

## Life History of Yellow Baboons: Physical Development, Reproductive Parameters, and Infant Mortality

JEANNE ALTMANN, STUART A. ALTMANN,  
*University of Chicago*

GLENN HAUSFATER, and SUE ANN MCCUSKEY  
*University of Virginia*

**ABSTRACT.** Longitudinal data from a population of yellow baboons, *Papio cynocephalus*, in the Amboseli National Park, Kenya, provide life history parameter estimates. Females reached menarche at approximately four-and-a-half years of age and then cycled for approximately a year before first conception. Postpartum anestrus averaged 12 months but ranged from six to 16 months. In cases of still births or infant death during postpartum amenorrhea, females commenced cycling after approximately one month. In mature females the time spent cycling before conception was five months on the average with a range from one to over 18 months. Only half of all full-term pregnancies resulted in infants who survived the first year of life; only a third, in infants who survived until the birth of their mother's next infant. In comparison with data from laboratory colonies, our data indicate that female baboons in Amboseli are older at birth of first infant. They have, on the average, a somewhat shorter interbirth interval than was estimated from earlier crosssectional field data, and therefore spend a larger portion of their adult life pregnant, but have a much longer interval—at least three years on the average—between the birth of an infant and the birth of that infant's next older surviving sibling. A number of morphological changes in immature baboons are described.

### INTRODUCTION

Early field studies of baboons (ALTMANN & ALTMANN, 1970; DEVORE, 1965; HALL, 1965; KUMMER, 1968; RANSOM & ROWELL, 1972; ROWELL, 1966; STOLTZ & SAAYMAN, 1970) either were conducted on groups in which individuals were not identifiable or were of such short duration that the oldest individuals of known age were under one year of age. Age estimates of other individuals were made primarily by extrapolation from these young individuals of known age and from maturational studies of rhesus monkeys (e.g., VAN WAGENEN 1972 & earlier), supplemented by limited data from laboratory colonies of baboons (e.g., GILBERT & GILLMAN, 1956, 1960; GILLMAN, 1951, GILLMAN & GILBERT, 1956). Until recently, no thorough developmental study of any baboon species had been completed in either laboratory or field setting. Only scanty longitudinal field data have been available for estimation of demographic parameters such as birth and death rates (ALTMANN & ALTMANN, 1970; COHEN, 1969). Recent laboratory studies by HENDRICKX and KRAEMER (1971), REED (1965), and SNOW (1967a, b) provide important relevant information. However, only SNOW utilized any developmental characteristics that are observable in the field.

Since 1963, several studies have been conducted on yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, a recently gazetted portion of the former

Masai-Amboseli Game Reserve, Kenya. Our observations since July 1971 have provided sufficient continuity in records that we can now make more accurate estimates of the ages at which various maturational changes occur, the length of time a female cycles before becoming pregnant, the length of pregnancy, rates of infant mortality, length of postpartum amenorrhea under conditions both of infant mortality and of infant survival, and length of interbirth intervals. Although our knowledge is still far from complete, the accumulated data are sufficient to warrant a major revision of our description of maturational and demographic parameters in Amboseli baboons. Continued long-term study will provide additional longitudinal data and the larger sample sizes needed for more thorough demographic analysis and for refinement of the maturational stages described below.

### POPULATION AND METHODS

The data to be presented come from three baboon groups (Main Group, Alto's Group, and High Tail's Group) in Amboseli National Park. The groups and the periods they were under observation are listed in Table 1. In what follows, infant mortality is based on data through February 1975. For all other purposes we have incorporated data through May 1976. During each day of observation on identifiable animals, census data on all known individuals and reproductive state of each adult female are recorded. During each previous study we have assigned each individual one of seven age-sex classes as noted elsewhere (ALTMANN & ALTMANN, 1970) following DEVORE (1965). The classes and the ages that we earlier ought corresponded to

**Table 1.** Amboseli studies.

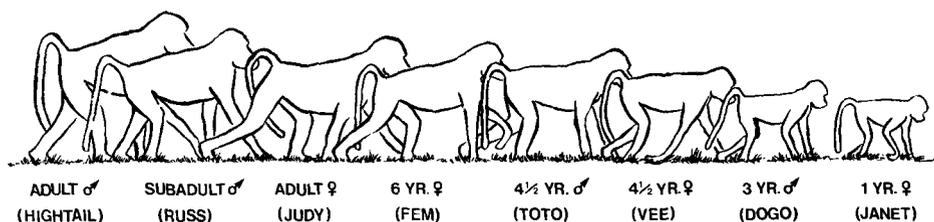
Group name	Dates of studies	Observation frequency	Observers
Main Group	Sept. through Nov. 1963	Almost daily	S. & J. ALTMANN
	Dec. 1963	Five days	S. & J. ALTMANN
Alto's Group	Feb. through July 1964	Almost daily	S. & J. ALTMANN
	July through Sept. 1969	Censuses plus occasional days of observation—few individuals identified	S. & J. ALTMANN J. COHEN
	July 1971 through Aug. 1972	Almost daily	S. & J. ALTMANN (4 months) G. HAUSFATER (14 months) S.A. MCCUSKEY (14 months) M. SLATKIN (3 months)
	Sept. 1972 through April 1973	Occasional censuses	M. FULLER
	Mid-June 1973 through mid-Sept. 1973	Almost daily	G. HAUSFATER S.A. MCCUSKEY
	Mid-May 1974 through Aug. 1974	Almost daily	S. & J. ALTMANN G. HAUSFATER
	Sept. 1974 through July 1975	Approximately 3 days per week	D. POST J. SCOTT
	July 1975—present (May 1976)	Almost daily	S. & J. ALTMANN
High Tail's Group*	Nov. 1971 through July 1972	Almost daily	G. HAUSFATER S.A. MCCUSKEY

\*In October of 1972, this group completed a fusion with Alto's Group; subsequent observations are listed under Alto's Group.

