

Dominance and Reproductive Rates in Captive Female Olive Baboons, *Papio anubis*

C. Garcia,¹ P.C. Lee,² and L. Rosetta^{1*}

¹Laboratoire de Dynamique de l'Evolution Humaine, CNRS UPR 2147, 75014 Paris, France

²Department of Psychology, University of Stirling, Stirling FK9 4LA, Scotland, United Kingdom

KEY WORDS postpartum amenorrhea; resumption of cycling; interbirth interval; dominance rank; fertility

ABSTRACT The reproductive cycles of 23 captive olive baboons were studied over two successive parturitions. Interbirth intervals of 450 days were reduced by 60% in comparison to wild baboons, and consisted of 145 days of postpartum amenorrhea, 3.5 cycles, and a gestation of 185 days. Dominance rank was found to be one significant factor affecting female fertility. Low-ranking females had longer total intervals between successive births and, in particular, they experienced a longer delay to conception once they had resumed sexual cycles. Mothers

of infants who were heavy for age resumed cycling more quickly and had fewer cycles before a subsequent conception. Mothers best able to sustain rapid early infant growth were those of high dominance rank and of high body mass; these females had more rapid reproductive rates. As female energy intake was unrelated to dominance, we suggest that social stresses are important suppressors of the hormonal and lactational competence of subordinate females. *Am J Phys Anthropol* 00:000–000, 2006. © 2006 Wiley-Liss, Inc.

The factors that potentially impose intrinsic physiological limits on fertility and fecundity in mammals have been the focus of considerable interest. In the last decade, studies of sportswomen attempted to disentangle the possible effects of energetics on the regulation of ovarian function, e.g., sustained endurance effort including daily training sessions, inadequate caloric intake, and short-term negative energy balance (Loucks, 1990; De Souza et al., 1998; Rosetta et al., 2001). Williams et al. (2001) experimentally induced reproductive dysfunction in female long-tailed macaques (*Macaca fascicularis*) after strenuous exercise training. Their monkey model exhibited many similarities to the pattern of menstrual impairment in exercising women, and led to questions about the role of metabolic adaptation to chronic energy restriction.

In nonhuman primates, both energy intake and travel costs influence net energy balance and female reproductive success (Altmann and Samuels, 1992; Isbell et al., 1999; Pontzer and Wrangham, 2004). Captive primates typically have shorter durations of postpartum inhibition of ovarian function and shorter interbirth intervals than do their wild counterparts (Gomendio, 1989; Johnson et al., 1993; Lee, 1996a; Gauthier, 1999), which may be a function of lower energy constraints in captivity. Reduced costs of traveling (i.e., less time and energy spent searching for food and carrying infants), and a plentiful and regular supply of food, may explain the early resumption of fertility as well as the greater reproductive success of captive compared to wild primates. Studies of free-ranging yellow and olive baboons and semifree-living mandrills also showed that seasonal or population food availability modifies reproductive performance (Altmann, 1980; Strum and Western, 1982; Bercovitch, 1987; Altmann et al., 1988; Smuts and Nicolson, 1989; Wasser et al., 1998; Setchell and Wickings, 2004).

In addition to energetics as a factor regulating mammal fertility, other key variables are the possible effects

of female age and the role of the hypothalamo-pituitary-adrenal axis driving physiological stress responses. There is a dramatic decrease in fertility with age in women, particularly after age 35 years (CECOS Federation et al., 1982), which is also seen in female nonhuman primates (Strum and Western, 1982; Smuts and Nicolson, 1989; Wasser et al., 1998), while there is less information on captive primates (but see Walker, 1995). The relationship between dominance rank and female fertility has been debated for over 20 years (Harcourt, 1987; Packer et al., 1995; Wasser, 1996; Altmann et al., 2004), with some studies showing clear reproductive advantages for individual of high rank, especially when resources are clumped or are large and monopolizable (Mathy and Isbell, 2001). Whether low-ranking female monkeys incur energy costs or stress costs which affect their fertility is also debated (Deutsch and Lee, 1991).

A preliminary survey at the CNRS Primatology Station (France) on a sample of 17 captive female olive baboons (*Papio anubis*) found that maternal rank influenced reproductive output, with high-ranking females having a shorter postpartum inhibition of ovarian function and interbirth intervals than did mid-ranking females (Garcia et al., 2002). The same animals were observed over a further 2 years, and six additional females were added to the sample. This longitudinal study was

Grant sponsor: CNRS; Grant number: GDR 2655.

*Correspondence to: Lyliane Rosetta, CNRS UPR 2147, 44 rue de l'Amiral Mouchez, 75014 Paris, France.
E-mail: rosetta@infobiogen.fr

Received 1 July 2005; accepted 18 November 2005.

DOI 10.1002/ajpa.20405
Published online in Wiley InterScience
(www.interscience.wiley.com).

designed to assess reproductive characteristics of semi-captive female olive baboons between two successive parturitions.

Here, we report on female reproductive parameters in relation to dominance rank, age of the female, and social context, focusing on the duration of postpartum amenorrhea, and waiting time to conception including the number of cycles, gestation length, and total interbirth interval. We controlled for infant mass and sex, as well as the physical characteristics of the mothers. Captive studies on socially housed, naturally reproducing females, where energy intake and expenditure are more closely controlled and exposure to environmental risks are limited, may allow us to distinguish between key social and ecological factors influencing fertility.

METHODS

Animals, housing, and diet

Twenty-three multiparous adult female olive baboons contributed to the study (16.9 ± 2.0 kg mass, range = 13.5–21.1 kg, and 13.9 ± 2.8 years of age, range = 10–21 years). These subjects belonged to two social groups housed in semifree-ranging conditions at the CNRS Primatology Station (France). Eight females were part of a group housed in Park 2, consisting of 63 individuals (two adult males, 17 adult females, two adolescent females, 33 juveniles, and nine infants). This enclosure measured 220 m², and had an outer park with climbing apparatus and an inner compartment. The areas were linked together by multiple runs. The other 15 animals belonged to another social group (Park 5) with 97 individuals (two adult males, one subadult male, 30 adult females, two adolescent females, 49 juveniles, and 13 infants). Park 5 measured 470 m², with both indoor and outdoor areas, and enrichment objects. These two groups were similar in terms of age-sex classes, with equivalent individual areas. The groups were artificially formed at least 2 years before the beginning of the initial study, and thus all individuals were familiar with each other, and some matriline (mothers and juveniles) had begun to form.

