Kim Hill
Department of Anthropology, University of New Mexico, Albuquerque, New Mexico 87131-1086, U.S.A.
kimhill@unm.edu

Christophe Boesch
Max Plank Institute for Evolutionary Anthropology, Leipzig, Germany.
boesch@eva.mpg.de

Jane Goodall, Anne Pusey and Jennifer Williams
Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution and Behavior, University of Minnesota, U.S.A.
pusey001@tc.umn.edu; williams@biosci.cbs.umn.edu

Richard Wrangham
Department of Anthropology, Harvard University, U.S.A.
wrangham@fas.harvard.edu

Received 31 October 2000
Revision received
21 February 2001 and
accepted 21 February 2001

Keywords: chimpanzees, mortality, hunter-gatherers, life history evolution.

Mortality rates among wild chimpanzees

In order to compare evolved human and chimpanzees' life histories we present a synthetic life table for free-living chimpanzees, derived from data collected in five study populations (Gombe, Taï, Kibale, Mahale, Bossou). The combined data from all populations represent 3711 chimpanzee years at risk and 278 deaths. Males show higher mortality than females and data suggest some inter-site variation in mortality. Despite this variation, however, wild chimpanzees generally have a life expectancy at birth of less than 15 years and mean adult lifespan (after sexual maturity) is only about 15 years. This is considerably lower survival than that reported for chimpanzees in zoos or captive breeding colonies, or that measured among modern human hunter-gatherers. The low mortality rate of human foragers relative to chimpanzees in the early adult years may partially explain why humans have evolved to senesce later than chimpanzees, and have a longer juvenile period.

Journal of Human Evolution (2001) **40,** 437–450
doi:10.1006/jhev.2001.0469

Introduction

Many assumptions are made about the differences in life-history between *Homo* and *Pan*, because they seem critical for understanding the transition from ape to human (e.g., Hawkes *et al.*, 1998; Kaplan *et al.*, 2000). Yet despite considerable interest, no robust life table for wild chimpanzees exists, due to problems of small sample size of known aged individuals and inter-site variability. Here, we present the first life table for wild chimpanzees derived from multiple sites in order to compare "natural" chimpanzee mortality to that of human hunter-gatherers and to test the hypothesis that there are differences between mortality rates in wild chimpanzees and human hunter-gatherers.

Although chimpanzee life tables have been previously constructed using large samples of captive individuals, it is unclear

0047–2484/01/050437+14$35.00/0

whether these data provide a valid estimate of mortality rates during chimpanzee evolutionary history. For example, synthetic life tables for chimpanzees at zoos (Courtney & Santow, 1989) and in breeding colonies (Dyke *et al.*, 1995) suggest that 35–50% of all individuals survive to age 30, yet juvenile mortality data in some wild populations show that less than 50% of individuals survive to age five (Nishida *et al.*, 1990). Likewise, adult mortality in captive populations appears particularly low compared with wild chimpanzees. For example, the survival curve for captive chimpanzees produced by Dyke *et al.* (1995) suggests that 47% of all females who reach age 15 survive to age 45 years, older than the estimated age for any chimpanzee that has ever been observed at Gombe.[1] These concerns about the utility of captive life tables led us to combine mortality data from various wild chimpanzee study sites.

Methods

Chimpanzees at Gombe have been continually monitored since 1963. The data analyzed here include 179 individuals monitored up to 1998. All infants born into the Kasakela community, all individuals in that group in 1963, and all immigrants to that group are included in the risk set from the year they were first observed. The sample also includes individuals from the Kahama subgroup when the Kasakela community divided. Some adult females who emigrated to the Mitumba group have been continually monitored and are also included. All other individuals were censored upon emigration or on 1 January 1998 if they were still alive at that time. Individuals who were not born in the study group or who were born before the observation period began were assigned ages based on age-characteristic behavioral and morphological traits. In both sexes, young adults (15–20 years) have thick glossy black hair, unworn and generally unbroken teeth, vigorous movements and relatively light facial creasing. Old individuals (about 35 years onwards) show thinning of hair (e.g., on shoulders, head or lower back), often with browner or grayer color and less sheen. Teeth are worn and may be broken, movements are slow, and facial skin shows sagging and wrinkling. Because observations continued for at least 10 years in each site, most individuals were seen as either young adults or old individuals. Later in the study period the age estimates for older individuals could be assessed against the appearance of individuals whose age was more tightly estimated because they were seen as juveniles or young adults. Most individuals were under age 15 when first observed (152 individuals), and only 24 individuals in the dataset are believed to have age estimates that could be in error of more than one or two years. Infants, juveniles and adult males were assumed dead if they disappeared. Nulliparous, sexually cycling females who disappeared after last being seen in good health were assumed to have emigrated. In Gombe, adult females sometimes transfer with their infant offspring to new communities, so disappearances of healthy adult females who were sexually cycling and observed less frequently toward the end of their tenure were likewise treated as cases of emigration. Thus, a disappeared adult female was classified as dead if her body was discovered, if she was observed ill before disappearing, if she disappeared during an epidemic, or if she left an infant offspring.

Demographic parameters of one community of Taï chimpanzees were continually monitored from 1982–1994 (Boesch &

---

[1] The old matriarch Flo, who was featured in early films about the Gombe chimpanzees and appeared ancient at that time was estimated to have been 43 years old at the time of her death. However, J. Goodall currently suspects that Flo's actual age at death may have been previously underestimated. Some chimpanzees at Gombe are now in their early 40s, yet appear to be younger than Flo at the time of her death based on tooth wear patterns.

