

Estrus cycle asynchrony in wild female chimpanzees, *Pan troglodytes schweinfurthii*

Akiko Matsumoto-Oda · Miya Hamai ·
Hitosige Hayaki · Kazuhiko Hosaka · Kevin D. Hunt ·
Eiiti Kasuya · Kenji Kawanaka · John C. Mitani ·
Hiroyuki Takasaki · Yukio Takahata

Received: 30 August 2005 / Revised: 8 October 2006 / Accepted: 8 October 2006 / Published online: 10 January 2007
© Springer-Verlag 2007

Abstract Although estrous synchrony has been reported in a number of mammalian species, most often among

Communicated by S. Alberts

A. Matsumoto-Oda (✉)
Department of Welfare and Culture, Okinawa University,
Naha, Okinawa 902-8521, Japan
e-mail: matumoto@okinawa-u.ac.jp

M. Hamai
Primate Research Institute, Kyoto University,
Kyoto, Japan

H. Hayaki
The Graduate School of Humanities and Sciences,
Kobe Gakuin University,
Kobe, Hyogo, Japan

K. Hosaka
Faculty of Child Studies, Kamakura Women's University,
Kamakura, Kanagawa, Japan

K. D. Hunt
Department of Anthropology, Indiana University,
Bloomington, IN, USA

E. Kasuya
Department of Biology, Kyushu University,
Fukuoka, Japan

K. Kawanaka · H. Takasaki
Department of Biosphere–Geosphere System Science,
Okayama University of Science,
Okayama, Japan

J. C. Mitani
Department of Anthropology, University of Michigan,
Ann Arbor, MI, USA

Y. Takahata
School of Policy Studies, Kwansai Gakuin University,
Nishinomiya, Hyogo, Japan

primates, methodological and analytical problems make it difficult to interpret these results. We developed a novel estrous synchrony index and employed a randomization procedure to analyze long-term observations of female chimpanzee (*Pan troglodytes schweinfurthii*) estrous cycles at the Mahale Mountains National Park, Tanzania. Our results revealed that female chimpanzees at Mahale avoid synchronizing their estrous periods with each other. We also found that birthrates decreased as the breeding sex ratio increased. We suggest that estrous asynchrony decreases female–female competition for mates. Asynchrony may also reduce the potential for male sexual coercion by nonpreferred mating partners.

Keywords Timing of estrus · Mating strategy · Female competition · Sexual conflict · Chimpanzees

Introduction

Reproductive synchrony is the tendency of individuals to time some part of their reproductive cycle with that of other population members (Findlay and Cooke 1982; Ims 1990). Reproductive synchrony is best understood when its two components, estrous synchrony and breeding synchrony, are distinguished, thus allowing each adaptation to be considered on its own. Estrous synchrony can be defined as the tendency of individuals to undergo the fertile period of the sexual cycle at the same time as other members of the population.

The distribution of females in time and space largely determines male–male competition for mates (e.g., Emlen and Oring 1977; Clutton-Brock 1989; Eberle and Kappeler 2002; Setchell and Kappeler 2003; Kappeler and van

Schaik 2004). At the same time, the timing of estrous may have evolved as a result of reproductive competition among females. When fertile periods are highly synchronized, fewer male mating partners are available, and female competition for access to males is increased (e.g., wood frog, *Rana sylvatica*, Howard 1980; Gowaty 2004; reviewed in Kappeler and van Schaik 2004). Estrous synchrony may nonetheless represent a strategy to enforce monogamy on males when paternal investment in young increases their probability of survival. Females who display asynchronous cycles might obtain different benefits. For example, asynchrony might decrease female–female competition for mates thereby increasing the opportunity for female mate choice, because each receptive female can attract more males when no other receptive females are available (e.g., natterjack toad, *Bufo calamita*, Arark 1988).