All animals had free access to water, and food was provided three times daily. Individuals were fed fruits (carrots and apples) at 11:30 hr and two types of commercial monkey pellets (SDS, Vigny, France; UAR, Villemoisson-sur-Orge, France) at 9:00 and 15:30 hr. The content of the SDS diet was 16.3% protein, 6.1% fat, 57.4% carbohydrates, and 4.4% total fiber, with a metabolizable energy value of 11.9 MJ/kg. The UAR diet was 18.8% protein, 6.7% fat, 55.1% carbohydrates, and 3.5% fiber, with a metabolizable energy value of 14.21 MJ/kg. Each day, the enclosure with 97 individuals (Park 5) received about 15 kg of carrots, 20 kg of apples, 6.5 kg of UAR pellets, and 12.5 kg of SDS pellets; the second park with 63 animals (Park 2) received about 10 kg of carrots, 13–14 kg of apples, 6.5 kg of UAR pellets, and 7–7.5 kg of SDS pellets. Fruit energy was determined from weighing different specimens over time and using averages of metabolizable energy per gram. Individuals in both parks had access to an equivalent quantity of food on a daily basis (0.59 kg/individual in Park 2, and 0.56 kg/individual in Park 5), and the major nutrient intake of focal females was monitored. One focal female was followed for 6–12 samples distributed equally over lactation/cycle phases (Garcia, 2005). The number of pellets and quantity and size of carrots and apples consumed by this individual during continuous focal samples, which started

when food was distributed and available and terminated when all food was eaten, were considered to represent energy intake over a 24-hr period (MJ/day).

Variables recorded

Analyses are based on data collected from October 2002 through December 2004.

Age. The age of adults was determined from dental estimates of age when the animals arrived at the CNRS Primatology Station, and their previous reproductive history if known.

Females were assigned to one of three age classes (Smuts and Nicolson, 1989). The younger adult age class (4–8 years) associated with first reproduction at 4–5 years was excluded:

Younger middle-aged (approximately 9–12 years): age class 1 (N = 8, 4 females in Park 2, and 4 in Park 5);
Older middle-aged (approximately 13–16 years): age class 2 (N = 11, 3 females in Park 2, and 8 in Park 5); and
Old and very old (≥ 17 years): age class 3 (N = 4, 1 female in Park 2, and 3 in Park 5).

For infants born during the study period, we recorded the exact birth date, and computed a new variable, birth season (1, winter: December 21–March 20; 2, spring: March 21–June 20; 3, summer: June 21–September 20; and 4, autumn: September 21–December 20). This variable was used to assess the distribution of reproductive events throughout the year, and to test for the presence or absence of seasonal birth peaks in this captive colony.

Reproductive parameters. The olive baboon is one of approximately 20 species in which nonpregnant females show obvious sexual swellings during the menstrual cycle (Dixson, 1983). The swelling affects the sex skin of the anogenital area (AGA); the AGA increases in tumescence due to estrogenic stimulation, and decreases after ovulation as estrogen concentrations fall (Dixson, 1998).

All study females were multiparous. They were systematically observed daily over 2 years and reproductive characteristics were recorded, including menstruation and morphological changes of the AGA. Swellings typically commenced 2.8 days after menstruation (Garcia, 2005), and reached maximum tumescence as ovulation approached (Hendrickx and Kraemer, 1969; Koyama et al., 1977; Shaikh et al., 1982). Our analyses focused on the following parameters: duration of postpartum amenorrhea and duration of cycling phase, waiting time to conception (duration between parturition and next conception), gestation length, and total interbirth interval. The day of conception (i.e., when a cycle resulted in pregnancy) was calculated as 2 days before detumescence. Gestation lengths were estimated retrospectively from day of birth to day of conception. The sex ratio at birth for the 23 focal females was 51.2% male (N = 43; 22 M:21 F), with an equal sex ratio for each category of maternal rank. There was no difference between the sex ratio of the focal females and the colony sex ratio at birth (30 M:29 F overall).

Rank. Female dominance rank was assessed as part of long-term behavioral monitoring, using ad libitum sampling (Altmann, 1974). The assessment of rank was based on all occurrences of submissive gestures (avoidances), initiation of attacks, threats, chases, and retreats during escalated aggression (Deutsch and Lee, 1991). We recorded the outcome of agonistic bouts, an agonistic bout being defined

as an interaction sequence between two individuals in which one exhibits at least one “submissive behavior” or “aggressive behavior” (Altmann, 1980). Dominance rank was determined using the criteria of Hausfater (1975) during agonistic bouts:

“A winner and a loser were determined in an agonistic bout only when one animal directed one or more submissive behaviors, and no aggressive behaviors, toward a second animal who directed no submissive behaviors toward the first animal. The individual who gave the submissive behaviors was considered the loser of the bout, and the individual who gave only aggressive and/or other nonsubmissive behaviors was considered the winner of the bout.”

Female rank was expressed as the proportion of females dominated (after Cheney et al., 1988), providing a relative rank ranging between 0 (low) and 1 (high). Rank was divided into quartiles, and we categorized individuals as high-ranking (upper quartile), mid-ranking (interquartile range), and low-ranking (lower quartile). If rank is not highly linear, but rather, power is skewed, the arbitrary division of females into quartiles will obscure potential differences between “alpha” individuals and a mass of relatively similar subordinate females. However, for the purposes of comparison between the parks and with other studies, we categorized the females into these high, mid, and low classes.

