

Female Reproductive Parameters of Tana River Yellow Baboons

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We describe the female reproductive parameters of yellow baboons at the Tana River National Primate Reserve, Kenya. We present data on menarche, cycle length, pregnancy, birth, postpartum amenorrhea, interbirth interval, and infant survival. We also briefly compare our data to those reported for yellow baboon females at the Amboseli Reserve, Kenya. Our results indicate statistically significant differences in some of these reproductive parameters between the two sites.

KEY WORDS: Reproductive strategies; reproductive parameters; *Papio hamadryas cynocephalus*; seasonality; females.

INTRODUCTION

The purpose of this article is to provide comparative demographic and reproductive data on a relatively unstudied population of baboons—the Tana River yellow baboons (*Papio hamadryas cynocephalus*). While the Tana database is significantly less extensive than those of Amboseli and Mikumi, it provides a valid and valuable point of comparison. This article includes a brief presentation of troop demographics, age estimates for the focal subjects, and a discussion of female reproductive parameters: menarche, cycle length, pregnancy and birth, postpartum amenorrhea and interbirth interval, and infant survival. Collectively, these parameters determine how well a female's genes compete with those of her peers for representation in future

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generations. Of particular interest are data we present regarding reproductive clustering—the appearance of seasonality—among this population. As yellow baboons live in a female-bonded group (Wrangham, 1980) and have a matrilineal society (Hausfater *et al.*, 1982), their reproductive parameters affect not only an individual's lifetime reproductive success but potentially matriline and troop viability also.

METHODS

We collected data at the Tana River National Primate Reserve, Kenya, between February 1988 and November 1992 (Condit and Smith, 1994a; Marsh, 1976). While other primates had been examined at this site over the past 20 years [*Colobus badius rufomitratu*s (Marsh, 1978; Decker, 1989; Mowry *et al.*, 1996); *Cercocebus galeritus galeritus* (Kinnaird, 1990)], the yellow baboon population was virtually unstudied. A 5-year demographic database existed for the study (Mchelelo) troop, though no female behavioral datum had been collected (Bentley-Condit and Smith, 1996a,b).

We initiated systematic observations of the study troop in 1988 to collect daily demographic data. We added focal samples on the Mchelelo troop males to the demographic data in April 1991. In November 1990, we captured the troop and obtained biomedical samples—serum, dentition casts—for age estimates and DNA fingerprinting. We darted the baboons missed in the initial capture and sampled them during September 1992–October 1992.

Troop membership fluctuated somewhat over the represented period (Table I), which we attribute to natural causes. However, mean troop size during the November 1991–October 1992 study ($n = 76$) is significantly smaller than the mean troop size throughout the entire 49-month database ($n = 79.6$) ($t = 3.27$, $df = 59$). Additionally, there was an unusually large exodus immediately following the capture in November 1990.

Twenty-five females served as focal subjects (Altmann, 1974) during the November 1991–September 1992 female behavior project. Not all females were sampled for the entire duration of the project due to deaths, disappearances, or late joining of the study, *i.e.*, due to onset/resumption of cycles. (See Bentley-Condit, 1995). The age estimate techniques and reproductive parameter calculations follow; statistically significant results are at $p \leq 0.05$.

Age Estimates

Using a slightly modified version of Altmann and co-workers' (1981) aging schema, we classified females as subadult, rather than adult, at the

Table I. Mchelelo Troop Census Data by Age Class^a and Sex^b

A♀	SA♀	J♀	I♀	A♂	SA♂	J♂	I♂	Total	Date
23	5	7	4	3	3	26	7	78	1 Oct 88
23	2	7	8	4	2	28	8	82	1 Oct 89
22	2	13	7	6	7	22	4	83	1 Oct 90
22	3	15	4	5	5	18	5	77	1 Oct 91
19	4	12	4	5	2	23	5	74	1 Oct 92

^aModified from Altmann *et al.* (1981, p. 395).

