Current Biology 17, 2150–2156, December 18, 2007 ©2007 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2007.11.033

Report

Aging and Fertility Patterns in Wild Chimpanzees Provide Insights into the Evolution of Menopause

Melissa Emery Thompson,[1,*] James H. Jones,[2] Anne E. Pusey,[3] Stella Brewer-Marsden,[4] Jane Goodall,[5] David Marsden,[4] Tetsuro Matsuzawa,[6] Toshisada Nishida,[7,8] Vernon Reynolds,[9] Yukimaru Sugiyama,[7] and Richard W. Wrangham[1]

[1]Department of Anthropology
Harvard University
11 Divinity Avenue
Cambridge, Massachusetts 02138
[2]Department of Anthropological Sciences
Stanford University
Main Quad, Building 360, Room 361D
Stanford, California 94305
[3]Jane Goodall Institute's Center for Primate Studies
Department of Ecology, Evolution, and Behavior
University of Minnesota
100 Ecology Building
St. Paul, Minnesota 55108
[4]Chimpanzee Rehabilitation Trust
P.O. Box 2208
Serrekunda Post Office
The Gambia
[5]Jane Goodall Institute
4245 North Fairfax Drive, Suite 600
Arlington, Virginia 22203
[6]Primate Research Institute
Kyoto University
Inuyama, Aichi 484-8506
Japan
[7]Emeritus
Kyoto University
Kyoto 606-8501
Japan
[8]Japan Monkey Center
26 Kanrin, Inuyama, Aichi 484-0081
Japan
[9]Emeritus, School of Anthropology
Oxford University
51 Banbury Road
Oxford OX2 6PF
United Kingdom

Summary

Human menopause is remarkable in that reproductive senescence is markedly accelerated relative to somatic aging, leaving an extended postreproductive period for a large proportion of women [1, 2]. Functional explanations for this are debated [3–11], in part because comparative data from closely related species are inadequate. Existing studies of chimpanzees are based on very small samples and have not provided clear conclusions about the reproductive function of aging females [12–19]. These studies have not examined whether reproductive senescence in chimpanzees exceeds the pace of general aging, as in humans, or occurs in parallel with declines in overall health, as in many other animals [20, 21]. In order to remedy these problems, we examined fertility and mortality patterns in six free-living chimpanzee populations. Chimpanzee and human birth rates show similar patterns of decline beginning in the fourth decade, suggesting that the physiology of reproductive senescence was relatively conserved in human evolution. However, in contrast to humans, chimpanzee fertility declines are consistent with declines in survivorship, and healthy females maintain high birth rates late into life. Thus, in contrast to recent claims [16], we find no evidence that menopause is a typical characteristic of chimpanzee life histories.

Results and Discussion

In this study, we contrast age patterns of fertility in chimpanzees and humans. Our analysis focuses on two interrelated but differentiated processes: reproductive senescence, characterized by reduced reproductive performance with age, and menopause, characterized by species-typical patterns of reproductive senescence that significantly exceed the general aging trajectory and result in a postreproductive life stage. We compared age-specific fertility patterns calculated from 534 chimpanzee births and 3416 female risk years with equivalent demographic data from two well-studied human foraging populations, the !Kung of Botswana [22] and the Ache of Paraguay [1]. In all datasets, age-specific fertility formed an inverted U shape, characterized by lower birth rates at the beginning and end of the reproductive life span. Compared with humans, chimpanzees reproduced more broadly across the life cycle, experiencing an earlier onset of fertility (Figure 1). Reproductive performance began to decline at a similar age group in chimpanzees and humans (25–35) and approached zero at approximately the same age (~50). Peak fertility rates of chimpanzees were similar to the !Kung population, who have reduced fertility because of a high incidence of secondary sterility [22], whereas Ache birth rates reached a markedly higher maximum. The slope of the age-related decline in chimpanzee fertility after age 25 was not significantly different from the hunter-gatherer populations (chimpanzees: −0.008; !Kung: −0.010, $t = 1.280$, $p = 0.237$; Ache: −0.013, $t = 1.821$, $p = 0.106$). These data support the hypothesis that the timing of human reproductive senescence has been largely conserved from our closest ancestors [2, 7].