Boesch, 2000). The data include observations on 123 different individuals. Individuals are included in the risk set and ages were assigned in the same manner described for Gombe above. Ages of older individuals rely partially on comparison to older individuals at Gombe whose ages are more precisely known due to the long observation period. Adolescent females who disappeared were coded as for Gombe; however, intercommunity transfers of adult females in Taï (and Kibale) have not been observed, thus all adult female disappearances were coded as deaths.

"Kibale chimpanzees" refers in this paper to individuals in the Kanyawara community (Wrangham *et al.*, 1992). Kanyawara chimpanzees have been monitored continuously since 1987. A total of 74 individuals entered the risk set, each in one of four ways: long-term members of the Kanyawara community identified by January 1989 ($n=33$); individuals assumed to be long-term members of the community, but first identified after January 1989 ($n=13$); immigrants since January 1989 ($n=8$); or born during the study period ($n=20$). The 54 individuals whose births occurred outside the study period were assigned an exact age (best guess) after first being divided into age categories based on morphological and behavioral characteristics described for Gombe and Taï. Deaths and disappearances of females were classified in the same way as described for Taï above. By the end of 1998, 47 individuals remained in the risk set, 11 had emigrated, and 16 had died.

Data for Mahale are coded directly from Nishida *et al.* (1990, Table 3.11). This database includes 92 juveniles who were born during the study period and carefully monitored. Risk years and deaths to unsexed infants were split equally between males and females. Since the data contain only juveniles all disappearances were counted as deaths. Data for Bossou are coded from Sugiyama (1994, Figure 3). Mortality data are restricted to observed infant births whose survival was monitored to age 4, as well as survival between ages 4–8 for a cohort of juveniles whose age was determined using standard juvenile age markers. Years at risk and deaths were assigned to individual years such that higher mortality occurred early in the 4-year intervals. Mortality/disappearance in the 8–11 year age interval was extremely high in this sample, but is not used here since migration and mortality are not distinguished in the published data.

Unsexed infants who died at all sites were evenly divided between male and female, and data reported for intervals longer than one year were divided up equally among intervals. These procedures led to fractions of chimpanzee years in the life table for some ages at some sites. Finally, all data from each yearly interval were summed across all sites to produce the synthetic life table. Standard discrete time demographic estimates were used. Yearly mortality rate (q_x) is calculated as number of deaths in a yearly interval/number of chimpanzees who began that yearly age interval. No correction was made for half years lived by those individuals who died in an interval or for those who emigrated during an interval since these data are available for only some sites. Yearly survival rate p_x is calculated as $1-q_x$, and probability of survival from birth to age x, l_x, is calculated as the product of all p_xs from age 0 to age $x-1$. Life expectancy at age x is the sum of all l_y values beginning with l_{x+1}, divided by l_x, and with an additional half year added (because the individual is assumed to live half a year in the year it dies).

Results

We combined unpublished mortality data from three long-term study sites with the published data from two other sites to form a synthetic life table (Tables 1 & 2). The

Table 1 The sample of individual risk years and deaths at each field site

	Females										Males									
	Gombe		Tai		Kibale		Mahale		Bossou		Gombe		Tai		Kibale		Mahale		Bossou	
Age	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die
0	50·5	10	33	4	10	0	44	10·5	11	1·5	60·5	13	27	3	10	1	48	15·5	11	1·5
1	42·5	4·5	29	4	10	0	29·5	5·5	9·5	1	48·5	4·5	24	4	11	1	31·5	10·5	9·5	1
2	38	1	24	5	8	0	23	3	8·5	0·5	43	3	21	3	11	2	21	1	8·5	0·5
3	35	2	20	0	8	1	20	2	8	0	38	0	18	1	9	1	18	3	8	0
4	34	1	20	0	7	0	17	1	7	1	36	3	18	1	6	1	14	0	7	1
5	33	1	19	7	6	0	16	0	6	0	32	1	15	2	4	0	14	0	6	1
6	32	0	14	2	7	0	13	1	6	0	29	1	12	4	4	0	11	0	5	1
7	30	1	16	1	8	0			6	0	31	0	9	1	5	0			4	0
8	29	1	14	1	8	0					32	1	9	0	5	0				
9	30	0	12	2	7	1					30	1	9	3	6	0				
10	33	1	15	1	4	0					28	2	6	0	6	0				
11	35	0	20	0	5	0					25	0	8	0	4	0				
12	36	1	23	0	5	0					27	1	10	0	4	1				
13	39	0	25	2	8	0					26	1	11	3	5	1				
14	37	0	23	1	8	0					25	1	9	3	4	0				
15	33	1	22	1	7	0					24	0	5	0	5	0				
16	31	0	23	0	6	0					25	1	7	0	5	0				
17	31	0	24	2	5	0					25	1	6	0	5	0				
18	30	1	22	4	5	0					24	1	7	1	5	0				
19	29	0	19	3	4	0					23	0	6	1	5	1				
20	29	1	15	1	5	0					23	1	6	0	5	0				
21	27	0	14	1	6	0					21	2	6	0	5	0				
22	26	0	13	2	6	1					19	0	7	1	7	0				
23	28	0	11	0	5	0					20	0	6	0	7	0				
24	29	1	9	3	4	0					20	0	7	2	6	0				
25	27	0	6	0	3	0					20	1	5	3	6	0				
26	25	1	9	1	3	0					18	2	2	1	5	0				
27	23	3	8	1	3	0					16	1	1	0	5	0				
28	18	2	8	0	3	0					14	1	1	0	5	0				
29	14	1	9	0	1	0					14	4	1	0	5	0				

