanzee populations differ strikingly in the feature (Knott 2001; Wrangham 2002). Though in wild chimpanzees interbirth intervals (IBIs) are rather similar between field sites, the duration of the postpartum amenorrhea period (PPA) is highly variable. In Gombe, e.g., average PPA for mothers with surviving infants is 3.9 yr (Wallis 1997), while it is 4.6 yr at Mahale (Nishida *et al.* 1990) and 4.4 yr at Kanyawara (Knott 2001). In contrast to the East African chimpanzee populations, PPA periods in the Taï population in West Africa are much shorter, averaging 2 yr (Boesch and Boesch-Achermann 2000).

Because, among the 4 populations, IBIs are similar while PPA are strikingly different, females at different field sites vary in the average number of menstrual cycles before conception. By assuming that once a female has resumed cycling she will continue having regular cycles until conception, Wrangham (2002) calculated the average number of cycles for female chimpanzees by subtracting the duration of PPA and the average duration of gestation (7.5 mo; Wallis 1997) from the average IBI. The lowest values are in Gombe (on average, 4.7 cycles before conception), followed by Kanyawara (5 cycles) and Mahale (8.9 cycles; Table I). Deschner *et al.* (2003) calculated the average number of cycles to conception (CTC) at Taï to be 29.2 cycles.

After immigrating into a new group, nulliparous East African females have on average a much higher number of cycles to conception than parous females do, with values ranging from 16 (Kanyawara) to 24 (Mahale) for nulliparous females vs. 5 (Kanyawara) to 8.9 (Mahale) cycles for parous females (Table I). The discrepancy in the average number of cycles to conception between parous and nulliparous females on the one hand and parous East African chimpanzees and parous West African chimpanzees on the other led to Wrangham's (2002) formulation of the cost- of-sexual-attraction hypothesis. The hypothesis is based on the observation that females differ not only in their PPA period and average number of cycles to conception but also in the degree of gregariousness and attractiveness to males. Though males in East African chimpanzee communities do not mate guard and compete over nulliparous females during their periovulatory period (POP), they do so for parous females during the few cycles that they experience. For West African chimpanzee females (nulliparous and parous) in Taï, Deschner *et al.* (2003) hypothesized that levels of competition between males and aggression toward females during the POP resemble more closely the situation for nulliparous East African chimpanzee females (Wrangham 2002). Therefore, whereas East African parous chimpanzee females seem to be highly attractive to males during their POP (loud POP), the low attractiveness of nulliparous East African chimpanzees and nulliparous as well as parous West African chimpanzee females indicates a silent POP. The cost-of-sexual-

Table I Reproductive parameters for female chimpanzees of different field sites

Study site	Period of adolescent sterility (yr)	IBI (yr)	Postpartum amenorrhea (yr)	Cycles to conception
Gombe[a]	2.4	5.2	3.9	4.7[h]
Mahale	2.7[b]	5.8[b]	4.6[b]	8.9[f,h]
Kanyawara	1.6[c]	6.0[e]	4.4[c]	5.0[e]
Taï NG (1980–1995)[d]	2.0	5.8	2.0	29.2[h]
Taï NG (1987–2002)[j]	1.7±0.5[l]	5.3±0.7[m]	1.8±1.2[n]	13.6±6.4[i,o]
Taï SG (1995–2002)[j]		5.3±0.8[p]	2.4±1.5[q]	9.0±3.2[i,r]
Taï (corrected value)[k]				19.4 (11.7)[g,o,r]

[a] Wallis (1997); [b] Nishida *et al.* (2003, recalculated); [c] Knott (2001);[d] Boesch and Boesch-Achermann (2000), [e] Wrangham (2002), [f] Nishida *et al.* (1990).

[g] Numbers in parentheses are for the South Group.

[h] Calculated by Wrangham (2002) by dividing the time period from the end of the PPA to the next conception through the average chimpanzee cycle duration of 36 d.

[i] Only observed cycles indicated by sexual swellings considered.

[j] Data are given as mean ± SD.

[k] Number of cycles to conception were calculated as described in the method section; [l] *n*=7; [m] *n*=18; [n] *n*=30; [o] *n*=18; [p] *n*=12; [q] *n*=13; [r] *n*=8

attraction hypothesis proposes that the factors ultimately responsible for the degree of female attractiveness during POP are the level of intragroup scramble competition for food between females and the difference in traveling costs for nulliparous and parous females. In this respect, the best strategy for chimpanzee females would be to have a high number of cycles per IBI and to reduce attractiveness to males, which in turn would reduce the level of male coercion. However, the display of sexual swellings as a result of ovarian cyclicity in females is generally associated with a higher association rate of males with the females (Wrangham 2000). A high level of association leads to more competition for food between females, which then leads to longer traveling distances. East African chimpanzee mothers cannot afford the long travel distances because they must carry their infants on the back (Wrangham 2000), and therefore they must reduce the number of cycles to conception. For Taï chimpanzee mothers, Wrangham (2002, p.205) suggested that higher food availability leads to a lower cost of grouping and, therefore, “affords females the luxury of many sexual cycles.”

Therefore, one prediction of the cost-of-sexual-attraction hypothesis is that both nulliparous and parous females at Taï should have a higher number of swellings to conception than their East African counterparts because feeding competition is relaxed and the females face a low cost of grouping.

However, sexual swellings are costly structures (Domb and Pagel 2001; Nunn 1999; Pagel 1994). Therefore, even in a situation in which females experience increased food availability and lower cost of grouping, females should exhibit a large number of swellings prior to conception only if there is a benefit to them. Consequently, the ecological and social pressures a female experiences during the different stages of her life history might lead to variations in the number of sexual swellings to conception.

By using long-term data from two different chimpanzee study groups in Taï and comparing the data with those of other chimpanzee field sites, we address the following questions: 1) Which factors influence the duration of the PPA and the number of cycles to conception in Taï females? 2) How do Taï females differ in their reproductive profiles (IBI, PPA, and cycles to conception) from East African chimpanzee females? 3) Can one explain the patterns by the cost-of-sexual-attraction hypothesis?