Estrous synchrony has been reported in two rodents (Norway rats: McClintock 1978; golden hamsters: Handelsmann et al. 1980) and a number of primates. Most studies of primates have indicated that females synchronize their reproductive activities (hamadryas baboon, *Papio hamadryas*, Kummer 1968, Zinner et al. 1994; gelada baboon, *Theropithecus gelada*, Dunbar 1980; chimpanzee, Wallis 1985, 1992; golden lion tamarin, *Leontopithecus rosalia*, French and Stribley 1987; human, McClintock 1971; Weller and Weller 1993). Analyses of the timing of reproductive activity in golden lion tamarins, ring-tailed lemurs (*Lemur catta*), and humans, however, have failed to find estrous synchrony (e.g., Pereira 1991; Sauter 1991; Wilson 1992; Monfort et al. 1996; Strassmann 1997; Schank 2000, 2001). Estrous synchrony may be difficult to achieve in long-lived animals such as primates because they have long cycles, leading some to suggest that previously reported cases of synchrony represent methodological artifacts (Strassmann 1997; Schank 2001). It is also very difficult to demonstrate analytically whether females synchronize their cycles. This difficulty underscores the need to develop new analytical techniques to examine estrous synchrony in primates.

In this paper, we develop a novel index and utilize a randomization procedure to analyze estrous synchrony in a group of chimpanzees (*Pan troglodytes schweinfurthii*) living in the Mahale Mountains National Park, Tanzania.

Subjects and methods

Study site and subjects

We studied the M-group chimpanzees at the Mahale Mountains National Park, Tanzania. These chimpanzees have been observed since 1965 and are well habituated to human presence (Nishida et al. 2003). We identified estrus

in females by the size of their anogenital swellings, which is related to increased levels of follicular estrogen. The weighted mean length of female sexual cycles from four previous studies was 34.3 days, and the weighted mean length of maximal tumescence was 12.3 days (Hasegawa and Hiraiwa-Hasegawa 1983; Wallis 1997; Deschner et al. 2003; this study). Daily observations of the turgidity of anogenital swellings of all cycling adult females in the study group were made and classified into three categories: flat, partial swelling, and maximal swelling. The period of maximal swelling was regarded as the ‘estrous period’ because almost all copulations were observed in this phase. The last 4 days of maximal swelling are referred to as the ‘perioovulatory period’ because ovulation occurs during the last few days of maximal swelling (Graham 1981; Deschner et al. 2003).

Data analysis

The estrus synchrony index

We counted the number of females with maximal swellings in the consecutive months from May to January in nine different years from 1981 to 1994. We excluded observations from February to April when the Mahale chimpanzees typically form small parties in response to fruit scarcity, which makes it difficult to monitor the reproductive states of individual females. We kept track of two female sexual states: (1) maximal swelling states and (2) perioovulatory periods. The data are summarized in Table 1.

The degree to which females synchronize their estrous cycles can be evaluated by the variation of the proportion of females with maximal swellings to cycling females observed among days. When the degree of synchronization is high, the females are more likely to show maximal swellings on the same days. This also results in a high proportion of the females with maximal swellings on some days and a lower proportion on other days. In other words, variation in the proportion of estrous females among days is high. In contrast, variation in the proportion of estrous females among days is smallest when females avoid cycling together. Variation is intermediate when there is neither synchrony nor avoidance of synchrony. In the extreme case, when all of the females completely synchronize their estrous cycles over the same time and durations, the proportions are one or zero, and the variation in proportions reaches its maximum value.

To evaluate whether females synchronize their estrous cycles, we used an estrus synchrony index (ESI) as a test statistic. This index is the variance in the proportion of females with maximal swellings to cycling females ob-

Table 1 The number of cycling females, average ages, average of maximal swelling, and nonmaximal swelling days during analyzed periods

