



Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers[☆]



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ABSTRACT

Demographic data on wild chimpanzees are crucial for understanding the evolution of chimpanzee and hominin life histories, but most data come from populations affected by disease outbreaks and anthropogenic disturbance. We present survivorship data from a relatively undisturbed and exceptionally large community of eastern chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda. We monitored births, deaths, immigrations, and emigrations in the community between 1995 and 2016. Using known and estimated ages, we calculated survivorship curves for the whole community, for males and females separately, and for individuals ≤ 2 years old when identified. We used a novel method to address age estimation error by calculating stochastic survivorship curves. We compared Ngogo life expectancy, survivorship, and mortality rates to those from other chimpanzee communities and human hunter-gatherers. Life expectancy at birth for both sexes combined was 32.8 years, far exceeding estimates of chimpanzee life expectancy in other communities, and falling within the range of human hunter-gatherers (i.e., 27–37 years). Overall, the pattern of survivorship at Ngogo was more similar to that of human hunter-gatherers than to other chimpanzee communities. Maximum lifespan for the Ngogo chimpanzees, however, was similar to that reported at other chimpanzee research sites and was less than that of human-hunter gatherers. The absence of predation by large carnivores may contribute to some of the higher survivorship at Ngogo, but this cannot explain the much higher survivorship at Ngogo than at Kanyawara, another chimpanzee community in the same forest, which also lacks large carnivores. Higher survivorship at Ngogo appears to be an adaptive response to a food supply that is more abundant and varies less than that of Kanyawara. Future analyses of hominin life history evolution should take these results into account.

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1. Introduction

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are the closest living relatives of humans, which makes data on their life histories and demography invaluable for comparative analysis of human life history evolution and for reconstructing life history parameters of extinct hominin taxa (Hill et al., 2001; Emery Thompson et al., 2007; Kachel and Premo, 2012; Lee, 2012; Schwartz, 2012; Duda and Zrzavý, 2013; Smith, 2013; van Noordwijk et al., 2013; Muller and Wrangham, 2014; Chan et al., 2016). Relative to other mammals of similar body size,

chimpanzees grow slowly, start to reproduce late, and live long: chimpanzee infants are weaned around five years of age; females give birth for the first time when they are about 14 years old; interbirth intervals are typically 5–6 years (Boesch and Boesch-Achermann, 2000; Nishida et al., 2003; Emery Thompson et al., 2007; Stumpf, 2007). While the longest precisely measured lifespan among captive chimpanzees is 62 years, one female alive today is estimated to be 78 years old (Ross, 2015). Maximum longevity in the wild is estimated to be well over 60 years (Emery Thompson et al., 2007). These growth, development, and longevity parameters are expected because chimpanzees are large-bodied, have relatively large brains, and are highly frugivorous (Ross, 1998; Mumby and Vinicius, 2008; van Schaik and Isler, 2012). However, it is hard to obtain large samples of chimpanzee demographic and life history data. This paucity of information creates difficulties when making comparisons with humans.

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Published data on chimpanzee demography and life histories reveal similarities and differences with human hunter-gatherer societies. Curves that plot the relationship between female fertility and age in chimpanzees, calculated from several wild populations, have an inverted u-shape similar to that documented for several human hunter-gatherer populations. Because of shorter interbirth intervals, female reproductive rates are higher in humans despite later ages at first reproduction (Kaplan et al., 2000). Delayed onset of reproduction and short interbirth intervals are associated with our species' reliance on skill-intensive foraging, extensive food sharing, allocaretaking, and the evolution of childhood (Bogin, 1997; Kaplan et al., 2000; Hill and Hurtado, 2009; Kramer, 2010; Hrdy, 2011; van Noordwijk et al., 2013). Also in contrast to humans, reproductive senescence in female chimpanzees is not decoupled from somatic senescence. Available data from long-term chimpanzee research sites indicate that few female chimpanzees survive long enough to become post-reproductive, and post-reproductive life expectancy is short (Emery Thompson et al., 2007; Alberts et al., 2013). Analysis of pooled data from five chimpanzee research sites (Bossou, Republic of Guinea; Gombe, Tanzania; Kanyawara, Uganda; Mahale, Tanzania; Tai, Ivory Coast) has shown much higher juvenile and adult mortality and much lower life expectancy at birth and at maturity in chimpanzees than in hunter-gatherers (Hill et al., 2001). An additional composite survivorship curve based on data from all of these sites except Tai plus data from Budongo (Emery Thompson et al., 2007) yielded somewhat lower estimates of mortality, but still showed a steep, steady decline in survival with age, with only about 40% of females surviving to the age of peak fertility and 20% surviving to age 40.