Anthropometric measurements. Females were anesthetized with ketamine (10 mg/kg by intramuscular injection), a widely accepted dissociative anesthetic used in studies requiring transient animal tranquilization. Infants were maintained with their mothers and not sedated, so as to minimize physical stress or disturbance to the mother-infant relationship during the measurement period. Measures of body size and mass were carried out on the anesthetized females and their infants. Body weight was measured with a standard scale (accurate to the nearest 50 g) and expressed in kilograms, accurate to two decimal places. We weighed the female with her infant, and then weighed the female only, and the infant weight was calculated from the difference, again to minimize any handling stress on the infant. The same investigators (C.G. and L.R.) were responsible for all body measures, to minimize interobserver error. Two series of body-weight measurements were made for each animal during the study period: one measurement at 11–12 postpartum weeks, and another at 4 weeks after resumption of cycling. Heavy individuals (mothers and infants) were those with mass in the upper 75%, and light individuals were those in the lowest 25%, with infant age taken into account.

Ethical considerations. All manipulations and treatments of subjects had ethical approval from the Comité Régional d’Ethique sur l’Expérimentation Animale (Marseille, France), and followed European Science Foundation animal-handling guidelines to minimize pain and distress. Since the aim of the study was to assess normative reproductive behavior in the social context, the social separation stress to the female was kept as limited as possible. Trapping, taking of blood, and measurements were considered to be interventions, but not invasive procedures.

Statistics

Subjects entered the study when they gave birth to an infant, and were excluded from the study at the second parturition. When the study terminated, several subjects

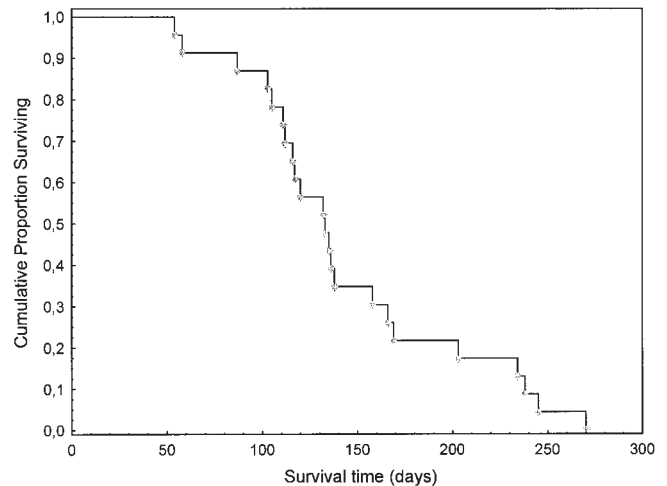


Fig. 1. Survival curve for postpartum amenorrhea duration in captive female olive baboons.

had not yet given birth a second time and contributed differentially to the data, since they had incomplete life histories. We therefore used survival analysis techniques that take into account the time that each subject was at risk for events of interest such as resumption of cycling, whether or not the event occurred during the study. Although the number of censored events was small, a time to event analysis was considered more appropriate for two further reasons. We were interested in exploring the underlying biology rather than statistical goodness of fit, and we had potential time-dependent covariates such as infant and maternal mass (see Wood, 1994).

We used Kaplan-Meier survival analyses to examine duration of postpartum amenorrhea, duration of cycling phase, gestation lengths, and interbirth intervals. The results are described by median and mean survival time with standard error and Brookmeyer-Crowley 95% confidence intervals for median survivorship. The log-rank test (L) was used to assess whether the survivorship functions differed significantly between groups (Hill et al., 1996). A second technique, the Cox proportional hazards regression model, was used to investigate the multivariate influence of several variables on reproductive intervals (Hill et al., 1996). The analysis estimated a set of regression coefficients that related the effect of each covariate to the hazard function. The test statistic used here was the regression coefficient divided by the standard error of the sample (RC/SE). For each analysis, a significant effect indicated that the covariate influenced the hazard function when the effects of other covariates were taken into account, i.e., the results were analogous to those obtained by standard multiple regression techniques. All statistical analyses were performed with BMDP for Windows, release 8.0 (BMDP, Inc., Cork, Ireland), or SPSS version 11, with the significance level set at $P < 0.05$.

Where we used parametric statistics, we first confirmed a normal distribution of the variables.

RESULTS

Most (65%) females resumed cycling within 5 months after giving birth (Fig. 1). The mean duration of postpartum amenorrhea was 145.2 ± 12.1 days (mean \pm SEM), with a median of 132.5 ± 12.0 days (median \pm asymptotic SE), and a range of 54–270 days ($N = 23$). Three

TABLE 1. Postpartum amenorrhea duration in female olive baboons, calculated from survival analyses¹

Class of female	N ²	Median \pm SE ³	95% CI ⁴	Mean \pm SE ³
All	23	132.5 \pm 12.0	116–158	145.2 \pm 12.1
With male infant	13	118.0 \pm 14.4	105–158	136.3 \pm 15.0
With female infant	10	133.0 \pm 3.2	117–203	156.8 \pm 20.2
High-ranking	6	133.0 \pm 31.2	87–158	122.7 \pm 17.8
Mid-ranking	11	114.0 \pm 3.3	105–136	127.9 \pm 14.3
Low-ranking	6	203.0 \pm 62.5	132–238	199.5 \pm 24.9
Age class 1	8	132.0 \pm 12.7	111–238	153.6 \pm 24.8
Age class 2	11	124.5 \pm 13.2	103–169	138.2 \pm 16.1
Age class 3	4	117.0 \pm 15.0	105 ⁵	147.8 \pm 29.4
Low body weight, <15.5 kg	6	158.0 \pm 35.5	111–203	163.3 \pm 20.6
Medium body weight, 15.5–17.7 kg	12	135.0 \pm 2.6	132–166	149.3 \pm 20.3
High body weight, >17.7 kg	5	114.0 \pm 4.4	103 ⁵	113.6 \pm 2.9

¹ Statistical comparisons between the groups are presented in Table 2.

² Sample size.

³ Median and mean survival time with standard error (SE) in days.

⁴ Brookmeyer-Crowley 95% confidence interval for median survival time in days.

⁵ Lower one-sided Brookmeyer-Crowley 95% confidence interval.