Methods

Study Site and Subjects

We studied 2 groups of wild West African chimpanzees inhabiting an evergreen lowland rain forest in the Taï National Park in Côte d’Ivoire. Habituation of the North Group started in 1979 (Boesch and Boesch-Achermann 2000), and we provide data of the group for 1987–2002 (Table II). We have observed the South Group since 1990 and the data used for the study is from 1995–2002 (Table III). Both groups experienced a considerable decline in group size during the study periods. While in 1987 North Group consisted of 80 individuals (including 8 adult males, 2 adolescent males, 27 parous females, and 4 nulliparous females), the number shrank

Table II Reproductive and demographic parameters for Taï North Group females from 1987 to 2002

Female	Parity	IBI (months)	PPA (months)	Min number of cycles to conception	Rank[a]	Age at start of IBI	Start of IBI	Number of males during 1.year of IBI[b]	Number of females during 1.year of IBI[b]
BIJOU	1		5			14	1989	6.0	23.5
BIJOU	2		7			17	1992	6.0	16
CASTOR	1		6		1	14	1990	6.0	20.5
CASTOR	2		7		1	16	1992	6.0	16
CASTOR	3	53	9	10	1	18	1994	3.0	13.5
DILLY	1	59	4	29	1	13	1991	6.0	19.5
FANNY	2	60	12	12	1	18	1987	7.5	27
FOSSEY	2	62	11	15	1	14	1993	5.5	15.5
FOSSEY	3		22		1	20	1999	1.5	9
GOMA	1	66	9	28	1	13	1986	8.5	27
GOMA	2	56	12	15	1	18	1991	6.0	19.5
GOMA	3		54		1	23	1996	2.0	10.5
HERA	3		25		1	22	1987	7.5	27
HERA	4	56	37	8	1	25	1990	6.0	20.5
KIRI	2		25		1	18	1987	7.5	27
LOUKOUM	2	67	28	6	2	14	1986	8.5	27
LOUKOUM	3	70	60	3	2	19	1991	6.0	19.5
MALIBU	2		11			17	1988	6.5	26
MYSTERE	2	64	41	7	2	15	1990	6.0	20.5
MYSTERE	3	64	23	13	2	20	1995	2.0	11
NARCISSE	1	75	29	13	1	14	1997	2.0	10.5
ONDINE	4[c]	60	20	12	2	33	1987	7.5	27
PERLA	1	70	13	32	1	13	1989	6.0	23.6
PERLA	2	59	43	6	2	19	1995	2.0	11
POKOU	4[c]		17		1	32	1988	6.5	26
POUPEE	3		20			14	1987	7.5	27
RICCI	3	77	57	10	1	25	1988	6.5	26
RICCI	4				1	31	1994	3.0	13.5
VENUS	1	74	2	18	1	13	1991	6.0	19.5
VENUS	2	49	29	7	2	19	1997	2.0	10.5
XERES	3		4		1	20	1990	6.0	20.5

[a] Rank categories: 1 = low-ranking, 2 = high-ranking, data from Boesch and Boesch-Achermann (2000) and Wittig and Boesch (2003).

[b] Calculated as mean of the number on January 1 and December 31 of each year.

[c] Minimum estimate.

to 21 individuals in 2002 (including 2 adult males, no subadult males, 6 parous females, and no nulliparous females). In 1995 South Group consisted of 62 individuals, including 8 adult males, no subadult male, 24 parous females, and no nulliparous female. By 2002 there were 48 individuals left, including 3 adult males, 2 subadult males, 16 parous females, and no nulliparous female. In North Group, mortality was mainly attributable to epidemics and leopard predation (Boesch and Boesch-Achermann 2000; Formenty *et al.* 1999), while mortality in South Group was mainly due to leopard predation and unknown causes (Boesch, *unpublished data*).

Table III Reproductive and demographic parameters for Taï South Group females from 1995 to 2002

Female	Parity	IBI (months)	PPA (months)	Min. number of cycles to conception	Age at start of IBI	Start of IBI	Number of males during 1 .year of IBI[a]	Number of females during 1 .year of IBI[a]
ATRA	1	51	15	13	14	1995	7.5	24
ATRA	2		13		18	1999	2.5	21
COCO	2	81	11	11	15	1995	7.5	24
EVA	?		57		29	1996	5.5	23
ISHA	?	60	40	7	25	1995	7.5	24
JULIA	?	60	24		28	1998	3.5	21.5
KABISHA	2	67	51	9	19	1996	5.5	23
LOUISE	2		40		18	1998	3.5	21.5
MARGOT	?	66	13	3	20	1995	7.5	24
OLIVIA	?	54	23		25	1998	3.5	21.5
RUBRA	?	59			29	1999	2.5	21
SUMATRA	?	69	21	9	31	1996	5.5	23
VIRUNGA	?	51			34	1999	2.5	21
YUCCA	?	69	52		25	1995	7.5	24
ZORA	?	71	4	12	39	1996	5.5	23

[a] Calculated as mean of the number on January 1 and December 31 of each year.