^bA, adult; SA, subadult; J, juvenile; I, infant.

signs of first menses and as adults at first pregnancy. This slight deviation does not affect comparisons of our data with other baboon data as it is the chronological ages that are important to our discussion, not the classification of adult/subadult. Age estimates for the 25 focal females are based primarily on a combination of dental eruption patterns and menarche, as body weight and crown–rump length guidelines (Coelho, 1985) proved largely ineffectual. Full dental eruption in female olive and yellow baboons appears to occur at between 7 and 8 years of age, and dental eruption age estimates appeared to be the most reliable indicator of the Mchelelo female minimum ages (Phillips-Conroy and Jolly, 1988; Phillips-Conroy, 1990; and Kahumbu and Eley, 1991). Where dental eruption data were not available, we used menarche to estimate minimum age.

Cycle Length

We collected data on Mchelelo female perineal swelling once per day, 5 days per week, from February 1988 to September 1992 following Hausfater *et al.* (1983). We also noted menstrual bleeding. Although we missed many of the Mchelelo females' menses, we observed most of the tumescent phases. Accordingly, we used tumescence rather than menses to determine cycle length. Specifically, we calculated cycle length from the nadir of tumescence of one cycle to the nadir of tumescence of the succeeding cycle.

Pregnancy, Birth, Postpartum Amenorrhea, and Interbirth Interval

Following Altmann *et al.* (1977), we counted gestation length from the day of detumescence of the conception cycle until the day of infant birth. We calculated postpartum amenorrhea from the infant's birth to the first day of the female's subsequent estrous cycle or the infant's

death—whichever occurred first. We calculated interbirth intervals by counting from conception cycle to conception cycle for subsequent live births.

RESULTS

Age Estimates

Table II is a summary of data on menarche, weight, dental eruption, and age estimate for the Mchelelo focal females. For 1989–1992, the Mchelelo troop averaged three females reaching menarche per year (range = 1–4, \bar{X} = 2.75, n = 11).

Table II. Female Subjects—Age Estimates

Female	Date of menarche	Weight (kg) ^a	Dental eruption ^a	Age estimate (yr) ^a
AL	27 Nov 91	6.75	Partial	7.00
CO	Pre-Feb 88	9.50	Full	≥9.80 ^{2,b}
DD	17 Dec 91	7.50	Partial	7.38
HQ	Pre-Feb 88	10.5	Full	≥9.80 ²
KM	Pre-Feb 88	—	—	≥9.80
KN	Pre-Feb 88	—	—	≥9.80
LL	Pre-Feb 88	11.0	Full	≥9.80 ³
LS	Pre-Feb 88	—	—	≥9.80
LY	19 Jan 89	9.00	Partial	7.70
MM	Pre-Feb 88	—	—	≥9.80
ML	Pre-Feb 88	10.5	Full	≥9.80 ²
MN	Pre-Feb 88	10.0	Full	≥9.80 ²
MH	Pre-Feb 88	—	—	≥9.80
NY	Pre-Feb 88	10.7	Full	≥9.80 ³
NQ	31 Jan 89	—	—	8.80
PA	7 Jan 92	—	—	5.80
PS	Pre-Feb 88	—	—	≥9.80
PO	Pre-Feb 88	10.1	Full	≥9.80 ¹
PH	21 Feb 89	—	—	8.66
PT	13 May 91	—	—	7.16
RS	18 Oct 90	7.50	Partial	6.70
ST	1 Nov 90	7.00	Partial	7.40
SK	31 Dec 91	5.70	Partial	4.20
SY	Pre-Feb 88	10.5	Full	≥9.80
WK	23 Oct 89	—	—	8.10

^aData from November 1991 troop capture. ¹

^bRelative ages: ¹, older; ², middle-aged; ³, younger.

Reproductive Parameters

Menarche

Using dental eruption patterns as the best age estimate, a wide range of age of menarche became apparent. For the females on which both dental and menarcheal data are available, the first sex skin swelling appeared at 6 years of age (\bar{X} = 6.0 years, range = 4.37–7.51 years, SD = 1.19 years, n = 6). There is a clustering of menarcheal onset times for the Mchelelo females. For the females with known menarcheal onset dates (n = 11), 91% (10/11) occurred from mid-October through late February. A chi-square goodness of fit test for these data showed that this distribution differs significantly from an expected even distribution over a 12-month period [$\chi^2_{(1)} = 10.895$]. In other words, menses onsets occurred more frequently in the 5-month period October–February than in the remainder of the year (March–September). Altmann *et al.* (1977) and Scott (1984) described some clustering of menarche during the November–February period at Amboseli.

