



## Life history of wild Sumatran orangutans (*Pongo abelii*)

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### Abstract

We present life history data on wild Sumatran orangutans gleaned from a 32-year and a 5.5-year study. Estimated age at first reproduction was 15.4 years. At 9.3 years, the average interbirth interval for this population is the longest ever recorded for any great ape population, significantly longer than that of a Bornean orangutan population. We find that age-specific mortality of Sumatran orangutans does not differ between sexes and is significantly lower than that of wild chimpanzees. We conclude that orangutan life history is the slowest among extant great apes. In accordance with their slow life history, longevity in the wild is estimated to be at least 58 years for males and at least 53 for females. We find no evidence for menopause. These data suggest that compared to the ancestral state, humans have undergone less of an increase in longevity than commonly assumed, and have experienced selection on earlier cessation of reproduction.

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### Introduction

Great ape life histories are of great interest for two main reasons. First, great apes are the

primates with the largest body sizes and the slowest life histories, and such extreme values are especially useful to test hypotheses about life history evolution (Kappeler and Pereira, 2003; Purvis and Harvey, 1995; Ross and Jones, 1999). Second, life-history information on great apes is uniquely relevant for firmly establishing the derived features of human life history and thus the changes that took place during hominin evolution.

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Nonetheless, it has been difficult to obtain life history data on great apes due to their longevity. As a result, great apes are underrepresented in life history comparisons (Kappeler and Pereira, 2003), except for the chimpanzee (*Pan troglodytes*: Nishida et al., 1990; Boesch and Boesch-Achermann, 2000; Hill et al., 2001) and to some extent the gorilla (*Gorilla gorilla*: Watts, 1991; Yamagiwa and Kahekwa, 2001). There is, however, a serious lack of data from the orangutan (*Pongo* spp.) and bonobo (*Pan paniscus*). As a result, captive demography is often used to characterize life history parameters, which are then used in comparative analyses (e.g., Ross and Jones, 1999; Kappeler and Pereira, 2003). However, because of systematic differences between wild and captive life histories (e.g., Zihlman et al., 2004), such substitution may reduce the resolution of comparative tests.

The aim of this paper is to partly fill the gap for orangutans by providing an overview of demographic data from a natural population of Sumatran orangutans at Ketambe (32 years) and Suaq Balimbing (5.5 years) to infer the life history of Sumatran orangutans. In addition, we compare Sumatran with Bornean orangutans, and orangutans with chimpanzees, bonobos, gorillas, and humans.

## Methods

### *Study site and population*

The Ketambe research station (3° 41' N; 97° 39' E) is located in the Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia. The research area was mostly covered by pristine rainforest, from the alluvial lowlands at ca. 350 m above sea level up to higher altitudes around 1000 m above sea level (Rijksen, 1978; van Schaik and Mirmanto, 1985).

Orangutan research at the site started in 1971, when Herman Rijksen established the research station. The following main researchers have worked in the area: Herman Rijksen (1971–1974), Chris Schürmann (1975–1979), Sugardjito (1980–1983), Suharto (1984–1987),

Tatang Mitra Setia (1988–1991), Suci Utami (1992–1995), Abu Hanifah Lubis (1996–1998), and Serge Wich (1999–2003). In addition, many students worked at the site for shorter periods. Continuity across study periods of individual main researchers was provided in four ways: (i) photographs were handed down; (ii) long-term field assistants bridged periods of individual researchers; (iii) previous researchers often revisited and provided feedback on photographs sent to them; and (iv) DNA samples of individuals (see Utami et al., 2002). In all, the orangutan research has produced ca. 50,000 h of focal animal samples, and has continued more or less continuously until the end of 2002, when it had to be halted due to the political situation in Aceh. Nevertheless, we were able to visit the area on several occasions to keep track of the demography of the orangutans in the study population. In August 2003, S.A. Wich resumed research there.

Most animals in the sample were wild. However, two ex-captive females were left in the area after rehabilitation efforts in the area were terminated in 1978. These females were included in the sample used here, but we began using their data only three years after we stopped provisioning them. Several analyses were repeated without these females, as there was a risk that they might produce a bias. Dominance ranks of females were determined from agonistic interactions, and taken from Utami et al. (1997) and additional unpublished records.

### *Estimating orangutan ages*

Because wild orangutans are likely to live for decades, even a 32-year study will produce neither a large sample nor life-history estimates for older individuals. For individuals that were not known from birth (younger and older immigrants as well as older residents already present at the start of the study), we therefore developed a procedure to derive both *conservative minimum estimates* and *realistic minimum estimates* of their ages. We use the term “conservative” to indicate the earliest age at which an animal was observed or estimated to enter a life stage, and “realistic” to indicate the age at which the average animal in the population

entered the life stage. Both estimates are “minimum” because they refer to age at entry into the particular life stage, rather than the mean age in this life stage.

We used the following procedure to develop conservative estimates of the age at which animals of unknown age entered different life-stages. We estimated the age of younger animals by comparing them directly with photographs of orangutans with known ages (i.e., born during the study). Older animals were compared with a composite estimate of ages for the major changes in life stage. This composite was produced in three steps. First, we assessed the developmental trajectory of all known-age animals by comparing photographs taken at different ages, and recorded the ages at which major changes in appearance occurred. We consider the estimates thus derived to be conservative, because, although they are based on the averages, the variation in the timing of entry at these earlier life stages is modest (see Results). Second, we used this developmental trajectory to estimate the ages at the time of the earliest photographs of individuals that immigrated into the study area during the study or that were resident at the start of the study. Third, we then compared photographs at different intervals after that time to estimate the earliest ages at which individuals entered subsequent life stages (see Table 1).