Analyzed period (Days)	1981–1982 Aug–Dec	1982–1983 Jun–Jan	1983–1984 May–Jan	1985–1986 Aug–Jan	1987–1988 Jul–Jan	1989–1990 May–Jan	1991–1992 May–Jan	1992–1993 May–Jan	1993–1994 May–Jan
The number of cycling females analyzed	15	11	13	13	17	15	9	11	10
The average ages of cycling females ^a	27.2±8.9	29.9±9.9	28.0±9.9	23.8±10.1	26.9±8.6	22.3±10.1	25.4±7.2	25.6±7.0	29.7±6.8
The average maximal swelling days ^b	12.7±2.9	10.3±2.9	12.1±5.3	12.7±4.3	13.4±3.8	13.5±3.0	12.3±1.7	12.2±4.2	10.4±4.8
The average nonmaximal swelling days ^c	20.2±6.6	27.3±4.6	20.4±6.7	23.3±5.6	22.1±6.2	20.1±6.8	20.6±2.5	21.2±6.4	21.2±7.7

^a There was no difference in ages (Kruskal–Wallis, $df=8$, $H=10.0$, $p=0.27$).

^b There was no difference in maximal swelling days (Kruskal–Wallis, $df=8$, $H=13.4$, $p=0.10$).

^c There was no difference in nonmaximal swelling days (Kruskal–Wallis, $df=8$, $H=6.6$, $p=0.59$).

served per day normalized by the variance of frequencies from the binomial distribution. Thus, the ESI is:

$$\text{var}(F_m/F_c)/[\text{mean}(F_m/F_c)\{1 - \text{mean}(F_m/F_c)\}]$$

where F_m is the number of females in maximal swelling and F_c is the number of cycling females. The number of days over which variances are computed is constant and therefore not included in computations of the test statistic.

ESI values will be large when females synchronize their estrous cycles and will be small when they avoid synchronizing. It is not immediately clear how large ESI values must be before concluding that females synchronize their estrous cycles. In addition, females typically remain swollen over consecutive days, and daily frequencies may not be independent from those on other days. These factors make it difficult to evaluate the statistical significance of the ESI. We circumvented these problems by using a randomization test (Edgington 1995).

We tested the null hypothesis that females neither synchronize nor avoid overlapping their estrous cycles with each other by comparing observed test statistics each year with expected distributions. We produced these expected distributions by generating 10,000 values of the test statistic for each study year via Monte Carlo simulation. We began by simulating maximum swelling periods for each female in the sample. To do so, we used a random number generator to select an integer c_i that varied from one to T_i , where T_i equaled the observed cycle length of the i th female. We used this value to determine the first day of maximum swelling of the i th female by shifting the start of her observed maximum swelling period by $c_i - 1$ day. Thus, if the start of maximum swelling of the i th female began on

day j in the observed sample, her start day in the simulation was computed as $c_i - 1 + j$. This procedure was repeated to simulate maximum swelling periods for the remaining cycles that the i th female experienced in any given year. The simulation process was duplicated for every female in the sample using new randomly selected c_i values for each individual. After these simulations, we computed a new ESI value to derive one data point of the expected distribution and then repeated the process 9,998 more times. We generated the final expected distribution by using the 9,999 simulated values plus the observed ESI value.

We compared test statistics against expected distributions computed for each year and applied Fisher's combined probability test (Rosenthal 1991) to evaluate whether females displayed a significant tendency to synchronize or avoid synchronizing their estrous cycles over the 9 years of study. For this meta-analysis, we combined the one-tailed probabilities (p) in each of the i years of study ($=1-9$) to compute, $-2\sum \log p_i$. This statistic follows a chi-square distribution with $2k$ degrees of freedom, where k equals to the number of separate tests and probabilities.

Birthrate, mortality rate and sex ratio

We also examined the relationships between birthrate, breeding sex ratio, and mortality rates. For these analyses, we took the numbers of males and births from long-term demographic data (Nishida et al. 2003). We counted the number of cycling females each year between 1980–1999. We defined birthrate as the number of births per cycling female per year, and mortality rate as the number of infant deaths per cycling female per year. Breeding sex ratio was

assayed by the number of cycling females per adult male. We excluded data from the years 1981 and 1982 due to a paucity of observations.