Table 1 ***Continued***

	Females										Males									
	Gombe		Tai		Kibale		Mahale		Bossou		Gombe		Tai		Kibale		Mahale		Bossou	
Age	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die	Enter	Die
30	10	2	9	1	0	0					12	2	1	0	5	0				
31	9	0	7	0	0	0					11	0	1	0	4	0				
32	9	0	7	1	1	0					11	1	2	0	4	1				
33	9	1	6	2	6	0					11	2	2	0	3	0				
34	8	1	4	1	6	0					8	1	3	1	3	0				
35	7	0	3	0	7	0					7	0	2	0	2	0				
36	8	1	3	1	7	0					7	3	2	0	2	0				
37	7	0	2	0	7	0					4	1	2	0	2	0				
38	7	1	2	0	7	0					3	1	2	0	3	0				
39	5	2	2	1	5	0					2	0	2	1	2	0				
40	3	0	2	0	5	0					2	0	1	0	2	0				
41	2	0	2	0	5	0					2	0	1	0	2	0				
42	2	0	2	0	4	1					2	2	1	0	2	0				
43	2	1	2	0	5	1							1	0	2	0				
44	1	0	2	0	2	0							1	0	1	0				
45	1	1	2	1	3	1									1	0				
46			1	1	3	1									1	1				
47					2	0														
48					2	0														
49					2	0														
50					2	0														
51					2	0														
52					2	0														
53					2	1														
54					1	0														
55					1	0														
Total	1024·0	44·5	577·0	58·0	264·0	8·0	162·5	23·0	62·0	4·0	899·0	60·5	303·0	39·0	216·0	11·00	157·5	30·0	59·0	6·0

largest data set, Gombe, represents a total of 1923 chimpanzee years at risk with 105 deaths. Another 1360 individual years at risk covering all ages were recorded at the Taï and Kibale sites. Finally, published data on juvenile mortality only provides another 441 chimpanzee years at risk from Mahale and Bossou. The data contain about 30% more observations on females than males (2090 *vs.* 1635 chimapnzee years, respectively), but an approximately equal number of deaths to both sexes (138 female deaths *vs.* 147 male deaths). The resultant life tables are truncated at age 55, the oldest age estimate reported for an individual from any of the five sites. Although some sites show temporal heterogeneity in mortality, we have chosen to include all time periods and all deaths reported at each site. The data include viral epidemics (polio and respiratory epidemics at Gomba, Ebola and Taï, influenza and an "Aids-like" epidemic at Mahale), deaths from poaching, warfare, infanticide, cannibalism and predation.

Mortality rates are high in the synthetic life table, with life expectancy at birth being less than 15 years for both sexes. Infant mortality is about 20% in the first year, dropping to a minimum of about 3·5% between ages 10–15. At age 15 the life expectancy is about another 15 years. By age 30 the annual mortality rate is about 8·5% and life expectancy an additional eight years.

The life table also suggests that males experience higher mortality than females throughout the lifespan (logistic regression controlling for age, age^2 and study site: sex difference age 0–15, $P=0{\cdot}033$; sex difference age 16–40, $P=0{\cdot}071$). Life expectancy at birth is three years higher for females than males (14·6 years *vs.* 11·2 years, respectively). Only 27% of all males born, but 41% of all females born are expected to survive to age 15. Likewise, only 11% of males but 18% of females are expected to survive from age 15 to age 40.

The life tables at the five different study sites also show differences in survival with Kibale and Gombe showing best survival and Taï and Mahale worst survival (Figure 1). However, we cannot reject the null hypothesis that mortality data at all sites are drawn from a single mortality sample (GENMOD procedure in SAS with sites as random effects in logistic regression, age, age^2 and sex controlled, for age 0–14: Gombe $P=0{\cdot}12$, Taï $P=0{\cdot}15$, Kibale $P=0{\cdot}37$, Mahale $P=0{\cdot}25$, Bossou $P=1{\cdot}0$; for age 15–40: Gombe $P=0{\cdot}81$, Taï $P=0{\cdot}14$; Kibale $P=0{\cdot}11$).

The procedure of summing the raw data to create the life table makes sense if differences between the study sites are due mainly to sample size (as the above analysis suggests). However, if the differences are due mainly to ecological conditions, it might be more appropriate to construct a life table that weights data from each site equally. This procedure increases the sex difference in survival, but does not substantially change our conclusions. The site-weighted life table shows a change in life expectancy at birth of $+1{\cdot}1$ years for females but $-0{\cdot}5$ years for males. Life expectancy at age 15 is increased 0·4 years for females and is decreased 0·2 years for males.

Since our goal is to estimate the mortality profile of wild chimpanzees under conditions that may be typical of their natural history, we should consider whether the data include deaths that are "unnatural" for chimpanzees. We have included disease deaths in our analyses because even diseases acquired from human hosts may be part of chimpanzee natural history in areas where both species co-resided for long periods. However, removal of some observation periods that appear exceptional does not have a large effect on the synthetic life table. For example, removal of all data collected at Taï during the "Ebola virus period" of mortality (114 risk years and 25 deaths) increases the estimate of life expectancy at

