

## RESEARCH ARTICLE

# Demography, Female Life History, and Reproductive Profiles Among the Chimpanzees of Mahale

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Demography provides critical data to increase our understanding of the evolution, ecology, and conservation of primate populations. The chimpanzees of the Mahale Mountains National Park, Tanzania, have been studied for more than 34 yr on the basis of individual identification and standardized attendance records. From this long-term study, we derived the following demographic data: The major cause of death was disease (48%), followed by senescence (24%) and within-species aggression (16%). Fifty percent of Mahale chimpanzees died before weaning. The median ages of female life history variables were: first maximal swelling, 10.0 yr ( $n = 5$ ); emigration, 11.0 yr ( $n = 11$ ); and first birth, 13.1 yr ( $n = 5$ ). The median period of adolescent infertility was 2.8 yr ( $n = 4$ ) when calculated from the age at immigration to that at first birth. Female fecundity was highest between 20 and 35 yr of age, with an annual birth rate of 0.2. Twenty-six females that were observed from a young age (10–13 yr) to death at various ages (15–40 yr) gave birth to an average of 3.9 and weaned an average of 1.4 offspring. Twenty-five females that were observed from middle age (18–33 yr) to death in older age (31–48) gave

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birth to an average of 2.7 and weaned an average of 2.0 offspring. The post-reproductive lifespan for female chimpanzees was defined as the number of years that passed from the year when the last offspring was born to the year when the female died, minus 5. Twenty-five percent of old females had a post-reproductive lifespan. The interbirth interval after the birth of a son ( $\bar{x} = 72$  mo) tended to be longer than that after the birth of a daughter ( $\bar{x} = 66$  mo). The extent of female transfer, which is a rule in chimpanzees, is influenced by the size and composition of the unit group and size of the overall local community. *Am. J. Primatol.* 59: 99–121, 2003. © 2003 Wiley-Liss, Inc.

**Key words:** chimpanzee; Mahale; demography; life history; reproduction

## INTRODUCTION

There are few data concerning the demography of great apes, despite the obvious implications for the evolution, ecology, and conservation of primate populations, and the important role these data could play in reconstructing the society of early hominids and our common ancestors. Great apes typically live in small populations and display relatively long gestation periods, interbirth intervals, and longevity coupled with slow growth rates [e.g., Harvey et al., 1987]. This makes it difficult to record relevant observations. With the notable exception of Gombe [Goodall, 1986; Wallis, 1997], demographic records of great apes collected for more than 30 yr do not exist. To fill this gap in knowledge, we present new demographic records from chimpanzees living in the Mahale Mountains National Park, Tanzania. We pay particular attention to several demographic features that appear to characterize the Mahale chimpanzees. These include high infant mortality, long interbirth intervals, late age at first birth, and a long period of female infertility after immigration [Hiraiwa-Hasegawa et al., 1984; Nishida et al., 1990]. We compare our data to those presented from other populations, and discuss the factors that influence chimpanzee reproduction and their conservation in the wild.

## METHODS

### Study Groups and Attendance Records

We provide data on two groups (“K” and “M”) for the period of 1966–1999. All of the chimpanzees in K group were identified in 1966, and their daily presence was recorded from then until 1983, when most male members disappeared and the female members immigrated into M group [Nishida et al., 1985]. Data from K group thus spanned 18 yr between 1966 and 1983. Study of the M group began in 1965, but 50% of these animals were not identified until 1980 [Hiraiwa-Hasegawa et al., 1984]. Researchers and Tanzanian research assistants have recorded the daily presence of M group chimpanzees almost continuously for the past two decades. Thus, the data from M group are derived from 19 yr between 1980 and 1999 (see Nishida [1990] for details of the research conditions). Most of the results reported here were derived from M group, but we use observations from both K and M group to describe individual female life history variables, including age at first birth, natal emigration, and death. Combining the two groups, we observed 305 chimpanzees for 34 yr. This is the largest data set analyzed to date, surpassing even that from Gombe (Pusey,

personal communication). Chimpanzees were provisioned from the onset of research to 1987, but since 1987 no food has been given to the chimpanzees. Individuals were therefore not fed during most of the study period.

### Definition of Age-Sex Classes

Infants of both sexes were defined as 0–4 yr 11 mo old, and juveniles of both sexes as 5–8 yr old. Adolescent males were defined as 9–15 yr old, and adolescent females as 9–12 yr old. Mature males were 16 yr or older, while mature females were 13 yr or older. We adhered strictly to these age standards, and did not consider any behavioral or physiological traits to define age-sex classes. For example, suppose that a 14-yr-old male was mature in size and behaviorally dominant over at least one of the mature males, i.e., the latter pant-grunted to the former. In this case, the individual in question may be physically, behaviorally, and socially mature, but not chronologically mature. Thus, we treated this male as an adolescent. The 13-yr criterion to define mature females was based on the fact that the median age at first birth was 13 (see below).

### Estimates of Age

For those subjects born before the start of the study, the age of a parous mature female was taken to be the estimated age of her oldest offspring plus 15 yr [Nishida et al., 1990]. Since the current data (see below) show that the median age at first birth is 13, we may have sometimes overestimated the ages of the older females.

### Definition of Terms

#### *Group.*

“Unit group” [Nishida, 1968] or “community” [Goodall, 1973].

#### *Group size.*

Annual group size was established at the end of the year, i.e., December 31.

#### *Death and emigration.*

The death of infants was easy to determine, since mothers were typically observed carrying their dead infants for prolonged periods, even up to 3 mo. The dead bodies of larger individuals, and emaciated individuals that were clearly dying were occasionally witnessed. Individuals that were not in good health when last seen were judged to be dead regardless of their age-sex class.

When females in late adolescence or young adulthood disappeared but were in good health when last seen, they were regarded as having emigrated. On the other hand, when males and mothers with small infants disappeared, they were assumed to be dead, regardless of their health condition when last seen [Nishida et al., 1990]. These assumptions are justified because we have never seen mature males immigrate into the K or M group in 34 yr of observation. This has also been the case at Gombe [Goodall, 1986; Williams et al., 2002], Tai [Boesch & Boesch-Achermann, 2000], and for the Ngogo unit group at Kibale (Mitani, unpublished data). We have also never seen mother–infant transfer between groups, except during a short period when K group became extinct [Nishida et al., 1985]. Our assumptions concerning death and dispersal are similar to those of previous authors [Goodall, 1986; Nishida et al., 1990; Reynolds, 1998; Boesch & Bosch-Achermann, 2000].

### *Mortality and birth rate.*

The annual mortality rate was calculated by dividing the number of deaths that occurred in a year by the group size at the beginning of the year. The annual birth rate equals the number of births that occurred in a year divided by the group size at the beginning of the year.