In 1990, only two focal females experienced menarche, even though there were four that reached the expected age of menses that year. If, indeed, there is clustering of menarche among the Mchelelo females, then the lack of onsets between November 1990 and February 1991 may be correlated with the November 1990 troop capture. There was no unusual environmental event, e.g., drought, during this period. Stress can affect non-human primate reproduction (Rowell, 1970; Wasser and Barash, 1983), and it is likely that this was a stressful event that may have affected reproductive states. This capture-induced stress may account for both delayed menarches (n = 2 females) and missed cycles (n = 8 females). While we cannot be certain that the capture caused the delayed menarches/missed cycles, we know that it was a particularly traumatic event that resulted in the deaths of two other troop members.

Cycle Length

Cycle length for the Mchelelo females showed great individual variability, at least some of which may have been due to the subadult females. Before regular cycling commences, it is common for adolescent females to have a brief swelling followed by a tumescent phase that lasts longer than that of the average adult (Altmann *et al.*, 1981) and for their first few cycles to be irregular and anovulatory (Altmann *et al.*, 1977). For the parous females that occasionally had abnormally long periods between tumescence,

one potential explanation is undetected pregnancies resulting in early miscarriages. While it is certainly feasible that other factors affected the observed variability—female age and resource availability—our age estimates and resource data are insufficient to measure these effects.

Since cycle lengths of nulliparous females are often very different from those of parous females (Altmann *et al.*, 1981), we divided the data in Table III to represent average cycle lengths for three categories of females—nulliparous, primiparous, multiparous—as well as all Mchelelo females combined. Data for primiparous females are only those for which we know first birth. Consequently, we split some female data between two categories, beginning in the nulliparous category and moving to the primiparous category with their conception cycle.

Although Harvey *et al.* (1987) give a species average estrous cycle of 31 days for yellow baboons, the data in Table III indicate that 33 days is a more realistic average cycle length for wild female yellow baboons. Thus, it is possible to compare the average cycle length for all females at Mchelelo ($\bar{X} = 38.94$ days) with the average for Amboseli ($\bar{X} = 33$ days), which reveals that the Mchelelo females have significantly longer cycles ($z = 5.21$, one-tailed). This significant difference prevails when the three re-

Table III. Summary of Average Cycle Length (Days)

	Mchelelo mean cycle length		
	Conception	Nonconception	All cycles
Nulliparous	—	41.38 ($n = 29$)	41.38 ($n = 29$)
(Range)	—	(16–65)	(16–65)
Primiparous	46.33 ($n = 6$)	42.00 ($n = 7$)	44.00 ($n = 13$)
(Range)	(26–60)	(29–60)	(26–60)
Multiparous	37.40 ($n = 20$)	37.12 ($n = 58$)	37.19 ($n = 78$)
(Range)	(16–68)	(14–65)	(14–68)
All females	39.46 ($n = 26$)	38.80 ($n = 94$)	38.94 ($n = 120$)
(Range)	(16–68)	(14–65)	(14–68)
Comparative data			
Subspecies	Cycle length	Method	Source
Yellow (wild)	32–34	Deturgescence	Hausfater (1975)
			Hausfater & Skoblick (1985)
Yellow (captive)	35	Tumescence	Hendrickx & Kraemer (1969)
		Menses	Zuckerman (1937)
Anubis (wild)	35–40	Follicular	Scott (1984)
		Detumescence	Smuts & Nicolson (1989)
Yellow & anubis (captive)	35.7	Tumescence	Wildt <i>et al.</i> , (1977)

productive categorizations are examined independently: multiparous $z = 3.01$, primiparous $z = 3.44$, and nulliparous $z = 3.48$. Although the Mchelelo cycle-length distribution appears to be slightly skewed ($\bar{X} = 38.94$ days, median = 38 days, mode = 42 days), the direction of the skew does not seem to negate our interpretation that Mchelelo cycles are significantly longer than those of Amboseli females. Additional analyses showed that the Mchelelo nulliparous/primiparous cycles are significantly longer than the multiparous cycles ($z = 2.11$, one tailed). However, there is no significant difference (across all females) between conceptive and non-conception cycles. We did not examine cycle-length differences by female age because our age estimates are most accurate for only a portion of the females, most of which are classed as nulliparous.