We also developed realistic minimum estimates because animals spend a highly variable number of years in the later life stages, and the conservative

minimum estimate may lead to serious underestimates. This was especially needed (and possible) for the large unflanged and flanged male classes (see Table 1).

Here, we describe both procedures in more detail. For adolescents (weaned individuals showing some sexual activity), age estimation was straightforward, as several infants of both sexes born during the study are now adolescents or already past that stage. Therefore, minimum age estimates for adolescents were accurate and both estimates were set at 10 years.

For adult females, the conservative minimum estimate was based on known mean age at first reproduction (AFR) in this population (see Results). If a female with infant was accompanied by an independent immature animal, or if she appeared to have had a previous infant (as suggested by large body size and large nipples and/or effects of aging such as more bald spots on the body and more wrinkles on the face than young females), the realistic minimum estimate was set at 1 AFR + 1 interbirth interval (i.e., 24).

Small unflanged males were assigned the observed age at which known-age adolescent males in the study population acquired “subadult” characteristics, probably coinciding with the attainment of full reproductive maturity (Kingsley, 1982; Utami et al., 2002), including a developing beard, long hair on the shoulders and arms, completely dark facial coloration, and usually hard rims of undeveloped cheek pads (Rijksen, 1978). As there were four males in the study population that were followed from birth into this life-phase, it was relatively easy to classify newly encountered small unflanged males. These males were also smaller than middle-aged adult females. Because there was little known variation in the age at entry into this life stage, conservative and realistic minimum estimates were the same.

For medium unflanged males, which are similar in size to full-grown adult females, we used the conservative minimum estimate based on known-aged medium unflanged males. The realistic estimate has to be the same, because no obvious variability in the rate at which males move through the small unflanged stage has been observed in the known animals.

Table 1

Conventions used to estimate the age of animals in the sample that were not born during the study (see text for detailed explanation).

Class	Conservative minimum estimated age at first encounter	Realistic minimum estimated age at first encounter
Adolescent	10	10
Adult female	15	15 or 24
Small unflanged male	14	14
Medium unflanged male	21	21
Large unflanged male	23	29
Flanged male	24	35

For large unflanged males, which are larger than the largest adult females, conservative minimum estimates are based on the minimum age of medium unflanged males of known age plus the minimum time period in which known medium unflanged males grew into large unflanged males, hence an age of 23 (21 + 2) years. Several other males that were already in the medium unflanged stage when first encountered took from five to a maximum of 18 years to enter into the large unflanged stage, with an average of around eight years ( $n = 6$ ). The realistic minimum estimate was therefore set at 29 (21 + 8) years.

The conservative minimum age of flanged males was based on the conservative minimum age of large unflanged males plus the minimum period that is needed to develop flanges (approximately one year, based on observations of known males in the study population and captive individuals; Rijkssen, 1978; Kingsley, 1982). However, since males in our study population remained in the large unflanged male class for an average of six years ( $n = 4$ ), we adopted a realistic minimum age estimate at entry into the flanged male stage of 35 (29 + 6) years.

### Demography

For the calculation of interbirth intervals we included only cases where the infant survived until weaning (complete intervals) or was alive at the end of observation (right-censored intervals). Left-censored intervals (i.e., females first encountered with an infant of unknown age) were not included.

In Ketambe, death was observed directly in two cases (one adult male and one mother-infant pair). In all other cases, death was inferred if one of the following occurred: (i) the individual was a resident and looked ill when last observed; (ii) the individual was a resident and disappeared; or (iii) the individual was a yearly or bi-yearly visitor to the area (cf. te Boekhorst et al., 1990), but was not seen for more than five years after the last observation. Five years is longer than the longest interval that an individual disappeared and reappeared again and it therefore seems reasonable to assume that these individuals had died. In such cases, age at death was conservatively set in the

year that the individual was last observed. In Suaq Balimbing, the death of a dependent infant was inferred within a month from its disappearance from the mother's vicinity.

To construct a life-table we used three methods. First, we constructed separate life-tables for all male and female infants born during the study. This yielded two reliable life-tables for individuals that were followed from birth onward. One infant of undetermined sex disappeared before the age of one year, and was divided evenly between male and female life-tables (Hill et al., 2001). Because the study started in 1971 and data used for this paper were collected until 2003, this life table cannot be used to estimate mortality of older individuals. Therefore, we also constructed a life-table for individuals for whom we conservatively estimated their ages (Table 1). This life-table was then combined with the first life-table (i.e., that of individuals born during the study) to construct the second, overall life-table. Finally, we created a third life-table that also included realistic age estimates for individuals not born during the study period (Table 1).

For the life table, we used standard discrete time measures (e.g., Hill et al., 2001). Yearly mortality rate ( $q_x$ ) was used to calculate yearly survival rate  $p_x (= 1 - q_x)$ . The probability of surviving from birth to age  $x$  ( $l_x$ ) is calculated as the product of all  $p_x$  values from age 0 to age  $x-1$ . The life expectancy at age  $x$  ( $e_x$ ) is the sum of all  $l_x$  values, starting at  $l_{x+1}$ , divided by  $l_x$ , and with half a year added due to the fact that individuals are assumed to live half a year in the year it dies.