Despite these similarities, the fertility patterns of chimpanzees and humans are markedly different when compared with each species' age-specific mortality patterns (Figure 1). Fertility in chimpanzees declines at a similar pace to the decline in survival probability, whereas human reproduction nearly ceases at a time when mortality is still very low. This suggests that

*Correspondence: memery@fas.harvard.edu

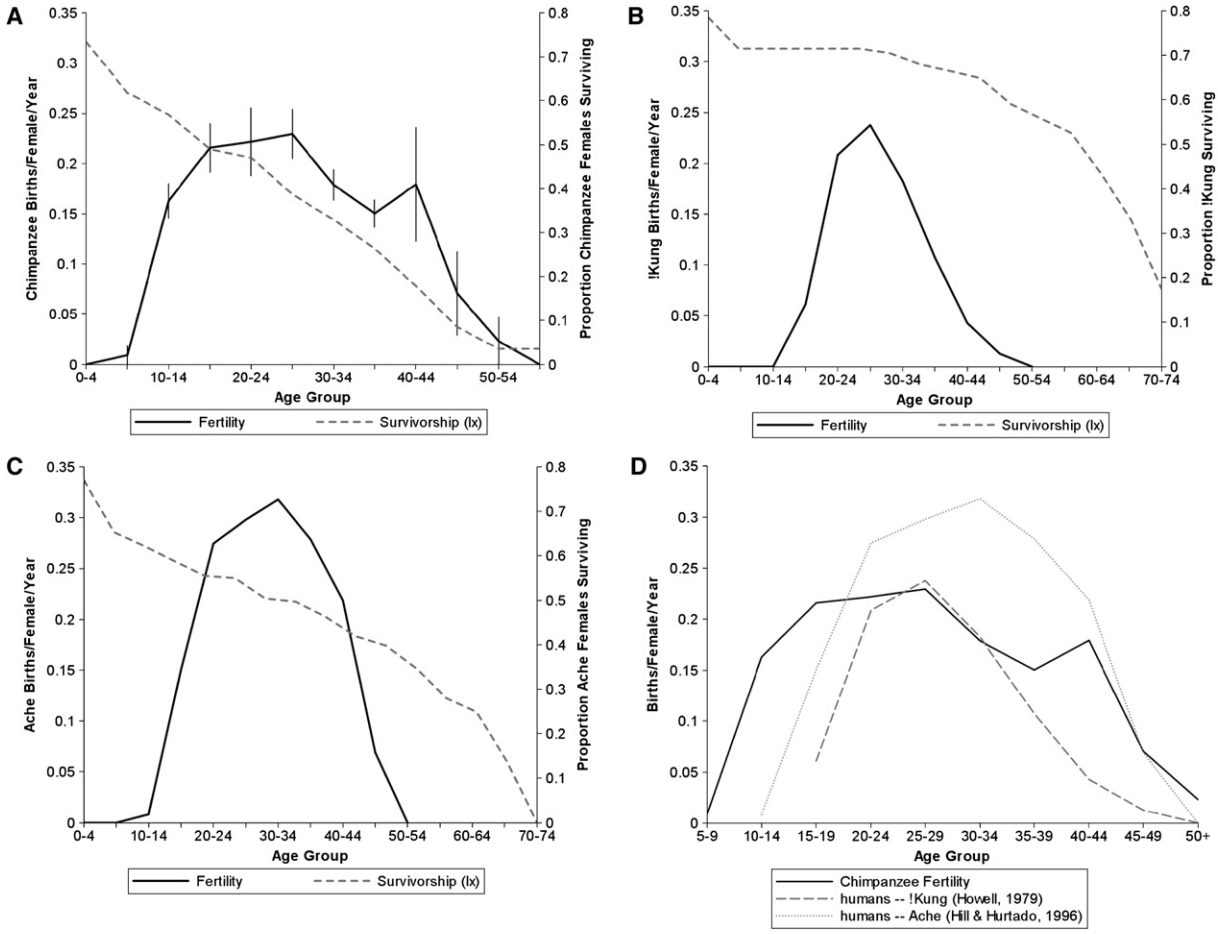

Figure 1. Comparison of Chimpanzee and Human Age-Specific Fertility and Mortality Patterns

(A) Chimpanzee age-specific fertility (mean ± standard error [SE] of six populations) and female probability of surviving (l_x) to end of each age class (five wild populations only).

(B) Dobe !Kung hunter-gatherers, 1963–1973 [22].

(C) Ache hunter-gatherers, Forest Period [1].

(D) Comparison plot of chimpanzee and human hunter-gatherer age-specific fertility. Age-specific fertility was calculated as the number of births as a fraction of risk years in each 5 year age interval. Intervals with two or fewer risk years in any population were excluded. All data are derived from true fertility and mortality rates rather than from model-fitted data.

reproductive senescence in chimpanzees, unlike in humans, is consistent with the somatic aging process.