**Table 2.** Age estimates of Amboseli baboons.

Class	Physical characteristics	1963-71 age estimates for these classes (yr.)	1974 age estimates for these classes (yr.)
Infant-1	Hair completely or partially black (natal coat). Black spots in tail and shoulders remain longest. Skin pink or red from skin vascularity—ears and nose retain pink longest. Male scrotum remains pink until three to four years of age.	0-1/2	0-2/3
Infant-2	Hair brown to cream-colored, often lighter (in Amboseli) than that of adults. Skin pigmented black, as in adults.	1/2-1	2/3-2
Juvenile-1	Not sharply demarcated from previous class. Light hair retained. Face wrinkles disappear. Scrotum changes from pink to gray near end of this period.	1-2	2-4
Juvenile-2	Not sharply demarcated from previous class. Hair often darker, as in adult. Males' testes descend about five and a half to six years of age.	2-4	4-5 for ♀♀ 4-7 for ♂♂
Adult female	Sexually mature; sexual skin swells periodically. Nipples button-like when nulliparous, elongated in more mature, multiparous females. First pregnancy at about six years of age; full size reached about seven years of age for females.	Over 4	Over 5
Subadult male	Development of secondary sexual characters: mantle, long canine teeth, large size, greater musculature than females. Scrotum (testes) larger than in juvenile-2. White streaks on muzzle. Canine ridges.	4-6	7-10
Adult male	Secondary sexual characteristics fully developed	Over 6	Over 10

these classes appear in Table 2, along with our present estimates of the ages of individuals that were placed in these categories. Comparisons of standing height for individuals in various age classes are shown in Figure 1. The oldest individuals of known birthdate were almost five years of age at the time of the most recent developmental observations reported here (May 1976). Thus, age estimates for older individuals still require extrapolation. The advantage of the present estimates over earlier attempts at age determination is that we can now use the developmental information on the one-five year olds of known age to compare with immatures from 1971, we can estimate fairly well the ages of those who were one to five years old in July 1971



**Fig. 1.** Relative sizes of Amboseli baboons.

(using as a further check the developmental progress of the younger members of this group as compared to those of known age) and we can estimate, albeit more grossly, the ages of those who were over five years of age, again, improving the estimates through comparison with the next younger age group.

## RESULTS

In the next sections we present (1) age-estimates for the 1971 immatures of Alto's Group and recent observations on age changes in physical development, which should prove useful in making field estimates of age, and (2) analysis of data on infant mortality, survivorship, reproductive parameters, and interbirth intervals.

### AGE ESTIMATES OF IMMATURES

The following background data were used to obtain estimates of the ages in 1971, when our current series of studies began, of individuals that were then infants or juveniles. Those individuals are now our oldest individuals whose ages are reasonable well known. (See the section on reproductive parameters below for details.) The length of pregnancy for Amboseli baboons was just under six months, on the average. The mean length of postpartum amenorrhea was 12 months. All adult females that were neither cycling nor pregnant for more than a month had associated offspring. In cases of neonatal death or stillbirth females resumed cycles within a month's time. All infants of known age "suckled" (nipple in mouth for extended periods) and rode on their mothers occasionally, including in most alarm situations, through approximately 17 months of age. In almost every case of a female who had an infant associated as described above, and who disappeared from the group and was presumed dead, the infant disappeared as well. The one exception is a 17-month old who has survived the first month since her mother's death.

During 1974-1976 we made observations of external physical differences that can readily be observed in the field and seem to reflect maturational changes. With comparable data for individuals of known age as they mature, we hope to continue to improve our age estimates for individuals born before 1971 and to improve age estimates in the field. In the following two sections, we describe developmental changes for two age-sex classes, infants from seven to 15 months of age, whom we shall call "yearlings," and males from about three years of age to sexual maturity. After that we discuss data on age at menarche, at first pregnancy and at birth of first infant.

### "Yearlings"

Data on "yearlings" (7 to 15 months old) are based primarily on observations of 17 members of Alto's Group born since mid-1973. At birth all infants had pink skin. By seven months of age, they all had grey hands and feet, primarily grey paracallosal skin, only a little grey pigmentation on a primarily pink muzzle, and pink ears. By 15 months, and by 12 months for many individuals, skin pigmentation was complete except for males' scrota which remained pink until about the fourth year of life. All "yearlings" still had quite wrinkled faces. Three-year-olds, but not members of older classes, had considerable facial wrinkling as well. On the youngest yearlings, the

callosities did not stand out in as clear relief from the paracallosal skin as in the 12- to 15-month-olds.

Although individuals over six months of age no longer had an overall black natal coats, coat color change proved to be extremely variable. Some individuals began showing gold splotches in their black coats early in the third month of life, others not for another month. Some had no black hair in their coats by six months of age, but more commonly, remnants of the natal coat persisted at least into the fourteenth month of life as black splotches or lines, particularly on the tail, shoulders, and upper arms.