Table 2 Synthetic life table for wild chimpanzees derived from five field sites

	Females						Males					
Age	Enter	Die	q_x	*5 yrq_x	l_x	e_x	Enter	Die	q_x	*5 yrq_x	l_x	e_x
0	**148·5**	**26·0**	**0·18**		**1·00**	**14·6**	**156·5**	**34·0**	**0·22**		**1·00**	**11·2**
1	120·5	15·0	0·12		0·82	16·6	124·5	21·0	0·17		0·78	13·1
2	101·5	9·5	0·09		0·72	17·8	104·5	9·5	0·009		0·65	14·7
3	91·0	5·0	0·05		0·65	18·6	91·0	5·0	0·05		0·59	15·1
4	85·0	3·0	0·04		0·62	18·7	81·0	6·0	0·07		0·56	15·0
5	**80·0**	**8·0**	**0·10**		**0·60**	**18·3**	**71·0**	**4·0**	**0·06**		**0·52**	**15·1**
6	72·0	3·0	0·04		0·54	19·3	61·0	6·0	0·10		0·49	15·0
7	60·0	2·0	0·03		0·51	19·1	49·0	1·0	0·02		0·44	15·6
8	51·0	2·0	0·04		0·50	18·8	46·0	1·0	0·02		0·43	14·9
9	49·0	3·0	0·06		0·48	18·5	45·0	4·0	0·09		0·42	14·2
10	**52·0**	**2·0**	**0·04**	0·03	**0·45**	**18·7**	**40·0**	**2·0**	**0·05**	0·04	**0·38**	**14·5**
11	60·0	0·0	0·00	0·03	0·43	18·4	37·0	0·0	0·00	0·06	0·37	14·3
12	64·0	1·0	0·02	0·02	0·43	17·4	41·0	2·0	0·05	0·07	0·37	13·3
13	72·0	2·0	0·03	0·02	0·42	16·7	42·0	5·0	0·12	0·06	0·35	12·9
14	68·0	1·0	0·01	0·02	0·41	16·2	38·0	4·0	0·11	0·06	0·31	13·6
15	**62·0**	**2·0**	**0·03**	0·02	**0·41**	**15·4**	**34·0**	**0·0**	**0·00**	0·06	**0·27**	**14·2**
16	60·0	0·0	0·00	0·03	0·39	14·9	37·0	1·0	0·03	0·04	0·27	13·2
17	60·0	2·0	0·03	0·04	0·39	13·9	36·0	1·0	0·03	0·03	0·27	12·5
18	57·0	5·0	0·09	0·04	0·38	13·4	36·0	2·0	0·06	0·04	0·26	11·9
19	52·0	3·0	0·06	0·05	0·35	13·6	34·0	2·0	0·06	0·05	0·24	11·5
20	**49·0**	**2·0**	**0·04**	0·06	**0·33**	**13·4**	**34·0**	**1·0**	**0·03**	0·05	**0·23**	**11·2**
21	47·0	1·0	0·02	0·04	0·31	13·0	32·0	2·0	0·06	0·04	0·22	10·5
22	45·0	3·0	0·07	0·04	0·31	12·2	33·0	1·0	0·03	0·04	0·21	10·2
23	44·0	0·0	0·00	0·04	0·29	12·1	33·0	0·0	0·00	0·06	0·20	9·5
24	42·0	4·0	0·10	0·04	0·29	11·1	33·0	2·0	0·06	0·06	0·20	8·5
25	**36·0**	**0·0**	**0·00**	0·05	**0·26**	**11·2**	**31·0**	**4·0**	**0·13**	0·07	**0·19**	**8·0**
26	37·0	2·0	0·05	0·07	0·26	10·2	25·0	3·0	0·12	0·08	0·17	8·1
27	34·0	4·0	0·12	0·06	0·25	9·7	22·0	1·0	0·05	0·11	0·15	8·2
28	29·0	2·0	0·07	0·08	0·22	10·0	20·0	1·0	0·05	0·10	0·14	7·6
29	24·0	1·0	0·04	0·08	0·20	9·7	20·0	4·0	0·20	0·08	0·13	6·9
30	**19·0**	**3·0**	**0·16**	0·07	**0·19**	**9·1**	**18·0**	**2·0**	**0·11**	0·10	**0·11**	**7·5**
31	16·0	0·0	0·00	0·08	0·16	9·7	16·0	0·0	0·00	0·11	0·09	7·4
32	17·0	1·0	0·06	0·10	0·16	8·7	17·0	2·0	0·12	0·10	0·09	6·4
33	21·0	3·0	0·14	0·07	0·15	8·2	16·0	2·0	0·13	0·08	0·08	6·2
34	18·0	2·0	0·11	0·09	0·13	8·5	14·0	2·0	0·14	0·13	0·07	6·0
35	**17·0**	**0·0**	**0·00**	0·08	**0·12**	**8·4**	**11·0**	**0·0**	**0·00**	0·13	**0·06**	**5·9**
36	18·0	2·0	0·11	0·06	0·12	7·4	11·0	3·0	0·27	0·13	0·06	4·9
37	16·0	0·0	0·00	0·08	0·10	7·3	8·0	1·0	0·13	0·14	0·05	5·6
38	16·0	1·0	0·06	0·08	0·10	6·3	8·0	1·0	0·13	0·16	0·04	5·3
39	12·0	3·0	0·25	0·06	0·10	5·7	6·0	1·0	0·17	0·09	0·03	5·0
40	**10·0**	**0·0**	**0·00**	0·09	**0·07**	**6·4**	**5·0**	**0·0**	*0·00*	0·14	**0·03**	**4·9**
41	9·0	0·0	0·00	0·13	0·07	5·4	5·0	0·0	0·00	0·13	0·03	3·9
42	8·0	1·0	0·13	0·07	0·07	4·4	5·0	2·0	0·40	0·10	0·03	2·9
43	9·0	2·0	0·22	0·16	0·06	4·0	3·0	0·0	0·00	0·13	0·02	3·5
44	5·0	0·0	0·00	0·25	0·05	4·0	2·0	0·0	0·00	0·25	0·02	2·5
45	**6·0**	**3·0**	**0·50**	0·27	**0·05**	**3·0**	**1·0**	**0·0**	**0·00**	0·14	**0·02**	**1·5**
46	4·0	2·0	0·50	0·26	0·02	4·5	1·0	1·0	1·00	0·25	0·02	0·5
47	2·0	0·0	0·00	0·31	0·01	7·5						
48	2·0	0·0	0·00	0·17	0·01	6·5						
49	2·0	0·0	0·00	0·00	0·01	5·5						
50	**2·0**	**0·0**	**0·00**	0·00	**0·01**	**4·5**						
51	2·0	0·0	0·00	0·10	0·01	3·5						
52	2·0	0·0	0·00	0·11	0·01	2·5						
53	2·0	1·0	0·50	0·13	0·01	1·5						
54	1·0	0·0	0·00	0·17	0·01	1·5						
55	**1·0**	**0·0**	**0·00**	0·25	**0·01**							

*Running 5 year average smooth of q_x.