To further test this idea, we divided our age-specific fertility data for age classes over 25 into two subsets, with each birth and female risk year classified according to the subsequent survival of the female. The "unhealthy" subset contained risk years and births that occurred within 5 years of a female's death; the "healthy" subset consisted of data from females that lived an additional 5 or more years (an approximate chimpanzee birth interval). The cause of death is unknown in the majority of cases; thus, this sample surely includes deaths from acute illness or violence [23], therefore underestimating the health-related differences in birth rate between the two groups. Even so, healthy individuals had higher fertility than did unhealthy individuals (Wilcoxon signed-ranks test, Gombe: $z = -1.924$, $n = 19$ years, $p = 0.054$, Mahale: $z = -2.172$, $n = 18$, $p = 0.030$, Mean of two populations: $z = -2.461$, $n = 19$, $p = 0.014$). Healthy individuals did not have a significant age-specific decline in fertility (Figure 2; $R^2 = 0.169$, $df = 6$ age groups ≥ 15, $p = 0.419$), whereas unhealthy individuals reproduced less well at later ages ($R^2 = 0.760$, $df = 6$, $p = 0.023$). This suggests that variance in somatic aging is systematically related to variance in reproductive senescence. Thus, these data are consistent with the hypothesis that the population-wide age decline in fertility reflects patterns of overall senescence, i.e., an increasing proportion of unhealthy individuals in older age groups.

As a further test of age influences on reproduction, we investigated whether the duration of interbirth intervals increased with age by calculating a Cox proportional-hazards model with an individual random effect to control for repeated intervals from the same individual. In this model, the length of interbirth intervals increased significantly with maternal age in chimpanzees (Figure 3A; $X^2 = 28.2$, $df = 1$, $p < 0.0001$). However, the effect size was very small ($\beta = -0.05$), particularly in relation to the age-related effect in humans (Figure 3C). For chimpanzees, the individual effect of maternal identity was the strongest predictor of interbirth interval

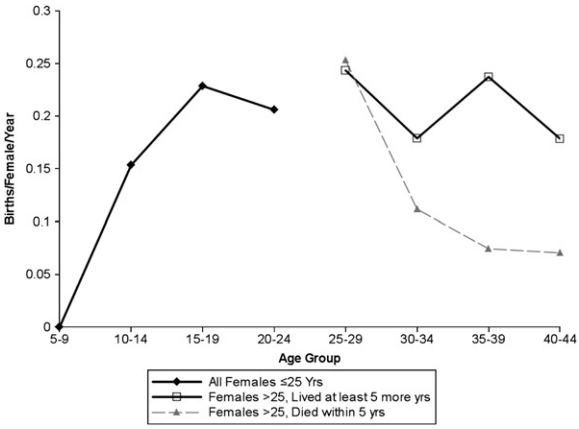

Figure 2. Impact of Somatic Health on Chimpanzee Fertility Rates

In females at or above the age of 25, healthy individuals had significantly higher fertility than did females who died within 5 years of the birth or risk year considered. We used data for the two sufficiently-sampled long-term populations, Gombe and Mahale, and indicate the mean of the two populations. Other populations have small samples but similar trends.

duration ($X^2 = 236.2$, df = 81, $p < 0.0001$). As with the age-specific fertility analysis, we attempted to control for declining maternal health by eliminating birth intervals that culminated in maternal death. This substantially mitigated the effect, with healthy chimpanzees over 35 years of age experiencing a 20% decline in fertility, further supporting the hypothesis that fertility decline in chimpanzees is closely related to somatic senescence (Figure 3B).

Even with this combined dataset, the sample of females in the oldest age classes is low, given that only 7% of female chimpanzees born in the wild survive to 40 years of age. However, reproduction after the age of 40 years occurred in all five wild chimpanzee populations. Thus, out of 34 mothers from the five sites that are estimated to have lived beyond the age of 40 (mean last age 45.3 years), 47% subsequently produced at least one offspring, and four females (mean last age 51.3 years) had two births after 40 years of age. Thus, we find little support in the wild data for the recent conclusion from captive studies that menopause occurs in chimpanzees at the age 35–40 years [16].

Our data on the reproductive patterns of wild chimpanzees help shed light on three aspects of the evolution of the human reproductive life span. First, age-specific fertility profiles of chimpanzees differ from those of humans. Chimpanzees had a wider, flatter profile than hunter-gatherer populations. This reflects in part the earlier maturity of chimpanzee females relative to humans [24]. In addition, the chimpanzee data do not indicate a strong peak in fertility, as is clear in the human datasets at approximately ages 25–35. This has several potential explanations. Ovarian hormone production in humans follows a very similar pattern, suggesting an increased ability to conceive at these ages [25]. Available data suggest that estrogen levels do not change significantly with age in captive chimpanzees [16], but data for wild chimpanzees are not yet available. In addition, human mothers often care for more than one dependent offspring at a time, which might contribute to shortened birth intervals, particularly at ages when they are most likely to have living mothers or other relatives to assist with care [7, 10]; this is rare in chimpanzees [26]. Also, chimpanzees experience significant mortality in this age group, possibly leading to substantial variance in reproductive function. However, even our data on ostensibly healthy chimpanzees does not suggest a significant peak in fertility within the reproductive life span.