### *Causes of death.*

If an individual was clearly ill when last seen, it was regarded as having died of that illness. If dead infants were found being carried by their mothers, with no external injuries on their bodies, they were regarded as having died of sickness. Dead chimpanzees with many wounds on their bodies were assumed to be victims of within-species aggression, except for a few years when lions were roaming in the study area. No evidence of predation on chimpanzees by leopards or eagles was found. If a mother was considered dead because of an epidemic, and the infant disappeared together at the same time, the infant was also regarded as having died of the same epidemic. If a mother was considered dead because of disease, an epidemic was not prevalent, and the infant disappeared at the same time or was seen alone without its mother, and then disappeared after being cared for by allomothers, we assumed that the infant died from the loss of its mother. If individuals estimated to be 40 yr or older disappeared, they were categorized as having died of old age, even if they were in good health when last seen.

## **Life Table**

We calculated “cohort life tables” using the following variables:  $n_x$  is the total number of individuals included in the risk set from age  $x$  to age  $x+1$ . Newborns enter at age 0 in the column of  $n_x$ , and immigrants enter at their presumed age at immigration;  $d_x$  represents the number of individuals that died between specific age intervals; and  $c_x$  is the number of individuals that were censored between particular age intervals. This indicates the number of all individuals that emigrated from the group. The annual mortality rate ( $q_x$ ) is the probability of death between particular age intervals, and is calculated from the equation  $d_x/(N_x-c_x/2)$ . Here  $c_x$  is divided by 2, assuming that individuals emigrate from the group at the midpoint of any given year [Courtenay & Santow, 1989].

## **Age-Specific Birth Rate**

Age cohorts were calculated every 5 yr from 11–15 to 41–45 yr. Age-specific birth rates were calculated as the total number of infants born in a specific interval divided by the total number of female chimpanzee months in that interval [= (# of females) × (# of months females were observed)]. Five-year intervals were biologically meaningful insofar as the period of infancy is approximately 5 yr [cf. Caro et al., 1995].

## **RESULTS**

### **Overall Demographic Trends: Changes in Group Size and Age-Sex Composition**

First, we report the demographic trends of the M group during the 19 yr from the end of 1980 to the end of 1999 (Table I, Fig. 1). Overall group size decreased from 88 in 1980 to 51 in 1999. Group size was a maximum of 102 in 1984 and a minimum of 46 in 1997.

TABLE I. Age-sex Composition of M Group

Age-sex class	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Aver	
Mature male	9	10	9	9	10	11	9	8	9	10	10	9	9	8	9	6	5	6	7	7	8.5	
Adolescent male	6	7	9	6	8	8	9	10	9	7	9	9	8	8	9	9	7	5	4	4	7.6	
Juvenile male	7	6	3	7	5	4	5	6	7	6	6	4	4	4	2	2	5	3	3	3	4.6	
Infant male	7	7	9	7	11	9	8	4	8	5	3	8	9	5	4	4	3	3	3	3	6.0	
Subtotal	29	30	30	29	34	32	31	28	33	28	28	30	30	25	24	21	20	17	17	17	26.7	
Mature female	36	38	38	37	36	37	35	33	33	31	26	29	28	25	23	21	17	16	16	16	28.6	
Adolescent female	7	7	7	9	11	11	11	11	6	6	9	8	9	9	7	6	3	6	5	6	7.7	
Juvenile female	3	7	9	12	8	8	8	10	9	8	5	3	7	7	8	7	3	1	3	1	6.5	
Infant female	13	13	15	11	12	11	5	6	12	11	11	11	7	8	8	7	4	5	9	10	9.5	
Subtotal	59	65	69	69	67	67	59	60	60	56	51	51	51	51	46	41	27	28	33	33	52.2	
Unsexed infant	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	
Total	88	95	100	98	101	99	90	89	93	84	80	81	82	82	76	70	62	47	45	50	51	79.1
Total of adults	45	48	47	46	46	48	44	41	42	41	36	38	37	33	32	27	22	22	23	23	23	37.1
Total of immatures	43	47	53	52	55	51	46	48	51	43	44	43	45	43	38	35	25	23	27	28	42.0	
Immature/total	0.489	0.495	0.530	0.531	0.545	0.515	0.511	0.539	0.548	0.512	0.550	0.531	0.549	0.566	0.543	0.565	0.532	0.511	0.540	0.549	0.532	

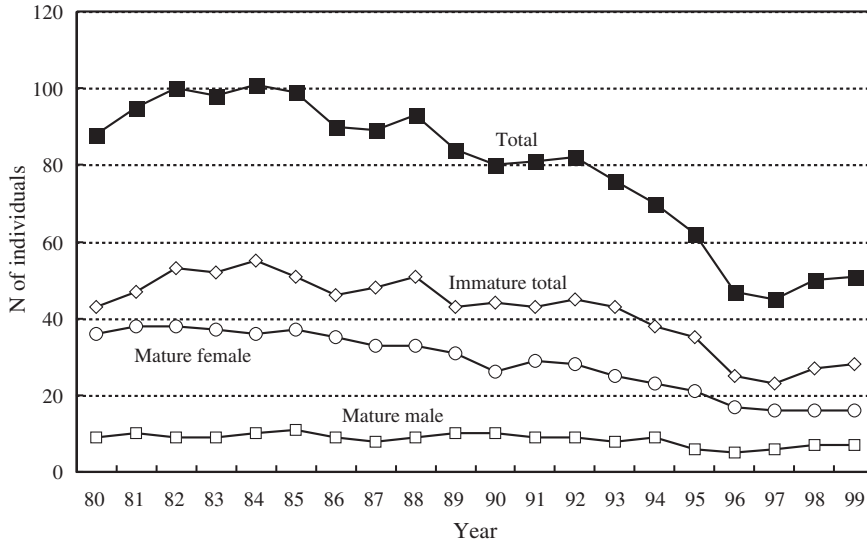


Fig. 1. Changes in the number of mature males, mature females, immature (adolescent, juvenile, and infant) individuals, and the size of M group (Total) calculated from Table I.

During the 19-yr observation period, the number of mature females and immature individuals decreased significantly. In contrast, the number of mature males fell less drastically. The resulting sex ratio (male/female) of mature individuals increased markedly from 0.25 to 0.44. In contrast, the proportion of immature individuals relative to group size remained relatively stable. The total number of immature individuals was slightly more than that of mature individuals (Fig. 2).

The number of mature M-group males ranged between 5 and 11, and averaged 8.5 during the 19 yr of the study. The number of mature females varied between 16 and 38, with a mean of 28.6 individuals. On average, there were three times as many mature females as mature males during the 19-yr study period. Table I provides similar data for other age/sex classes.