TABLE 2. Maternal, infant, and habitat factors affecting reproductive parameters in 23 semifree-ranging female olive baboons¹

	Postpartum amenorrhea	Number of cycles to conception	Waiting time to conception	Gestation length	Interbirth interval
<i>Maternal factors</i>					
Age class (df = 2)	L = 0.53	L = 0.31	L = 0.11	L = 1.00	L = 0.38
Relative mass (df = 2)	L = 1.95	L = 2.61	<i>L = 5.30*</i>	L = 0.01	<i>L = 5.24*</i>
Rank (df = 2)	<i>L = 3.39</i>	<i>L = 2.92</i>	<i>L = 7.67**</i>	<i>L = 8.94**</i>	<i>L = 8.14**</i>
<i>Infant factors</i>					
Sex (df = 1)	L = 0.93	L = 0.31	L = 0.05	L = 1.89	L = 0.05
Relative mass (df = 2)	<i>L = 5.07*</i>	<i>L = 4.29*</i>	L = 0.11	L = 0.25	<i>L = 3.64</i>
Birth season (df = 3)	L = 3.71	L = 3.72	L = 3.43	L = 3.64	L = 6.21
<i>Habitat factors</i>					
Park (df = 1)	L = 1.42	<i>L = 5.36*</i>	<i>L = 5.87**</i>	L = 0.26	<i>L = 4.78*</i>

¹ Postpartum amenorrhea, number of cycles to conception, waiting time to conception, gestation length, and interbirth interval. Statistics represent log-rank test (L) on survival functions.

* $P < 0.05$.

** $P < 0.01$ (italics, $0.05 < P < 0.1$).

females resumed cycling within 100 days of giving birth, while five females took over 170 days to resume cycling. Overall, resumption of cycles was influenced by dominance rank (Table 1). Short postpartum amenorrhea was associated with being of mid or high rank, while low-ranking females took significantly longer than dominant counterparts before they resumed their cycles ($L = 4.03$, $P = 0.04$). The relationship between duration of postpartum amenorrhea and infant mass (Table 2) was consistent with predictions: females with light, potentially slowly growing infants took significantly longer to resume cycling than did females with heavy, rapidly growing infants (Fig. 2).

Once a female resumed cycling, on average (N censored = 1) she would experienced three or four cycles before conception (mean \pm SEM, 3.6 ± 0.6 ; median, 2.5; range, 1–10). Conception resulted during 17% of first cycles, while a total of 48% had occurred within two cycles, and 70% within three. Low-ranking females tended to take longer to start cycling, but were then slightly more likely to conceive on the first cycle (17%) than were mid-ranking females (9%). High-ranking females took the least time to start cycling, and 33% of first cycles resulted in conception. Females in the smaller Park 2 had significantly more cycles prior to conception (Table 2) than did those in Park 5 (5.3 ± 1.3 vs. 2.7 ± 0.4). There was also a further effect of infant mass (Table 2), with mothers of infants who were heavy after the resumption of cycling experiencing fewer cycles than did

mothers of lighter infants. Female rank (proportion of females dominated) and park were entered simultaneously as covariates with the number of cycles to conception. The trend for an effect of rank (RC/SE = 1.79, $P = 0.07$) was confirmed, while the park effect was again significant (RC/SE = 1.93, $P = 0.05$) when the other factors were taken into account.

Total time between resumption of cycles and conception was 126.4 ± 20.7 days (N censored = 1; median, 96.5 days; range, 18–370 days). Taking a combined measure of the waiting time to conception, which includes postpartum amenorrhea and the duration of cycling until conception, the mean delay was 270.8 ± 23.4 days (N = 1 censored bout). The median delay was 237 days (SE = 30.3), with a range of 110 to over 553 days. As expected from previous findings (Table 2), rank was a major influence on the waiting time to conception, with low-ranking females taking significantly longer to conceive than high-ranking females ($L = 9.99$, $P < 0.01$). Females in the larger Park 5 took less time to conceive again, while light mothers took longer to conceive (light vs. mid, $L = 5.37$, $P = 0.02$; light vs. heavy, $L = 4.04$, $P = 0.04$). Park, female rank category, and maternal mass were entered simultaneously as covariates. The three factors all had significant independent associations with waiting time to conception (park, RC/SE = 2.28, $P = 0.02$; maternal mass, RC/SE = 2.89, $P < 0.01$; high- vs. mid-ranking, RC/SE = -2.21 , $P = 0.03$; high- vs. low-ranking, RC/SE = -3.27 , $P = 0.001$).

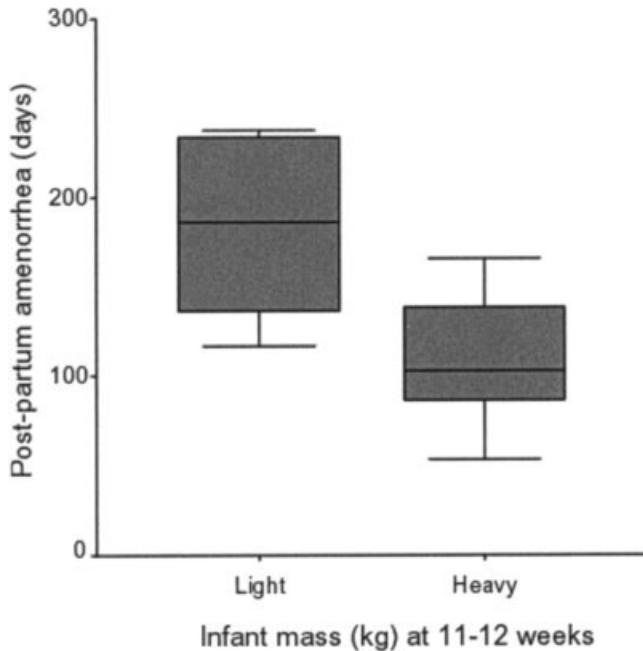


Fig. 2. Duration of postpartum amenorrhea for mothers of light infants (<1.4 kg, $N = 6$), compared to those with heavy infants (>1.7 kg, $N = 5$). Plot shows median (bar), interquartile range (box), and highest and lowest values (whiskers).

Gestation length could be accurately determined for 20 females, when the date of conception and date of birth were known to within 1 day. Gestation averaged 185.1 ± 0.8 days (median, 185.0 ± 1.7 days; range, 177–192 days). The variation in gestation length was associated with maternal rank (Table 2), with low-ranking females having shorter gestations (mean \pm SE = 182.6 ± 0.7 days) than high-ranking females (188.4 ± 1.0 days, $L = 9.73$, $P < 0.002$).