### The Suaq sample

A smaller sample was collected at Suaq Balimbing (3°04' N; 97°26' E), where orangutans were followed continuously from early 1994 until September 1999. Suaq is a coastal swamp at near sea level, located some 70 km southwest of Ketambe, where orangutans occur at higher density, are more likely to form travel bands (van Schaik, 1999), and use tools regularly (van Schaik et al., 2003). Here, we report on infant and juvenile survival, using infants of known ages, as well as

those whose ages were estimated using various comparisons with known-age animals elsewhere and photographs (see van Noordwijk and van Schaik, *in press*, for details). Although we did not have a long enough time period to estimate adult mortality, we did not record any deaths among resident individuals (those recorded each year).

## Results

### *Sex ratio at birth*

A total of 29 births were recorded during the study period. Of the 28 sexed infants, 16 were male and 12 female, which yields a proportion of males at birth of 0.57. This ratio is not significantly different from 0.50 (binomial test, ns). There was no significant correlation between female dominance and percentage of male offspring (Spearman correlation:  $r_s = -0.383$ , ns,  $n = 9$ ).

### *Age at first reproduction*

There are only three females for which we know birth year and therefore age of producing first offspring (9.0, 12.5 and 15.5 years, average 12.3). For another seven females we inferred the age of first reproduction by estimating their own birth year from the age estimate when first observed. The mean age of first reproduction among all of them was 14.4 years (SD = 2.4, range 9–18). Of the known-age females, two were born to a reintroduced mother, the first one during provisioning, and the other one four years after provisioning ended. Because it is possible that a better physical condition of the mother could have caused early maturation, we also removed these two females from the sample. If we also exclude one reintroduced females of estimated age, we obtain a mean value of 15.4 years ( $n = 7$ , SD = 1.6, range 13–18). We consider this latter value to be the more accurate one.

### *Interbirth intervals*

During the study period, 16 complete interbirth intervals were recorded for nine females. The mean

of these intervals was 111.3 months ( $n = 16$ , SE = 6.3), or 9.3 years. If the average closed interbirth interval was calculated per female, the average interbirth interval among females was 110.1 ( $n = 9$ , SE = 5.8), or 9.2 years. If we treat all interbirth intervals as separate events and include right-censored data (i.e., incomplete intervals), a Kaplan-Meier survival analysis yields an average interbirth interval of 111.5 months ( $n = 23$ , SE = 6.3, 95% CI = 99.3–123.8) or 9.3 years.

Excluding the two ex-captive reintroduced females produces a mean for complete interbirth intervals of 110.6 months ( $n = 13$ , SE = 7.9), or 9.2 years, and a mean of 111.7 months, or 9.3 years, if the female means are averaged ( $n = 7$ , SE = 7.5). Including censored intervals, the mean interbirth interval for the locally born females becomes 111.1 months ( $n = 19$ , SE = 7.5, 95% CI = 96.3–125.8), or 9.3 years, for the sample including complete and censored intervals. In short, 9.3 years is the best estimate for the interbirth intervals following surviving infants in this population.

Variation in interbirth intervals did not depend on the sex of the last infant: The Kaplan-Meier estimates for intervals were 111.5 months ( $n = 14$ , SE = 8.0, CI = 95.8–127.1) following males and 110.8 months ( $n = 9$ , SE = 11.3, CI = 88.7–132.9) following females. Analysis of only completed intervals gives the same result ( $n_{\text{male}} = 11$ ,  $n_{\text{female}} = 5$ , U = 28.5, ns).

Interbirth intervals showed variation between females, but could not be explained by female rank (Spearman correlation:  $r_s = -0.281$ ,  $n = 9$ , ns; ranking based on Utami et al. [1997], and Wich [unpubl. data]. No relationship with age was detected ( $r_s = -0.067$ ,  $n = 14$ , ns), nor was there any indication of a non-linear effect of age.

### *Infant and juvenile survival*

Only two infants out of 29 born died before the first year (one of them because his mother died), bringing infant mortality in the first year to 6.9%. No infants died between the ages of one and three. Two individuals died during the juvenile life phase, ages 4 and 7, respectively.

The smaller data set for Suaq (Table 2b) shows a somewhat higher infant mortality, with four