#### Juvenile and Subadult Males

In July and August of 1974, males *Kub* and *Dogo* both became three years old, yet they were quite different from each other in size. From physical appearance we would have classified *Kub* as a juvenile-1, *Dogo* as an infant-2 or small juvenile-1, and we would have estimated that they were about a year apart in age. This suggests that the revised age estimates in Table 2 should be even further advanced for some classes. At three years of age, *Kub* and *Dogo* still had pink scrota, and their testes had not yet descended. Their faces were still somewhat wrinkled and showed no development of the canine ridge, *Dogo's* scrotum turned grey during the fourth years of life. *Kub* disappeared from the group that year.

At about five years of age, juvenile males *Swat* and *Toto* had black scrota, but no bulges from testes were visible. *Swat* had a slight canine ridge on the muzzle with some white zygomatic hairs. *Swat* and *Toto* were then the size of an average adult female. In the sixth year, they became larger than all adult females and their testes descended. The change from pink to black scrota apparently occurs at approximately three to four years of age. Descent of the testes occurs at five and a half to six years. These should be useful age criteria for these difficult age classes.

In July–August, 1974, the subadult males of Alto's Group, *Stu*, *Russ*, *Red*, and *Stiff*, all had testes descended in somewhat pendulant scrota. *Stiff* and *Red* had the most clearly sacculated scrota but no separation of the two testes was visible. The canine ridge and adjacent furrow were clearly visible.

*Ben* and *Even*, classified as young adult males in 1974, had large, pendulant scrota, with two separate testicular bulges visible on *Ben*. Whereas *Ben's* scrotum was pendulant in 1973, *Even's* was then more like those of the 1974 subadults. Since 1971, we have judged *Even* to be at least one year younger than *Ben*. *Ben* was ninth- or tenth-ranking in 1973, twelfth in 1974, second in 1975. In the summer of 1975 *Red* made the transition to adult male; the other three 1974 subadults did so in the following nine months. A rapid rise in dominance rank followed physical maturation.

#### Juvenile and Young Adult Females

In July of 1971 four individuals that had completed infant color-change (*Spot*, *Vee*, *Gin*, and *Major*), were judged to be about the same age, about one year old, and were called infant-2's. Since none of their mothers were cycling at that time, it is unlikely that these infants were as old as 16 months. In September of 1971, one of the infants (*Major*), disappeared along with his mother, and both were presumed dead. All of the three surviving yearlings commenced regular menstrual cycles, one in

November and two in December of 1974, presumably at four and a half to five years of age. (However, from 1971–1974, one of these three, *Spot*, had a visible though small penis, but ischial callosities that were unfused at the mid-line, a female characteristic.) *Spot*, *Gin*, and *Vee* became pregnant after 11, 9 and 15 months of cycles, respectively. *Spot* and *Gin* produced viable infants. *Vee* is pregnant (May, 1976).

*Fem* was called a juvenile-1 in July of 1971. During the 1971–1972 study she was associated with adult female *Ring*, mother of infant-2 *Gin*, the only instance of a strong association of a juvenile and an adult female that HAUSFATER could detect in 1971–1972. Assuming that *Fem* was, in fact, *Ring*'s offspring and combined with other evidence, we estimate that *Fem* was probably three, perhaps as much as four years old in the summer of 1971. *Fem* began menstrual cycles sometime between January and June of 1973, probably during the latter half of that period, at about five years of age. She gave birth to her first infant near the end of December, 1974.

For four females who were first identified as juveniles in High Tail's Group in November, 1971, we have some information on first menstrual cycles and first pregnancy. After cycling for less than nine months, *Brush* became pregnant at the end of May, 1974. Her infant, born with some injury, died shortly after birth. *Handle* became pregnant after nine months of cycling and produced a healthy infant in October, 1975. *Plum*'s first pregnancy, after 11–17 months of cycling, resulted in a viable infant. *Slinky* cycled for 18 months before becoming pregnant. Her first infant was stillborn. In 1971, *Plum*, *Slinky*, and *Brush* were classed as juvenile-2's, *Handle* as a juvenile-1.

In summary then, Amboseli female baboons commence cycling at about four and a half of five years of age, experience the onset of their first pregnancy at about six years of age, and give birth to their first infant at six and a half years of age.

#### INFANT MORTALITY AND SURVIVORSHIP

For the period from birth through approximately two years of age a preliminary survivorship curve has been constructed from data for the three Amboseli groups combined (Fig. 2). From this Figure and from our records on individual females, it is clear that no more than half of all full-term pregnancies resulted in infants who survived their mother's full 7–16 month postpartum amenorrhea period. Less than one third survived to the completion of their mother's next full-term pregnancy, that is, to 22 months of age on the average. Thus, in their first year of life Amboseli infants very rarely have a next-older sibling only two years older than themselves. For most infants a surviving older sibling will be at least three and often four or five years older.

The combined survivorship curve consists primarily of data from individuals whose birthdate was known to within two weeks. Individuals who were estimated to be no more than 18 months of age at the start of the studies are included as well. In this category is one color-change infant (approximately four months of age) and six yearlings who were members of either High Tail's Group or Alto's Group in 1971 and whose ages were estimated. The 1963–1964 Main Group sample contributes primarily to the estimates for the first several months of life, the estimated-age sample contributes primarily to the estimates for the second year of life.