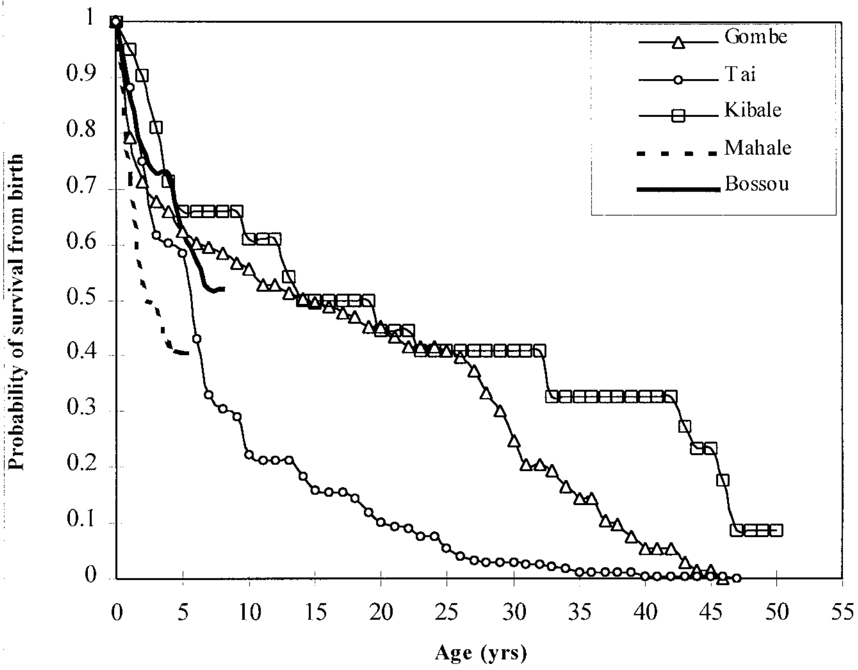

Figure 1. Age specific probability of survival from birth (l_x) for the five chimpanzee study sites mentioned in this paper.

birth in our synthetic table by only about 0·8 year and life expectancy at age 15 by about 3·1 years.

We also include human predation as part of the natural history of wild chimpanzee populations. In support of this assumption, faunal assemblages from several archeological sites suggest that humans often preyed upon great apes (Brooks & Robertshaw, 1990; Chen & Olsen, 1990; Harrison, 1996, 1998, 2001) long before the advent of modern weapons.

Our results strongly suggest that free-living chimpanzees experience lower survival than captive individuals in zoos or breeding colonies. Courtenay & Santow (1989), using a smaller sample from Gombe, also concluded that wild chimpanzees have lower survival in all age categories except perinatal. In our synthetic life table, from age two onward, there is no overlap in the standard errors for the survival curves of same-sex wild chimpanzees *vs.* those in breeding colonies (Figure 2). Juvenile mortality is also higher in wild chimpanzees than among reported zoo populations (Courtenay & Santow, 1989) (ages 0–14 logistic regression controlling for age, age^2, wild *vs.* captive, $P=0·03$) and adult mortality in the wild is marginally higher (ages 15–30 logistic regression controlling for age, age^2, wild *vs.* captive, $P=0·11$). These differences are probably due to a combination of advantages to captive chimpanzees including better nutrition, health care and vaccination programs, and the elimination of some natural hazards (e.g., predators, unchecked conspecific violence).

Comparison with other apes is more difficult due to the scarcity of demographic data on bonobos, gorillas and orang-utans in the wild. A recent study of bonobos (Furuichi