Second, our data have implications for understanding the evolution of human menopause. Like recent data on follicular depletion in chimpanzees [17], age-specific fertility data show that reproductive senescence follows a similar time course in chimpanzees and humans. But although the decline in chimpanzee fertility mirrors declines in survival, humans experience an extended postreproductive life span. Our findings thus support the hypothesis that the pattern of reproductive decline in both species has its origins in our last common ancestor and that human evolution has resulted in an extended life span without complementary selection on extended reproduction [2, 4]. On the other hand, our data suggest that healthy chimpanzees maintain high fertility at ages when even healthy humans experience marked declines in reproductive function. This difference might provide some evidence that natural selection has slightly reduced the reproductive span of humans (or, less likely, extended that of chimpanzees). However, we have two caveats to this conclusion. Relatively few chimpanzees reach these oldest age classes; thus, our sample size is still too small to draw strong conclusions about this difference. Additionally, later menopause has been linked with longevity in humans, suggesting that reproductive senescence might also be slower in relatively healthy humans [27–29]. Were there a similar relationship in chimpanzees, it could also mean that those chimpanzees left in the sample at late ages were those with particularly high fertility.

Finally, although some studies have emphasized an age-related decline in the fertility of captive chimpanzees as evidence of menopause, our examination of wild chimpanzees emphasizes the need to consider the general aging trajectory of the species in conjunction with reproductive senescence. In contrast to recent conclusions from captivity [16], we find no evidence to support the hypothesis that chimpanzees routinely experience menopause in the wild. On the contrary, our data on reproductive senescence conform to known differences in survivorship of individual animals. Somatic health has not been considered in previous studies on the fertility of captive chimpanzees, but it might explain the very mixed results of these studies. Parallel contrasts are found between careful captive studies of aging gorillas, which support the occurrence of menopause [30], and wild studies, which do not [31].

Age declines in fertility are a common feature of mammalian life histories, and, particularly among other primates, some older individuals cease reproducing years before death [20, 21, 32–37]. Likewise, some chimpanzees clearly do experience a short postreproductive lifespan. However, we argue that this is not inconsistent with their generally slow reproductive schedule and the decline in general health that accompanies the aging process. Although true menopause results when the supply of ovarian follicles is too depleted to sustain ovarian cycling [38, 39], other factors, such as inflammatory