### Mortality Rate

Five peaks in the mortality rate were apparent over the 19-yr period (Fig. 3). Mortality was less than 10% in 11 yr and surpassed 10% in 8 yr. We cannot associate any epidemic or other obvious source of mortality to the first peak in 1983. The second peak in 1986 was caused by what our African field assistants termed an “AIDS-like” disease [Nishida et al., 1990]. The third peak in 1989 resulted from predation by lions [Tsukahara, 1993]. The fourth peak was caused by a devastating flu-like disease that began in 1993 and continued into 1994. At least 11 chimpanzees died of this disease [Hosaka, 1995; Hosaka et al., 2000]. Finally, in 1995 and 1996, M group experienced the most catastrophic drop in number since the beginning of the research. The die-off peaked in 1996 and reached the highest mortality rate of the entire study period—over 30% of the population. The chimpanzees suffered high mortality in the preceding (1995; 20%) and succeeding (1997; 12%) years as well. In sum, more than 20% of the

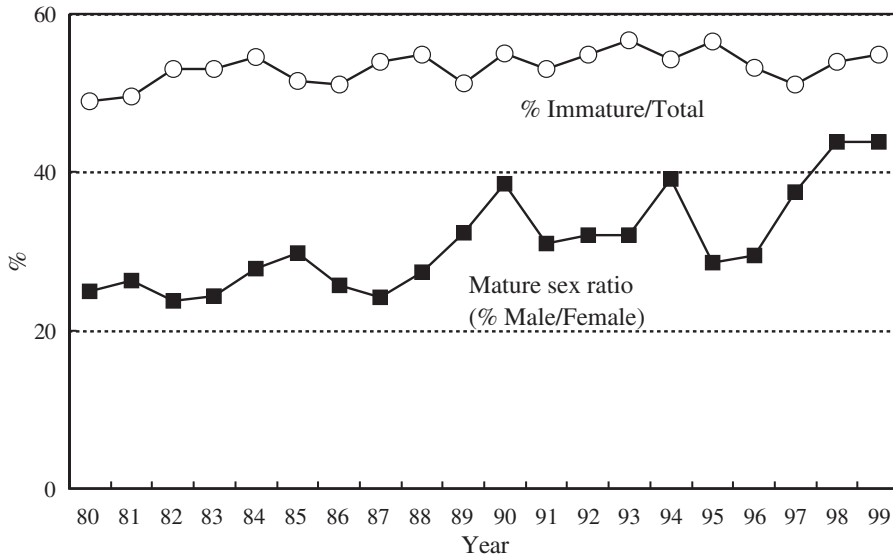


Fig. 2. Percentage of immature individuals and mature sex ratio calculated from Table 1.

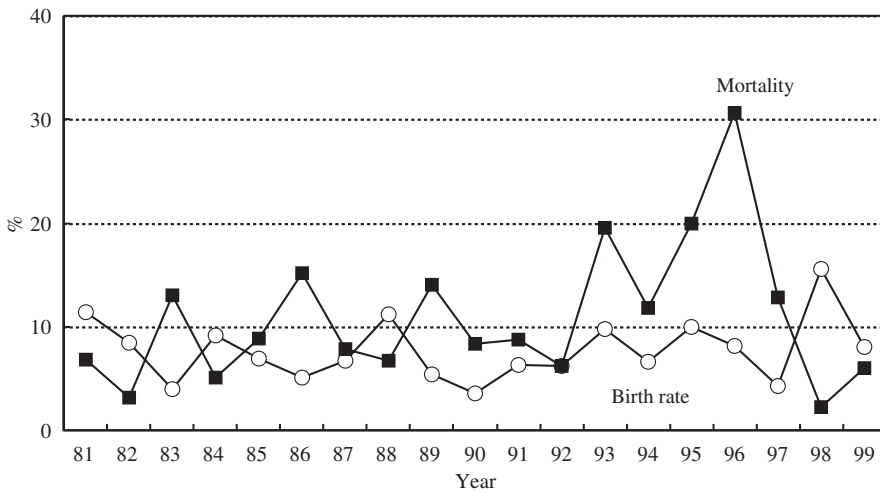


Fig. 3. Mortality and birth rates.

population was lost in these 3 yr. Only four corpses of mature chimpanzees were recovered. Since many more mature males and females disappeared during this period, observers at the time assumed that M group might have split up. Observers consequently traveled around the periphery of M group to look for a “branch” or “splinter” group, but the search was in vain. The sources of the dramatic population loss remain unknown. Several factors (discussed below) may have been involved.

### Sources of Mortality

During the 19-yr study period, 116 individuals (56% of the 207 individuals that died) died from causes that were known or estimated. For the other 91 individuals, the cause of death was unknown.

#### *Disease.*

Disease was the most common cause of death among the M-group chimpanzees. Fifty-six chimpanzees died of illness, accounting for 48% of all deaths. Because we assumed that missing individuals that were ill when last seen had succumbed to disease (see above), it is likely that we overestimated the effects of disease as a source of mortality. Despite this possible bias, we are confident that disease was the single most significant cause of death, given the relatively low rates of mortality attributed to other possible sources.

*“AIDS-like” disease.* An “AIDS-like” disease killed at least three mother–infant pairs. The animals that suffered from this disease became thinner and thinner, and their hair color became paler. They died a few months after the onset of disease. At least three chimpanzees recovered from this illness, although recovery took 1–2 yr.

*Flu-like disease.* From 1993 to 1994, as many as 11 chimpanzees were suspected to have fallen victim to a flu-like epidemic [Hosaka, 1995; Hosaka et al., 2000]. The chimpanzees had runny noses, coughed, lay on the ground, and showed other symptoms of lethargy. A similar disease at Gombe was described as “pneumonia” by Wallis and Lee [1999].

#### *Senescence.*

Twenty-four percent of the chimpanzees died due to senescence. Hosaka et al. [2000] reported following an old female (BO), who appeared to be tired and could not catch up with her group mates, until she succumbed on the ground.

#### *Within-species aggression.*

Eighteen chimpanzees were killed by mature male conspecifics [Hamai et al., 1992]. Seventeen of the 18 victims were infants, 12 of which (71%) were less than 1 yr of age, and were probably victims of within-group aggression. Of the 17 infants, 13 were males and three were females; the sex of one infant was not ascertained. If new immigrant females are assumed to have given birth without any bias to sons or daughters, male infants were attacked significantly more often than females (binomial,  $Z = 2.5$ , two-tailed,  $P < 0.05$ ). This bias disappears, however, when one controls for the fact that new female immigrants gave birth to more sons than daughters. Only one mature male was suspected to have been killed by conspecifics. An ex-alpha male (NT) was probably gang-attacked by his group mates. Two of the present authors (T.N. and N.I.) found him lying in the bush in a coma, with many gashes and wounds over his entire body. He was found in the center of M group’s range, and thus was probably not attacked by individuals from another unit group [Nishida, 1996]. Within-species attacks were responsible for 16% of all M-group deaths.



*Predation.*

In 1989, lions preyed upon at least six chimpanzees [Tsukahara, 1993]. The lions stayed within M group's range for some time, but since 1991 no lions have been seen. There has been no evidence of leopard predation upon M-group chimpanzees. We have only occasionally examined leopard feces, however. Five percent of all deaths can be attributed to predation.