For 21 females, interbirth interval could be calculated to within 1 day (N censored = 2). The mean interbirth interval in this population was 450.6 ± 21.2 days (median, 422.0 ± 29.6 days; range, 299–649 days). A small proportion (22%) gave birth again in less than 1 year, while only 13% took longer than 18 months. Although the interbirth interval is obviously the sum of the waiting time to conception plus gestation, there were differences in the rank effects on the separate durations and events that make up this total interval. A number of factors influenced interbirth intervals (Table 2).

Again, dominant individuals had significantly shorter intervals than did subordinates (Fig. 3), while lighter females had longer intervals than did mid or heavy females (light: 547.3 ± 52.0 days vs. 415.1 ± 22.1 days for mid, and 419.6 ± 25.2 days for heavy females). Females in the larger Park 5 also had shorter intervals than did those in Park 2 (415.1 ± 22.5 days vs. 497.6 ± 23.0 days). As was noted for duration of postpartum amenorrhea and number of cycles to conception, mothers of heavy infants experienced less of a delay between reproductive events (390.0 ± 26.6 days for heavy infants vs. 505.3 ± 51.5 days for light ones). Female rank category, mother's weight, and park were again explored as simultaneous covariates influencing interbirth intervals, and all were significant (high- vs. mid-ranking: RC/SE = -2.34 , $P = 0.02$; high- vs. low-ranking: RC/SE = -3.27 , $P = 0.001$; park: RC/SE = 2.07 , $P = 0.04$; mother's weight: RC/SE = 2.76 , $P < 0.01$).

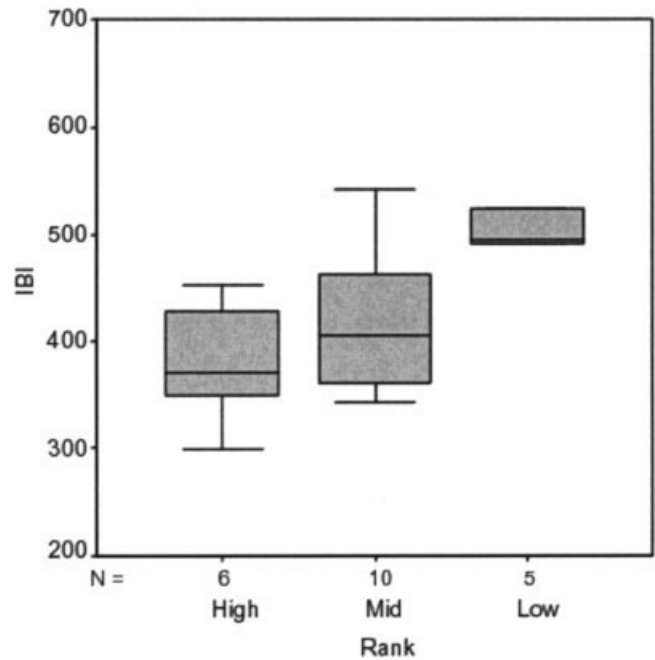


Fig. 3. Interbirth interval (IBI) for high-, mid-, and low-ranking female baboons. Plot shows median (bar), interquartile range (box), and highest and lowest values (whiskers).

In order to examine any potential interactions among factors influencing interbirth intervals, we ran a general linear model on the noncensored data. There were no significant interactions between any of the independent variables, and the main effect of rank was still strongly demonstrated (ANOVA: $F = 7.56$, $df = 2, 21$, $P = 0.04$). We suggest that each factor highlighted above is acting independently to influence interbirth intervals.

There were no rank-related differences in body mass among females (ANOVA: $F = 0.40$, $df = 2, 23$, NS), nor were there rank-related differences in estimated individual food intake per day (median = 4.20 MJ, $r_s = 0.23$, NS) or individual intake per kg body mass ($r_s = 0.10$, NS). Thus, for this sample, dominance status did not appear to influence energy acquisition directly.

DISCUSSION

We present longitudinal data on the complete reproductive cycles of captive female baboons from delivery through postpartum amenorrhea (4–5 months), the number of cycles to conception (2–4 cycles), and pregnancy and new delivery (interbirth interval = 450 days). The intervals reported here are only 60% of those found in the wild (see below).

Baboons typically show an even distribution of reproduction throughout the year, with no strong seasonal birth peaks (Altmann et al., 1988; Bercovitch and Harding, 1993). We found a slight seasonal trend in births but only for females in Park 5, with a peak in February and a trough in July–August. However, the sample sizes are too small to test statistically. Furthermore, we found no effect of time of year (birth season) on any of the reproductive variables examined. Infant sex also had no marked effect on the reproductive parameters assessed here. While breeding in captivity appears to be subject to the positive benefits of food enhancement increasing the rate of reproduction,

the trends described here suggest that social variables also influenced individual reproductive output.

Effects of female age on reproductive performance

In this colony, no reproductive parameter was significantly related to maternal age. Among wild olive baboons at Gilgil, Kenya, interbirth intervals either shortened significantly as females aged (Smuts and Nicolson, 1989), or they initially shortened with age and then lengthened toward the end of the females' reproductive lives, i.e., the classic mammalian inverse U-shaped relationship between age and reproductive performance (Strum and Western, 1982; Bercovitch et al., 2003). In wild chimpanzees, fertility declines substantially after age 35 (Nishida et al., 2003). In free-ranging yellow baboons, Wasser et al. (1998) reported that the number of cycles to conception decreased significantly with age and that the duration of lactation showed a U-shaped pattern with age, but they found no significant effect of age on interbirth interval. Our failure to find any association between fertility and age may be due to all females having commenced reproduction (multiparity), and thus being unlikely to show reduced fertility associated with early reproductive careers, while the lack of a decline in fertility with increasing age may be due to small sample sizes, with only one female being very old (i.e., >20 years) and 3 females being old (17–20 years). Furthermore, life span and, concomitantly, reproductive life span are lengthened in captivity (Colman et al., 1999), and thus we might only observe such effects with females over age 25 years.