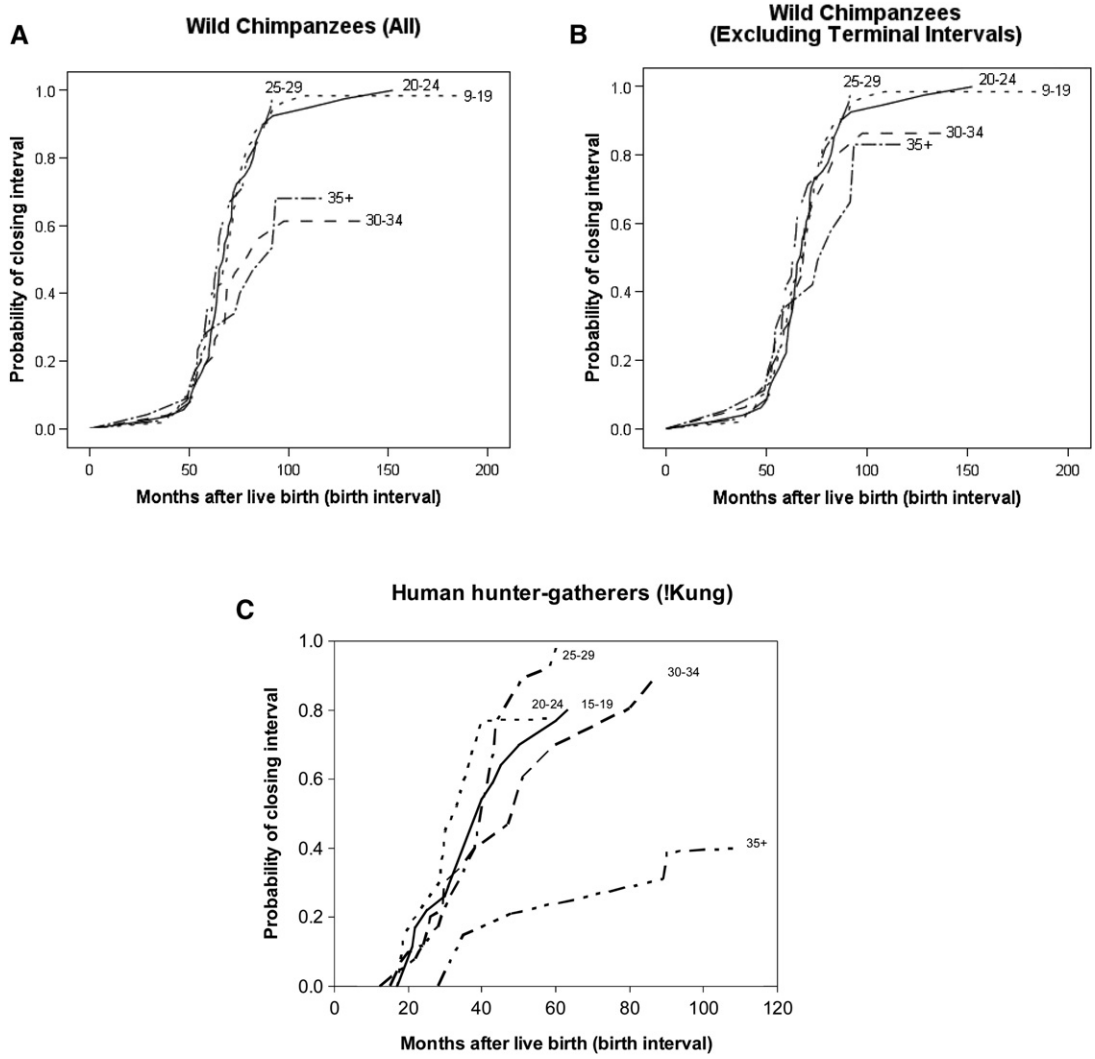

Figure 3. Hazard for Chimpanzee and Human Interbirth Intervals According to the Age of Mother at the Start of the Interval

Lines reflect the probability of a chimpanzee bearing a new infant at each time point when the previous infant has survived.

(A) All wild chimpanzee birth intervals.

(B) Wild chimpanzee birth intervals, excluding intervals that terminated with the mother's death.

(C) Birth intervals of human hunter-gatherers in the Dobe !Kung population, adapted from Howell, 1979 [22].

processes, probably also contribute to secondary infertility in some individuals [40]. These cannot be ruled out as causes of reproductive cessation in aging individuals. Additionally, evidence from other large-bodied mammals suggests that captive breeding schedules can artificially accelerate reproductive senescence; prolonged nonreproductive periods led to an increase in genital pathologies and accelerated follicular loss in captive elephants and rhinoceros [41–43]. Some studies have reported a correlation between contraceptive use or an increase in nonconceptive cycles and early menopause in humans [44, 45], but this phenomenon has not yet been investigated in other primates.

The adaptive significance of human menopause, or postreproductive life span, is still debated. This study provides greater evolutionary context to this debate by demonstrating that chimpanzees and humans experience a similar pace of reproductive senescence but that this pace does not exceed expectations from the overall somatic aging process in chimpanzees. These results, as well as recent data from wild gorillas [31] and orangutans [46], indicate that menopause is not a part of the life cycle of living apes and is a uniquely derived feature of humans.

Experimental Procedures

Study Populations

Our subjects represent four wild populations of *Pan troglodytes schweinfurthii* in Gombe National Park (Tanzania), Mahale National Park (Tanzania), Kibale National Park (Uganda), and Budongo Forest (Uganda), one wild population of *Pan troglodytes verus* in Bossou, Guinea, and one free-ranging, provisioned population at the Chimpanzee Rehabilitation Project in the Gambia with reproductive parameters comparable to wild populations [47]. Although these populations exhibit small differences in reproductive parameters (Table 1), variance in completed (birth to birth) interbirth intervals within each population was larger than the interpopulation variance (F tests, all $p < 0.02$). Thus, age-specific fertility patterns were comparable whether we weighed each geographic population equally or

Table 1. Comparative Data on Reproduction in Free-Ranging Chimpanzees

Chimpanzee Community	n Birth Intervals[a]	n Females	Median IBI (mos) ± SE after Offspring Death[b]	Median IBI (mos) ± SE after Surviving Offspring[c]	Median IBI after Surviving—Controlled by Female[c]	Shortest Completed Interval[c]	Longest Completed Interval[c]	Youngest to Give Birth[d]	Oldest to Give Birth to Surviving Offspring[e]
Gombe	74/41	41	23.2 ± 2.5	67.4 ± 4.0	73.1	39.4	97.5	11.1	49.2
Mahale	116/58	62	26.6 ± 3.8	71.9 ± 2.0	69.0	44.1	132.0	12.0	44.0
Kibale	21/16	17	29.6 ± 8.1	79.1 ± 13.9	70.5	28.9	98.4	14.1	55.0
Budongo	13/17	17	37.1 ± 0.0	62.7 ± 3.0	63.8	57.5	83.7	n/a	40.6
Bossou	21/10	10	24.0 ± 0.4	63.9 ± 2.7	77.9	23.2	128.0	9.5	39.5
Gambia	43/25	25	29.6 ± 2.8	67.2 ± 5.8	73.4	21.7	110.7	12.6	32.7
Composite	288/173	165	26.6 ± 2.7	68.9 ± 1.2	70.6	21.7	132.0	9.5	55.0