Table 2a  
Synthetic life table of realistic age estimates for Ketambe

Age	Females					Males				
	Enter	Die	$q_x$	$l_x$	$e_x$	Enter	Die	$q_x$	$l_x$	$e_x$
0	13.5	1.5	0.11	1.00	28.78	15.5	0.5	0.03	1.00	33.68
1	12	0	0.00	0.89	31.32	15	0	0.00	0.97	33.79
2	10	0	0.00	0.89	30.32	15	0	0.00	0.97	32.79
3	10	0	0.00	0.89	29.32	15	0	0.00	0.97	31.79
4	8	0	0.00	0.89	28.32	14	1	0.07	0.97	30.79
5	7	0	0.00	0.89	27.32	13	0	0.00	0.90	32.12
6	8	0	0.00	0.89	26.32	11	0	0.00	0.90	31.12
7	8	0	0.00	0.89	25.32	10	1	0.10	0.90	30.12
8	10	0	0.00	0.89	24.32	10	0	0.00	0.81	32.41
9	11	0	0.00	0.89	23.32	10	0	0.00	0.81	31.41
10	8	2	0.25	0.89	22.32	6	1	0.17	0.81	30.41
11	8	0	0.00	0.67	28.59	4	0	0.00	0.67	35.39
12	7	0	0.00	0.67	27.59	5	0	0.00	0.67	34.39
13	8	0	0.00	0.67	26.59	4	0	0.00	0.67	33.39
14	8	0	0.00	0.67	25.59	11	0	0.00	0.67	32.39
15	7	0	0.00	0.67	24.59	10	0	0.00	0.67	31.39
16	6	0	0.00	0.67	23.59	10	0	0.00	0.67	30.39
17	6	0	0.00	0.67	22.59	10	0	0.00	0.67	29.39
18	6	0	0.00	0.67	21.59	10	0	0.00	0.67	28.39
19	6	0	0.00	0.67	20.59	10	0	0.00	0.67	27.39
20	6	0	0.00	0.67	19.59	8	0	0.00	0.67	26.39
21	6	0	0.00	0.67	18.59	12	0	0.00	0.67	25.39
22	6	0	0.00	0.67	17.59	12	0	0.00	0.67	24.39
23	7	0	0.00	0.67	16.59	12	0	0.00	0.67	23.39
24	12	1	0.08	0.67	15.59	11	0	0.00	0.67	22.39
25	11	0	0.00	0.61	15.96	11	1	0.09	0.67	21.39
26	11	1	0.09	0.61	14.96	10	0	0.00	0.61	22.48
27	9	1	0.11	0.56	15.40	10	0	0.00	0.61	21.48
28	7	0	0.00	0.49	16.27	9	0	0.00	0.61	20.48
29	7	1	0.14	0.49	15.27	9	0	0.00	0.61	19.48
30	6	1	0.17	0.42	16.73	9	0	0.00	0.61	18.48
31	5	0	0.00	0.35	18.97	9	0	0.00	0.61	17.48
32	5	0	0.00	0.35	17.97	8	0	0.00	0.61	16.48
33	5	0	0.00	0.35	16.97	7	0	0.00	0.61	15.48
34	5	0	0.00	0.35	15.97	6	0	0.00	0.61	14.48
35	5	0	0.00	0.35	14.97	14	1	0.07	0.61	13.48
36	4	0	0.00	0.35	13.97	13	1	0.08	0.57	13.47
37	4	0	0.00	0.35	12.97	12	0	0.00	0.53	13.56
38	4	0	0.00	0.35	11.97	11	0	0.00	0.53	12.56
39	4	0	0.00	0.35	10.97	10	0	0.00	0.53	11.56
40	2	0	0.00	0.35	9.97	9	0	0.00	0.53	10.56
41	2	0	0.00	0.35	8.97	9	2	0.22	0.53	9.56
42	2	0	0.00	0.35	7.97	7	0	0.00	0.41	11.14
43	2	0	0.00	0.35	6.97	7	0	0.00	0.41	10.14
44	2	0	0.00	0.35	5.97	6	0	0.00	0.41	9.14
45	2	0	0.00	0.35	4.97	6	0	0.00	0.41	8.14
46	2	0	0.00	0.35	3.97	6	0	0.00	0.41	7.14
47	2	1	0.50	0.35	2.97	6	0	0.00	0.41	6.14
48	1	0	0.00	0.18	4.45	6	0	0.00	0.41	5.14
49	1	0	0.00	0.18	3.45	6	0	0.00	0.41	4.14
50	1	0	0.00	0.18	2.45	6	2	0.33	0.41	3.14
51	1	0	0.00	0.18	1.45	3	1	0.33	0.27	3.46

Table 2a (continued)

Age	Females					Males				
	Enter	Die	$q_x$	$l_x$	$e_x$	Enter	Die	$q_x$	$l_x$	$e_x$
52	1	0	0.00	0.18	0.45	2	0	0.00	0.18	3.95
53						2	1	0.50	0.18	2.95
54						1	0	0.00	0.09	4.39
55						1	0	0.00	0.09	3.39
56						1	0	0.00	0.09	2.39
57						1	0	0.00	0.09	1.39
58						1	1	1.00	0.09	0.39

Notes:  $q_x$  = mortality rate;  $l_x$  = probability of survival from birth to age  $x$ ;  $e_x$  = life expectancy at age  $x$ . See text for further explanation.

infant deaths recorded for infants aged one and two years, although all other infants and juveniles survived, leading to a survival of ca. 56% until age 11, compared to 67% in the far larger Ketambe sample. No juvenile deaths were recorded. The higher infant mortality may be a response to recent disturbance, as two of the infants died after extensive illegal logging had begun and because all but one female at the beginning of the study were accompanied by infants.

#### Synthetic life-table

The results of the life table with realistic minimum age estimates are presented in Tables 2a and 2b. These results indicate that there was no significant difference in the age-specific mortality rates of female and male orangutans when realistic age estimates were used (logistic regression controlling for age and age<sup>2</sup>;  $P = 0.338$ ). Using conservative minimum estimates gave a similar result (Fig. 1a, b).

#### Longevity and age at last reproduction

Several individuals present at the start of the study are still alive. By using their estimated ages at the start of the study we can derive reasonable longevity estimates. When we used conservative minimum ages, the oldest surviving female in the population is 44 years old, with two others with an age of 39. With realistic minimum estimates the oldest female alive is about 53. The oldest female (44 or 53 depending on conservative or realistic

age estimate) in the Ketambe population gave birth to her last infant at the age of 41 or 50 and still appeared healthy. Two other healthy-looking females gave birth at the age of 38 (irrespective of estimate used).