Pregnancy and Birth

The average length of gestation for the Mchelelo females is 181.5 days ($n = 28$). A total of 46 known conceptions—based on observed births, miscarriages, and stillbirths—occurred among the focal females between February 1, 1988, and November 3, 1992. Of 46 conceptions, 37 went full-term, resulting in 35 live births and 2 stillbirths (Condit and Smith, 1994b). Average age at first birth could not be determined due to the limited number of individuals that met the criteria of known first birth plus adequate age estimates.

For the Mchelelo females, births are not evenly dispersed throughout the year. Over the approximately 5-year period for which data are available, more live births occurred in January ($n = 8$) and September ($n = 7$) than in other months. Dividing the year into two 6-month blocks (to maintain the October–February period examined in the discussion of menses) revealed that 24 live births (69%) occurred during the September–February block, compared to 11 (31%) during the March–August block. A chi-square goodness-of-fit analysis of the birth data showed a significant difference from the theoretical distribution for live births if they were evenly distributed [$\chi^2_{(1)} = 4.82$]. Birth and stillbirth/miscarriage data are in Fig. 1.

Examination of the stillbirth/miscarriage data ($n = 11$; based on observed pregnancy terminations) reveals a similar but nonsignificant distribution. Over the same period, a total of eight (73%) miscarriages and stillbirths occurred between September and February, compared to three (27%) between March and August.

To assess whether there are birth peaks among the Mchelelo females similar to those reported at Amboseli by Altmann (1980), we further divided the years into 2-month blocks—January–February, March–April,

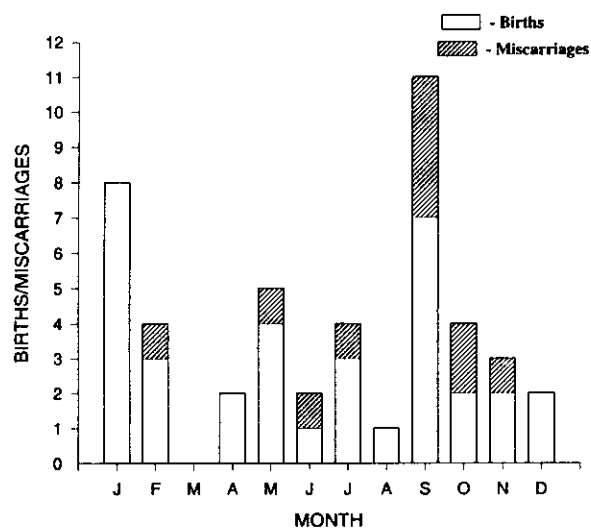


Fig. 1. Mchelelo births and stillbirths/miscarriages by month: February 1988–September 1992.

etc.—which revealed two apparent peaks for the live births ($n = 35$). Eleven (31%) live births occurred during January–February and nine (26%) occurred during September–October throughout the total period of data collection. The data for these two 2-month blocks differ significantly from expected frequencies if births were evenly distributed [chi-square goodness of fit test; $\chi^2_{(5)} = 10.08$]. Significantly more births occur during these two times (4 months) of the year ($n = 20$) compared to the remaining 8 months of the year ($n = 15$). When the years are examined independently, at least one of the peaks (January–February or September–October) is evident in each year except 1990. For 4 of the 5 years, the births during the two peaks are greater than that which would be expected with an equal distribution throughout the year. Even during 1990, the births for the peak months ($n = 2$) equal the expected distribution despite the fact that there was no birth in 7 of 12 months. These data offer further support that there are, indeed, two birth peaks among the Mchelelo females.