Comparative data on reproduction in free-ranging chimpanzees. Sample sizes and reproductive parameters are given for each chimpanzee community, and the composite dataset is underlined. The following abbreviations are used: interbirth interval (IBI) and months (mos).
[a] Data are presented as complete/censored.
[b] Offspring died < 4 years.
[c] Offspring survived at least 4 years.
[d] Ages known.
[e] Ages estimated.

considered all females to be members of the same statistical population (see Supplemental Data available online). In an additional analysis, we coded each female risk year and birth according to whether the female (1) subsequently died within 5 years of the datapoint in question or (2) lived an additional 5 years beyond that date, with indeterminate data (i.e., the most recent 5 years of living females) excluded. For ages over 25, we then calculated age-specific fertility rates separately and used a paired analysis to compare birth rates between healthy and unhealthy groups at each age.

Female dispersal in chimpanzees precludes the precise assignment of birth dates to most females in the study. The majority of females (n = 300) were either first identified as juveniles or as young, nulliparous immigrants; thus, we can be confident of their ages at least to within 5 years. Females who were first identified as mothers or older residents (n = 55) were assigned ages based on their reproductive histories, including age and number of known or suspected offspring. Age estimates derived in this manner were typically conservative, though clues related to appearance were also used to rank the relative ages of individuals [48]. To include older females from all populations, we conducted analyses on the entire dataset for years of researcher presence. A more conservative analysis, excluding all females whose age estimates included more than a 5 year error, was also conducted with qualitatively similar results (Supplemental Data).

We compared chimpanzee data with the two available demographic datasets from human forager populations [1, 22]. It should be noted that !Kung women were adversely impacted by infectious infertility; Howell [22] estimated that this might have lowered reproductive output by approximately 3% per year, though she concludes that this does not fully account for the relatively low fertility rates of the !Kung compared to other populations. This might or might not reflect a valid comparison with wild chimpanzees; therefore, curves of both available hunter-gatherer datasets are provided for comparison. Comparative data for Figure 3 are available only for the !Kung. However, because birth rates were lower throughout the life course for the !Kung relative to the Ache, data from the !Kung should provide accurate information on relative fertility in each age group. For Ache and chimpanzees, mortality data pertains to females specifically. Published data for !Kung mortality were available for the combined population only; this is a marginal overestimate because female mortality in this population was approximately 10%–20% lower than was male mortality, depending on the age group [22].

Interbirth Intervals

Interbirth interval calculations were performed with Kaplan-Meier survival analyses. These analyses consider both completed birth intervals (i.e., those that conclude with a birth) and censored intervals (those that had not resulted in a birth by the date of study or the mother's death) in which the first infant survived to weaning. We considered only births with dates known to within one year (though more commonly within days or weeks). We also calculated a Cox proportional-hazards model incorporating dependent variables of "infant survival to age 4" and "mother's age at start of interval." To address the nonindependence of multiple intervals contributed by each female, we incorporated a gamma-frailty term [49] that specifies an individual-level multiplicative random effect on the fertility hazard with unit mean and variance estimated by using a method of penalized likelihood [50]. The frailty term is essentially a latent trait that models additional variance in birth intervals not accounted for by the measured covariates. The model fit for 459 birth intervals was the following: $R^2 = 0.606$, Wald statistic = 206, df = 82.6, $p < 0.0001$.

Supplemental Data

Supplemental Results and Discussion, three figures, and two tables are available at http://www.current-biology.com/cgi/content/full/17/24/2150/DC1/.

Acknowledgments

We are indebted to the work of the African field assistants who maintain continuous data collections on chimpanzees at our study sites. Long-term research was supported by the following: Department for International Development (Budongo [Bd]), Direction National de la Recherche Scientifique et de la Tehcnique République de Guinée (Bossou [Bo]), Getty Foundation (Bd), Golden Ark (Chimpanzee Rehabilitation Trust, Gambia [Ga]), JGI (Gombe [Go]), JSPS-HOPE Program (Bo), Government of the Gambia (Ga), International Primate Protection League (Ga), Japan International Cooperation Agency (Mahale [M]), Louis S.B. Leakey Foundation (Kibale [K], Bd), Makerere University Biological Field Station (K), MEXT Japan (M, Bo), Harris Steel Group (Go), National Geographic Society (K, Bd), United States National Institutes of Health (Go), Tanzanian Council for Science and Technology (Go, M), Norwegian Agency for Development Cooperation (Bd), Tanzanian National Parks (Go, M), Tanzanian Wildlife Research Institute (Go, M), Ugandan National Council for Science and Technology (K, Bd), Uganda Forest Deptartment (Bd), Uganda Wildlife Authority (K, Bd), National Science Foundation (K, Go), University of Minnesota (Go), Wenner-Gren Foundation (K), and World Wildlife Foundation (Ga). We thank Peter Ellison, Craig Packer, Kristen Hawkes, Martin Muller, Michael Cant, and several anonymous reviewers for valuable suggestions.