Other factors affecting fertility

Female dominance rank was related to the waiting time to conception, gestation length, and total interbirth interval. Rank was also weakly associated with duration of postpartum amenorrhea and cycling phase duration, as seen in many wild and captive primates (Smuts and Nicolson, 1989; Wasser et al., 1998; Setchell et al., 2002; Setchell and Wickings, 2004). However, the underlying physiological mechanisms remain to be clarified. Several were suggested as explanations of the links between dominance rank and reproduction. Foremost among these are nutritional status and energy balance or stress.

Reproductive rates of captive and provisioned free-ranging primates tend to be higher than those of unprovisioned groups (reviewed by Lee, 1996b). Maternal nutrition is associated with milk production in nonhuman mammals (Oftedal, 1984), and interacts with suckling rates. Suckling and consequent infant growth underlie the resumption of cycling, ability to conceive, and ultimately interbirth intervals. Food-enhanced wild baboon populations have shorter interbirth intervals than do those with only natural forage (Bercovitch and Strum, 1993; Altmann and Alberts, 2003), mirroring the difference between captive and wild populations.

We found a very short duration of postpartum amenorrhea (145 days) in our sample compared to wild populations (Altmann, 1980: 360 days in wild *Papio cynocephalus*; Smuts and Nicolson, 1989: 407 days in wild *Papio anubis*). Our data are similar to those of Gauthier (1999: 161 days in captive *Papio papio*), and confirm that captive primates have a shorter duration of inhibition on ovarian function than do their wild counterparts (Altmann et al., 1977). It is notable that of the total interval between successive births, the duration of lactational amenorrhea

accounts for the majority of the difference between our captive females and wild baboons. Shortening the duration of postpartum amenorrhea may be a function of reduced energy constraints in the captive environment. A lower cost of travel (i.e., time and energy spent foraging and carrying infants), combined with a plentiful and regular supply of food, and access to health interventions when ill, may all explain the early resumption of fertility as well as the greater reproductive success of captive primates compared to wild ones. In our captive sample, about 3.5 cycles are needed for a new conception, which is similar to the 3 or 4 cycles usually occurring before conception in wild yellow baboons (Altmann et al., 1978).

Better nutrition may influence reproductive parameters among populations or groups, but is not sufficient to explain interindividual differences in reproductive capacities within a group. Similar to the pattern observed in these captive females, dominance influenced the duration of postpartum amenorrhea in free-ranging olive baboons, with 365 days for high-ranking females and 456 days for low-ranking females. Unlike our sample, however, the total time cycling almost doubled between high (127 days) and low (217 days) ranks (Smuts and Nicolson, 1989). Significantly shorter interbirth intervals for high-ranking females are generally observed (Gomendio, 1990; Wasser et al., 1998; Setchell et al., 2002).

In this captive colony, food was widely delivered and fairly evenly dispersed inside the parks, and there was little possibility for dominants to monopolize patches of high-quality food. Consequently, high-ranking females did not have feeding advantages over low-ranking ones, and no rank-related differences in total food intake were found (see also Garcia, 2005). In this context, where rank-related differences in energy intake cannot account for the fertility patterns we found, it is unlikely that nutritional mechanisms (Schneider, 2004) alone mediate the relationship between dominance and fertility. Nutritional factors are expected to have the greatest impact on the duration of postpartum amenorrhea, as the period of peak lactation and maximum infant growth rate represents the highest energetic costs to the mother (Oftedal, 1984; Lee, 1987; Altmann and Samuels, 1992). However, our data show that the strongest effect of female status is on the waiting time to conception and on gestation length, suggesting that stress rather than nutrition alone may play a crucial role.

Chronic social stress has long been proposed as an alternative explanation for rank effects on female reproduction. Social constraints play an important role in the regulation of reproductive function in a variety of mammalian species (Wasser and Barash, 1983; Altmann et al., 1988; Packer et al., 1995). In marmosets, social subordination hormonally suppresses reproduction (Abbott et al., 1990). Stress can thus disrupt menstrual cycles, can reduce the probability of ovulation or likelihood of a conception, and might lead to abortion. Aggression toward subordinate females on the part of reproductively active dominant females was suggested as the major mechanism interfering with cycling through the adrenal-hypothalamus network (Weingrill et al., 2004). In our study, the chronic stress hypothesis is supported by an increased wait to conception among low-ranking females, which is the main cause of their longer interbirth intervals. Low-ranking females tended to cycle for longer than high-ranking females because their cycles may have been less fertile or even anovulatory. In addition, gestation length was also related to dominance rank, with low-ranking females having shorter

gestations, which may have been a hormonal or growth response to harassment, attacks, and chases. Since rank in this colony was determined on the basis of threats, chases, attacks, and submissions, potentially stressful interactions occurred and with some frequency. However, it should be noted that the harassment of subordinates by dominants could impose additional energy expenditure costs on the subordinates as they flee to avoid interaction, which could result in a negative energy balance even with similar intakes. Whether such interactions translate into chronic hormonal stresses is currently being explored.

Infant and male effects

Infant mass at 11–12 weeks postpartum had an important effect on the duration of postpartum amenorrhea: the lighter the infant, the longer the postpartum amenorrhea. If infants must reach a threshold weight before they are weaned (Lee et al., 1991; Bowman and Lee, 1995), then more time will be required to reach this threshold. When the infant was lighter at 11–12 weeks (peak suckling and peak growth), the duration of postpartum amenorrhea was longer. Similarly, infant mass 4 weeks after the mother's resumption of cycle was associated with the number of cycles she experienced before another conception: the heavier the infant, the fewer the number of cycles. Stress could potentially interact with the efficiency of milk production to reduce output, so that light, slowly growing infants had to suck more frequently, extending lactation duration or the hypofertility of females once cycles resumed. Maternal mass also influenced the competence and quality of individual cycles, e.g., a mother's ability to conceive and capacity to become pregnant quickly after resuming cycling was enhanced when her mass was greater and maternal mass was unrelated to rank. Individual variation in condition and energy balance appears to play a role in reproductive potential, while stress interacted with these individual characteristics through social status.