The oldest male in the area was 47 using conservative minimum age estimates; several other males died between 39 and 42. Using realistic estimates, the oldest male was 58 when he died and several others between 50 and 53 at death. Irrespective of the age estimate used, the oldest male currently alive in the population is estimated to be 50, with several others between 40 and 47 years old. All these males still appear strong (i.e., no bald areas on the body and strong muscles that keep the flanges flat and taut), suggesting that our realistic estimate of 58 years is unlikely to be overly optimistic.

**Discussion**

*Results or artifacts?*

Given the fact that many variables had to be estimated rather than measured directly, the first question that arises is how reliable the results reported here really are. First, two kinds of age estimates (conservative and realistic) were used in this study to compile life-tables and estimate longevity. The mortality trajectory, however, does not change appreciably for the two data sets based

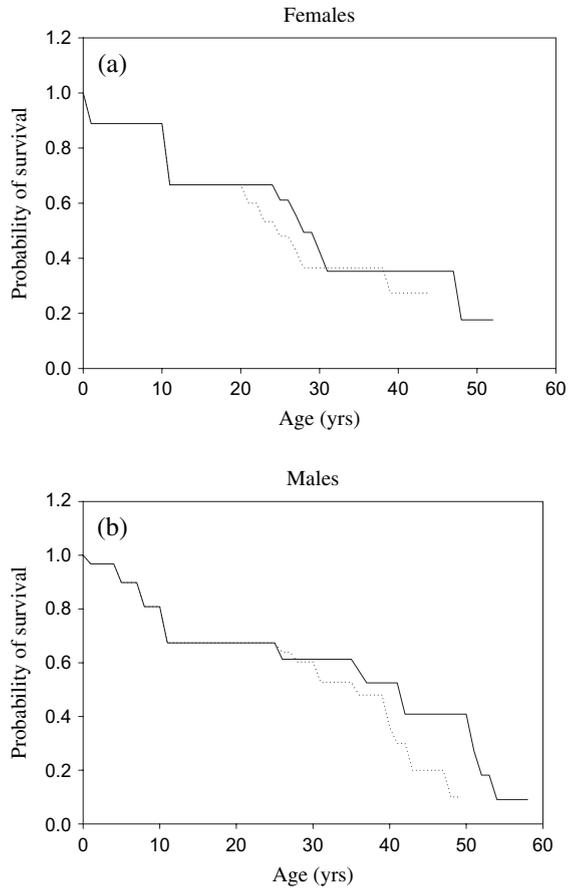


Fig. 1. Age-specific probability of survival for wild orangutans. Solid lines represent the minimum realistic age estimates and the dotted lines the minimum conservative estimates: (a) females and (b) males.

Table 2b  
Survival of immatures in Suaq Balimbing

Age	Enter	Die	$q_x$	$l_x$
0	10	0	0	1
1	9	2	0.22	0.78
2	9	2	0.22	0.56
3	3	0	0	0.56
4	4	0	0	0.56
5	6	0	0	0.56
6	15	0	0	0.56
7	16	0	0	0.56
8	10	0	0	0.56
9	7	0	0	0.56
10	5	0	0	0.56
11	4	0	0	0.56

Notes: Abbreviations as in Table 2a

on these different age estimates. Second, mortality was usually inferred when animals had not been seen for at least five years. This procedure would work well for residents, but is unlikely to capture the survival of transients, i.e., animals that spend some time at the site (long enough to be named) and then move on. If these events are common, we may have especially overestimated the mortality of males, the sex more likely to migrate over longer distances (Delgado and van Schaik, 2000). Interestingly, no sex difference in mortality was inferred (see below).

Another way to assess the validity of the results is to estimate the population’s intrinsic rate of

increase, which is expected to be only marginally above zero for orangutans. Based on our results, the deterministic growth rate of the Ketambe orangutan population is in fact slightly negative: the deterministic rate of increase  $[r] = -0.003$  (calculated in a vortex [Lacy et al., 2003] model using an interbirth interval corrected for infant and juvenile mortality). While this indicates that our results are nearly accurate (or that errors tend to cancel), it also raises the question whether the Ketambe population (and that of Suaq) has a higher mortality or longer interbirth intervals than a stable population. Because the last 30 years has seen a large reduction of orangutan habitat around the Ketambe and Suaq research areas, it is possible that there has been some crowding of orangutans in these areas. However, an analysis of interbirth intervals of non-reintroduced females as a function of year of birth at Ketambe shows no correlation ( $r_s = -0.216$ ,  $n = 13$ , n.s.). Neither was there any indication that mortality was concentrated in the more recent years. Finally, density at the study sites has remained more or less stable (van Schaik, 2004). Taken together, then, these findings show that crowding can be ignored as a source of bias in our estimates of demography.

#### Patterns at Ketambe

The observed birth sex ratio at Ketambe (0.57;  $n = 28$ ) was very similar to the infant sex ratio observed at Suaq Balimbing (0.56,  $n = 25$ ; Singleton and van Schaik 2002). Changes in sex ratios at different age-sex classes were used by Singleton and van Schaik (2002) to infer higher mortality among reproductive males. Similarly, higher male mortality was observed among chimpanzees (Hill et al., 2001). Yet, no sex difference in mortality was seen at Ketambe. Due to the lack of detailed home range data at Ketambe, it is not possible to determine an appropriate adult female/male ratio for the population, and thus we cannot derive this second estimate of a sex difference in mortality. It is not clear whether the lack of sex difference in mortality observed at Ketambe is real, due to small sample size, or due to the relative underestimation of female age because adult females of unknown age (but possibly quite old)

were assigned an age of 24, whereas similar males could be assigned an age of 35.