*Maternal death.*

Maternal death was considered to have resulted in the death of four infants. Infants < 3 yr of age do not survive their mother's death.

There were three cases of adoption of 3-yr-old orphans by unrelated caretakers. An adolescent female (TL) adopted a 3-yr-old female (MG), and an infertile mature female (GW) adopted a 3-yr-old female (PP). They transported, groomed, protected, and slept with the orphans. In sum, they provided all maternal care except lactation for more than 2 yr. Both orphans survived to adulthood and emigrated from M group after 11 yr of age. A 3-yr-old female (CS), was adopted by an old female (GK) for 3 yr, but died 1 yr after the presumed death of GK. We assumed that CS was unable to survive her adoptive mother's death.

*Twin birth.*

We recorded only one twin birth during 34 yr of observation. Both died because the mother could not care for them properly [Matsumoto-Oda, 1995].

*Snares.*

Refugees from the Democratic Republic of the Congo (formerly Zaire) came to Mahale between 1970 and the early half of the 1980s, and established camps along the shore of Lake Tanganyika. They set wire snares within the M-group range. Many chimpanzees were observed with snares around their wrists, but they freed themselves after a few months. One juvenile female became thinner and thinner after she was ensnared. In a previous report [Nishida et al., 1990], this female was considered to be dying of disease, but here we make the more plausible assumption that she fell victim to the snare.

*Other causes.*

Falling from trees can be fatal [Goodall, 1986]. However, although we saw a few individuals fall from a considerable height, no chimpanzee at Mahale has died as the result of a fall.

**Birth**

One hundred twenty-six births were recorded in the 19-yr study period: 60 were females, 49 were males, and the sex of 17 was not determined because they died shortly after birth. The birth sex ratio did not deviate significantly from parity (binomial,  $Z = 1.05$ , two-tailed,  $P > 0.05$ ).

*Birth rate.*

In contrast to the mortality rate (see above), the birth rate did not fluctuate much during the 19-yr study period, and remained at 5–10% of the total population per year. The highest birth rate was recorded in 1998. This peak can be ascribed to the fact that many infants died in the preceding years, after which females resumed estrus and became pregnant.

## Immigration

Forty-five cases of immigration were recorded during the 19-yr study period. Most of the immigrants (34/45 = 76%) were late adolescent females. However, three prime females (ZP, WD, and FH) also immigrated, accompanied by a juvenile female (ZD), a juvenile male (MA), or a juvenile male (SS) and an adolescent male (FN), respectively. One infant female (CS) and three juvenile males (HT, HR, and CL) were probably orphans of peripheral females that had immigrated into M group but had not been identified by researchers, presumably because they were shy and occupied areas toward the periphery of the group range. After their mothers died, it is likely that these immature individuals joined the core party (of which the main members were mature males), after which they were individually recognized by researchers. For example, we identified a 3-yr-old female (CS) after (presumably) her mother died. As noted above, CS was adopted by an old female (GK). No mature male has immigrated into M group.

Most immigrants stayed in M group for several years. Seven adolescent female immigrants, however, disappeared within 2 yr. We assume that all seven individuals emigrated to another unit group.

## Emigration

Thirty-three chimpanzees were regarded as having emigrated from M group. Because all male chimpanzees and mature females were assumed to have died if they disappeared permanently, all of the 33 emigrants were adolescent females. Nonetheless, we observed immigration of immature males into M group (see above), and thus it is possible that we underestimated the emigration and overestimated the mortality of the immature males. This possibility is not very likely, however, given the aggressive territorial behavior of mature males. The numbers of immigrant and emigrant adolescent females were similar: 34 immigrants vs. 33 emigrants.

## Female Life History Variables

Ages at first and last birth, and interbirth intervals are variables that influence the lifetime reproduction of females. Several factors similarly influence the age at which females give birth for the first time. These include the age of the first estrous swelling, the age of natal transfer, the period of adolescent infertility, and the length of time between immigration to first parturition. In a previous report [Nishida et al., 1990], we largely estimated the ages of the females. In this report we limited our analysis to females of known ages. These individuals were followed from their birth to the time they gave birth for the first time.

### *Age at first maximal swelling.*

The median ages of the first indication of the swelling of the perineal part and maximal swelling were 120 ( $\bar{x} = 117.20 \pm 10.35$ ,  $n = 5$ ) and 128 mo ( $\bar{x} = 127.60 \pm 6.19$ ,  $n = 5$ ), respectively.

### *Age of emigration from natal groups.*

One female (NK) of known age from K group transferred to M group. One M-group female (TL) of known age transferred to B group (Fukuda, personal communication). Nine females of known ages from M group were presumed to have transferred to unknown groups. The median age of transfer was 11 ( $\bar{x} = 11.27 \pm 1.50$ , range = 9.7–14.0,  $n = 11$ ).

*Adolescent infertility.*

We defined adolescent infertility as the period between the time of the first maximal swelling and the first birth. Only four females failed to disperse, and subsequently gave birth for the first time in their natal M group. Adolescent infertility was quite variable, ranging from 1 yr 2 mo to 4 yr 1 mo (median = 2 yr 10 mo).

*Time between immigration and first birth.*

Thirty-four females immigrated into the M and K groups. Of these, the four youngest adolescent females—two of which had immigrated from K group into M group with their mothers—soon disappeared, apparently retransferring to groups other than the K and M groups. Two females immigrated to M group only recently (after 2000) and were therefore excluded from analysis.

Twenty-six females gave birth a considerably long time after they immigrated into the K or M group (when they were late adolescents or young adults). The median number of months that elapsed from immigration to first birth was 32, but varied considerably, ranging from 24 to 143 mo ( $\bar{x} = 40.04 \pm 30.37$ ,  $n = 26$ , Fig. 4). This means that more than 2 yr usually pass before females conceive for the first time. This may include a period of adolescent infertility and an additional stressful period following immigration. NK, who was an immigrant from the K to the M group, had the longest record. It took NK 11 yr to give birth for the first time after her first sexual swelling was observed.

Parous females that emigrated from the K to the M group during the K group extinction tended to give birth earlier than females that migrated from other groups. Two factors might account for this. First, these females were typically older and thus further along in their reproductive career than the other immigrants. Second, all of these K-group immigrants continued to use their original core areas in their original home ranges.