Data Collection

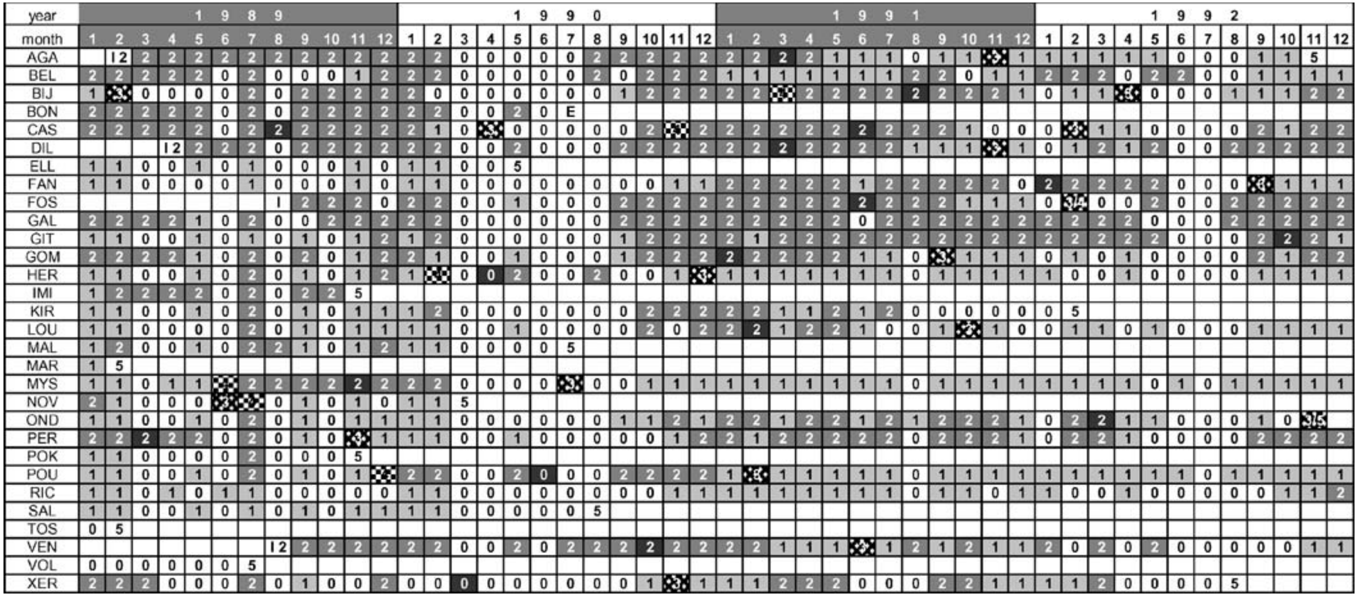
Beginning in 1987 (North Group) and 1995 (South Group), field assistants noted the presence of every individual encountered on a given day (hereafter referred to as the presence list). We paid particular attention to the presence of a female with a maximally tumescent sexual swelling. We defined maximum tumescence as a swelling with a shiny, tight appearance and no wrinkles (Furuichi 1987). We especially noted females displaying a sexual swelling in the presence list of the group. We did not always observe the groups daily because sometimes we could not find them or assistants did not work because of illness. The average number of observation days per month is 21 d for North Group and 24.6 d for South Group during the periods relevant to the study.

Data Analysis

We entered the presence lists of the 2 groups into a database. We scored females in the following categories: 1) not seen on a certain day, 2) seen without a swelling, 3) seen with a swelling, and 4) first seen in a group (immigration). In addition, we recorded new infants, the death of a dependent infant, and the death of a female (Fig. 1). We considered infants to be dependent until the next infant was born. Because all females except 1 immigrated into the groups, ages of females are estimates (Boesch and Boesch-Achermann 2000).

Defining Cycles by Observations of Swellings

The average female chimpanzee cycle in Taï South lasts about 40.3 d and the average maximum tumescence period lasts about 11.4 d (Deschner *et al.* 2003). When we did not see a female for several consecutive days, we defined observed swellings as



year	1 9 8 9												1 9 9 0												1 9 9 1												1 9 9 2											
month	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12
AGA		I 2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	2	2	2	2	2	2	2	2	2	1	1	1	0	1	1	3	1	1	1	1	1	1	0	0	0	1	1	5	
BEL	2	2	2	2	2	0	2	0	0	0	1	2	2	2	0	0	0	0	0	2	0	2	2	2	1	1	1	1	1	1	1	2	2	0	1	1	2	2	2	0	2	2	0	0	1	1	1	1
BIJ	1	3	0	0	0	0	2	0	2	2	2	2	2	0	0	0	0	0	0	0	1	2	2	2	2	2	4	2	2	2	2	2	2	2	2	1	0	1	1	3	0	0	0	1	1	1	2	2
BON	2	2	2	2	2	0	2	0	2	2	2	2	2	2	0	0	2	0	E																													
CAS	2	2	2	2	2	0	2	2	2	2	2	2	2	1	0	3	0	0	0	0	0	2	4	2	2	2	2	2	2	2	2	2	2	1	0	0	0	3	1	1	0	0	0	0	2	1	2	2
DIL				I 2	2	2	2	0	2	2	2	2	2	2	0	0	2	0	0	0	2	2	2	2	2	2	2	2	2	2	2	1	1	1	3	1	0	1	2	1	2	0	0	2	2	2	2	2
ELL	1	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	5																															
FAN	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	1	2	2	2	2	2	0	2	2	2	2	2	0	0	0	3	1	1	1
FOS								I	2	2	2	0	2	2	0	0	1	0	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	0	3/4	0	0	2	0	0	2	2	2	2	2
GAL	2	2	2	2	1	0	2	0	0	2	2	2	2	2	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	0	0	0	2	2	2	2	2
GIT	1	1	0	0	1	0	1	0	1	0	1	2	1	2	0	0	0	0	0	0	1	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	2	2	2	1
GOM	2	2	2	2	1	0	2	0	2	0	1	2	2	1	0	0	1	0	0	0	1	2	2	2	2	2	2	2	2	1	1	0	3	1	1	1	0	1	0	1	0	0	0	0	2	1	2	2
HER	1	1	0	0	1	0	2	0	1	0	1	2	1	4	0	0	2	0	0	2	0	0	1	3	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	1	1	1	1
IMI	1	2	2	2	2	0	2	0	2	2	5																																					
KIR	1	1	0	0	1	0	2	0	1	0	1	1	1	2	0	0	0	0	0	0	0	2	2	2	2	2	1	1	2	1	2	0	0	0	0	0	0	5										
LOU	1	1	0	0	0	0	2	0	1	0	1	1	1	1	0	0	1	0	0	0	0	2	0	2	2	2	1	2	2	1	0	0	1	3	1	0	0	1	1	0	1	0	0	0	1	1	1	1
MAL	1	2	0	0	1	0	2	2	1	0	1	2	1	1	0	0	0	0	5																													
MAR	1	5																																														
MYS	1	1	0	1	1	4	2	2	2	2	2	2	2	2	0	0	0	0	3	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1
NOV	2	1	0	0	0	3	4	0	1	0	1	0	1	1	5																																	
OND	1	1	0	0	1	0	2	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	2	1	2	2	1	2	2	1	2	1	2	2	2	1	0	2	2	1	1	0	0	0	1	0	3/5	
PER	2	2	2	2	2	0	2	0	1	0	3	1	1	1	0	0	1	0	0	0	0	0	1	2	2	1	2	2	2	2	2	0	2	2	2	1	0	2	2	1	0	0	0	0	2	2	2	2
POK	1	1	0	0	0	0	2	0	0	0	5																																					
POU	1	1	0	0	1	0	2	0	1	0	1	4	2	2	0	0	2	0	0	0	2	2	2	2	1	3	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
RIC	1	1	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	1	1	2
SAL	1	1	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	5																												
TOS	0	5																																														
VEN								I 2	2	2	2	2	2	2	0	0	2	0	2	2	2	2	2	2	2	2	1	1	1	3	1	2	1	2	1	1	2	0	2	0	2	0	0	0	0	0	1	1
VOL	0	0	0	0	0	0	5																																									
XER	2	2	2	0	0	0	2	0	1	0	0	2	0	0	0	0	0	0	0	0	0	1	3	1	1	1	2	2	2	0	0	0	2	2	1	1	1	1	2	0	0	0	0	5				