Postpartum Amenorrhea and Interbirth Interval

Further evidence of clustering of menses was apparent in the resumption of estrus by Mchelelo females following the birth of an infant. During

the period February 1, 1988 through November 3, 1992, there were 22 births in which the infants lived beyond mothers' resumptions of estrous cycles. Newborn survival is important, as Altmann *et al.*, (1977) have shown that the period of postpartum amenorrhea is significantly shortened by the early death or miscarriage of the infant. Of the 22 births in which the infant survived beyond mother's resumption of estrus, in 20 (82%) of the cases the mothers resumed cycling in the September–February time block—the same period used in the previous discussions of menstrual onsets, births, and miscarriages. These 20 female cycles represent all of the parous females with known surviving offspring. Only two resumptions occurred outside of the September–February period: one each in May and June.

Again, a chi-square goodness-of-fit test applied to these return-to-estrus-following-birth data show a statistically significant difference from the expected distribution [$\chi^2_{(1)} = 14.72$, $n = 22$]. Significantly more females resumed cycling in the 6-month period September–February than in the remainder of the year following the birth and weaning of an infant. This significant concentration exists despite a wide duration range of postpartum amenorrhea (range = 8–23 months, $\bar{X} = 14.55$ months) for the 22 cases.

Clustering was not apparent in cases in which a female's infant died before weaning or the female miscarried ($n = 10$). Females resumed cycling significantly sooner following the miscarriage of an infant (range = 0.5–5 months, $\bar{X} = 1.88$ months; $n = 8$) than in cases where the infant lived and was successfully weaned (range = 8–23 months, $\bar{X} = 14.55$ months; $n = 22$) [$t_{(28)} = 19.20$].

Based on data for 16 females, Mchelelo females had, on average, 4.13 cycles (range = 1–16 cycles; $n = 24$) or 150.13 days between subsequent pregnancies (range = 16–570 days; $n = 24$), i.e., approximately 5 months. Examination of the Mchelelo data on observed interbirth intervals revealed an average interbirth interval of 27.94 months (range = 14.43–35.93 months, SD = 5.95 months, $n = 13$).

Infant Survival

There were 35 live births and 11 miscarriages/stillbirths within the February 1988–November 1992 period. Thus, the probability that a pregnancy would result in a live birth is 0.76 and the miscarriage/stillbirth rate is 0.24. The Mchelelo miscarriage/stillbirth rate of $\geq 20\%$ is higher than the Amboseli rate of 10% (Altmann *et al.*, 1988). The Mchelelo data may, in fact, be grossly underestimated, as it is possible that there were frequent undetected pregnancies with early spontaneous abortions.

Following Altmann *et al.*, (1977) and Altmann (1980), an infant survivorship curve is presented in Fig. 2. The data from which it was obtained indicate that of the pregnancies that went full term and resulted in live births ($n = 35$), 12% (4/35) of the infants died during their first year of life. Of those remaining ($n = 31$), an additional 13% (4/31) died during their second year. During the third year of life, only 4% (1/27) of the infants died. Thus, of all live births, 12% (4/35) of the infants will not reach age 1 year and 23% (8/35) will not attain age 2 years.

Summary and Comparison with Amboseli

A brief review of the reproductive parameters data presented in the preceding sections for Mchelelo females is presented in Table IV. Significant differences compared to the Amboseli females are indicated, as are the results of some within-group—Mchelelo only—comparisons.

Menarche. The average age at menarche at Amboseli is 4.8 years [range = 4–5.75 years; $n = 10$ (Altmann *et al.*, 1981)]. The average