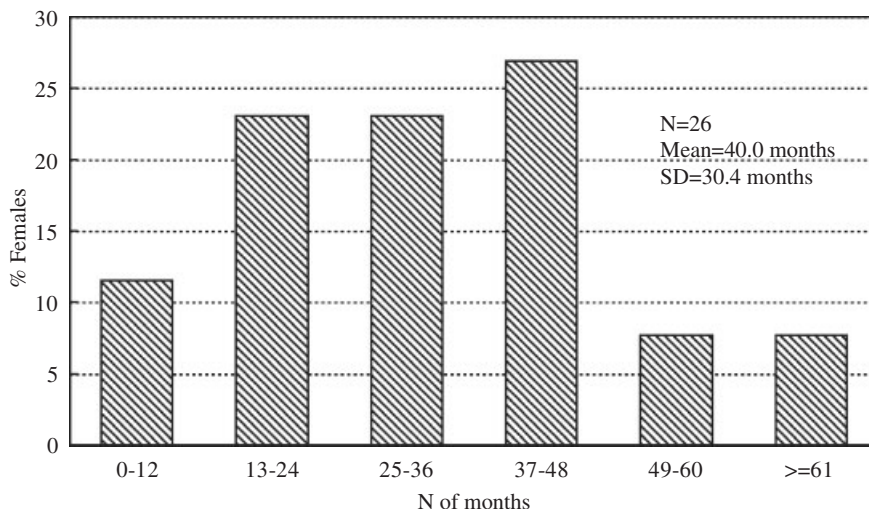


Fig. 4. Number of months that passed from immigration to first birth.

*Age at first birth.*

Because females usually transfer to unknown unit groups, we were able to confirm the age at first birth for only five females. One K-group-born female (NK) of known age transferred to M group and gave birth. One M-group-born female (TL) gave birth for the first time before transferring to the adjacent B group. Three natal M-group females (AB, TZ, and RB) gave birth without transferring from M group. The median age at first birth for these females was 13.2 ( $\bar{x} = 15.6 \pm 4.52$ , range = 12.0–23.0,  $n = 5$ ). The median estimated age at first birth for females that immigrated into M group was 14 yr ( $\bar{x} = 14.65 \pm 2.58$ ,  $n = 26$ ). On the other hand, the median age at first birth for four females (TL, AB, TZ, and RB) that gave birth in their natal group was 13. Thus, females that give birth in their natal group had an earlier age at first birth (Mann-Whitney,  $Z = 1.75$ ,  $n_1 = 26$ ,  $n_2 = 4$ ,  $P < 0.04$ ).

*Interbirth interval.*

The median interbirth interval when the previous offspring survived was 68 mo ( $\bar{x} = 72.5 \pm 8.4$ , range = 63–87,  $n = 15$ ) if the previous offspring was male, and 66 mo ( $\bar{x} = 66.2 \pm 7.6$ , range = 52–78,  $n = 18$ , Table II) if it was female. Thus, mothers tended to have a shorter interbirth interval when the previous offspring was a daughter than when it was a son (Mann-Whitney,  $U = 85.5$ ,  $n_1 = 15$ ,  $n_2 = 18$ ,  $0.05 < P < 0.1$ , two-tailed). The interbirth interval was not correlated with the age of the mother (son:  $r_s = 0.17$ ,  $P > 0.05$ ,  $n = 15$ , daughter:  $r_s = -0.32$ ,  $P > 0.05$ ,  $n = 18$ ).

TABLE II. Interbirth Interval (mo)

Male				Female			
Name	Age	Postpartum estrus	Birth interval	Name	Age	Postpartum estrus	Birth interval
CH	16	57	72	WN	33	64	
CH	27	55		SA	20	53	63
SA	13	35	67	WE	19	58	74
ND	19	53	66	WO	17	56	78
WA	18	63	83	WO	29	50	58
WA	30	74		FT	17	56	75
WD	16	36	68	FT	30	52	73
WO	23	59	68	SO	29	67	77
FT	25	54	63	SL	27	33	53
SO	23	43	63	SL	32		52
SL	23	46		TY	15	56	72
BO	29	66	87	TY	21	59	69
WX	21	67	80	WX	27	61	69
IK	17	53	69	IK	23	56	64
OP	20	52	85	IK	28	51	59
PI	19	51	82	FB	14	58	67
CA	31	58	68	FB	20	50	65
DA	40	68		OP	15	51	61
XT	20	54	67	JN	21	46	62
				DO	28	65	
Total		1044	1088			1042	1191
Average		54.9	72.5			54.8	66.1

The median first postpartum estrus after lactational amenorrhea when the offspring survived occurred 54 mo after delivery for males ( $\bar{x} = 54.9 \pm 10.3$ , range = 35–74,  $n = 19$ ), and 56 mo after delivery for females ( $\bar{x} = 54.8 \pm 7.7$ , range = 33–67,  $n = 19$ , Table II). Thus, the females experienced postpartum estrus at a similar date regardless of whether they had previously given birth to a son or daughter (Mann-Whitney U-test, ns).

Data concerning the interbirth interval were not always congruent with the first postpartum data, because swelling itself can be more easily influenced by the unstable rhythm of sex hormones, as suggested by occasional occurrences of extremely early postpartum resumption of estrus [Takasaki et al., 1986]. Therefore, the period from birth to first postpartum resumption of estrus is probably not a good indicator of reproductive cost.

#### *Lifetime reproductive output.*

Our research did not cover a long enough period to provide unbiased data on female lifetime reproductive output. However, we provide some preliminary data below.

Twenty-six females whose entire birth record is available were observed from a young age (10–13 yr) to death at various ages. The average number of live births was 3.85 (daughters =  $1.73 \pm 1.25$ , sons =  $1.54 \pm 1.48$ , and unsexed offspring =  $0.54 \pm 0.87$ ). The average number of weaned offspring was  $1.35 \pm 1.23$  (daughters =  $0.85 \pm 0.92$ , sons =  $0.50 \pm 0.71$ ). Since females that died early tended to be included in this sample, the lifetime reproductive output calculated from this sample almost certainly underestimates the actual lifetime reproductive output.

Twenty-five females were observed from middle age (18–33 yr) to death in older age (31–48 yr). The average number of live births was  $2.68 \pm 1.25$  (daughters =  $1.52 \pm 1.12$ , sons =  $1.04 \pm 0.73$ , and unsexed offspring =  $0.12 \pm 0.33$ ). The average number of weaned offspring was  $1.96 \pm 1.06$  (daughters =  $1.20 \pm 1.04$ , sons =  $0.76 \pm 0.66$ ). Since some of their offspring may have died or emigrated before they began to be observed systematically, the number of both nonweaned and weaned offspring calculated from this sample is probably an underestimation of the actual lifetime reproductive output.

Figure 5, which is composed of combined data sets (26+25 above), suggests an overall picture of extremely low fecundity in female chimpanzees.

### **Age-Specific Mortality**

Table III shows age-specific mortality in Mahale chimpanzees. Fifty percent of the chimpanzees died before weaning, and 80% died before they became mature. This mortality is too high for the population to be maintained, if the current trend continues.

### **Age-Specific Birth Rate**

We calculated age-specific birth rates for 5-yr cohorts of females (see Methods). Females maintained a relatively high fecundity of  $> 0.2$  per year in the age cohorts from 16–20 to 26–30 yr (Fig. 6).