Fig. 1 Reproductive status of North Group females from 1989 to 1992. 0 = insufficient observation density, 1 = no swelling, 2 (light background) = swelling, 0 and 2 (dark background) = conception cycle, 3 = infant born, 4 = dependent infant died, 5 = female died, I = female immigrated, I 2 = female immigrated with swelling, E = female emigrated.

belonging to a different cycle if the time span between consecutive swellings exceeded 18 d because this was the longest observed duration of a maximum tumescent swelling period for a parous Taï female chimpanzee (Deschner *et al.* 2003). To compare among females and between seasons, we attributed swelling cycles to the month when we observed them. If a swelling period stretched from the end of 1 mo into the beginning of the following month, we attributed the cycle to the month in which the swelling began. This allowed us to distinguish among months in which we observed a female with a sexual swelling, months in which we could exclude the occurrence of a sexual swelling, and months in which the density of observations was not sufficient to document swelling occurrence. We excluded postconception swellings from our analysis by considering only swellings that happened ≥7.5 mo before the birth of an infant.

Missing Observations

Owing to fission-fusion in chimpanzee communities, we could not observe all group members on given day. Because the average maximum tumescence period of a female chimpanzee swelling lasts *ca.* 10 d, we marked every month in which we did not see a female for >10 consecutive days as a month in which her swelling could have passed unnoticed.

Number of Cycles

We calculated the number of cycles for each IBI for each female—given that the previous offspring survived at least until subsequent conception—by calculating the sum of all months in which we observed the female with a swelling after she gave birth until 8 mo before the next birth. Because we cannot exclude the possibility that females exhibited additional swellings during months when observation density was insufficient, the figure given here is the minimum number of cycles per IBI.

Duration of PPA

We defined the duration of PPA as the time span from birth to the first observed sexual swelling after the birth. Because it is possible that a female had a swelling in the period that was not observed owing to insufficient observation density, the figure given is the maximum PPA duration.

Probability of Swelling

We aligned all IBIs to the month of conception and subsequently calculated the probability that a female had a swelling for each month of the IBI by dividing the number of observed swellings in that month by the number of IBIs that had a sufficient density of observation then (Fig. 2). We used the probability of swelling for every month of the IBI to calculate the corrected number of swellings to conception.

Corrected Number of Swellings to Conception

For all months of a female's IBI after the end of the PPA when density of observation was not high enough to exclude that a swelling might have occurred

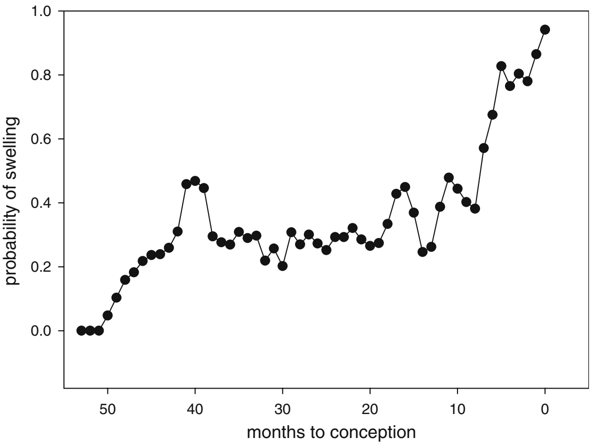


Fig. 2 Probability of exhibiting a maximum tumescent swelling on any given month during the IBI for females from the Taï North Group. Data are aligned to the month of conception and shown until 53 mo before conception, when sample size became <50% of the original data set. We smoothed the curve by averaging over the 2 neighboring months (females N=13).

undetected, we added the value out of the probability curve. By summing the number of observed swellings and the probability values during months with an inadequate density of observation, we obtained a corrected number of swellings to conception for all IBIs.

Female Rank

We based data on female rank on the exchange of pant-grunt vocalization (Bygott 1979; de Waal 1978; Noe *et al.* 1980) and on Boesch and Boesch-Achermann (2000) and Wittig and Boesch (2003). Because data collection in South Group covered 8 yr only, for a number of analyses, we used only the data of North Group.

Statistical Analysis

We used Pearson correlations to assess the relationship between different continuous variables. We analyzed differences in numbers of cycles to conception between nulliparous and primiparous females via a t-test for independent samples. We used general linear mixed models (GLMMs) to analyze the effect of several continuous and categorical independent variables on continuous dependent variables such as parity and age on PPA duration. A GLMM is an extension of the general linear model, which allows one to account for repeated observations of the same subjects by including subject (female individuality) as a random factor in the model (Coté and Festa-Bianchet 2001; Pinheiro and Bates 2000). As a covariance structure for the random factor, we selected compound symmetry. We used restricted maximum likelihood methods to estimate the models and Satterthwaites F-tests to test for fixed parameter effects. The methods are robust against unequal sample sizes and against violation of the assumption of multisphericity (Keselman *et al.* 2001). Because Satterthwaites F-tests do not have exact F-distributions, the denominator degrees of freedom are not integer. After a significant fixed effect of a categorical variable, we tested differences between the categories via contrasts. We calculated means and standard deviations from the average scores of the individuals and performed all statistical analyses via SPSS 11.5.

Results

Reproductive Parameters of Taï Female Chimpanzees and Corrected Estimates of Cycles to Conception

Taï females of North Group have an average period of adolescent sterility (from immigration to conception) of 1.7 yr (Table I). However, because nulliparous females already start exhibiting swellings before they immigrate into a new group, the number is a minimum estimate. The average IBI for the North (females $N=13$, IBI $N=18$) and South Group (females $N=12$, IBI $N=12$) is 5.3 yr. Postpartum amenorrhea lasted on average 1.8 yr in the North (females $N=19$, IBI $N=30$) and 2.4 yr in the South Group (females $N=12$, IBI $N=13$). Observed cycles to conception numbered 13.6 for the North (females $N=13$, IBI $N=18$) and 9 for the South Group (females $N=8$, IBI $N=8$). Density of observation, as described in Methods, was too low to exclude that a female had a swelling during a given month on average for 9.4 mo between the end of her PPA and the subsequent conception. Females ceased regular cyclic activity for an average of 7.2 mo between the end of the PPA and the subsequent conception. The number of months we observed a female without a swelling between the end of the PPA and the subsequent conception was higher for shorter PPAs (Pearson correlation: $r_{26}=-.60$, $p=.001$). The average adjusted number of cycles to conception for parous females calculated with the aid of the probability distribution as described in Method is 19.4 cycles for North Group females and 11.7 cycles for South Group females.