In Ketambe, interbirth intervals did not depend on the sex of the previous infant. A similar pattern has been reported for *G. g. beringei* and *G. g. graueri*, where the interbirth intervals also do not differ depending on the sex of the former infant (Watts, 1991; Yamagiwa and Kahekwa, 2001). We also did not find that higher ranked females had a shorter interbirth interval, contrary to patterns found in chimpanzees (Pusey et al., 1997). This is somewhat surprising since in both species linear hierarchies and contest competition for food occurs (Utami et al., 1997; Wittig and Boesch, 2003). The absence of an increased interbirth interval for lower ranking orangutan females might be related to the very high home-range overlap among Sumatran orangutan females (Singleton and van Schaik, 2001). Dominant orangutan females did not invest longer in male offspring, which differs from chimpanzees where such a pattern has been reported (Boesch and Boesch-Achermann, 2000).

#### Orangutans compared

Until recently, two subspecies of orangutan were recognized: *Pongo pygmaeus pygmaeus* in Borneo, and *Pongo pygmaeus abelii* in Sumatra. Today, however, as a result of genetic studies, the populations on the two islands are commonly regarded as two distinct species: *Pongo pygmaeus* on Borneo and *Pongo abelii* on Sumatra (Xu and Arnason, 1996; Groves, 2001). It is interesting to look for other differences as well.

Female orangutans at Ketambe had an age of first reproduction similar to those published for their Bornean counterparts (Table 3). It should be noted, however, that the sample for age of first reproduction in Bornean orangutans is extremely small ( $n = 3$ ) and may therefore change when larger samples become available.

The interbirth interval of 9.3 years for the Sumatran orangutan population at Ketambe is the longest reported so far for any orangutan population, and, indeed, for any great ape species (Table 3). Galdikas and Wood (1990) reported a mean interbirth interval for Bornean orangutans

Table 3  
Comparison with other orangutan populations and great ape species

Species	Site	Female body weight (kg)	IBI (yrs, means)	∅IBI after male/female	Infant mortality (%)	Proportion of males at birth	Age at first reproduction (mean, in yrs and range)	Refs
<i>Pongo abelii</i>	Ketambe	35.7 <sup>†</sup>	9.3	N	8.0 <sup>a</sup> , 0 <sup>b</sup>	0.57	15.4 (13-18)	This study
<i>Pongo abelii</i>	Suaq Balimbing		8.2 <sup>††</sup>			0.56 <sup>d</sup>		Singleton and van Schaik, 2002; van Noordwijk and van Schaik, in press;
<i>Pongo pygmaeus</i>	Tanjung Puting		7.7				15.7 (15-16)	Galdikas and Wood, 1990; Tilson et al., 1993;
<i>Pongo pygmaeus</i>	Gunung Palung		7.0					Knott, 2001;
<i>Gorilla gorilla beringei</i>	Karisoke	80 <sup>†</sup>	3.9 (median)	N	26.2 <sup>a</sup> ; 7.7 <sup>b</sup>	1.3	10.1 (median) (8.7-12.8)	Watts, 1991;
<i>G. g. graueri</i>	Kahuzi		4.6	N	19.6 <sup>a</sup> ; 6.5 <sup>b</sup>	1.1		Yamagiwa and Kahekwa, 2001;
<i>Pan troglodytes</i>	Tai	40.4 <sup>†</sup>	5.8		30 <sup>c</sup>	1.3	14.3 (12.5-18.5)	Boesch and Boesch-Achermann, 2000;
<i>Pan troglodytes</i>	Gombe		5.5				13.3 (11.1-17.2)	Knott, 2001;
<i>Pan troglodytes</i>	Kanyawara		6.2				15.4 (14-18)	Wrangham in Knott, 2001;
<i>Pan troglodytes</i>	Bossou		5.1				13.0 (12-14)	Sugiyama, 1994;
<i>Pan troglodytes</i>	Mahale		6.0	N	28 <sup>a</sup> ; 19 <sup>b</sup>	1.0	14.6 (12-20)	Nishida et al., 1990;
<i>Pan paniscus</i>	Wamba	33.2 <sup>†</sup>	4.5				14.2 (13-15)	Kuroda, 1979; Furuichi, 1987; Takahata et al., 1996;
<i>Pan paniscus</i>	Lomako		8.0					Fruth in Knott, 2001.

Notes: IBI = interbirth interval, † = body weights from Smith and Jungers (1997), and do not actually come from the sites itself, †† = based on right censored data only, a = for infants 1 yrs, b = infants 1–3 yrs, c = for infants < 2 yrs (adapted from Table 2.4 in Boesch and Boesch-Achermann (2000)), d = infant sex ratio.

at Tanjung Puting, based on survival analysis, of 7.7 years (92.6 months; SE = 2.4), or 1.6 years lower than Ketambe. The Tanjung Puting confidence limits do not overlap those of the Ketambe estimate. Comparison of the completed intervals confirms that this difference is statistically significant (Mann-Whitney-U test:  $n_{\text{Ketambe}} = 16$ ,  $n_{\text{Tanjung Puting}} = 12$ ,  $U = 44.5$ ,  $P = 0.02$ ). The only published mean interbirth interval for another Bornean population (Gunung Palung; Knott, 2001) is 7.0 years (based on  $n = 4$  complete intervals), whereas the only other Sumatran site for which an interbirth interval estimate is reported (Suaq) is at least 8.2 years (based on estimated infant ages and censored intervals; van Noordwijk and van Schaik, in press). In addition, recent data from the Kutai research site in East Borneo suggest a short interbirth interval of ca. 6.1 years (A. Suzuki, pers. comm.). Thus, the data available so far clearly support a generally longer interbirth interval for Sumatran than Bornean orangutans.