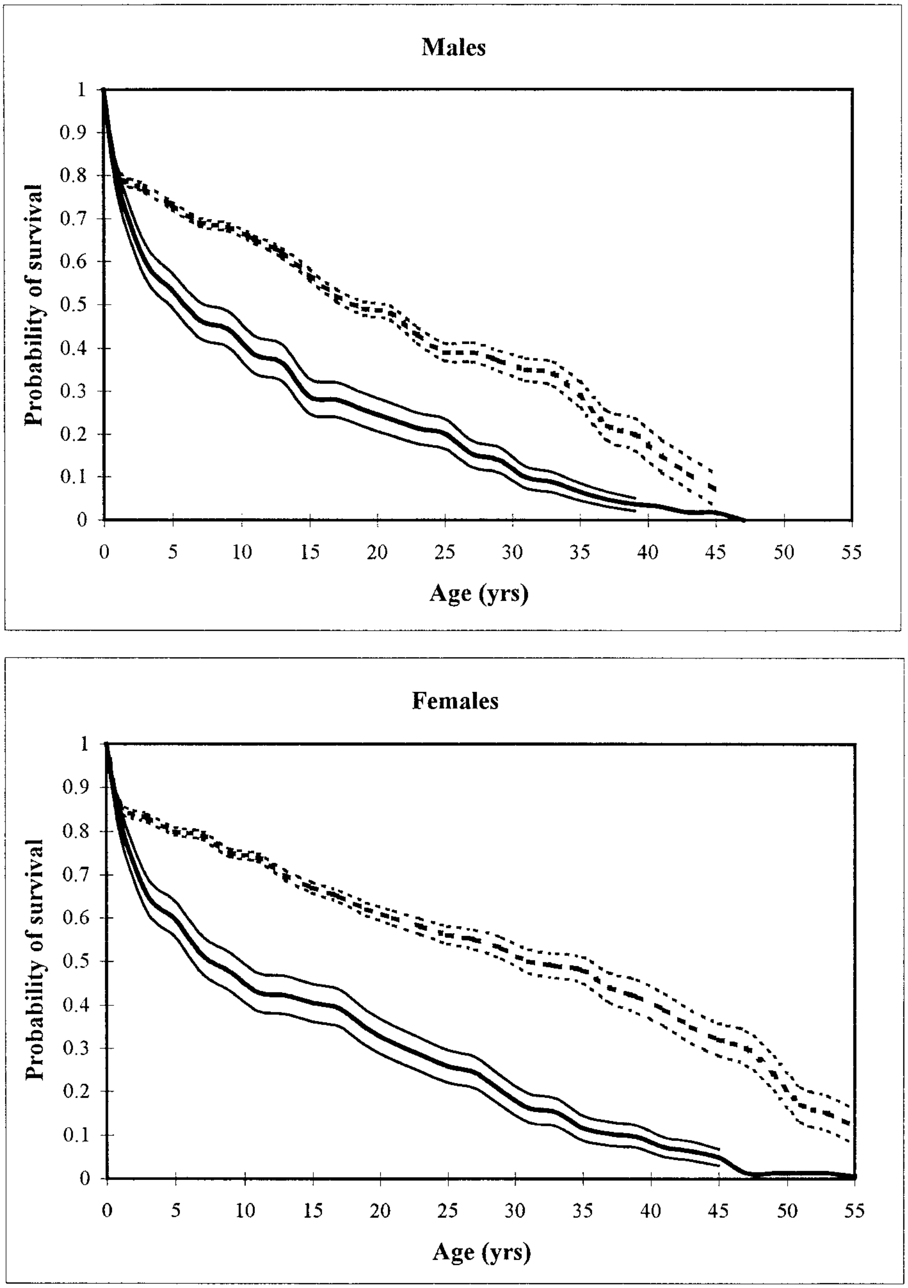

Figure 2. Age specific probability of survival from birth for wild chimpanzees (solid lines with 1 S.E. shown) and captive chimpanzees in breeding colonies (dotted lines with 1 S.E. shown). Standard error of survival is calculated as specified in Greenwood (1926). Captive date are adapted from Dyke *et al.* (1995, Figure 2).

et al., 1998), based on a small sample, shows 73% survival to age six, considerably higher than the 52% survival of chimpanzees to age six. The sparse demographic data on mountain gorillas suggest about 65% survival to age three (Robbins, 1995), nearly the same as that for female chimpanzees estimated here.

Comparison with modern hunter-gatherers

Because of human language we know a great deal more about the levels of human mortality in isolated, hunter-gatherer and tribal populations (e.g., Howell, 1979; Early & Peters, 1990; Hill & Hurtado, 1996; Early & Headland, 1998) than is known about chimpanzee mortality. For example, this study analyzes 3724 chimpanzee years at risk of death, whereas the demographic study of pre-contact Ache hunter-gatherers is based on 9978 person years at risk (Hill & Hurtado, 1996: ch. 6) and the well-known !Kung demographic analyses is based on 7556 person years at risk (Howell, 1979: ch. 4). Recent studies on hunter-gatherers during periods when they were dependent on wild foods, had no modern weapons and no modern medical treatment or state intervention in patterns of warfare and violence, show that all human hunter-gatherers for which there are good demographic data experience higher survival than we report here for wild chimpanzees (Kaplan *et al.*, 2000). A detailed comparison of chimpanzees with the Ache hunter-gatherers of Paraguay, for example, shows that chimpanzees experience higher mortality throughout the entire lifespan after infancy (logistic regression with age and sex controlled: ages 0–15 parameter estimate for Ache $= -0{\cdot}8893$, $P=0{\cdot}001$; Ages 16–40 parameter estimate $-1{\cdot}7584$, $P=0{\cdot}0001$). Even the site of lowest chimpanzee mortality, Kibale, shows only 9% of chimpanzees surviving to age 50, whereas 42% of Ache foragers survived to age 50 in the pre-contact forest-living period.

The data suggest that wild chimpanzees experience about 3·5 times the early adult mortality rate estimated for hunter-gatherers (4% per year *vs.* 1·2% per year). According to mammalian life history models (Charnov, 1993; Hill, 1993; Hawkes *et al.*, 1998) this should lead to earlier sexual maturity and more rapid senescence in chimpanzees. Both of these predictions appear correct. Chimpanzee females first give birth at approximately 14 years of age (Nishida *et al.*, 1990; Pusey, 1990; Tutin, 1994; Wallis, 1997; Boesch & Boesch, 2000) whereas humans in traditional settings generally experience first birth around age 19 (Wood, 1994; Hill & Hurtado, 1996). The respective mortality curves (Figure 3) also show that chimpanzees begin to senesce about 20 years earlier than do, for example, Ache hunter-gatherers. The mortality rate between 30–35 years is seven times higher among wild chimpanzees than among the Ache (12/123 chimps died *vs.* 14/1011 Ache who died in this interval). Importantly, captive chimpanzees also senesce at about the same age as wild chimpanzees, suggesting that genetically based mechanisms of aging differ between *Homo* and *Pan*. The timing of chimpanzee senescence, expressed both in captivity and in the wild, is consistent with life history theory, which suggests that natural selection is weak beyond ages to which few individuals survive during their evolutionary history (Hamilton, 1966).