We also observed a park effect on the number of cycles prior to conception, on the total duration of the cycling phase, and on interbirth intervals, but no effect for the duration of postpartum amenorrhea. Females in Park 5 with short interbirth intervals had a similar total food intake and density as in Park 2 (Garcia, 2005). While there were twice as many female competitors in Park 5, some females had been together for longer, matrilineal lines had developed, and the area allowed for more escape, which may have resulted in reduced social conflict.

Stress, nutrition, and energetics appear to be insufficient to explain park differences. One alternative explanation is that male quality influenced the fertility of females. Both parks contained two adult males, and the ratio of adult males to adult females was similar. Males in Park 2 may be less fertile than males in Park 5, leading to higher reproductive rates in Park 5. Lower male fertility can result from the absence of sperm, insufficient sperm concentration, lack of sperm viability, malformations of sperm, and a low proportion of normal sperm, or insufficient mobility (see Dixson, 1998). Alternatively, the males in Park 2 may have experienced sperm depletion due to higher cycle synchronization (e.g., Zinner et al., 1994), but Park 2 showed less cycle synchrony than did Park 5. Finally, females in Park 2 could have had less attractive sexual swellings than did females in Park 5, resulting in fewer mounts and a reduced probability of conception (Domb and Pagel, 2001; Dunbar,

2001; Nunn et al., 2001; Zinner et al., 2002). The shape of Park 5 (with two separated polygons permitting copulations hidden from view) might also be responsible for enhanced mating opportunities in this park.

CONCLUSIONS

All females in the captive colony exhibited enhanced reproductive rates by contrast to wild baboons. Despite excellent nutrition and a relatively low energy expenditure on travel or foraging, individual variation in reproductive rates was marked. Significant rank-related effects were observed, with low-ranking females experiencing the slowest rates of reproduction. These data suggest that chronic social stresses were critical influences on reproductive rates, primarily affecting the waiting time to conception. Interesting influences of infant growth (mass attained for age) were also found, such that when infants grew rapidly in early lactation, their mothers were more likely to resume sexual cycling early. Infants who were heavier after their mothers had resumed cycles also had mothers who experienced fewer cycles prior to conception. Heavier mothers also appeared to be at an advantage, as expected if there are additional costs to lactation even in a well-fed captive colony. Dominance status, energy acquisition, individual characteristics, and the physical environment all interacted to produce variation in reproductive rates for these captive females.

ACKNOWLEDGMENTS

The authors thank Guy Dubreuil for allowing our research to be carried out at the CNRS Primatology Station. Thanks also go to the animal keepers for their field assistance. Special thanks go to Laurence Joubin for very helpful statistical advice. We are grateful to the referees for helpful comments. This study was funded by a CNRS grant from the Department of Sciences de l'Homme et de la Société to L.R.; Downing College, Cambridge University, provided travel funds for P.C.L.

LITERATURE CITED

- Abbott D, George LM, Barrett J, Hodges JK, O'Byrne KE, Sheffield JW, et al. 1990. Social control of ovulation in marmoset monkeys: a neuroendocrine basis for the study of infertility. In: Ziegler TE, Bercovitch FB, editors. Socioendocrinology of primate reproduction. New York: Wiley Liss. p 135–158.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Altmann J. 1980. Baboon mothers and infants. Cambridge, MA: Harvard University Press.
- Altmann J, Alberts SC. 2003. Variability in reproductive success viewed from a life-history perspective in baboons. *Am J Hum Biol* 15:401–409.
- Altmann J, Samuels A. 1992. Costs of maternal care: infant carrying in baboons. *Behav Ecol Sociobiol* 29:391–398.
- 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.
- Altmann J, Altmann SA, Hausfater G. 1978. Primate infant's effects on mother's future reproduction. *Science* 201:1028–1030.
- Altmann J, Hausfater G, Altmann SA. 1988. Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In: Clutton-Brock TH, editor. Reproductive success. Chicago: University of Chicago Press. p 403–418.