If the variation in interbirth intervals had been simply due to phenotypic plasticity, we would have expected the opposite difference. Bornean orangutans are generally less frugivorous (Delgado and van Schaik, 2000) and tend to experience long periods of very low fruit abundance (Knott, 1998; pers. obs.). With this lower energy supply, one would expect slower infant development and hence long interbirth intervals, opposite to the observed pattern. Thus, this pattern supports the position that the Bornean and Sumatran orangutans represent genetically distinct meta-populations, with different life histories.

Other features also suggest systematic differences between Sumatran and Bornean orangutans (Delgado and van Schaik, 2000). First, Sumatran orangutans tend to be more frugivorous and especially insectivorous, and spend far less time feeding on the inner bark of trees (Fox et al., 2004) than do Bornean orangutans. Second, female orangutans on Borneo spend much less time in associations than females on Sumatra (Galdikas, 1985; Wich et al., 1999; van Schaik, 1999), which might indicate that food availability is lower in Borneo, since in general the time that female orangutans spend in associations beyond the mother-offspring unit increases with an increase

in food availability (Sugardjito et al., 1987; but see van Schaik, 1999). Finally, it appears that there are more adult (flanged) males than subadult (sexually mature but unflanged) males on Borneo, but more subadult males than adult males on Sumatra (Delgado and van Schaik, 2000), which has been interpreted as indicating the absence of arrested development in Borneo. These further differences all suggest that a clear taxonomic distinction between Sumatran and Bornean orangutans is warranted.

#### *Orangutan life history compared with other great apes*

A comparison of orangutan life history data with that of other great apes shows two clear contrasts. First, as has been reported previously (Galdikas and Wood, 1990; Knott, 2001), orangutans have a longer interbirth interval than gorillas (*Gorilla gorilla beringei* and *G. g. graueri*), chimpanzees (*Pan troglodytes*), and bonobos (*P. paniscus*) (Table 3). It has been suggested (van Noordwijk and van Schaik, in press) that the lower fruit availability in Southeast Asian forests, as compared with African forests, forces orangutan mothers to forage alone, and hence to postpone weaning until their offspring can forage and range more or less on their own. Chimpanzee mothers, on the other hand, can wean offspring earlier and have another infant sooner since food availability allows the weaned offspring to remain in association with the mother and her new infant.

The second contrast is that orangutan mortality is low when compared with that in the other great apes. Mortality of infants less than one year old is more than three times lower than that for chimpanzees and around 2.5 times lower than for gorillas (there is no information for bonobos). No mortality was recorded for orangutan infants between 1–3 years old at Ketambe, compared to mortality rates of 7% for gorillas and 19% for chimpanzees. In general, female and male chimpanzees experience a significantly higher mortality than female and male orangutans throughout the lifespan (Fig. 2, logistic regression controlling for age and age<sup>2</sup>,  $P = 0.015$  and  $P < 0.001$ , respectively).

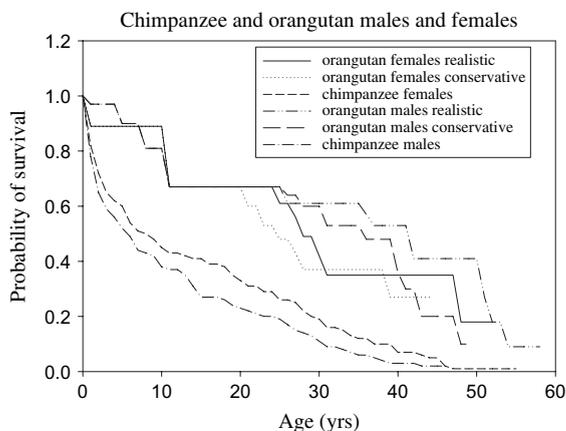


Fig. 2. Age-specific probability of survival for wild orangutans (Ketambe sample only) and wild chimpanzees. Chimpanzee data from Hill et al. (2001). Realistic and conservative refer to the realistic and conservative minimum age estimates of orangutans.

Adding the data from Suaq to the data set does not affect this conclusion.

The lower mortality of orangutans relative to chimpanzees (Fig. 2) strongly suggests that orangutans have greater longevity. Current estimates of maximum observed life spans in the wild are rather similar, which might mean that there is no species difference in longevity. The oldest recorded wild female chimpanzee (from the Kibale population) was estimated to be 55 years old and still alive when the Hill et al. (2001) paper was written, three years older than the oldest living female orangutan at Ketambe. The oldest chimpanzee male was estimated to be 46 at death (Hill et al., 2001), 12 years younger than the estimated age of 58 at which the oldest male in the Ketambe population died. Although this suggests similar longevity, it should be remembered that the chimpanzee sample is far larger than that for the orangutans. Moreover, because adult female orangutans of unknown age were estimated to be at most 24 years at the start of the study, although they may have been older, whereas chimpanzee females were assigned the most probable ages, we have probably underestimated female ages for the orangutans.