Results

Estrus asynchrony

Female cycle length was 33.4 ± 6.3 ($n=108$) when the cycle was defined as the period of nonmaximal swelling and maximal swelling. Females averaged 12.5 ± 4.0 ($n=194$) days in maximal swelling, and 21.2 ± 6.4 days in nonmaximal swelling ($n=155$, Table 1). The ages of cycling females and the number of maximal swelling days they experienced did not differ between years.

Analysis of female maximal swelling periods on an annual basis revealed that females did not synchronize their estrous cycles in any year (Table 2). In contrast, females avoided synchronizing their cycles in 4 years, whereas their estrous cycles occurred randomly in 5 years (Table 2). A more consistent pattern emerged when we examined the timing of female reproduction over the entire 1980–1995 study period. During this time, females avoided synchronizing their maximal swelling periods with each other (combined probability test, $p < 0.001$). Overlap of periovulatory periods was evident only in 1987–1988, when many females resumed cycling after a period of high infant mortality.

Birthrate, mortality rate, and sex ratio

Figure 1 reveals a significant inverse correlation between female birthrate and the breeding sex ratio (Kendall partial correlation coefficient, $n=15$, $\tau=-0.40$, $z=-2.08$, $p=0.04$). In contrast, birthrate showed no relationship with the current annual mortality rate or the mortality rate from the prior year (same year: $n=14$, $\tau=-0.25$, $z=-1.30$, $p=0.20$; last year: $n=15$, $\tau=-0.08$, $z=-0.41$, $p=0.68$).

Discussion

Estrus asynchrony

Results of our analyses indicate that female chimpanzees in the M-group at Mahale display asynchronous estrous cycles. This pattern of asynchrony contrasts with most other primate data published thus far, which suggest that females frequently synchronize their reproductive activities (Kummer 1968; Dunbar 1980; French and Stribley 1987; Wallis 1985, 1992; Zinner et al. 1994).

Although a previous study (Wallis 1985) showed that onset of estrus was synchronized among female chimpan-

zees caged in the same building, inappropriate statistical analyses used in the study were pointed out later by Shank (2001). Another study at Gombe, which is only 200 km north of Mahale, investigated estrous synchrony among some females in the entire group. Results showed that females that had lost an infant tended to synchronize their subsequent estrous cycles with their female travel companions (Wallis 1992). In baboons and chimpanzees, when postpartum females lose infants, they need fewer cycles on average to conceive than fertile females who have successfully weaned infants (Altmann et al. 1977; Nishida et al. 1990; Zinner et al. 1994; Wallis 1997; Boesch and Boesch-Achermann 2000). Wallis (1992) suggested that females who have lost infants may resume cycling with other fertile females from whom they receive cues that the environment is suitable for reproduction to replace the loss. Even if females synchronize the start days of their subsequent estrous cycles with travel companions, such synchrony does not persist at Mahale. The degree of estrous synchrony between females who maintained close proximity did not differ significantly from that of other pairs (Matsumoto-Oda and Kasuya 2005).

Female chimpanzee mating strategies

Female reproductive success is widely regarded as closely linked to resource availability. Rarely is it considered that female reproductive success is limited by mating opportunities. Female primates are expected to compete for mating opportunities only when males vary in quality: when access to high-quality males is limited, and when the cost of competing for high-quality males is low compared to the benefits of mating these males. If competing for males were energetically expensive enough that it increased interbirth intervals significantly while only marginally improving offspring quality, little competition would be expected. However, if competition was not costly and offspring quality improved significantly, female–female competition for males would be expected. Such competition has been observed among female Norway rats (*Rattus norvegicus*) where it has been shown that synchrony both decreases the expected male phenotypic quality and decreases the number of matings (Schank 2004).