- Altmann J, Lynch JW, Nguyen N, Alberts SC, Geschiere LR. 2004. Life-history correlates of steroid concentrations in wild peripartum baboons. *Am J Primatol* 64:95–106.
- Bercovitch FB. 1987. Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *Am J Primatol* 12:189–195.
- Bercovitch FB, Harding RS. 1993. Annual birth patterns of savanna baboons (*Papio cynocephalus anubis*) over a ten-year period at Gilgil, Kenya. *Folia Primatol (Basel)* 61:115–122.
- Bercovitch F, Strum S. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behav Ecol Sociobiol* 33:313–318.
- Bercovitch FB, Widdig A, Trefilov A, Kessler MJ, Berard JD, Schmidtke J, Nurnberg P, Krawczak M. 2003. A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften* 90:309–312.
- Bowman JE, Lee PC. 1995. Growth and threshold weaning weights among captive rhesus macaques. *Am J Phys Anthropol* 96:159–175.
- CECOS Federation, Schwartz D, Mayaux MJ. 1982. Female fecundity as a function of age. *N Engl J Med* 306:404–406.
- Cheney DL, Seyfarth RM, Andelman SJ, Lee PC. 1988. Reproductive success in vervet monkeys. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago: University of Chicago Press. p 384–402.
- Colman RJ, Kemnitz JW, Lane MA, Abbott DH, Binkley N. 1999. Skeletal effects of aging and menopausal status in female rhesus macaques. *J Clin Endocrinol Metab* 84:4144–4148.
- De Souza MJ, Miller BE, Loucks AB, Luciano AA, Pescatello LS, Campbell CG, Lasley BL. 1998. High frequency of luteal phase deficiency and anovulation in recreational women runners: blunted elevation in follicle-stimulating hormone observed during luteal-follicular transition. *J Clin Endocrinol Metab* 83:4220–4232.
- Deutsch JC, Lee PC. 1991. Dominance and feeding competition in captive rhesus monkeys. *Int J Primatol* 12:615–628.
- Dixon AF. 1983. Observations on the evolution and behavioral significance of “sexual skin” in female primates. *Adv Stud Behav* 13:63–106.
- Dixon AF. 1998. *Primate sexuality: comparative studies of the prosimians, monkeys, apes and human beings*. Oxford: Oxford University Press.
- Domb LG, Pagel M. 2001. Sexual swellings advertise female quality in wild baboons. *Nature* 410:204–206.
- Dunbar RIM. 2001. What’s in a baboon’s behind? *Nature* 410:158.
- Garcia C. 2005. *Energétique et régulation de la fonction de reproduction chez des femelles captives babouins olive (Papio anubis)*. Ph.D. dissertation, Université d’Aix-Marseille II, France.
- Garcia C, Lee PC, Rousselière E, Dubreuil G, Rosetta L. 2002. Etude préliminaire chez des femelles captives babouins olive (*Papio anubis*): détermination des paramètres reproductifs. *Primatologie* 5:369–395.
- Gauthier CA. 1999. Reproductive parameters and paracallosal skin color changes in captive female Guinea baboons, *Papio papio*. *Am J Primatol* 47:67–74.
- Gomendio M. 1989. Differences in fertility and suckling patterns between primiparous and multiparous rhesus mothers (*Macaca mulatta*). *J Reprod Fertil* 87:529–542.
- Gomendio M. 1990. The influence of maternal rank and infant sex on maternal investment trends in rhesus macaques: birth sex ratios, inter-birth intervals and suckling patterns. *Behav Ecol Sociobiol* 27:365–375.
- Harcourt AH. 1987. Dominance and fertility among female primates. *J Zool* 213:471–487.
- Hausfater G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). *Contrib Primatol* 7:1–150.
- Hendrickx AG, Kraemer DC. 1969. Observations of the menstrual cycle, optimal mating time and preimplantation embryos of the baboon, *Papio anubis* and *Papio cynocephalus*. *J Reprod Fertil [Suppl]* 6:119–128.
- Hill C, Com-Nougé C, Kramar A, Moreau T, O’Quigley J, Senoussi R, Chastang C. 1996. *Analyse statistique des données de survie*. Paris: Flammarion Médecine-Sciences.
- Isbell LA, Pruettz JD, Nzuma BM, Young TP. 1999. Comparing measures of travel distances in primates: methodological considerations and sociological implications. *Am J Primatol* 48:87–98.
- Johnson RL, Berman CM, Malik I. 1993. An integrative model of the lactational and environmental control of mating in female rhesus monkeys. *Anim Behav* 46:63–78.
- Koyama T, De La Pena A, Hagino N. 1977. Plasma estrogen, progesterin, and luteinizing hormone during the normal menstrual cycle in the baboon: role of luteinizing hormone. *Am J Obstet Gynecol* 127:67–72.
- Lee PC. 1987. Nutrition, fertility and maternal investment in primates. *J Zool Lond* 213:409–422.
- Lee PC. 1996a. The meaning of weaning: growth, lactation, and life history. *Evol Anthropol* 5:87–96.
- Lee PC. 1996b. Lactation, condition and sociality: constraints on fertility of non-human mammals. In: Rosetta L, Mascie-Taylor CGN, editors. *Variability in human fertility*. Cambridge: Cambridge University Press. p 25–45.
- Lee PC, Majluf P, Gordon IJ. 1991. Growth, weaning and maternal investment from a comparative perspective. *J Zool Lond* 225:99–114.
- Loucks AB. 1990. Effects of exercise training on the menstrual cycle: existence and mechanisms. *Med Sci Sports Exerc* 22:275–280.
- Mathy JW, Isbell LA. 2001. The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatol (Basel)* 72:268–277.
- 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.
- Nunn CL, van Schaik CP, Zinner D. 2001. Do exaggerated sexual swellings function in female mating competition in primates? A comparative test of the reliable indicator hypothesis. *Behav Ecol* 12:646–654.
- Oftedal OT. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp Zool Soc Lond* 51:33–85.
- Packer C, Collins DA, Sindimwo A, Goodall J. 1995. Reproductive constraints on aggressive competition in female baboons. *Nature* 373:60–63.
- Pontzer H, Wrangham RW. 2004. Climbing and the daily energy costs of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317–335.
- Rosetta L, Condé da Silva Fraga E, Mascie-Taylor CGN. 2001. Relationship between self reported food and fluid intake and menstrual disturbance in female recreational runners. *Ann Hum Biol* 28:444–454.
- Schneider JE. 2004. Energy balance and reproduction. *Physiol Behav* 81:289–317.
- Setchell JM, Wickings EJ. 2004. Social and seasonal influences on the reproductive cycle in female mandrills (*Mandrillus sphinx*). *Am J Phys Anthropol* 125:73–84.
- Setchell JM, Lee PC, Wickings EJ. 2002. Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). *Int J Primatol* 23:51–68.
- Shaikh AA, Celaya CL, Gomez I, Shaikh SA. 1982. Temporal relationship of hormonal peaks to ovulation and skin deturgescence in the baboon. *Primates* 23:444–452.
- Smuts B, Nicolson N. 1989. Reproduction in wild female olive baboons. *Am J Primatol* 19:229–246.
- Strum SC, Western JD. 1982. Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *Am J Primatol* 3:61–76.
- Walker ML. 1995. Menopause in female rhesus monkeys. *Am J Primatol* 35:59–71.
- Wasser SK. 1996. Reproductive control in wild baboons measured by fecal steroids. *Biol Reprod* 55:393–399.

- Wasser SK, Barash DP. 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Q Rev Biol* 58:513–538.
- Wasser SK, Norton GW, Rhine RJ, 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. *Hum Reprod Update* 4:430–438.
- Weingrill T, Gray DA, Barrett L, Henzi SP. 2004. Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Horm Behav* 45:259–269.
- Williams NI, Caston-Balderrama AL, Helmreich DL, Parfitt DB, Nosbisch C, Cameron JL. 2001. Longitudinal changes in reproductive hormones and menstrual cyclicity in cynomolgus monkeys during strenuous exercise training: abrupt transition to exercise-induced amenorrhea. *Endocrinology* 142:2381–2389.
- Wood JW. 1994. Dynamics of human reproduction. New York: Aldine.
- Zinner D, Schwibbe MH, Kaumanns W. 1994. Cycle synchrony and probability of conception in female hamadryas baboons *Papio hamadryas*. *Behav Ecol Sociobiol* 35:175–183.
- Zinner D, Alberts SC, Nunn CL, Altmann J. 2002. Significance of primate sexual swellings. *Nature* 420:142–143.