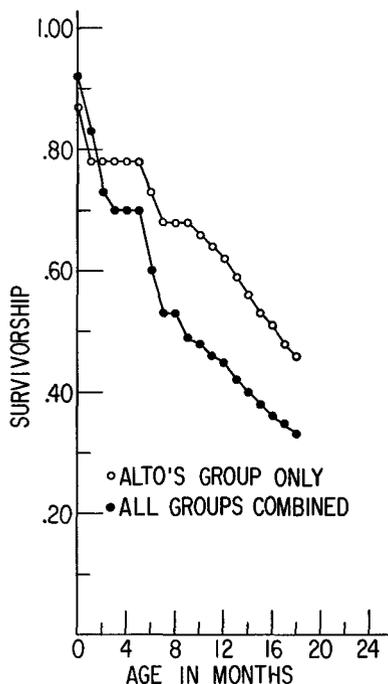


Fig. 2. Probability that a full-term infant will survive through the indicated ages. See text for details.

In Table 3 we present the data used to calculate mortality rates and thus to construct the survivorship figures, first for data from all three groups combined and then for Alto's Group alone, i.e., including members of High Tail's group only after the two groups merged. Despite some gaps in the study periods, we are confident that all full-term pregnancies since 1971 are known. All infants that died during such study discontinuities were over nine months of age and do not affect the mortality rates for younger ages. All infants that survived such discontinuities were counted in calculating survivorship in each intervening interval. All full-term births have been included whether viable or not. Thus, the survivorship at age zero was estimated as the proportion of full-term births that were viable (i.e., one minus the proportion of stillbirths).

Estimation of mortality rates for the first year and a half of life were calculated as follows. The sample population consisted of all individuals that were observed alive at the earliest age of that interval and that either were observed alive at the end of the interval, or died during the interval but would have been observed at the end of the interval (because we were present) if they had survived that period (See the exception for discontinuity between studies noted above). The mortality rate,  $q_x$ , for an interval was estimated as the proportion of individuals who died during the age interval out of the number in the sample population for that interval. The survival rate,  $p_x$ , for the interval was, of course, one minus the death rate. The product,  $l_x$ , of such survival rates up to any age of interest was taken as an estimate of surviving from full-term

**Table 3.** Life table for all three Amboseli groups combined and for Alto's Group only. See text for details. Mortality rates for the 10th, 11th, and 12th months of life were calculated as the simple average of the rate for the nine to 12 month period for which we had only pooled data. The same was done for the 12-18 month period.

Age interval in months [x, x+1]	Sample size $N_x$		Mortality rate $q_x$		Survival rate $p_x = 1 - q_x$		Survival from full-term pregnancy through age $X+1$ $l_{x+1} = l_0 p_0 p_1 \dots p_x$		Survival from full-term pregnancy through Age $X$ but not through age $X+1$ $d_x = l_x - l_{x+1}$	
	Combined	Alto's Group	Combined	Alto's Group	Combined	Alto's Group	Combined $l_0 = l_{-1}$ - rate of stillbirth = .92 (N=36)	Alto's Group $l_0 = .87$ (N=24)	Combined	Alto's Group
[0,1]	30	21	.10	.10	.90	.90	.83	.78	.09	.09
[1,2]	26	16	.12	0	.88	1.00	.73	.78	.10	0
[2,3]	22	16	.05	0	.95	1.00	.70	.78	.03	0
[3,4]	21	16	0	0	1.00	1.00	.70	.78	0	0
[4,5]	20	15	0	0	1.00	1.00	.70	.78	0	0
[5,6]	20	15	.15	.07	.85	.93	.60	.73	.10	.05
[6,7]	17	14	.12	.07	.88	.93	.53	.68	.07	.05
[7,8]	15	13	0	0	1.00	1.00	.53	.68	0	0
[8,9]	14	13	.07	0	.93	1.00	.49	.68	.04	0
[9,10]	13	13	.03	.03	.97	.97	.48	.66	.01	.02
[10,11]	13	13	.03	.03	.97	.97	.46	.64	.02	.02
[11,12]	13	13	.03	.03	.97	.97	.45	.62	.01	.02
[12,13]	15	14	.05	.05	.95	.95	.42	.59	.03	.03
[13,14]	15	14	.05	.05	.95	.95	.40	.56	.02	.03
[14,15]	15	14	.05	.05	.95	.95	.38	.53	.02	.03
[15,16]	15	14	.05	.05	.95	.95	.36	.51	.02	.02
[16,17]	15	14	.05	.05	.95	.95	.35	.48	.01	.03
[17,18]	15	14	.05	.05	.95	.95	.33	.46	.02	.02

pregnancy to that age. The product of survival rates through the interval immediately preceding the one of interest times the mortality rate for the interval of interest, provides an estimate of the probability that an individual will live up to that interval and then die in that interval. One could, of course, calculate the comparable probabilities under the assumption of live-birth, but the form which included all full-term pregnancies was used by us here to facilitate calculation of interbirth intervals, as described below. Fitting an exponential curve to these data yields a monthly mortality rate of .05 plus a stillbirth rate of .15 for the combined data and a mortality rate of .03 plus a stillbirth rate of .13 for Alto's Group alone. It is not yet clear whether survivorship is now improving in Amboseli in general, is better for Alto's Group than for the other groups, or whether these results reflect small-sample fluctuations. Demographic parameters for other Amboseli groups and for later stages of the life cycle will be treated elsewhere and must depend heavily on cross-sectional census data at this time (ALTMANN & ALTMANN, 1970; COHEN, 1969, 1972).

#### INTERBIRTH INTERVALS

The interval between a female's successive births consists of several components: postpartum amenorrhea, the subsequent menstrual cycles, and then pregnancy. We

present estimates of the duration of each of these components below. In a number of instances data are incomplete. For example, we have only lower limits on durations of intervals that are interrupted by beginnings and endings of study periods. Omitting such data from calculations of mean values not only reduces the sample size but often also produces biased results. Where appropriate, we have used the technique of KAPLAN and MEIER (1958) for utilizing such incomplete or "censored" data. Other techniques that deal with similar problems are those of ALTMANN and WAGNER (1970) and COX (1972).