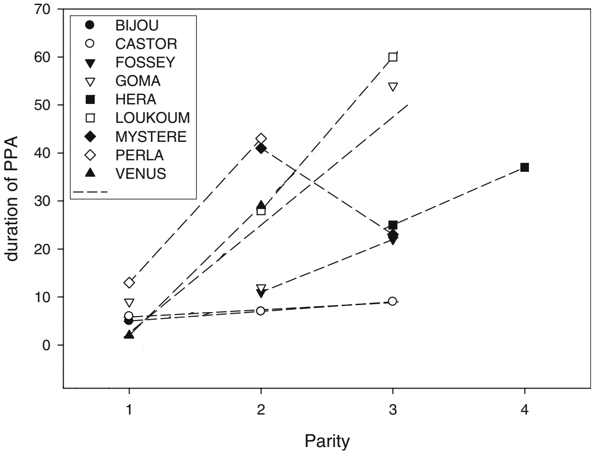
Parity, Cycles to Conception, and PPA Duration

Nulliparous North Group females average 17 observed cycles from immigration to conception while primiparous females average 24 observed cycles from the end of the PPA to the next conception. The difference is not significant (t-test for independent samples: $t_{11}=-1.6$, $p=.15$). We could not test the influence of parity within females on the number of cycles to conception owing to the small sample size of the number of cycles to conception. However, because there is a strong negative correlation between duration of PPA and the number of cycles to conception (Pearson correlation: $r_{11}=-.76$, $p=.007$) we used the duration of PPA as a substitute for numbers of cycles to conception when sample size for intrafemale comparisons was too small. An intrafemale comparison for parous females showed that females with higher parity had longer PPAs (GLMM; $F_{18.9,\ 18.3}=11.9$; $p=.003$; Fig. 3).

Factors Influencing the PPA and the Number of Cycles

To test which factors might influence the number of swellings to conception and the duration of PPA, we conducted a GLMM using duration of IBI, female rank, age at start of the IBI, number of adult males in the group at start of IBI, and number of adult females in the group at start of IBI as predictor variables. Age at the start of the IBI correlates significantly with the duration of the PPA, with younger females having shorter PPAs than older females (GLMM, $F_{18.4,\ 17.2}=19.5$; $p<.001$; Fig. 4). The result remained significant when we excluded 2 females that experienced a clear rise in rank

Fig. 3 Duration of PPA in months in relation to female parity (0 = nulliparous, 1 = primiparous, etc.).



from one IBI to the next (GLMM, $F_{14.9,\ 14.3}=11.6$; $p=.004$). When we introduced the other factors as covariates, age at the start of the IBI remained highly significant, whereas no other factor had a significant influence on the duration of the PPA.

Changes in Female Age Distribution for Taï North and South Groups

The average proportion of days we observed a parous North Group female with a sexual swelling per year decreased from 17.3% in 1987 to 0.7% in 2002 (Fig. 5). The decrease is significant over time (Pearson correlation: $r_{16}=-.67$, $p=.004$). Within the same period, the number of adult females in North Group decreased from 27 to 6 and the number of males decreased from 8 to 2. Because the number of adult females and males in the group did not predict the duration of PPA but female age did, we asked if changes in the female age distribution could explain the decrease in observed swellings per year. Though the average age for North Group females did not change dramatically (from 21.4 in 1987 to 24.0 in 2002), female age distribution did. In 1987, the majority (52%) of North Group parous

Fig. 4 Duration of PPA in relation to age at the start of the IBI.

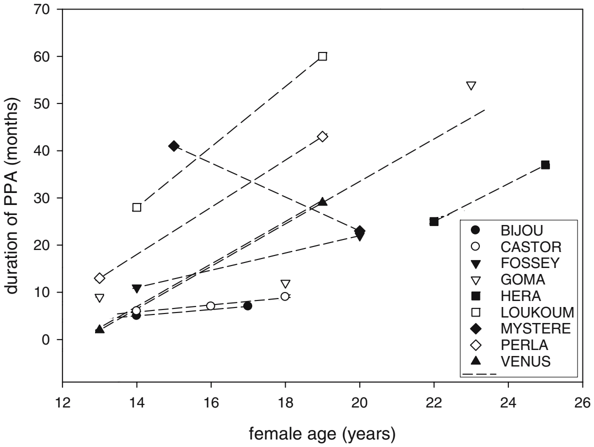
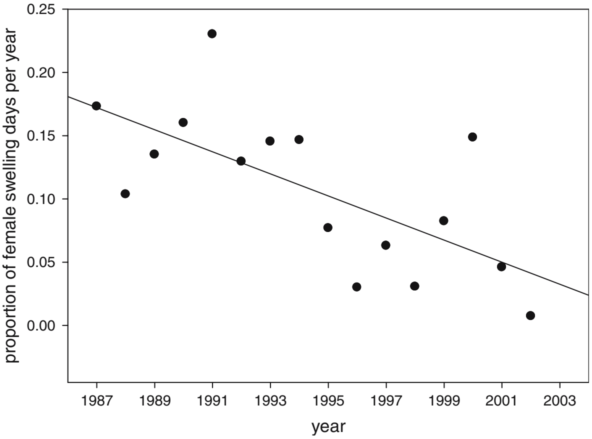


Fig. 5 Proportion of days we observed a parous female with a maximum swelling for the North Group from 1987 to 2002. Dots indicate averages across females, sample sizes vary from *N*=22 in 1987 to *N*=6 in 2002.



females were <20 yr of age (Fig. 6a). The proportion decreased (to 17%) in 2002, at which time, the majority (83%) were between 20 and 29 yr, and there was no female >30 yr.