When female–female mating competition is high, a decrease in female reproductive success can follow. Dunbar and Sharman (1983) reported an inverse correlation between the number of breeding females per male and birthrates in one-male breeding units of gelada baboons. Likewise, in captive hamadryas baboons, which also have one-male breeding units, the number of females that are simultaneously in estrus is inversely correlated with the probability of conception (Zinner et al. 1994). These studies suggest that access to males or sperm is a limiting resource

Table 2 The synchronized indexes of maximal swelling period and preovulatory period (the last 4 days of maximal swelling), and results of meta-analysis

Maximal swelling period	Analyzed year	The number of maximal swelling females in a day (range, median)	Observed ESI	ESI by Monte Carlo simulation			Standardized ESI	Two-tailed probability	Results		
				Mean±SD of ESI	Larger than observed ESI	Equal to observed ESI				Smaller than observed ESI	
Maximal swelling period	1981–1982	0–7, 3	0.20	0.20±0.04	4,088	1	5,911	0.09	0.82	Random	
	1982–1983	0–7, 0	0.46	0.75±0.03	9,999	1	0	-9.31	0.0002	Asynchrony	
	1983–1984	0–6, 1	0.32	0.40±0.03	9,929	1	70	-2.30	0.01	Asynchrony	
	1985–1986	0–6, 1	0.27	0.36±0.05	9,950	1	49	-2.14	0.01	Asynchrony	
	1987–1988	0–10, 2	0.33	0.31±0.03	1,796	1	8,203	0.89	0.36	Random	
	1989–1990	0–6, 0	0.32	0.38±0.03	9,832	1	167	-2.00	0.03	Asynchrony	
	1991–1992	0–4, 0	0.56	0.62±0.05	8,868	1	1,131	-1.13	0.23	Random	
	1992–1993	0–7, 1	0.41	0.45±0.03	8,020	1	1,979	-1.07	0.40	Random	
	1993–1994	0–5, 1	0.21	0.25±0.05	8,118	1	1,881	-0.89	0.38	Random	
	Meta-analysis										Asynchrony
	Adding log		Chi-square								47.18
			<i>df</i> ×2								18
	Preovulatory period	1981–1982	0–3, 0	0.17	0.20±0.03	8,110	1	1,889	-0.88	0.38	<i>p</i> <0.001
		1982–1983	0–1, 0	0.28	0.68±0.12	9,999	1	0	-3.41	0.0002	Random
1983–1984		0–3, 0	0.40	0.38±0.05	2,649	1	7,350	0.62	0.53	Asynchrony	
1985–1986		0–2, 0	0.19	0.32±0.05	9,999	1	0	-2.67	0.0002	Random	
1987–1988		0–3, 0	0.37	0.28±0.04	246	1	9,753	2.19	0.05	Asynchrony	
1989–1990		0–3, 0	0.16	0.32±0.05	9,999	1	0	-3.57	0.0002	Synchrony	
1991–1992		0–3, 0	0.42	0.60±0.05	9,994	1	5	-3.80	0.0012	Asynchrony	
1992–1993		0–3, 0	0.45	0.41±0.05	2,581	1	7,418	0.67	0.52	Asynchrony	
1993–1994		0–3, 0	0.22	0.27±0.05	7,836	1	2,163	-0.84	0.43	Random	
Meta-analysis											Random
Adding log			Chi-square								Asynchrony
			<i>df</i> ×2								74.42
											18
											<i>p</i> <0.001

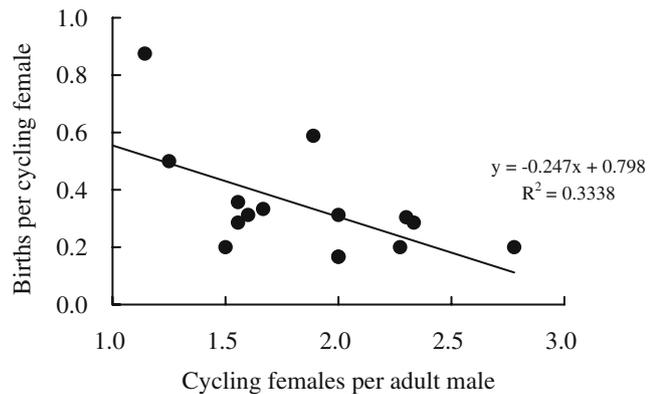


Fig. 1 Birthrate (number of births per cycling female per year) plotted against breeding sex ratio (number of cycling females per adult male) for each year. The birth rate decreased as the more females cycled synchronously. There were 14 points in this figure because the data of 1983 and 1997 were the same value

in some nonhuman primates. Among chimpanzees, sperm depletion leading to female–female mating competition seems possible, because males copulated, on average, four times a day (Short 1981).