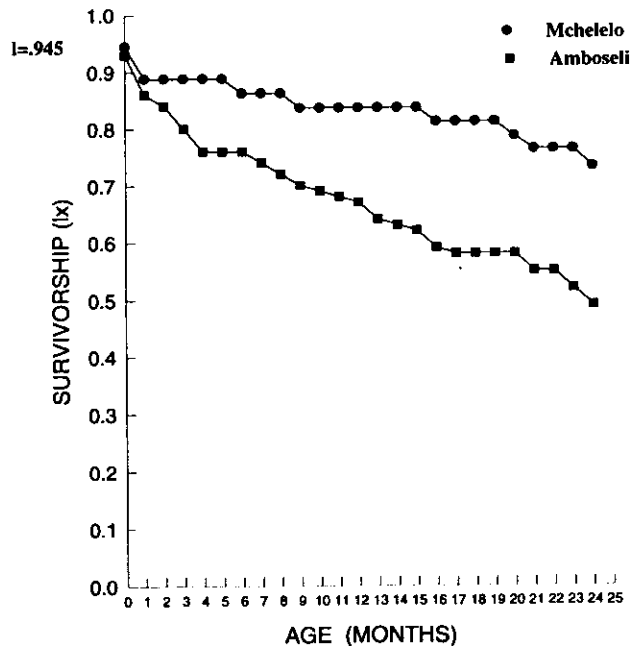


Fig. 2. Infant survivorship curve [Amboseli data adapted from Altmann (1980, p. 34)].

Mchelelo female is significantly older than the average Amboseli female at menarche [$t_{(5)} = 2.474$, one tailed].

Gestation. The average Mchelelo female's gestation ($\bar{X} = 181.5$ days) is significantly longer than that of the average Amboseli female [$\bar{X} = 175$ days; $n = 23$ (Altmann *et al.*, 1977)] [$t_{(27)} = 2.73$, one-tailed].

Births. Altmann (1980) noted 54 full-term births over a 7-year period, resulting in 49 live births for Amboseli females. The Mchelelo birth peak data differ from those for the Amboseli yellow baboons, for which only a June–July birth peak was reported by Altmann (1980).

Postpartum Amenorrhea. Altmann *et al.* (1977) reported amenorrheal lengths for the Amboseli females following infant death/stillbirth as $\bar{X} = 0.88$ months, (range = 0.25–1.25 months; $n = 14$) and following live birth as $\bar{X} = 12$ –12.5 months (range = 6–16 months; $n = 20$). Comparisons of the Amboseli with the Mchelelo data showed no significant difference in the length of amenorrhea following miscarriage but a significant difference in length of postpartum amenorrhea following a live birth [$t_{(21)} = 3.71$, one-tailed]. On average, postpartum Mchelelo females spent significantly more time amenorrheic than the Amboseli females did; this difference may be linked to cycle clustering.

Interbirth Interval. Altmann *et al.* (1977) reported a mean cycling duration before subsequent pregnancy of 5 months and a mean interbirth interval of 21 months for the Amboseli females. The observed mean interbirth interval for the Mchelelo females differs significantly from that observed at Amboseli [$t_{(12)} = 3.636$]. This is not surprising given that Mchelelo females had a significantly longer postpartum amenorrhea. Since number of cycles and gestation length corresponded between Mchelelo and Amboseli females, it appeared that the difference in interbirth interval could be attributed to the postpartum amenorrheal phase.

Infant Survival. In Fig. 2 we compare the Mchelelo infant survival data with those for Amboseli (Altmann, 1980). Although full-term Mchelelo and Amboseli infants began their lives with very similar survival rates (Mchelelo = 0.945, Amboseli = 0.93), the Amboseli rates quickly fell far below those for an Mchelelo infant. These two distributions are significantly different [$t_{(46)} = 2.13$]. While it should be noted that the Amboseli data were based on a longer time period and a larger sample size (7 years; $n = 54$) than those of Mchelelo (4.75 years; $n = 37$), an Amboseli infant had only a 49% chance of reaching the age of 2, while a Mchelelo infant had a 76% chance. This survival rate had a direct effect on the average female interbirth interval and fecundity.

Thus, our data indicate that Mchelelo females have a later age at menarche—based on first tumescence—longer gestations, longer postpartum amenorrheas, longer interbirth intervals, and a higher infant survival