Orangutans have longer interbirth intervals and later age at first reproduction (Table 3) than chimpanzees. Especially if orangutans also turn

out to have greater longevity, they therefore have the slowest life history among extant apes. The pattern across apes suggests that pace of life history is affected by frugivory, with the more folivorous (gorilla) having faster-paced life history than the more frugivorous chimpanzee (and bonobo being intermediate in both) (Doran et al., 2002; Yamagiwa et al., 2003).

The chimpanzee-orangutan contrasts could be linked to arboreality or a more solitary lifestyle. Since arboreal mammals in general have a slower life history than terrestrial mammals (van Schaik and Deaner, 2003), the lower mortality rates of orangutans compared to chimpanzees could be due to the fact that orangutans are far more arboreal than chimpanzees. Another, related possibility is that orangutans suffer less from parasitic infections. Several factors such as body mass, social contact, population density, diet, and habitat diversity appear to be related to parasite prevalence and diversity in hosts (e.g., Nunn et al., 2003). Body mass, population density, diet, and habitat diversity are fairly similar between orangutans and chimpanzees (Rodman, 1984; Wich et al., 1999). Hence, the lower overall mortality for orangutans may reflect a lower risk of parasite transmission due to an arboreal and more solitary lifestyle (van Noordwijk and van Schaik, *in press*) and the virtual absence of body contact due to grooming (Rijksen, 1978).

#### Comparison with humans

This new information can also be used to refine ideas on life-history evolution in hominins. If the last common ancestor of chimpanzees and humans was frugivorous, we may expect the life history of both orangutans and chimpanzees to be a reasonable approximation of that ancestor's life history. In particular because our estimates of chimpanzee life history in the wild may be poor (see above), these new data on orangutans may modify our view of the main derived human life-history features (shorter interbirth intervals, longer life spans, and menopause).

First, the decrease in interbirth interval in the hominin lineage may be even greater than usually thought: the interbirth intervals for orangutans

(6.1–9.3 years) are even greater than those for chimpanzees (5.1–6.2 years), which are longer than for hunter-gatherers (3.2–3.8 years, Kaplan et al., 2000).

Second, the increase in longevity in hominins may be less than commonly thought (Smith and Tompkins, 1995): the expected age at death for individuals of age 15 is between 46 and 40 years for orangutan males and females, respectively, whereas it is between 53 and 56 for hunter-gatherers (Kaplan et al., 2000; Hill et al., 2001), a difference of around 7 and 16 years. For wild chimpanzees, these ages lie between 24 and 41 years for males and females, respectively (Hill et al., 2001), suggesting a far larger difference, but for captive chimpanzees it would be 33 and 41 years (Dyke et al., 1995). Thus, the reconstructed first hominin and modern humans may have shown a difference of about 10–15 years in life expectancy at age 15. Sample sizes for great apes are inadequate for estimation of the differences in longevity.

Third, menopause in humans may not just be a result of selection for increased post-reproductive survival (e.g., Hawkes et al., 2003), but also of selection for reduced age at last reproduction. It has been suggested (e.g., Hawkes, 2003) that the key evolutionary shift during hominin evolution was that age at last reproduction was conserved, whereas post-reproductive lifespan increased. We found no evidence for menopause in orangutan females, at least not until the ages observed here. Likewise, in two other populations (Suq Balimbing and Tuanan), there are no clearly aged females without infants (SW, CvS, unpubl.), suggesting that reproductive and somatic senescence are not decoupled in orangutans. This inferred absence of menopause is consistent with other analyses of primates in the wild (e.g., Packer et al., 1998), with the possible exception of one chimpanzee population, Mahale (Nishida et al., 1990; Boesch and Boesch-Achermann, 2000), and with analyses of captive primates, including orangutans (Caro et al., 1995). At least one wild orangutan female (this study) and two chimpanzee females (Boesch and Boesch-Achermann, 2000) have now been observed to reproduce into their forties (and more orangutan females may do so, as a result of our conservative age estimation), whereas mean age of

menopause among hunter-gatherer females is 39 (Kaplan et al., 2000). Moreover, there was no evidence among orangutans for an increase in interbirth intervals with maternal age. Thus, although much more information is obviously needed, and assuming that the combined information on orangutans and chimpanzees can be used to provide a realistic assessment of the life history of the first hominins, the currently available information suggests that there was selection on earlier cessation of reproduction among hominins, rather than merely an increase in life span.

## Summary

This analysis of long-term demographic data for Sumatran orangutans refined our estimates of orangutan life history. Interbirth intervals were longer than that reported for Bornean sites, but age at first reproduction similar. The first longevity estimates from the wild indicate life spans of over 50 years, with no evidence for menopause. Mortality rates were very low for both males and females, with no clear sex difference. These estimates established the Sumatran orangutan as the nonhuman primate with the slowest life history pace. They also helped to refine the life-history contrasts between humans and great apes. Inclusion of orangutan data into the reconstructed life history of the first hominins suggests that humans have evolved even shorter interbirth intervals than hitherto assumed, less dramatically increased total life spans, and have been subject to active selection on menopause. Recent data on dental development in extinct hominins (Dean et al., 2001) and wild chimpanzees (Zihlman et al., 2004) suggest that the distinct human life history suite did not arise with the origin of the genus *Homo*, as commonly inferred (e.g., Hawkes et al., 2003), but much more recently.

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