Our results showed an inverse correlation between birthrate and the number of cycling females per male (see Fig. 1), as was observed in baboons. Among baboons, birthrates increased when food was abundant, or when many females had recently lost infants (e.g., Dunbar 1984). This was not the case among Mahale chimpanzees. Birthrates fluctuated little over 19 years (5–10%, Nishida et al. 2003), and our data showed that infant mortality and birthrate were not positively correlated. In other words, the birthrate rose when there were few cycling females, and as a general phenomenon, there were few females in estrus at the same time.

Female–female competition for mating can be expressed as direct aggression to secure matings. Female–female competition for mates through aggression, harassment, or inhibition by simple physical presence has been reported for some primate species when the sex ratio is extremely female-biased, as in polygynous mating systems (e.g., patas monkeys: Loy and Loy 1977; gelada baboons: Dunbar 1984; gorillas: Watts 1990; hamadryas: Zinner et al. 1994), or when there are long recovery periods for sperm replacement (Smuts 1987; Small 1988). In wild chimpanzees, such competition has not been observed. When anestrus, females are relatively dispersed; aggression among anestrus females was very low both at Gombe (one time/106 h, Goodall 1986) and at Mahale (4.6 times/100 h, Nishida 1989). Females are more likely to be in proximity when they are in estrus and therefore clumped near males, yet female aggression in sexual contexts was not observed at Gombe (Goodall 1986). These low occurrences of female–female contest competition for mates may be attributable to a female scramble strategy, expressed as avoiding estrous synchrony.

Avoiding synchronizing estrous cycles may be a female strategy to reduce male sexual coercion. Males of many animals, including chimpanzees, increase their reproductive success through coercive tactics such as physical aggression against females, forced copulation, harassment and intimidation, induced abortion (followed by insemination by a second male), and sexually selected male infanticide (Smuts and Smuts 1993; Clutton-Brock and Parker 1995). Sexual coercion is a particularly effective male mating strategy in unimale groups or multimale groups in which males compete for access to females like chimpanzees (Tutin 1979; Kappeler 2000; Constable et al. 2001).

Previously, the presence of sexual coercion in chimpanzees has been taken as evidence that males “win” the battle over mating, forcing females to mate with the only partner available. From the perspective of females, the presence of coercion increases the probability that they may be forced to copulate with nonpreferred partners and requires a counterstrategy, because nonpreferred partners lower female reproductive success. The opportunity for males to coerce females is reduced when females avoid synchronizing their estrous cycles with each other. When there are few females in estrus at the same time, male–male mating competition intensifies, and by thus inciting male–male competition, estrous asynchrony increases the probability that high-ranking males will mate females. Although this may be a suboptimal strategy for females, as it precludes an unfettered choice of mates, it may be the best one available given the potential for coercion. High-ranking males are likely to possess important social or physical characteristics that their offspring can inherit (e.g., ‘best genes hypothesis’; northern fur seal, *Callorhinus ursinus*, Bartholomew 1970; elephant seal, Cox and Le Boeuf 1977). Synchrony avoidance may therefore represent a tactic that permits a female to exercise limited choice for high-ranking males, rather than mating the first male that encounters and coerces her.