#### Postpartum Amenorrhea

Following the birth of an infant, the mother experiences a period of postpartum amenorrhea. This period terminated quickly if the infant died. We have adequate records of 14 such cases (including two stillbirths). The mean time from infant death to onset of sex skin turgescence was three and a half weeks with a range of one-and-a-half to five weeks. There was no relationship between infant age at death and the length of time it took the mother to resume cycles, hardly surprising in a sample of this size with such little variability. If an infant survived, postpartum amenorrhea lasted six to at least 16 months, with a mean of 12–12.5 months, calculated by the KAPLAN-MEIER technique ( $N = 20$ ).

#### Cycling

The length of the interval spent cycling before multiparous females became pregnant was very variable for our sample of 32 such intervals, ranging from one month to over 18. Due to this wide range and to lack of total continuity in the Amboseli studies, the data are incomplete for five cases. Five intervals, including both the longest intervals of known duration, one thirteen and one nine months long, and one interval only known to of at least 18 months, included a "skipped" cycle, perhaps indicating a pregnancy with early spontaneous abortion. In none of these cases has the female shown the characteristic pregnancy sign (ALTMANN, 1970). No other interval of known length was over eight and a half months. The mean, median, and the mode for all intervals of known duration, excluding the one of length 13, above, were all four months. Using the KAPLAN-MEIER technique to include four of the five cases of incomplete data gives a mean duration of approximately five months. (The "over 18" duration cannot be incorporated in this technique.) It is not clear what value is most appropriate to use in this situation. More data definitely are needed. For calculation of the interbirth intervals below, we have used the value of four months for the cycling time. Use of a longer interval would just extend the expected interbirth interval correspondingly.

#### Gestation

The average duration, from last detumescence of the sex skin to birth, in 23 pregnancies of known length, was 25 weeks. All births were within two weeks of that value. For the calculation of interbirth intervals in terms of months, we have used the value of six months.

#### Interbirth Interval

Utilizing the data from the previous section, the expected time between successive births was calculated using the following assumptions:

- (1) All infant deaths in an age interval occur at the mid-point of the interval.
- (2) All pregnancies result in full-term births, either births of viable infants or stillbirths. (Spontaneous abortion apparently is quite rare or occurs at a very early stage of pregnancy.)
- (3) A female whose infant dies in the first 12 months of life resumes cycling one month later, and females whose infants survive the first year of life resume cycles after 12 months of postpartum amenorrhea.
- (4) Females cycle for four months and then experience a six-month pregnancy. Both these durations are considered to be independent of the length of post-partum amenorrhea or infant survival. Likewise, no demographic or sociological effects on interbirth interval, such as maternal age or dominance status, have been detected and therefore they have not been considered here.

Variability in interbirth interval was thus considered to be entirely a function of infant mortality. The expected interbirth interval was calculated as the sum of the possible interval lengths from 11 months (representing a stillbirth plus a minimal one month post-partum amenorrhea plus four months cycling plus six months pregnancy) through 22 months (i.e., infant surviving 12 months), each multiplied by the probability of an interval of that length. The probability of a minimum interbirth interval of 11 months is equal to the probability of a stillbirth: .08 for the combined sample, .13 for Alto's Group alone. The probability of a maximum interbirth interval of 22 months, i.e., the probability of surviving the first year of life, is .45 for the combined sample and .62 for Alto's Group alone. For each age interval in Table 3 through the twelfth month of life we add 11 to the mid-point of the interval to obtain the interbirth interval for females whose infants died in that age interval. The probability of an interbirth interval of that length is found in the  $d_x$  row for the corresponding age interval. For example, the probability of death between two and three months of age,  $d_2$ , is .03 for the combined sample. The interbirth interval corresponding to deaths at that age is  $2.5 + 11 = 13.5$ . The product (.03)(13.5) is that interval's contribution to the expected value. The sum of all such contributions is the expected interbirth interval. The expected, or average, interbirth interval is 18.0 months for the combined sample and 19.1 for Alto's Group alone, the latter reflecting the lower mortality rates for the first year of life in Alto's Group.

Our limited sample of complete interbirth intervals is consistent with the above estimates, which were based on the components of the interval. We have adequate samples only for females whose infant survived the first year of life. Ten infants survived the first year of life; nine of these had mothers who survived to complete another pregnancy. According to estimates as calculated for the separate components, we would expect intervals to average 22 months in length. The mean interval for the nine cases was 21 months. The remaining female died 26 months after the birth of her most recent offspring. She was cycling at the time of her death. Thus, these data agree quite closely with the estimates computed by looking at much of the same data but pooled over all females and separated into components of the interbirth interval.

## DISCUSSION

The methods used in this paper for estimating mortality rates and interbirth

intervals seem the most reasonable with the present sample sizes and in the absence of data on the possible functional dependencies among the variables involved. Variability and dependence should of course be taken into account as appropriate data become available. The mean length of gestation and of menstrual cycles apparently vary little, either between species or between laboratory and various field habitats (cf. ALTMANN & ALTMANN, 1970; HAUSFATER, 1975; GILLMAN & GILBERT, 1946; KRIEWALDT & HENDRICKX, 1968). The small differences that may exist are not of a magnitude with which we are concerned in this paper. All workers report a gestation period of just under six months and a cycle length of just over one month.