Table IV. Reproductive Parameters: Summary and Comparison with Amboseli^a

Parameter	Mchelelo average	Amboseli average	Significance ^b
Menarche	6.00y	4.80y	*
Clustering	—	—	*
Cycle length	38.94d	32–34d	*
Nulliparous	41.38d	—	
Primiparous	44.00d	—	
Multiparous	37.19d	32–34d	*
Gestation	181.50d	175d	*
Conceptions	9.70@y	—	
Births			
Clustering	—	—	*
Peaks	—	—	*
Prob. live birth	0.945	0.93	
Miscarriages			
Clustering	—	—	*
Prob. miscarriage and stillbirth	0.24	0.10	
Return to estrous			
Clustering	—	—	*
Postpartum amenorrhea			
Live birth	14.55m	12–12.5m	*
Miscarriage	1.88m	0.88m	NS
Months cycled between pregnancies	5.00m	5.00m	NS
Interbirth interval	27.94m	21.00m	*
Probability of infant survival to 24 months	0.73	0.49	

^ay, years; d, days; m, months.

^b*p* ≤ 0.05; NS, nonsignificant.

rate than the yellow baboon females of Amboseli do. We are assuming, based on estimates for other populations (Jones, 1962; Strum, 1982; Altmann *et al.*, 1988), that a female baboon has, on average, a maximum life span of approximately 20 years. We realize, of course, that this may be an overestimation or perhaps even an underestimation given that we have no long-term data from the Mchelelo site to confirm our estimate. However, it seems a reasonable estimate based upon these other populations. Accordingly, menarche at age 6 years would leave 14 reproductive years. With the average interbirth interval of 27.94 months for live births and 5.88 months for miscarriages (1.88 months of amenorrhea plus 4 months of gestation), a Mchelelo female could expect to conceive 7 times, 1.68 of which would result in miscarriages/stillbirths and 5.32 of which would result in live births. Actually, the average Mchelelo female would have two miscar-

riages/stillbirths and give birth to five live offspring during her reproductive career. Only three of her offspring would live to the age of 24 months.

DISCUSSION

We aimed to present and describe the reproductive parameters of a virtually unstudied population of yellow baboons and to compare these reproductive data for the Mchelelo females to those for the Amboseli yellow baboons. From our findings, several points deserve further attention and research. The major point in need of further consideration is the fact that Mchelelo and Amboseli females seem to differ significantly on several reproductive parameters, which indicates that there may be substantial dissimilarity between the two populations. The cause of these differences, however, is yet to be determined. While we admit that we are unable now to address the range of possibilities fully, we believe that our data are representative of the Mchelelo population and not merely due to some prior, novel ecological event. We base this deduction upon the fact that the patterns that we reported were detected across an approximately 5-year period.

While Altmann (1980) reported a birth peak in June–July for the Amboseli females, our data indicate two birth peaks for the Mchelelo females: January–February and September–October. In order to maximize reproductive success, births should occur at a time when conditions are best for the survival of both mother and offspring (Butynski, 1988). This implies that environmental conditions must be predictable. Whether this is the case for the Tana Reserve remains to be investigated. Our data indicate that environmental conditions at the Tana—rainfall and resource availability—are predictable enough to allow for two birth peaks and perhaps influence the clustering discussed previously. However, we lack systematic data on rainfall and resources utilized for the entire period encompassed by the database. Accordingly, we are unable to address the role of the environment in the Mchelelo–Amboseli differences reported herein. We would, however, expect a strong environmental influence given the relationship between resource availability and female reproduction (Bercovitch and Strum, 1993). While there is also the possibility that genetic differences between the two populations are a significant factor affecting reproductive parameters, we do not have comparative genetic data for them.

Data on resource consumption by the Mchelelo troop based upon *ad libitum* observations between November 1991 and September 1992 indicate that Mchelelo infants tended to be in the weaning process when soft, easily processed food items (e.g., *Dobera glabara* berries) were available. These data support Altmann's (1980) observations regarding correlations between

timing of infant births and weanings so as to have appropriate weaning foods available. We would expect births to be timed so as to maximize the infant's chances of survival, and the availability of soft, easily processed foods—grass shoots, fruit, and flowers—at the time of weaning may be a crucial component of infant viability.

Our inability to explain fully the differences between the Mchelelo and Amboseli populations does not lessen the importance of our data. The implications are significant not only for the Mchelelo population but also to our understanding of baboon reproductive processes. In particular, they provide further indication of the significance of interpopulational differences. The data offer further evidence of the caution we should exercise in generalizing between populations or species.

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