Acknowledgement T. Nishida, the late S. Uehara, and many others who shared the fieldwork in the Mahale Mountains National Park, Tanzania; their contribution to the data was indispensable. Besides some of them, F. W. Marlowe, R. Oda, A. E. Pusey, and K. Tsuji commented on earlier versions, which greatly improved this paper. The Japan Ministry of Education, Culture, Sports, Science and Technology mainly supported the fieldwork financially. The Tanzania National Parks, Scientific Research Council, Serengeti Wildlife Research Institute, and their subsidiaries facilitated our research. We make grateful acknowledgement to these people and institutions.

References

- Altmann J, Altmann SA, Hausfater G, McCuskey SA (1977) Life history of yellow baboons: physical development, reproductive parameters and infant mortality. *Primates* 18:315–330

- Arark A (1988) Callers and satellites in the natterjack toad: evolutionarily stable decision rules. *Anim Behav* 36:416–432
- Bartholomew GA (1970) A model for the evolution of pinniped polygyny. *Evolution* 24:546–559
- Boesch C, Boesch-Achermann H (2000) *The chimpanzees of the Tai Forest*. Oxford University Press, New York
- Clutton-Brock TH (1989) Mammalian mating systems. *Proc R Soc Lond B* 236:339–372
- Clutton-Brock TH, Parker GA (1995) Sexual selection and the potential reproductive rates of male and females. *Nature* 351:58–60
- Constable JL, Ashley MV, Goodall J, Pusey AE (2001) Noninvasive paternity assignment in Gombe chimpanzees. *Mol Ecol* 10:1279–1300
- Cox CR, Le Boeuf BJ (1977) Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317–335
- 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*. *Anim Behav* 66:551–560
- Dunbar RIM (1980) Demographic and life history variables of a population of Gelada baboons (*Theropithecus gelada*). *Behav Ecol Sociobiol* 7:253–265
- Dunbar RIM (1984) *Reproductive decisions*. Princeton University Press, Princeton
- Dunbar RIM, Sharman M (1983) Female competition for access to males affects birth rate in baboons. *Behav Ecol Sociobiol* 13:157–159
- Eberle M, Kappeler PM (2002) Mouse lemurs in space and time: a test of the socioecological model. *Behav Ecol Sociobiol* 51:131–139
- Edgington ES (1995) *Randomization tests*. Marcel Dekker, New York
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Findlay CS, Cooke F (1982) Breeding synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. *Evolution* 36:342–351
- French JA, Stribley JA (1987) Synchronization of ovarian cycles within and between social groups in golden lion tamarins (*Leontopithecus rosalia*). *Am J Primatol* 12:469–478
- Goodall J (1986) *The chimpanzees of Gombe*. Harvard University Press, Cambridge
- Gowaty PA (2004) Sex roles, contents for the control of reproduction, and sexual selection. In: Kappeler PM, van Schaik CP (eds) *Sexual selection in primates*. Cambridge University Press, Cambridge, UK, pp 37–54
- Graham C (1981) Menstrual cycle physiology of the great apes. In: Graham CE (ed) *Reproductive biology of the great apes*. Academic Press, New York, pp 286–303
- Handelmann G, Ravizza R, Ray WJ (1980) Social dominance determines estrous entrainment among female hamsters. *Horm Behav* 14:107–115
- Hasegawa T, Hiraiwa-Hasegawa M (1983) Opportunistic and restrictive mating among wild chimpanzees in the Mahale Mountains, Tanzania. *J Ethol* 1:75–85
- Howard RD (1980) Mating behaviour and mating success in wood frog *Rana sylvatica*. *Anim Behav* 28:705–716
- Ims RA (1990) The ecology and evolution of reproductive synchrony. *TREE* 5:135–140
- Kappeler PM, van Schaik CP (2004) Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP (eds) *Sexual selection in primates*. Cambridge University Press, Cambridge, UK, pp 3–23
- Kappeler PM (2000) Primate males. In: Kappeler PM (ed) *Primate males*. Cambridge University Press, Cambridge, UK, pp 3–7