Hill et al. (2001) themselves questioned whether their analysis accurately represented chimpanzee demography, given that their results described a declining population, something that cannot hold over evolutionary time. As both they and Muller and Wrangham (2014) pointed out, chimpanzee populations across Africa are declining due to habitat loss, hunting, and disease; perhaps the intensity of these factors in the 20th and 21st century have systematically increased measured chimpanzee mortality rates. Zoonotic and anthroponotic diseases have had particularly large impacts at Tai (Boesch and Boesch-Achermann, 2000; Leendertz et al., 2004; Köndgen et al., 2008), and serious epidemics have occurred at Mahale (Nishida et al., 2003) and Gombe (Pusey et al., 2007, 2008; Williams et al., 2008; Lonsdorf et al., 2011). Pathogenicity associated with SIV_{cpz} infection is known at Gombe (Keele et al., 2009) and researchers at Mahale reported multiple fatalities associated with an "AIDS-like syndrome" (Nishida et al., 2003). Hunting has also had a serious impact at Tai (Boesch et al., 2008), and snare injuries are common at Budongo (Reynolds, 2005) and Kanyawara (Wrangham and Mugume, 2000), even though little or no deliberate targeting of chimpanzees by hunters has occurred during the history of research at those sites. Bossou has only a single, small, isolated chimpanzee community heavily subjected to anthropogenic influence (Hockings et al., 2012).

which has escaped the worst impacts of human contact and experienced moderate population growth. They contrasted this with a life table assembled from the original Hill et al. (2001) sample with the Kanyawara data removed (the "four-site sample") and one for the Hadza, a contemporary human foraging society (Blurton Jones, 2016). Yearly mortality rates and life expectancy at Kanyawara mostly lay between the four-site sample and the Hadza. For example, infant mortality in year 1 was 11% at Kanyawara versus 21% in the four-site sample, and life expectancy at birth was almost 20 years at Kanyawara versus 13 years in the four-site sample. Mortality risk was significantly higher in the four-site sample for the 0–14 and 15–30 year intervals. The risk of death in the first two years was actually greater for Hadza infants than for chimpanzees at Kanyawara. The Kanyawara survivorship curve leveled off in the 15–30 year interval in a manner similar to the Hadza and unlike the continued steep decline in survivorship in the four-site sample. However, it still diverged markedly from that for the Hadza after 30 years of age, with survival dropping sharply at 30 years for the chimpanzees but remaining relatively flat for another 10 years for the Hadza. Only 18% of Kanyawara chimpanzees reached age 30, and those who did had a life expectancy of only 12 more years. In contrast, 42% of all Hadza lived until 30; those who did survived another 32 years on average.

Muller and Wrangham (2014) were cautious about the importance of the apparent plateau in Kanyawara chimpanzee survivorship between 15 and 30 years, noting that their sample was small and that the 95% confidence intervals around their survival estimates were large. But they pointed out that the Kanyawara chimpanzees had not experienced serious epidemics and argued that overall, "the data suggest an important downward revision in adult mortality rates in wild chimpanzees", although they "do not appear to challenge the existence of a substantial difference in adult mortality between humans and chimpanzees" (Muller and Wrangham, 2014: 113).

Kanyawara is in Kibale National Park, Uganda, and in reaching these conclusions, Muller and Wrangham (2014) noted that preliminary analysis of demographic data from Ngogo, a second site in Kibale, indicated that survival was also relatively high there (Watts, 2012). These two chimpanzee communities belong to the same population, but their territories are not adjacent and they have had different recent histories of disturbance by humans (Struhsaker, 1997). Moreover, forest composition at the two sites differs in ways that substantially affect chimpanzee diets and help to explain why the Ngogo community is much larger than that at Kanyawara (Potts et al., 2011; Watts et al., 2012a). Chimpanzees are ecologically flexible and their historical range included a wide variety of habitat types, from closed-canopy lowland and mid-altitude rainforest to montane forest, open woodland, and savanna-woodland-gallery forest mosaics (reviewed in Watts et al., 2012b). Population density estimates vary correspondingly, from as low as one individual per 10 km² in relatively dry, open habitats (e.g., Fongoli: Pruett et al., 2002) to about five individuals per 1 km² in evergreen for-

Table 1
Comparative measures of mortality and life expectancy in wild chimpanzee communities.^a

Site	e ₀ Male	e ₀ Female	e ₀ All	q ₀ Male	q ₀ Female	q ₀ All	l ₄₅ Male	l ₄₅ Female	l ₄₅ All	Maximum age
Ngogo	30	36	33	0.12	0.17	0.15	0.20	0.51	0.35	66
Kanyawara	17	22	20	0.11	0.11	0.11	0.14	0.10	0.12	64
Gombe	15	20	18	0.17	0.19	0.18	0.00	0.03	0.03	55
Tai	8	7	13	0.12	0.11	0.08	0.01	0.00	0.04	46

^a Measures defined in the text. All life table measures (q_x, l_x, e_x) were calculated using the methods of Hill et al. (2001) and Muller and Wrangham (2014).

Muller and Wrangham (2014) recently constructed a life table using updated data on the Kanyawara chimpanzee community,

ests (e.g., Ngogo; below). Ecological variation leads to life history variation in some nonhuman primates (e.g., Hanuman langurs,

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