#### Postpartum Amenorrhea

There are large discrepancies in estimates of the duration of postpartum amenorrhea, ranging from five months according to ROWELL (1966) to 12–15 months according to DEVORE (1962). Neither author indicates the data base on which their estimate was made. A sample of only complete anestrus intervals for olive baboons in Gilgil, Kenya (STRUM, pers. comm.) gives a mean value of 11 months ( $N = 16$ ). Assuming that the bias due to exclusion of incomplete intervals will not be too great these data certainly agree well with those from Amboseli. However, even small differences in length of postpartum anestrus may have considerable effects on population growth, as demonstrated with simulation techniques for human populations by SKOLNICK (1972). Life history consequences of changes in reproductive parameters have been discussed by COLE (1954).

#### Cycling

For the length of time a multiparous female spends cycling before becoming pregnant, ROWELL (1966) indicates five to 15 weeks (i.e., one to three cycles), DEVORE (1962) "two or more months to the next breeding season." ROWELL's report may be based in part on the caged colony she kept in Kampala, in part on field observations.

#### Birth Season

Although there does seem to be some slight seasonality in baboon births (ALTMANN & ALTMANN, 1970; HAUSFATER, 1975; DEVORE, 1962) no data have yet been published that clarify the source of this seasonality. Variance in gestation length is extremely low and variance in cycling time and in length of postpartum amenorrhea is high, but our data are not yet adequate to demonstrate functional dependence between season and either of these other two variables. If there is any seasonality in infant deaths, seasonality in births could result.

#### Interbirth Interval

Previously published discussions of interbirth intervals in baboons have involved the implicit assumption of survival of the infant. Clearly, such maximum intervals are the exception, not the rule in Amboseli. Near Gilgil, Kenya, the contrary is apparently true: S. STRUM (pers. comm.) indicates only two infant death in first year of life ( $N=31$ ).

Average interbirth interval varies inversely with infant mortality rate. It also varies

inversely with the number of births per female-day in a group of baboons. However, the mean number of births per female-day will not be exactly the inverse of the mean interbirth interval if a different base population of females is used for each. In a monograph on Amboseli baboons (ALTMANN & ALTMANN, 1970), births per female-day were calculated for our own and other data in the literature using census data that included all post-menarchical females, whereas the calculation of mean interbirth interval used in the present paper did not include infertile females, or even sufficient data for those low fertility females whose infertile periods may extend beyond our study periods.

Included in the first category, infertile females, would probably be one female, *Lulu*, who was identified in Alto's Group during censuses in 1969, at which time she was cycling. She had no associated infant then or in July of 1971 and has been cycling since 1971 without interruption and without becoming pregnant. Her nipples are not elongated. At least one Main Group female, *Blondy*, did not cycle throughout the 1963–1964 study, despite the fact that her associated offspring was probably at least a year of age at the beginning of the study. *Judy*, of Alto's Group, is an example of a low-fertility female. She cycled for over 18 months before becoming pregnant; her infant was born in April of 1973. If included, data from both these classes of females would reduce the estimated number of births per female-day. Data on rarely fertile females would also lead to longer estimates of the length of the interbirth interval. The Gilgil olive baboons apparently include no such rarely fertile or infertile females. All multiparous females have about four cycles (about five months) before pregnancy (S. STRUM, pers. comm.).

The interbirth intervals calculated in this paper also do not include nulliparous females, that is, females that had reached menarche and are classified as adult on that basis, but that had not yet had an infant. As we indicated, nulliparous females in Amboseli cycled for approximately a year before becoming pregnant. Their inclusion would affect estimates of birth per female-day but not interbirth intervals.

In Amboseli one can expect approximately two to three females in a group of 14 adult females to be nulliparous or infertile. Consequently, the inverse of the expected interbirth intervals calculated here provides an estimate of the births per female-day for about 11.5/14 of the adult female population. By multiplying these estimates by 11.5/14, we obtain an estimate of births per female-day, on the average, for the population of females as a whole. Doing so, we obtain  $4.56 \times 10^{-2}$  births per female-month or  $1.495 \times 10^{-3}$  births per female-day for the combined sample (three groups, 1963–1964 and 1971–1974),  $4.30 \times 10^{-2}$  births per female-month or  $1.410 \times 10^{-3}$  births per female-day for Alto's Group alone (1971–1974). These figures agree remarkably well with the estimate given in ALTMANN and ALTMANN (1970) for Main Group during 1963–1964, namely  $1.513 \times 10^{-3}$  births per female-day. The decision of whether to include nulliparous and infertile females in the calculations will depend, of course, on the problems of interest. They should be if demographic projection is the goal, but not if, for example, differences in age of siblings is the relevant variable.

#### Menarche

Amboseli females reach menarche almost two years later than laboratory or zoo-raised baboons (GILBERT & GILLMAN, 1960; SNOW, 1967b). In Amboseli, the cycling

period before nulliparous females become pregnant is longer than has been assumed in the field literature, and other developmental stages seem to occur at later ages for both males and females. No relevant data on any of these parameters have been published from other baboon field studies.

### Ecological Factors

Evidence from numerous species of mammals (SADLEIR, 1969) indicates that if animals are feeding on material of low nutritional value, puberty is delayed. In addition, infant mortality is often higher, but the anestrus period may be longer and subsequent fertility lower (cf. JAIN et al., 1970, re humans), producing opposite effects on interbirth intervals. BUSS (1968) and BUSS and REED (1970) demonstrated that growth rates were slower in baboon infants whose mothers were on low protein diets and suggested that the effect was due to the lowered milk production rather than to the lower protein content of the milk, since low protein milk formulas fed to infant monkeys in the larger quantities did not affect growth rates. Thus, additional nutritional stress may adversely affect survival rates for Amboseli infants.