Data on oldest survivors in our long term study sites also support our conclusions about the chimpanzee lifespan. The oldest individual in the Gombe dataset is a female who died at an assigned age of 45 and was first observed at an estimated age of 24. The oldest individual in the Taï dataset is a female who died at an assigned age of 46 and was first observed at an estimated age of 33. The oldest individual in the Kibale dataset is a living female estimated to be

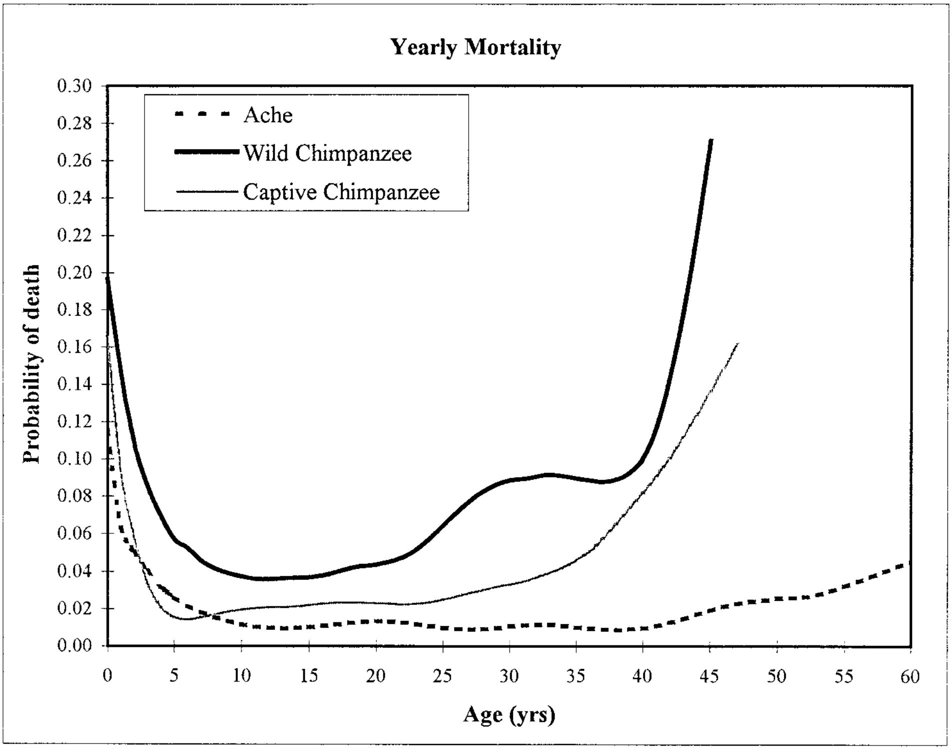

Figure 3. Age specific yearly probability of death (average for both sexes, spline smooth in SAS) for wild chimpanzees, captive chimpanzees (Dyke *et al.*, 1995) and Ache hunter-gatherers (Hill & Hurtado, 1996). Captive chimpanzees show lower early adult mortality than wild chimpanzees, but both populations show increased mortality due to senescence beginning in the early twenties.

aged 55. The oldest male at Kibale disappeared in 1996 (still looking strong). He was described as "past prime" when first observed in 1980, and is accordingly estimated to be at least 46 years old at the time of death.

Nevertheless, some field workers have commented that they believe some free-living chimpanzees are older than the oldest individuals with good age estimates in our life table. Wrangham reports two very senile females who were believed to be well over 45 when observed (by comparison to known aged individuals observed at Gombe). Boesch also compared some of the oldest chimpanzees at Taï to those observed in Gombe of known age and concludes that they were probably well past age 45. Finally, Nishida (personal communication) mentions a white-haired and bent old male who continued to live another 13 years after he was identified, and he calculated that the mother of an alpha male who was first observed from age 15, must have been at least 48 years old at the time of her death if he was her first offspring. These anecdotal reports, along with life tables on captive chimpanzees suggesting that some live to the age of 60 and beyond, make us cautious about the current estimate of mortality rates beyond age 40 among wild chimpanzees. However, another independent estimate of chimpanzee life expectancy at age 35 based on the mortality doubling rate, shows good agreement with our measured estimate. Our current sample includes 123 chimpanzee years at risk in the 35–39 year age interval, a large enough sample to provide some confidence in the mean 10% mortality per year at that age. The chimpanzee life table shows a mortality doubling every 12·5 years from adulthood (age 12) to age 35. If the mortality doubling rate continues beyond age 35 and if the 10% death rate is correct for chimpanzees in the 35–40 year class, the average life expectancy at age 35 should be only another 5·9 years. This is quite close to our life table estimate of e_{35} at 6·3 years estimated only from observatios on chimpanzees over age 35. Furthermore, the mortality rate from known-aged individuals only at Gombe during this age interval is 8% per year, close to the 10% estimate we obtained using all individuals, even those of less certain ages. Thus, we are reasonably confident that the high mortality rates we estimate for older chimpanzees will be supported as better data on individuals of known age becomes available in the future. Of course, there may still be some exceptionally healthy or lucky chimpanzees who live well beyond the average lifespan.

The life table data also have alarming implications for chimpanzee conservation. Given the mean age at first birth for chimpanzee females (about 14·3 years), the probability of surviving to that age (about 0·41), the mean adult lifespan of chimpanzee females (about 16·2 years after first birth), and the mean interbirth interval (66·7 months) (see Kaplan *et al.*, 2000), we can estimate that each wild chimpanzee female born can expect to produce only 0·80 daughters on average. This is well below population replacement level, indicating that current chimpanzee populations may be in danger of extirpation. However, only very small changes in the parameters are required to produce zero growth. For example, increasing the probability of survival to adulthood by 4%, adding one year to the mean adult lifespan, and reducing mean interbirth interval by 10% leads to a stable population with zero growth. Since both mortality and fertility estimates show high variation across populations, we cannot be sure at this time which of these estimates is unrepresentative of chimpanzee evolutionary history. However, the data do suggest that we should be very concerned about the continued viability of chimpanzee populations in the five study sites reported here.