We also found a large change in the age distribution of South Group (Fig. 6b). The last female immigrated into the group in 1994 and gave birth to her first infant in 1997. Since then there has been no nulliparous female in the group. The number of females in South Group decreased from 23 in 1996 to 17 in 2002, and average female age increased from 25.2 yr in 1996 to 32 yr in 2002 (Fig. 6b). In 1996, the majority (65%) of females were between 20 and 29 yr, which shifted in 2002 when the majority (58%) of females were >29 yr. In 2002 there was no female <20 yr in South Group. The decrease in the average proportion of days we observed a female with a swelling therefore seems to be due mainly to a decrease in the proportion of young parous females in both groups.

Discussion

We confirmed that female chimpanzees of the Taï population experienced, on average, more cycles to conception and had a shorter postpartum amenorrhea period (PPA) than females from other populations did (Boesch and Boesch-Achermann 2000; Wrangham 2002). However, researchers based earlier calculations of the number of cycles to conception (Wrangham 2002) on the assumption that after the first postpartum cycle a chimpanzee female continues having regular cycles until conception. According to our data this is not the case, because females ceased cyclic activity for an average of 7.2 mo between the end of the PPA and the subsequent conception. By taking into account the periods in which a female did not exhibit regular cycles after the end of the PPA and at the same time correcting for periods with insufficient observations, we were able to provide a more realistic estimate of the number of cycles to conception in Taï chimpanzee females. The number is considerably lower than the one Wrangham (2002) calculated but still higher than numbers recorded for other chimpanzee populations in East Africa. Further, we show a variation in the length of the PPA in parous Taï chimpanzee females that one

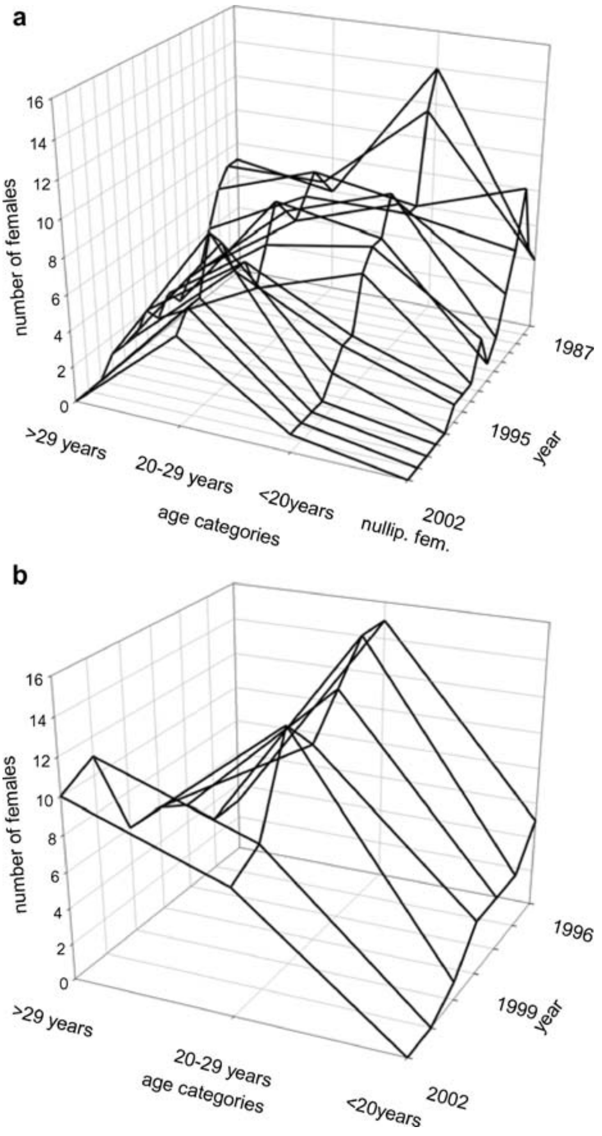


Fig. 6 Changes in age distribution over time in female Taï chimpanzees. (**a**) North Group. (**b**) South Group.

cannot explain by the cost-of-sexual-attraction hypothesis. Finally, intragroup comparisons indicated that the main factor determining the length of the PPA and the number of cycles to conception is the age of the female.

Though we confirmed the previously reported pattern that Taï chimpanzee females have a shorter PPA and exhibit more cycles to conception than females from East African field sites do, it became clear that the calculation of the numbers can become inaccurate depending on 1) the frequency with which one observes individual females and 2) the time period during which a female ceases having regular cycles after the end of the PPA. For a reliable comparison of data from different field sites, researchers should take the sources of error into consideration and use adapted methods such as the ones we described to estimate a female's number of cycles to conception more accurately.

Taï chimpanzee females exhibit swellings less often during June to August than during the rest of the year (Anderson 2001; Boesch and Boesch-Achermann 2000). The number of swellings correlates with general food abundance (Anderson 2001). It is therefore possible that cyclic activity is restricted then, resulting in an energetically induced temporary amenorrhea. However, because Taï chimpanzee females are less gregarious during this period (Doran 1997) one could as well interpret a reduction in the number of observed swellings as a reaction to the reduced social pressure on young females.

There is a difference in both the duration of PPA and the number of CTC between the 2 groups in Taï. Because we found for North Group that age influences the 2 traits, it is likely that the marked difference in age distribution observed between females of the 2 groups accounted for the difference between them in both PPA and CTC.

Though researchers have not described the consistent patterns between age and PPA to numbers of cycles to conception in chimpanzee populations other than Taï, authors have occasionally described resumptions of swelling cycles early after parturition at Mahale (Takasaki *et al.* 1986) and Gombe (Goodall 1986). While no information is available about the identity and age of the Gombe females, the case described for a female from Mahale M Group supports the pattern observed in Taï. A young immigrant female resumed estrous cycling only 7 mo after the birth of her first infant. Correlations between age and the number of cycles to conception exist also in baboons. The number of cycles to conception decreases with increasing age in yellow baboons at Mikumi National Park, Tanzania (Wasser *et al.* 1998) and at Amboseli National Park, Kenya (Altmann *et al.* 1988). However, as in chimpanzees, other populations such as the Olive baboons of Gombe National Park, Tanzania do not show the correlation (Packer *et al.* 1998). Because dominance rank rarely changes over time in female baboons (Hausfater *et al.* 1982), the existing correlation for some populations seems therefore completely age dependent. Further, female baboons are the philopatric sex while males disperse. A higher number of cycles serving as a social passport therefore could not explain the observed pattern as it could in Taï chimpanzees. More detailed combined behavioral and endocrinological studies in baboons are therefore needed to clarify the functional significance of age specific PPA duration and the number of cycles to conception.