If slower growth rates exists, they may account for the delayed onset of menarche relative to laboratory animals. Studies with humans (FRISCH & REVELLE, 1970) suggest that menarche occurs at attainment of a constant critical body weight despite variations in age and height. GILBERT and GILLMAN (1960) found no relationship between weight and age at menarche in a sample of 12 chacma baboons raised in a laboratory, all presumably under similar conditions, a result consistent with the findings with humans.

Maturation and other demographic parameters in baboons can be expected to be different in differing ecological situations, perhaps with those locales possessing abundant food supplies and low rates of predation and other sources of mortality at one extreme, areas of limited food supply and appreciable predator populations at the other. Moreover, because ecological factors change with time these parameters may not be stable in any one locale. Since 1964, the Amboseli woodland habitat has undergone an extensive decline (WESTERN & VAN PRAET, 1973). Vervet (STRUHSAKER, 1973) and baboon populations have experienced a parallel decline. In Amboseli, 1963 may have been near the beginning of the period of extensive population decline.

As we have indicated above, the period of postpartum amenorrhea and of cycling before pregnancy are considerably longer at both Gilgil and Amboseli than in the laboratory. Furthermore, infant mortality apparently has been much higher in recent years at Amboseli than at Gilgil. A possible explanation for both these facts may be differences in nutrition in these three situations, ranging from the best nutrition in the reporting laboratories to the poorest at Amboseli, with postpartum amenorrhea and fertility rates, apparently the more sensitive responses, affected in both of these wild populations but with marked effects on infant mortality being apparent only in Amboseli.

### Social Effects

There may be a number of behavioral and social effects of smaller groups, delayed onset of reproduction and high infant mortality rates such as prevail in Amboseli. First, infants grow up primarily with peers that are not their siblings, and in mixed

age- and sex-peer groups rather than in age- or sex-segregated cohorts. In this sense they resemble children growing up in very small towns and villages in America in the past or in some hunter-gatherer groups now, more than they resemble children of small, relatively insular nuclear families of, say, urban middle-class America. Some of the social implications of such situations have been discussed by KONNER (1972) for !Kung Bushman children, and by BARKER and GUMP (1964) and COLEMAN (1974) for American children. The different associations formed during the period of immaturity may have further implications for adult behavior and mating partner preferences. Second, if these demographic factors result in greater variance in the coefficients of relatedness within groups, altruism based on kin selection should be more potent and more readily distinguished from reciprocal altruism in populations like Amboseli than in those in which most of an individual's associates are closely related to him, as has been reported for expanding populations with groups in which a large number of kin survive to maturity (YAMADA, 1963; SADE, 1972; STRUM, 1975). Finally, the longer interbirth interval and longer pre-reproductive period of Amboseli baboons implies a greater number of years available for pre-adult socialization as well as for social and no-social learning opportunities. On the other hand, under present ecological conditions, more stringent demands on food-gathering, predator avoidance, and other essential activities may mean that the overall time available for such learning during immaturity is no greater for these animals.

**Acknowledgements.** Our field research on baboons has been supported by the American people through a series of grants, first from the National Science Foundation (GB 27030 and its predecessors) and more recently, from the National Institutes of Mental Health (MH-19, 617 and MH 24473). We are most grateful for this generous support. We offer our thanks to DAVID POST and JANE SCOTT for collecting and making available Amboseli demographic data from September 1974 through July 1975 and to SHIRLEY STRUM for making available some of her demographic data from Gilgil. We are grateful to LAURA PETERSON for doing the drawing for Figure 1, and to JOEL COHEN and MONTGOMERY SLATKIN for comments on an earlier draft of this paper. Finally, we would like to thank those people of the Republic of Kenya, in particular PEREZ OLINDO of the Kenya National Parks, and the Game Wardens of the Amboseli National Park, most recently JOSEPH KIOKO, who have made possible our field research in Amboseli.

## REFERENCES

- ALTMANN, S. A., 1970. The pregnancy sign in savannah baboons. *Lab. Anim. Dig.*, 6: 7-10.
- & J. ALTMANN, 1970. *Baboon Ecology: African Field Research*, Bibliotheca Primatologica, No. 12, University of Chicago Press, Chicago & S. Karger, Basel.
- & S. S. WAGNER, 1970. Estimating rates of behavior from Hansen frequencies. *Primates*, 11: 181-183.
- BARKER, R. G. & P. V. GUMP, 1964. *Big School, Small School*. Stanford University Press, Stanford.
- BUSS, D. H., 1968. Gross composition and variation of the components of baboon milk during natural lactation. *J. Nutr.*, 96: 421-426.
- & O. M. REED, 1970. Lactation of baboons fed a low protein maintenance diet. *Lab. Animal Care*, 20: 709-712.
- COHEN, J. E., 1969. Natural primate troops and a stochastic population model. *Amer. Nat.*, 103: 455-477.
- , 1972. Markov population processes as models of primate social and population dynamics. *Theo. Pop. Biol.*, 3: 119-134.