- Kummer H (1968) *Social Organization of hamadryas baboons*. University of Chicago Press, Chicago
- Loy J, Loy K (1977) Sexual harassment among captive patas monkeys *Erythrocebus patas*. *Primates* 18:691–699
- Matsumoto-Oda A, Kasuya E (2005) Proximity and estrous synchrony in Mahale chimpanzees. *Am J Primatol* 66:159–166
- McClintock MK (1971) Menstrual synchrony and suppression. *Nature* 229:244–255
- McClintock MK (1978) Estrous synchrony and its mediation by airborne chemical communication (*Rattus norvegicus*). *Horm Behav* 10:264–276
- Monfort SK, Bush M, Wildt DE (1996) Natural and induced ovarian synchrony in golden lion tamarins (*Leontopithecus rosalia rosalia*). *Biol Reprod* 55:875–882
- Nishida T (1989) Social interactions between resident and immigrant female chimpanzees. In: Heltn PG, Marquardt LA (eds) *Understanding chimpanzees*. Harvard University Press, Cambridge Mass, pp 68–89
- Nishida T, Takasaki H, Takahata Y (1990) Demography and reproductive profiles. In: Nishida T (ed) *The chimpanzees of the Mahale Mountains*. University of Tokyo Press, Tokyo, pp 63–68
- Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history and reproductive profiles among the chimpanzees of Mahale. *Am J Primatol* 59:99–121
- Pereira ME (1991) Asynchrony within estrous synchrony among ringtailed lemurs (Primates: *Lemuridae*). *Physiol Behav* 49:47–52
- Rosenthal R (1991) *Meta-analytic procedures for social research*. Sage Publications, London
- Sauther ML (1991) Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly special reserve, Madagascar. *Am J Phys Anthropol* 84:463–477
- Schank JC (2000) Menstrual-cycle variability and measurement: further cause for doubt. *Psychoneuroendocrinology* 25:837–847
- Schank JC (2001) Measurement and cycle variability: reexamining the case for ovarian-cycle synchrony in primates. *Behavioral Processes* 56:131–146
- Schank JC (2004) Avoiding synchrony as a strategy of female mate choice. *Nonlinear Dyn Psychol Life Sci* 8:147–176
- Setchell JM, Kappeler PM (2003) Selection in relation to sex in primates. *Adv Study Behav* 33:87–174
- Short RV (1981) Sexual selection in man and the great apes. In: Graham CE (ed) *Reproductive biology of the great apes*. Academic, New York, pp 319–341
- Small MF (1988) Female primate sexual behavior and conception. Are there really sperm to spare? *Curr Anthropol* 29:81–99
- Smuts BB (1987) Sexual competition and mate choice. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primates societies*. University of Chicago Press, Chicago, pp 385–399
- Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Stud Behav* 22:1–63
- Strassmann BI (1997) The biology of menstruation in Homo sapiens: total lifetime menses, fecundity, and nonsynchrony in a natural-fertility population. *Curr Anthropol* 18:123–129
- Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav Ecol Sociobiol* 6:29–38
- Wallis J (1985) Synchrony of estrous swelling in captive group-living chimpanzees (*Pan troglodytes*). *Int J Primatol* 6:335–350
- Wallis J (1992) Socioenvironmental effects on timing of first postpartum cycles in chimpanzees. In: Nishida T, McGrew WC,

- Marler P (eds) Topics in primatology, vol 1. University of Tokyo Press, Tokyo, pp 119–130
- Wallis J (1997) A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *J Reprod Fertil* 109:297–307
- Watts DP (1990) Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zoo Biol* 9:185–200
- Weller L, Weller A (1993) Human menstrual synchrony: a critical assessment. *Neurosci Biobehav Rev* 17:427–439
- Wilson HC (1992) A critical review of menstrual synchrony research. *Psychoneuroendocrinology* 17:565–591
- Zinner DP, Schwibbe MH, Kaumanns W (1994) Cycle synchrony and probability of conception in female hamadryas baboons *Papio hamadryas*. *Behav Ecol Sociobiol* 35:175–183