Though we could demonstrate the influence of age on CTC and PPA, we cannot exclude the possibility that female rank might have an influence on these factors as well. Rank had an influence on PPA in an earlier study of Taï North Group (Boesch and Boesch-Achermann 2000). However, because rank and age strongly correlate in female chimpanzees (Nishida 1979; Pusey *et al.* 1997; Wittig and Boesch 2003) and we did not have enough rank changes in our data set, it is difficult to determine which factor is the more important in influencing PPA and CTC. Though we could show that age remained significant after removing the cases in which a rank rise had occurred, indicating that age alone might be the determinant variable, one has to keep in mind that rank was divided into only 2 categories. We therefore did not detect minor rank changes in our analyses but they might still have affected the PPA and CTC. Further, in the few cases in which young females achieved a high rank position early after immigration, their PPA duration was longer and the number of CTC was lower than were those of other females of similar age (females Loukoum and Mystere in this study and Poupee in Boesch and Boesch-Achermann, 2000). Therefore, indications that rank alone might influence the PPA and CTC exist, though more detailed studies are needed to confirm the very preliminary findings.

We cannot explain some of our results by the cost-of-sexual-attraction hypothesis. If male coercion, the level of intragroup scramble competition for food between females, and the difference in traveling costs for nulliparous and parous females were the only factors determining the number of swellings to conception, one would expect no correlation between parity and the duration of PPA. However, the fact that females of high parity have a significantly longer PPA than that of primiparous females indicates that at Taï, additional factors influence the number of cycles to conception of females of different parities.

At Taï, Boesch and Boesch-Achermann (2000) and Lehmann and Boesch (submitted). proposed that higher food availability together with higher predation pressure led to increased female sociality. Indeed, the dyadic association index for Taï females is >3 times higher than in East African populations such as Gombe, Mahale, or Kibale (Wittig and Boesch 2003). In this social situation, contest competition for monopolizable food items between females becomes more important (Wittig and Boesch 2003).

We propose that at Taï the postpartum amenorrhea duration and the number of swellings to conception are less dependent on the balance between avoidance of male coercion and traveling costs, but much more on the need of male social support in conflicts with other females.

A high number of swellings to conception could work as a social passport by attracting males and soliciting their support in conflicts with other females (Boesch and Boesch-Achermann 2000; Wallis 1982). This could work in several contexts. Nulliparous females benefit at the time when they try to immigrate into the group and face aggression by resident females (Boesch and Boesch Achermann 2000; Goodall 1986; Nishida 1989). But younger females that already have an infant might still benefit from a high number of swellings to conception. The high sociality between females might increase their need of male support during conflicts with older, higher-ranking females, either in situations of contest competition over monopolizable food items or when supporting their infants during conflicts with infants of higher-ranking females (Boesch and Boesch-Achermann 2000). Older, higher-ranking females, which already have established social relationships with other females, might be able to rely on these relationships for support in conflicts and therefore might not need to invest into high numbers of costly swellings. However, differences in the number of swellings to conception might have implications as well on female reproductive strategies.

Having a high number of cycles to conception might offer females the possibility to confuse paternity and lure all adult males of the group into believing that they could be the father of the infant. In this context it is interesting that most of the cases of intragroup male infanticide occurred in a situation in which several females transferred into a new group, after the males of their own group had disappeared (Nishida and Kawanaka 1985).

Nunn (1999) and van Schaik *et al.* (1999) described the female dilemma in which females are caught between biasing the paternity to the dominant male to receive protection and support for their offspring and confusing paternity so that all males in the group consider themselves as putative fathers. In Taï chimpanzees, females might be able to balance their need of confusing and biasing paternity depending on their social situation. Though young females seem to be more dependent on paternity confusion, and therefore have a high number of swellings to conception, older and possibly higher-ranking females might have a greater possibility to bias paternity toward the dominant male by having a low number of swellings to conception in which they can be generally monopolized by the dominant male. Indeed, higher-ranking Taï females seem to be more successful in realizing their mate preferences than lower-ranking, younger ones are (Stumpf and Boesch 2006).

The social passport hypothesis allows us to explain the differences in PPA duration and the number of swellings to conception between younger and older parous females at Taï, as well as to generate predictions that one can then test. First, we expect young females to receive increased male support during conflicts with other females at times when they have sexual swellings. Second, we expect older, higher-ranking females to receive more support from their female allies than younger females would. Finally, on a reproductive level, we expect infants of younger, low-ranking females to be sired more often by low-ranking males, while a higher proportion of infants of older and higher-ranking females should be sired by high-ranking males.

Nothing is known about the proximate mechanisms inducing sexual swellings in young Taï chimpanzee females. Only combining behavioral and endocrinological data on cycles of young females can address this issue.

In summary, parous Taï females have on average a higher number of cycles to conception than parous East African chimpanzee females do. Within a group, the strongest factor influencing the number of cycles is female age, with young females having a higher number of cycles to conception than older females. The period between the resumption of cycling and subsequent conception in Taï females is regularly interrupted by periods of cyclic inactivity. Because age influences strongly the number of cycles to conception, researchers must take demography into consideration when comparing reproductive patterns among chimpanzee groups.

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References

Altmann, J., Hausfater, G., & Altmann, S. A. (1988). Determinants of reproductive success in Savannah baboons, Papio cynocephalus. In T. H. Clutton-Brock (Ed.), *Reproductive success. Studies of individual variation in contrasting breeding systems* (pp. 403–418). Chicago: Chicago University Press.

Anderson, D. P. (2001). *Tree phenology and distribution, and their relation to chimpanzee social ecology in the Tai National Park, Côte d'Ivoire*. University of Wisconsin-Madison.

Berger, J., & Cunningham, C. (1994). *Bison: Mating and conservation in small populations*. New York: Columbia University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest*. Oxford: Oxford University Press.

Bygott, J. D. (1979). Agonistic behavior, dominance, and social structure in wild chimpanzees of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 405–427). Menlo Park, CA: Benjamin/Cummings.

Connor, R. C., Richards, A. F., Smolker, R. A., & Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour, 133*, 37–69.