- COLE, L. C., 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.*, 29: 103-137.
- COLEMAN, J., 1974. *Youth: Transition to Adulthood*. University of Chicago Press, Chicago.
- COX, D. R., 1972. Regression models and life tables. *J. Roy. Stat. Soc.*, B, 34: 187-220.
- DEVORE, I., 1962. The social behavior and organization of baboon troops. Doctoral dissertation, Department of Anthropology, University of Chicago.
- (ed.), 1965. *Primate Behavior: Field Studies of Monkeys and Apes*. Holt, Rinehart, & Winston, N.Y.
- FRISCH, R. E. & R. REVELLE, 1970. Height and weight at menarche and a hypothesis of critical body weights and adolescent events. *Science*, 169: 397-399.
- GILBERT, C. & J. GILLMAN, 1956. The changing pattern of food intake and appetite during the menstrual cycle of the baboon (*Papio ursinus*) with a consideration of some of the controlling endocrine factors. *S. Afr. J. Med. Sci.*, 21: 75-88.
- & J. GILLMAN, 1960. Puberty in the baboon (*P. ursinus*) in relation to age and body weight. *S. Afr. J. Med. Sci.*, 25: 98-103.
- GILLMAN, J. 1951. Pregnancy in the baboon (*P. ursinus*). *S. Afr. J. Med. Sci.*, 16: 115-124.
- & C. GILBERT, 1946. The reproductive cycle of the chacma baboon (*Papio ursinus*) with special reference to the problems of menstrual irregularities as assessed by the behaviour of the sex skin. *S. Afr. J. Med. Sci.*, 11: 1-54 (Biol. Suppl.)
- & ———, 1956. Menstrual disorders induced in the baboon (*Papio ursinus*) by diet with a consideration of the endocrine factors underlying the menstrual disorders and the body weight changes. *S. Afr. J. Med. Sci.*, 21: 89-120.
- HALL, K. R. L., 1965. Ecology and behavior of baboons, patas, and vervet monkeys in Uganda. In: *The Baboon in Medical Research*, H. VAGTBORG (ed.), Univ. of Texas, Austin, pp. 43-61.
- HAUSFATER, G., 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). A quantitative analysis. Ph. D. dissertation, Univ. of Chicago [Contrib. Primatol. No. 7]
- HENDRICKX, A. G. & D. C. KRAEMER, 1971. *Reproductive Embryology of the Baboon*. University of Chicago Press, Chicago.
- JAIN, A. K., T. C. HSU, R. FREEDMAN, & M. C. CHANG, 1970. Demographic aspects of lactation and post partum amenorrhea. *Demography*, 7: 255-271.
- KAPLAN, E. L. & P. MEIER, 1958. Nonparametric estimations from incomplete observations. *Amer. Stat. Assoc. J.*, 53: 457-481.
- KONNER, M. J., 1972. Aspects of the developmental ethology of a foraging people. In: *Ethological Studies of Child Behavior*, N. BLURTON JONES (ed.), Cambridge University Press, Cambridge.
- KRIEWALDT, F. H. & A. G. HENDRICKX, 1968. Reproductive parameters of the baboon. *Lab. Anim. Care*, 18: 361-370.
- KUMMER, H., 1968. *Social Organization of Hamadryas Baboons. A Field Study*. Univ. of Chicago Press, Chicago.
- RANSOM, T. W. & T. E. ROWELL, 1972. Early social development of feral baboons. In: *Primate Socialization*, F. E. POIRIER (ed.), Random House, N.Y.
- REED, O. M., 1965. Studies of the dentition and eruption patterns in the San Antonio baboon colony. In: *The Baboon in Medical Research*, VAGTBORG (ed.), pp. 167-180.
- ROWELL, T. E., 1966. Forest living baboons in Uganda. *J. Zool.*, 147: 344-364.
- SADE, D. S., 1972. A longitudinal study of social behavior of rhesus. In: *The Functional and Evolutionary Biology of Primates*, R. H. TUTTLE (ed.), Aldine-Atherton, Chicago.
- SADLER, R. M. F. S., 1969. *The Ecology of Reproduction in Wild and Domestic Mammals*. Methuen & Co. Ltd., London.
- SKOLNICK, M. H., 1972. Natural regulation of numbers in primitive human populations. *Nature*, 239: 287-288.
- SNOW, C. C., 1967a. Some observations on the growth and development of the baboon. In: *The Baboon in Medical Research*, Vol. 2, H. VAGTBORG (ed.), Univ. of Texas, Austin, pp. 187-199.

- , 1967b. The physical growth and development of the open-land baboon, *Papio doguera*. Doctoral dissertation, Univ. of Arizona, 209 p.
- STOLTZ, L. P. & G. S. SAAYMAN, 1970. Ecology and behaviour of baboons in the Northern Transvaal. *Annals of the Transvaal Museum*, 26: 99–143.
- STRUM, S., 1975. Life of a baboon troop. *National Geographic*, 147: 672–692.
- STRUHSAKER, T. T., 1973. A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, 54: 930–932.
- VAN WAGENEN, G., 1972. Vital statistics from a breeding colony. *J. Med. Prim.*, 1: 3–28.
- WESTERN, D. & C. VAN PRAET, 1973. Cyclical changes in the habitat and climate of an East African ecosystem. *Nature*, 241: 104–106.
- YAMADA, M., 1963. A study of blood-relationship in the natural society of the Japanese macaque. *Primates*, 4: 43–65.

—Received August 11, 1975; Accepted May 15, 1976

Authors' Addresses: JEANNE ALTMANN and STUART A. ALTMANN, *Allee Laboratory of Animal Behavior University of Chicago, 5712 South Ingleside, Chicago, Illinois 60637, U.S.A.*; GLENN HAUSFATER and SUE ANN MCCUSKEY, *Department of Psychology and Biology, Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22907, U.S.A.*