Received: September 27, 2007
Revised: November 8, 2007
Accepted: November 9, 2007
Published online: December 13, 2007

References

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

2. Pavelka, M.S.M., and Fedigan, L.M. (1991). Menopause: A comparative life history perspective. Yearb. Phys. Anthropol. *34*, 13–38.
3. Williams, G. (1957). Pleiotropy, natural selection, and the evolution of senescence. Evolution Int. J. Org. Evolution *11*, 398–411.
4. Alexander, R. (1974). The evolution of social behavior. Annu. Rev. Ecol. Syst. *5*, 325–383.
5. Hawkes, K., O'Connell, J., and Blurton Jones, N. (1989). Hard-working Hadza grandmothers. In Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals, V. Standen and R. Foley, eds. (Oxford: Blackwell Scientific Publications), pp. 341–366.
6. Finn, C.A. (2001). Reproductive ageing and the menopause. Int. J. Dev. Biol. *45*, 613–617.
7. Hawkes, K., O'Connell, J., Blurton-Jones, N.G., Alvarez, H., and Charnov, E.L. (1998). Grandmothering, menopause, and the evolution of human life histories. Proc. Natl. Acad. Sci. USA *95*, 1336–1339.
8. Kaplan, H. (1997). The evolution of the human life course. In Between Zeus and the Salmon: The Biodemography of Longevity, K. Wachter and C. Finch, eds. (Washington, D.C.: National Academy of Sciences), pp. 175–211.
9. Hill, K., and Kaplan, H. (1999). Life history traits in humans: Theory and empirical studies. Annu. Rev. Anthropol. *28*, 397–430.
10. Kaplan, H., Hill, K.R., Lancaster, J.B., and Hurtado, A.M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. Evol. Anthropol. *9*, 156–184.
11. Marlowe, F. (2000). The patriarch hypothesis: An alternative explanation of menopause. Hum. Nat. *11*, 27–42.
12. Graham, C.E. (1979). Reproductive function in aged female chimpanzees. Am. J. Phys. Anthropol. *50*, 291–300.
13. Littleton, J. (2005). Fifty years of chimpanzee demography at Taronga Park Zoo. Am. J. Primatol. *67*, 281–298.
14. Roof, K.A., Hopkins, W.D., Izard, M.K., Hook, M., and Schapiro, S.J. (2005). Maternal age, parity, and reproductive outcome in captive chimpanzees (*Pan troglodytes*). Am. J. Primatol. *67*, 199–207.
15. Gould, K.G., Flint, M., and Graham, C.E. (1981). Chimpanzee reproductive senescence: A possible model for evolution of the menopause. Maturitas *3*, 157–166.
16. Videan, E.N., Fritz, J., Heward, C.B., and Murphy, J. (2006). The effects of aging on hormone and reproductive cycles in female chimpanzees (*Pan troglodytes*). Comp. Med. *56*, 291–299.
17. Jones, K., Walker, L., Anderson, D., Lacreuse, A., Robson, S.L., and Hawkes, K. (2007). Depletion of ovarian follicles with age in chimpanzees: Similarities to humans. Biol. Reprod. *77*, 247–251.
18. Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. Am. J. Phys. Anthropol. *124*, 154–165.
19. Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K.D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., et al. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am. J. Primatol. *59*, 99–121.
20. Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. Nature *392*, 807–811.
21. Moss, C.J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. J. Zool. *255*, 145–156.
22. Howell, N. (1979). Demography of the Dobe! Kung (New York: Aldine de Gruyter).
23. Wrangham, R.W., Wilson, M.L., and Muller, M.N. (2006). Comparative rates of violence in chimpanzees and humans. Primates *47*, 14–26.
24. Hill, K. (1993). Life history theory and evolutionary anthropology. Evol. Anthropol. *2*, 78–88.
25. Ellison, P.T., Panter-Brick, C., Lipson, S.F., and O'Rourke, M.T. (1993). The ecological context of human ovarian function. Hum. Reprod. *8*, 2248–2258.
26. Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior (Cambridge: Belknap Press).
27. Ossewaarde, M.E., Bots, M.L., Verbeek, A.L., Peeters, P.H., van der Graaf, Y., Grobbee, D.E., and van der Schouw, Y.T. (2005). Age at menopause, cause-specific mortality and total life expectancy. Epidemiology *16*, 556–562.
28. Amagai, Y., Ishikawa, S., Gotoh, T., Kayaba, K., Nakamur, Y., and Kajii, E. (2006). Age at menopause and mortality in Japan: The Jichi Medical School cohort study. J. Epidemiol. *16*, 161–166.