Summary

In order to assess different models of ape and human life history divergence we need comparable mortality data on humans and chimpanzees living under conditions that may be typical over long periods of evolutionary time. Recent data from foraging societies during periods when they were dependent on wild foods, had no modern weapons (to deter predators) and no modern medical treatment or state intervention in patterns of warfare and violence have provided a good understanding of "natural" human mortality levels. The same quality of data for chimpanzees has not been available, primarily due to problems of sample size. This study provides the first life table for wild chimpanzees derived from a large enough sample that the results are likely to be robust. Our data show that wild chimpanzees suffer high mortality relative to human foragers. Life expectancy is less than 15 years, and adult life expectancy is only an additional 15 years. Modern human foragers generally have twice the life expectancy at birth and more than twice the life expectancy once they reach adulthood (Kaplan *et al.*, 2000). These observations should lead researchers to consider when the hominid–ape divergence in mortality pattern evolved and what were its causes.

Chimpanzee data also show that males experience higher mortality than females. This is consistent with sexual selection theory, but a detailed analyses of causes of death should provide more information on

the mechanism. While males may experience more trauma due to conspecific violence, this must not be the cause of the differences in juvenile mortality, which seem more likely to be related to differential disease resistance. Finally, the data are suggestive of differences in mortality across current chimpanzee study sites. If this is true, discovering the causes of these differences may tell us a good deal about chimpanzee ecology and the evolution of the chimpanzee life history.

We have just entered an exciting era in which both chimpanzee and human life history traits under natural conditions can be established with some confidence. This should lead to new theoretical and empirical research concerning the differences between the two species as well as examination of the factors that determine mortality variation between ecologies and through time. Understanding such variation is certain to have wide reaching ramifications for studies of human longevity, and the evolution of social organization and behavior in both species.

Acknowledgements

KH would like to thank Jane Lancaster for helping accumulate the data and Garnett McMillan for statistical help.

References

Boesch, C. & Boesch, H. (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Brooks, A. S. & Robertshaw, P. (1990). The glacial maximum in tropical Africa: 22000–12000 BP. In (O. Soffer & C. Gamble, Eds) *The World at 18,000 BP*, Vol. 1, pp. 121–169. London: Unwin Hyman.

Charnov, E. L. (1993). *Life History Invariants*. Oxford: Oxford University Press.

Chen, C. & Olsen, J. (1990). China at the last Glacial Maximum. In (O. Soffer & C. Gamble, Eds) *The World at 18,000 BP*, Vol. 1, pp. 276–295. London: Unwin Hyman.

Courtenay, J. & Santow, G. (1989). Mortality of wild and captive chimpanzees. *Folia primatol.* **52,** 167–177.

Dyke, B., Gage, T., Alford, P., Swenson, B. & Williams-Blangero, S. (1995). Model life table for captive chimpanzees. *Am. J. Primatol.* **37,** 25–37.

Early, J. & Headland, T. (1998). *Population Dynamics of a Philippine Rain Forest People*. Gainsville: University of Florida Press.

Early, J. & Peters, J. (1990). *The Population Dynamics of the Mujacai Yanomamo*. New York: Academic Press.

Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C. & Kano, T. (1998). Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* **19,** 1029–1044.

Greenwood, M. (1926). Reports on Public Health and Statistical Subjects 33, Appendix I. London: HMSO.

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *J. Theoretical Biol.* **12,** 12–45.

Harrison, T. (1996). The paleoecological context at Niah Cave, Sarawak: Evidence from the primate fauna. *Bulletin of the Indo-Pacific Association* **14,** 90–100.

Harrison, T. (1998). Vertebrate faunal remains from Madai caves (MAD 1/28), Sabah, East Malaysia. *Bulletin of the Indo-Pacific Association* **17,** 85–92.

Harrison, T. (2001). Archeological and ecological implications of the primate fauna from prehistoric sites in Borneo. *Bulletin of the Indo-Pacific Association* **20,** 133–146.

Hawkes, K., O'Connell, J., Blurton-Jones, N., Alvarez, H. & Charnov, E. (1998). Grandmothering, menopause and the evolution of human life histories. *Proc. natn. Acad. Sci. USA* **95,** 1336–1339.

Hill, K. (1993). Life history theory and evolutionary anthropology. *Evol. Anthropol* **2,** 78–88.

Hill, K. H. & Hurtado, A. M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.

Howell, N. (1979). *Demography of the Dobe !Kung*. New York: Academic Press.

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence and longevity. *Evol. Anthropol* **9,** 156–184.

Nishida, T., Takasaki, H. & Takahata, Y. (1990). Demography and reproductive profiles. In (T. Nishida, Ed.) *The Chimpanzees of the Mahale Mountains*, pp. 3–97. Tokyo: University of Tokyo Press.

Pusey, A. (1990). Behavioral changes at adolescence in chimpanzees. *Behaviour* **115,** 203–246.

Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour* **132,** 21–47.

Sugiyama, Y. (1994). Age-specific birth rate and lifetime reproductive success of Chimpanzees at Bosou, Guinea. *Am. J. Primatol.* **32,** 311–318.

Tutin, C. E. G. (1994). Reproductive success story: variability among chimpanzees and comparison with gorillas. In (R. W. Wrangham, W. C. McGrew, F.

de Waal & P. Helte, Eds) *Chimpanzee Cultures*, pp. 181–193. Cambridge: Harvard University Press.

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *J. Reprod. Fert.* **109,** 297–307.

Wood, J. (1994). *Dynamics of Human Reproduction*. New York: Aldine de Gruyter.

Wrangham, R. W., Clark, A. P. & Isabirye-Basuta, G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In (T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal, Eds) *Topics in Primatology. Vol. 1: Human Origins*, pp. 81–98. Tokyo: University of Tokyo Press.