### **Menopause**

Some females ceased giving birth and developing sexual swellings. As indicated in column L of Table IV, 15 females did not show estrous swellings for

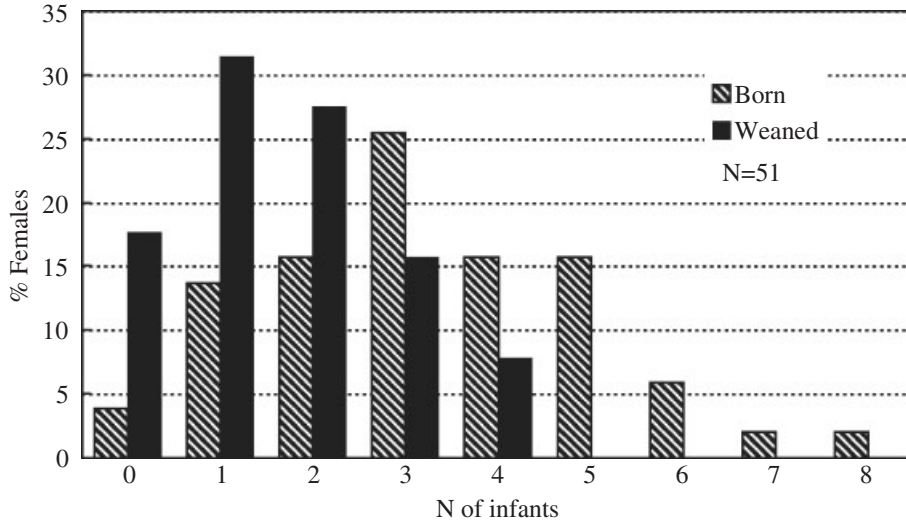


Fig. 5. Variation in lifetime number of offspring (all and weaned) for a female. The data sets of 26 females that were observed from adolescence or earlier until death, and 25 females that were observed from middle age until death were combined.

TABLE III. Life Table of M Group Chimpanzees

x	nx	dx	cx	qx	lx	Survival rate
0	152	53	0	0.34868	1.00000	1.00
1	99	24	8	0.25263	0.65132	0.90
2	67	9	1	0.13534	0.48678	0.72
3	57	7	3	0.12613	0.42090	0.63
4	47	1	2	0.02174	0.36781	0.57
5	44	3	0	0.06818	0.35981	0.52
6-10	178	7	11	0.04058	0.34521	0.31
11-15	79	3	9	0.04027	0.32940	0.21
16-20	38	1	4	0.02941	0.31614	0.10
21-25	20	1	1	0.05128	0.30684	0.08
26-30	11	0	2	0	0.29111	0.06

more than 1 yr before death. Four females did not show swelling for more than 3 yr before death.

Sexual swelling itself is not a good indicator of ovulation. Therefore, the period from the year when the last offspring was born to the year when the mother died was investigated (column J). If the period of maternal care of the last offspring is 5 yr, J-5 may be equivalent to the post-reproductive period that does not involve female reproduction. There were eight females that had more than 5 yr in this period, as shown in column K. This accounts for 23.5% of all old females.

**DISCUSSION**

The results presented above shed new light on several aspects of wild chimpanzee demography and behavior. Here we discuss how these data provide

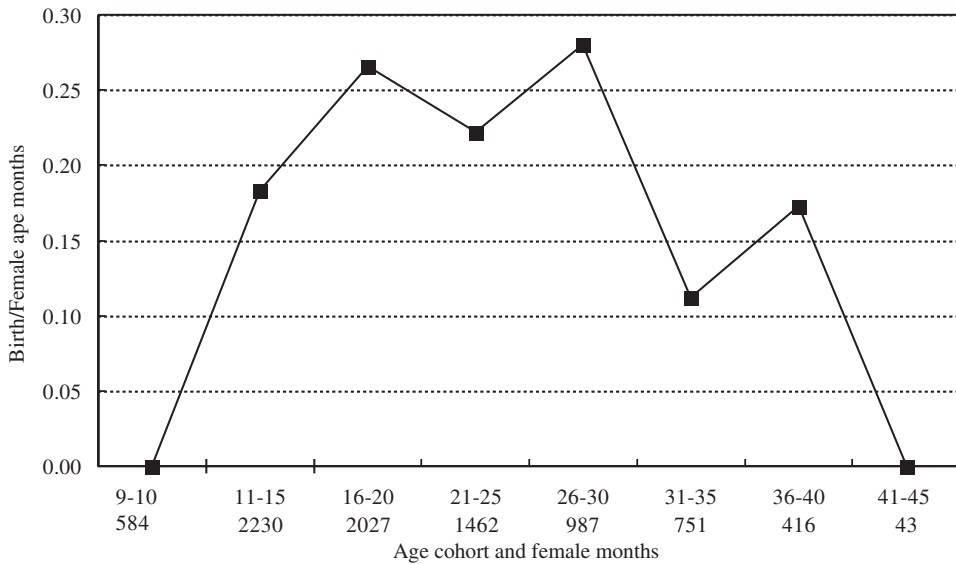


Fig. 6. Age changes in fertility. Number of births divided by number of female ape months that were observed.

new insights into the costs of transfer and maternal care, menopause, the effect of nutrition on life history variation, and implications for conservation.

### Costs of Transfer

The median estimated age at first birth for females that immigrated into M group was 14 yr. On the other hand, the median age at first birth for four females that gave birth in their natal group was 13. Natal females that remained in their group and gave birth did not need to establish new core areas. Moreover, natal females had less serious conflicts than new immigrants since the former had relatives, such as mothers and friends. Therefore, females that give birth in their natal group are predicted to have an earlier age at first birth. The data support this expectation, but should be viewed with caution because the ages of the immigrants were only estimated.

Females that transfer from their natal range are likely to suffer several costs [Williams et al., 2002]. After moving to a new, unknown area, such individuals are likely to experience reduced foraging efficiency, and to suffer increased social stress induced by resident female aggression [Pusey, 1980; Goodall, 1986; Nishida, 1989]. Given that females might benefit reproductively by remaining in their natal range, and the potential costs of dispersal, why do they emigrate? Here we assume that females transfer to avoid the deleterious effects of inbreeding [Pusey, 1980].