Coté, S. D., & Festa-Bianchet, M. (2001). Offspring sex ratio in relation to maternal age and social rank in mountain goats (Oreamnos americanus). *Behavioral Ecology and Sociobiology, 49*, 260–265.

Crews, D., & Moore, M. C. (1986). Evolution of mechanisms controlling mating behaviour. *Science, 231*, 121–125.

Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, Pan troglodytes verus. *Animal Behavior, 66*, 551–560.

de Waal, F. B. M. (1978). Exploitative and familiarity-dependent support strategies in a colony of semi-free living chimpanzees. *Behaviour, 66*, 268–311.

Domb, L. G., & Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature, 410*, 204–206.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology, 18*, 183–206.

Formenty, P., Boesch, C., Wyers, M., Steiner, C., Donati, F., Dind, F., *et al.* (1999). Ebola outbreak in wild chimpanzees living in a rainforest of Côte d'Ivoire. *Journal of Infectious Diseases, 179*, 120–126.

Furuichi, T. (1987). Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at Wamba Zaire. *Primates, 28*, 309–318.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: The Belknap Press of Harvard University Press.

Goossens, B., Graziani, L., Waits, L. P., Farand, E., Magnolon, S., Coulon, J., *et al.* (1998). Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behavioral Ecology and Sociobiology, 7*, 49–54.

Hausfater, G., Altmann, J., & Altmann, S. A. (1982). Long-term consistency of dominance relations among female baboons (Papio cynocephalus). *Science, 217*, 752–755.

Hayssen, V., van Tienhoven, A., & van Tienhoven, A. (1993). *Asdell's patterns of mammalian reproduction; a compendium of species-specific data*. Ithaca, NY: Comstock Publishing Associates.

Heistermann, M., Ziegler, T., van Schaik, C. P., Launhardt, K., Winkler, P., & Hodges, K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging hanuman langurs. *Proceedings of the Royal Society of London Series B-Biological Sciences, 268*, 2445–2451.

Hrdy, S. B., & Whitten, P. L. (1987). Patterning of sexual activity. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 370–384). Chicago: University of Chicago Press.

Keselman, H. J., Algina, J., & Kowalchuk, R. K. (2001). The analysis of repeated measures designs: A review. *British Journal of Mathematical and Statistical Psychology, 54*, 1–20.

Knott, C. D. (2001). Female reproductive ecology of the apes: Implications for human evolution. In P. T. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 429–463). New York: Aldine de Gruyter.

Lehmann, J., & Boesch, C. (submitted). Sex differences in sociality. *American Journal Primatology.*

Loy, J. (1987). The sexual behavior of african monkeys and the question of estrus. In E. Zucker (Ed.), *Comparative behavior of African monkeys* (pp. 175–195). New York: Alan R. Liss.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 73–122). Menlo Park, CA: Benjamin/Cummings.

Nishida, T. (1989). Social interactions between resident and immigrant female chimpanzees. In P. Heltne & L. Marquardt (Eds.), *Understanding chimpanzees* (pp. 68–89). Cambridge, MA: Harvard University Press.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., *et al.* (2003). Demography, female life history and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology, 59*, 99–121.

Nishida, T., & Kawanaka, K. (1985). Within-group cannibalism by adult male chimpanzees. *Primates, 26*, 274–284.

Nishida, T., Takasaki, H., & Takahata, Y. (1990). Demography and reproductive profiles. In T. Nishida (Ed.), *The chimpanzees of the Mahale mountains: Sexual and life history strategies* (pp. 63–97). Tokyo: Tokyo University Press.

Noe, R., de Waal, F. B. M., & van Hoof, J. A. R. A. M. (1980). Types of dominance in a chimpanzee colony. *Folia Primatologica, 34*, 90–110.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behavior, 58*, 229–246.

Packer, C., Tatar, M., & Collins, A. (1998). Reproductive cessation in female mammals. *Nature, 392*, 807–810.

Pagel, M. (1994). The evolution of conspicuous oestrous advertisement in old world monkeys. *Animal Behavior, 47*, 1333–1341.

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-PLUS*. New York: Springer.

Pusey, A. E., & Packer, C. (1994). Infanticide in lions: Consequences and counterstrategies. In S. Parmigiani & F. S. vom Saal (Eds.), *Infanticide and parental care* (pp. 277–299). Harwood, London.

Pusey, A. E., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science, 277*, 828–831.

Steklis, H. D., & Whiteman, C. H. (1989). Loss of estrus in human evolution: Too many questions, too few answers. *Ethology and Sociobiology, 10*, 417–434.

Stumpf, R., & Boesch, C. (2006). The efficiacy of female choice in chimpanzees of the Taï forest, Côte d'Ivoire. *Behavioral Ecology and Sociobiology, 60,* 749–765.

Takasaki, H., Hiraiwa-Hasegawa, M., Takahata, Y., Byrne, R. W. & Kano, T. (1986). A case of unusually early postpartum resumption of estrous cycling in a young female chimpanzee in the wild. *Primates, 27*, 517–519.

van Noordwijk, M. A., & van Schaik, C. P. (2000). Reproductive patterns in eutherian mammals: Adaptations against infanticide. In C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 322–360). Cambridge, UK: Cambridge University Press.

van Schaik, C. P., van Noordwijk, M. A., & Nunn, C. L. (1999). Sex and social evolution in primates. In P. C. Lee (Eds.), *Comparative primate socioecology* (pp. 204–231). Cambridge, UK: Cambridge University Press.

Wallis, J. (1982). Sexual behavior of captive chimpanzees (Pan troglodytes): Pregnant versus cycling females. *American Journal of Primatology, 3*, 77–88.

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility, 109*, 297–307.

Wasser, S. K., Norton, G. W., Rhine, R. J., Klein, N., & Kleindorfer, S. (1998). Ageing and social rank effects on the reproductive system of free-ranging yellow baboons (Papio cynocephalus) at Mikumi National Park, Tanzania. *Human Reproduction Update, 4*, 430–438.

Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology, 24*, 847–867.

Wolff, J. O., & MacDonald, D. W. (2004). Promiscuous females protect their offspring. *TREE, 19*, 127–134.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. Kappeler (Eds.), *Male primates* (pp. 248–258). Cambridge, UK: Cambridge University Press.

Wrangham, R. W. (2002). The cost of sexual attraction: Is there a trade-off in female Pan between sex appeal and received coercion? In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 204–215). Cambridge, UK: Cambridge University Press.