29. Hong, J.S., Yi, S., Kang, H.C., Kang, H.G., Bayasgalan, G., and Ohrr, H. (2006). Age at menopause and cause-specific mortality in South Korean women: Kangwha cohort study. Maturitas *56*, 411–419.
30. Atsalis, S., and Marguiles, S.W. (2006). Sexual and hormonal cycles in geriatric Gorilla gorilla gorilla. Int. J. Primatol. *27*, 1664–1685.
31. Robbins, A.M., Robbins, M.M., Gerald-Steklis, N., and Steklis, H.D. (2006). Age-related patterns of reproductive success among female mountain gorillas. Am. J. Phys. Anthropol. *131*, 511–521.
32. Berube, C.H., Festa-Bianchet, M., and Jorgenson, J.T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology *80*, 2555–2565.
33. Schwartz, C.C., Keating, K.A., Reynolds, H.V., III, Barnes, V.G., Jr., Sellers, R.A., Swenson, J.E., Miller, S.D., McLellan, B.N., Keay, J., McCann, R., et al. (2003). Reproductive maturation and senescence in the female brown bear. Ursus *14*, 109–119.
34. Henriksen, H.B., Anderson, R., Hewison, A., Gaillard, J., Bronndal, M., Jonsson, S., Linnell, J.D., and Odden, J. (2005). Reproductive biology of captive female Eurasian lynx, *Lynx lynx*. Eur. J. Wildl. Res. *51*, 151–156.
35. Harley, D. (1990). Aging and reproductive performance in langur monkeys (*Presbytis entellus*). Am. J. Phys. Anthropol. *83*, 253–261.
36. Strum, S.C., and Western, J.D. (1982). Variations in fecundity with age and environment in olive baboons (*Papio anubis*). Am. J. Primatol. *3*, 61–76.
37. Fedigan, L. (1991). Life span and reproduction in Japanese macaque females. In The Monkeys of Arashiyama: Thirty-Five Years of Research in Japan and the West, L.M. Fedigan and P.J. Asquith, eds. (New York: State University of New York Press), pp. 140–154.
38. Faddy, M.J., Gosden, R.G., Gougeon, A., Richardson, S.J., and Nelson, J.F. (1992). Accelerated disappearance of ovarian follicles in mid-life: Implications for forecasting menopause. Hum. Reprod. *7*, 1342–1346.
39. Faddy, M.J., and Gosden, R.G. (1996). A model conforming the decline in follicle numbers to the age of menopause in women. Hum. Reprod. *11*, 1484–1486.
40. Wood, J.W. (1994). Dynamics of Human Reproduction: Biology, Biometry, Demography (New York: Aldine de Gruyter).
41. Hildebrandt, T., Goritz, F., Pratt, N.C., Brown, J.L., Montali, R.J., Schmitt, D.L., Fritsch, G., and Hermes, R. (2000). Ultrasonagraphy of the urogenital tract in elephants (*Loxodonta africana* and *Elephas maximus*): An important tool for assessing female reproductive function. Zoo Biol. *19*, 321–333.
42. Hermes, R., Hildebrandt, T., and Goritz, F. (2004). Reproductive problems directly attributable to long-term captivity–asymmetric reproductive aging. Anim. Reprod. Sci. *82–83*, 49–60.
43. Hermes, R., Hildebrandt, T.B., Walzer, C., Goritz, F., Patton, M.L., Silinski, S., Anderson, M.J., Reid, C.E., Wibbelt, G., Tomasova, K., et al. (2006). The effect of long non-reproductive periods on the genital health in captive female white rhinoceroses (*Ceratotherium simum simum, C.s. cottoni*). Theriogenology *65*, 1492–1515.
44. Cramer, D.W., Xu, H., and Harlow, B.L. (1995). Gynecology: Does "incessant" ovulation increase risk for early menopause? Am. J. Obstet. Gynecol. *172*, 568–573.
45. Sowers, M.R., and La Pietra, M.T. (1995). Menopause: Its epidemiology and potential association with chronic disease. Epidemiol. Rev. *17*, 287–302.
46. Wich, S.A., Utami-Atmoko, S., Mitra Setia, T., Rijksen, H., Schurmann, C., van Hooff, J.A., and van Schaik, C.P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). J. Hum. Evol. *47*, 385–398.
47. Brewer-Marsden, S., Marsden, D., and Emery Thompson, M. (2006). Demographic and female life history parameters of free-ranging chimpanzees at the Chimpanzee Rehabilitation

Project, River Gambia National Park. Int. J. Primatol. *27*, 391–410.
48. Hill, K., Boesch, C., Goodall, J., Pusey, A.E., Williams, J., and Wrangham, R.W. (2001). Mortality rates among wild chimpanzees. J. Hum. Evol. *40*, 437–450.
49. R Development Core Team (2004). R: A language and environment for statistical computing (Vienna: R Foundation for Statistical Computing).
50. Therneau, T., and Grambash, P. (2000). Modeling survival data: Extending the Cox model (New York: Springer).