There is considerable intersite variation in the tendency for females to transfer. Almost all of the females in K group emigrated at adolescence [Nishida, 1979]. The rate of emigration was 90% among M-group females (this study) and only 50% among Gombe females [Pusey et al., 1997]. The rate of female transfer at Tai is similar to that at Mahale [Boesch & Boesch-Achermann, 2000], whereas

TABLE IV. Post-Reproductive Lifespan and Female Last Reproduction

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Name	Year of birth	Year of immigration	YB first offspring	YB last offspring	YD last offspring	Year last estrus	Age last estrus	Year of death	Duration last offspring	PRL1 J-5	PRL2 I-F	PRL3 I-G	Age of death1 I-D +11	Age of death2 I-C +11	Age of death3 I-B
	D-15/C-11						G-B		care I-E						
WK	1936	Unknown	?	1966	1966	1974	38	1974	8	3	8	0			
WM	1949	Unknown	1964 <sup>a</sup>	1972	-	1980.10		1982	10	5			33		
WW	1943	Unknown	1958 <sup>a</sup>	1977	1978			1978	1	-4	0		35		
GP	1949	Unknown	1964 <sup>a</sup>	1978	-	1984.09	35	1985	7	2		1	36		
GA	1952	Unknown	1967 <sup>a</sup>	1979	1983	1988.01	36	1988	9	4	5	0	36		
NG	1940	Unknown	1955 <sup>a</sup>	-	-	1986.01	46	1990	>17	>12		4	50		50
WT	1942	Unknown	1957 <sup>a</sup>	1974	1977			1979	5	0	2		37		
WB	1943	Unknown	1958 <sup>a</sup>	1974	1977	1983.12	39	1986	12	7	9	3	43		
WN	1945	Unknown	1960 <sup>a</sup>	1978	-	1984.09	39	1987	9	4		3	42		
UM	1956	Unknown	1971 <sup>a</sup>	1980	1981	1986.09	30	1987	7	2	6	1	41		
EA	1955	Unknown	1970 <sup>a</sup>	1992	1993	1990.10	35	1993	9	4	0	3	38		
DA	1960	Unknown	1975 <sup>a</sup>	1988	-	1994.09	34	1994	6	1		0	34		
HA		Unknown		1980	-	1992.09	47	1992	12	7		0			47
MP		Unknown		1976	?	1985.10	40	1985	9	4		0			
WS	1951	Unknown	1966 <sup>a</sup>	1981	1981	1984.08	33	1984	3	-2	3	0	33		
WG	1948	Unknown	1963	1963	-			1980	17	12					
TG	1955	Unknown	1970 <sup>a</sup>	1980	-			1990	10	5		1			
TI	1960	Unknown	1075 <sup>a</sup>	1982	-	1982.02	22	1983	1	-4					
AD	1956	Unknown	1971 <sup>a</sup>	1978	-			1983	5	0					
LN	1958	Unknown		1973	-	1989.08	31	1989	16	11		0			
FA	1952	Unknown	1967 <sup>a</sup>	1988	1988	1987.09	35	1988	0	-5	0	1	36		
IA	1956	Unknown	1971 <sup>a</sup>	1981	-			1986	5	0			30		
BO	1952	Unknown	1967 <sup>a</sup>	1988	1990	1993.01	41	1994	6	1	4	1	42		
SO	1953	Unknown	1968 <sup>a</sup>	1988	1989	1988.02	35	1989	1	-4	0	1	36		36
WA	1954	1966	1967	1984	1993	1993.11	39	1993	9	4	0	0	41	38	39
SL	1956	Unknown	1971 <sup>a</sup>	1994	1996	1994.01	38	1997	3	-2	1	3	41		42
OO	1956	Unknown	1971	1986	1986	1985.09	29	1986	0	-5	0	1	30		



WE	1955	Unknown	1970 <sup>a</sup>	1981	1985		30	1985	4	-1	0	30	
CH	1958	Unknown	1974	1985	-	1990.01	32	1990	5	0	0		32
WO	1958	1972	1975	1992	1995			1995	3	-2	0	35	34
WL	1959	1971	1979	1995	1992	1995.01	36	1996	1	-4	4	32	36
CA <sup>b</sup>	1960	Unknown	1976 <sup>a</sup>	1997	-	-							
DO	1961	Unknown	1981 <sup>a</sup>	1989	1995	1995.12	34	1996	7	2	1	1	
GK	1961	1973	1975	1983	1983	1995.04	34	1996	13	8	13	1	33
WX <sup>b</sup>	1961	Unknown	1977	1996	-	-							
FH	1963	Unknown	1978 <sup>a</sup>	1991	1996	1996.03	33	1996	5	0	0	33	
FT <sup>b</sup>	1963	1974	1976	1999	-	-							
IK <sup>b</sup>	1965	Unknown	1981	1998	-	-							
GM	1966	1975	1983	1993	1993	1996.01	30	1996	3	-2	3	28	33

<sup>a</sup>Presumed.

<sup>b</sup>Still in active reproduction.

YB, year of birth; YD, year of death; PRL, post reproductive lifespan; PRL1, see text; PRL2, years that passed from death of last offspring to mother's death; PRL3, years during which females remained anestrus directly before death.

at Bossou young females do not emigrate [Sugiyama, 1999]. How do we explain why female transfer is common at Mahale and Tai, and less common at Gombe and Bossou? One likely factor involves the small size and isolated conditions of the local populations at Gombe and Bossou. At these sites, young females have few, if any, options among neighboring groups in which to disperse. In this context it may be of interest to note that at Ngogo in Kibale, where there are many unit groups, it is the rule for adolescent females to transfer, as is the case at Mahale and Tai (Mitani, unpublished data). If our assumption about the relationship between inbreeding avoidance and female dispersal is true, then female chimpanzees at Gombe and Bossou are likely to gain fewer benefits and suffer greater costs by dispersing compared to females at other sites. This again may be a result of the relatively small local populations of chimpanzees at these sites, which leads to more genetically homogeneous populations and greater feeding competition among females.

It is significant that recently more natal females have remained without transferring in M group. During the time of this study, the size of M group decreased to half that of the largest size recorded, while the group range remained the same size, which reduced feeding competition considerably. If so, the benefit of not transferring would become greater. However, it should be pointed out that three of the four females that did not transfer had already reached 13 yr of age before the great size reduction of the M group in 1995. Therefore, the influence of group size reduction on these females was partial at most.

### Costs of Maternal Care

Because males in theory can producing more offspring compared to females, dominant females or females in better condition are expected to produce more sons than daughters [Trivers & Willard, 1973]. Additional considerations suggest that dispersal patterns may also affect differential maternal investment in sons and daughters. In animals such as baboons, where females are the philopatric sex, dominant mothers are expected to invest more in daughters that can inherit their mother's high dominance rank [Altmann, 1980]. Because chimpanzee females emigrate but do not show clear-cut dominance relationships, with gerontocracy being the rule [Nishida, 1989; Nishida et al., 1990; but see Pusey et al., 1997], there would be no point in investing more in daughters than in sons. In contrast, male reproductive success is likely to be strongly influenced by dominance ranks [Hasegawa & Hiraiwa-Hasegawa, 1983; Constable et al., 2000], and this leads to the prediction that chimpanzee mothers will invest more in sons than in daughters.

Our results are largely consistent with theoretical expectations. Among the M-group females, interbirth intervals tended to be longer after the birth of a son than after the birth of a daughter. Similar results were found at Tai, where high-ranking mothers experienced longer interbirth intervals after giving birth to sons than after the birth of daughters [Boesch & Boesch-Achermann, 2000]. In the light of these findings, recent evidence that giving birth to sons (relative to daughters) significantly shortened the expected lifespan of mothers in preindustrial northern Scandinavia [Helle et al., 2002] is an interesting parallel to which more attention should be paid.

## Menopause

Controversy exists over whether menopause is a characteristic unique to human beings [see Peccei, 2001, for recent review]. In a previous study [Nishida et al., 1990] we argued that female chimpanzees experience menopause. We defined as post-reproductive the old, noncycling females that had neither given birth nor showed cycling after their last offspring died. This procedure was criticized because the post-reproductive period should be considered to start only 5 yr after the last offspring are produced, because noncycling females will have devoted those years to offspring care if the offspring did not die [Caro et al., 1995; Takahata et al., 1995]. To address these criticisms, we subtracted 5 from the number of years that passed from the time a female's last offspring died to the year when she died. Using this procedure we still found that 25% of old females had a post-reproductive lifespan.

Based on long-term studies of baboons and lions, Packer et al. [1998] suggested that human menopause should not be regarded as a special adaptation. They found no evidence that reproductive costs were high for old females, or that post-reproductive females raise the fitness of their children or grandchildren. In contrast, Caro et al. [1995] argued that 99% of human females experience menopause, while only 13–60% of nonhuman primates live through a similar period. This estimate was based on investigations of 13 species of captive nonhuman primates, including chimpanzees, and German women living in the 18th and 19th centuries. They concluded that the 29-yr period from the birth of the last offspring to the mother's death in women is much longer than the corresponding 9-yr period in captive chimpanzees, and that human menopause is the result of selective forces acting uniquely upon human beings.

Although we have shown that a sizable proportion of female chimpanzees experience a post-reproductive life, it appears that differences exist between human and chimpanzee females.

## Factors Influencing Life History Variables

A comparison across study sites (Table V) suggests that several factors are responsible for differences in life history variables. First postpartum estrus and interbirth interval are remarkably short in the Taronga Zoo [Courtenay, 1987], a captive site where infants are left to maternal care. Nutritional factors likely affect these variables—a claim that is bolstered by observations in Bossou and Gombe. At these sites, chimpanzees have been provisioned with nutritious food (banana at Gombe and oil palm at Bossou), which may explain the relatively short interbirth intervals there. However, this should be viewed with caution since it is not apparent whether the differences are significant, and the influence of provisioning on the nutritional conditions of chimpanzees at Gombe and Bossou is ambiguous.

As the survivorship curve (Fig. 7) drawn from the life table of M-group chimpanzees (Table III) shows, M-group chimpanzees experience very high mortality rates during infancy. Compared with Tai chimpanzees [Boesch & Boesch-Achermann, 2000], those at Mahale experience higher infant mortality. This is partly because infanticide appears to be more of a problem at Mahale than at Tai. However, the mortality rate during the juvenile phase at Tai rises enormously and thereafter the rate of survival is always higher at Mahale. This is because many mature and adolescent individuals died of the Ebola virus and from

TABLE V. Inter-Site Comparison of Female Reproductive Variables

	Taronga Zoo		Bossou		Gombe		Mahale		Tai	
	Mean (year)	N	Median (year)	N	Mean (year)	N	Median (year)	N	Mean (year)	N
Provisioning	100		Oil-palm		Banana		Stopped in 1987		NA	
Vegetation	-		TRF		RF+W		RF+W		TRF	
Group size			16-22		38-60		45-101		29-82	
Representative value	Mean (year)	N	Median (year)	N	Mean (year)	N	Median (year)	N	Mean (year)	N
Age, first max. swelling	-				10.8	8	10.7	5		
Age, emigration							11.0	11		
Dura, adolescent infertility					2.4	4	2.8	4		
Age, first birth			13		13.3	4	13.2	5		
Dura, immigration-first birth	-						2.5	26	2.7	
First postpartum estrus	2.3	11			3.9	12	4.6		5.1	
Interbirth interval	3.8	15	5	15	5.2	11	5.6		5.7	
Oldest female that gave birth					37		39			
Number of adolescent female	-				6 (19)		20 (17)		7 (15)	
Number of adolescent female immigrants	-				12 (19)		22 (17)		13 (15)	
Source	Courtenay [1987]		Sugiyama [1994]		Wallis [1997]		This study		Boesch & Boesch-Achermann [2000]	

TRF, tropical rain forest; RF, riverine forest; W, woodland.

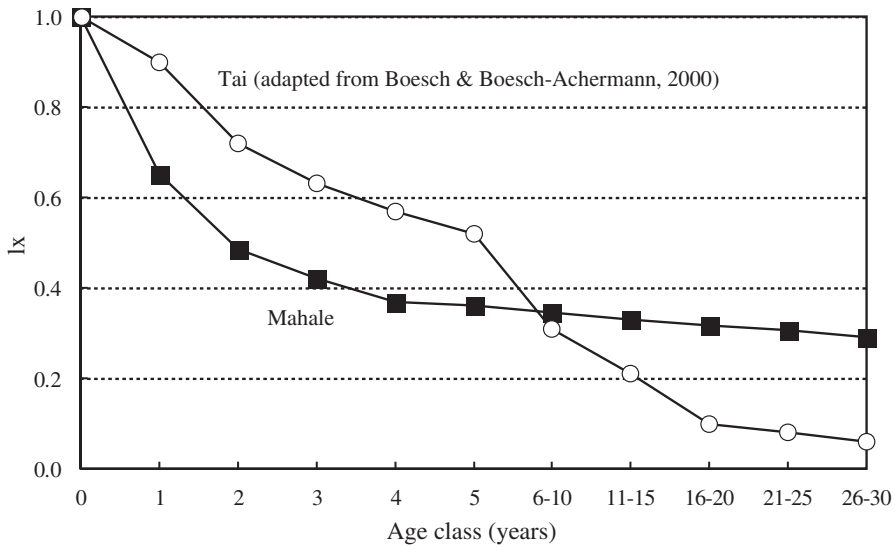


Fig. 7. Survivorship curves for Mahale and Tai chimpanzees.

leopard predation. According to the survival curve of Gombe, Kibale, and other locations recently drawn by Hill et al. [2001], Mahale has the highest infant mortality. The question of why this is so must be addressed in order to conserve this important population of chimpanzees.

### Implications for Conservation

Disease is a significant cause of mortality in Mahale chimpanzees. Although medical investigations have not been conducted, anthroponozoonotic epidemics [Wallis & Lee, 1999] might explain the catastrophic population decreases in M-group chimpanzees. Regular monitoring of chimpanzee health conditions by expert veterinarians is needed. We must also enforce more strict regulations for chimpanzee viewing by researchers, tourists, film crews, and park guides in order to decrease risks from stress and infection for wild chimpanzees [Woodford et al., 2002; Butynski, 2001].

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