HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR

https://www.openbookpublishers.com

Cover image: Ryota Nagasaka. Street Photography, April 20, 2020, https://unsplash.com/photos/w_5TUm7Xa00

Cover design: Jeevanjot Kaur Nagpal

19. Evolutionary Demography of the Great Apes

Melissa Emery Thompson and Kristin Sabbi

The living hominids share a suite of life history features that distinguishes them from other primates, including larger body size, extended juvenile growth and development, and a long lifespan. While modern humans exhibit many distinctions from their great ape relatives, these species provide an important reference by which to infer the life history characteristics of our last common ancestor. Demographic analysis of the great apes reveals specifically how life histories changed during recent human evolution and can provide perspective on inter- and intra-specific variation in life history features. In this chapter, we provide the most detailed information available on demographic characteristics of great apes, comparisons with humans, and discussion of the proximate factors that influence life history variation across the clade.

Introduction

Human life histories are extraordinary in many respects. Even in the poorest of conditions, we are capable of substantially longer lifespans compared with any other primates. Humans have slow growth rates and long periods of infant dependency, followed by prolonged juvenile and adolescent periods. Women reliably experience menopause and a prolonged post-reproductive lifespan, traits that are rare or insignificant in other primates. While weaning ages and interbirth intervals in humans are broadly consistent with allometric relationships to maternal weight across primates, they are substantially shorter than would be predicted from infant development (Harvey and Clutton-Brock 1985; Watts and Pusey 1993; Dettwyler 1995; Kennedy 2005) and much shorter than in other great apes, despite similarities in body mass and elevated costs of brain growth.

Part of our understanding of the origins of human life history requires examining our unique and recent evolutionary history, but a necessary step must come from recognizing our deeper evolutionary roots as primates and as hominids, taxa that evolved slower life history patterns than their ancestors (Charnov and Berrigan 1993). The hominid clade, comprising humans and other great apes, is arguably best defined by virtue of its life history features. A common ancestor of hominids experienced selection for a larger body, increased relative brain size and complexity, a longer lifespan, and an extended period of offspring dependency and juvenile development compared with its progenitors. These features are retained in the living great apes (hereafter, understood to refer to "non-human great apes"): 7 species comprising Sumatran orangutans (*Pongo abelii*), Bornean orangutans (*P. pygmaeus*), Tapanuli orangutans (*P. tapanuliensis*, recently identified), eastern gorillas (*Gorilla beringei*), western gorillas (*G.*

gorilla), common chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*). These species exemplify, in essence, multiple copies of a common template on which human life history evolved. This allows us to study the factors that can produce variation in life history features within and between species that have similar biology, uncovering potential pathways upon which human traits could have evolved. For example, if we want to know why our species can live for 100+ years, we must first ask how our closest relatives achieved long lifespans and what factors constrain them to 50–60 years.

A valuable feature of using great apes as a referent is that they retain the shared, derived slow life history complex despite having diverged into markedly different foraging environments and having evolved radically different social systems. All great apes, to a certain extent, use a complex diet and seem to prefer fruit — a high-quality, unevenly-distributed resource — when they can get it. All exhibit some social flexibility to minimize the costs of grouping when food is scarce, best exemplified by the fission-fusion organization of chimpanzees and bonobos. However, orangutans contend with radically fluctuating habitats, forcing them to weather periods of extreme food shortage (Knott 2005; Harrison, Morrogh-Bernard, and Chivers 2010; Vogel et al. 2012). They exhibit commensurate adaptations, such as enhanced fat storage, delayed male secondary sexual development, semi-solitary foraging behaviour, and extraordinarily slow metabolic rates (van Schaik 1999; Utami Atmoko and van Hooff 2004; Pontzer et al. 2010). Gorillas display adaptations for processing the large amounts of herbaceous material available in their habitats, effectively buffering both spatial and temporal variation in fruit availability (Remis 2003). At the extreme, mountain gorillas living in the Virunga Mountains can subsist with almost no fruit in their diet (Harrison and Marshall 2011).

While the utility of contextualizing human demographic features with primate data has long been recognized, high-quality data have been scarce, particularly for the great apes. The most prominent reference datasets on primate life history (e.g., Harvey and Clutton-Brock 1985; Smith and Jungers 1997; Leigh 2001), which continue to yield important analyses, incorporate small samples derived primarily from captivity. Captive data have a number of drawbacks, the most obvious of which is the influence of improved nutrition and medical care on features such as growth, reproductive rate, and mortality. Reproductive data are particularly fraught, due to contraceptive measures, separation of mothers and infants, and group management decisions that affect breeding opportunities. These practices are often applied intermittently (e.g., contraception only for certain individuals or at certain times), non-randomly (e.g., selection for breeding of certain individuals), and with poor documentation. Captive data are valuable for understanding the limits of variation within each species, by comparing them to wild data. Such comparisons have some less well-recognized problems. For example, all gorillas in captivity are lowland gorillas, overwhelmingly of the western species (Nsubuga et al. 2010), while data from the wild come primarily from one population of mountain gorillas, which lives at an extreme of gorilla habitat variation. Similarly, the vast majority of founder chimpanzees in captivity (along with most museum specimens) were caught in West Africa, and thus represent the subspecies *Pan troglodytes verus* (Ely et al. 2005), while the majority of wild demographic data are being generated by East African sites comprising *P.t. schweinfurthii*. To the extent that data on other subspecies are available, it is difficult to evaluate whether variation is due to true taxonomic differences or to phenotypic plasticity in response to local environments. Wild data also have their limitations. For example, ages of many individuals are estimated, particularly

for the dispersing sex. Limiting analyses to individuals with well-known ages can also impose bias, if the excluded individuals pursue specific strategies that might alter life history events (e.g., transient male orangutans). Nevertheless, great ape research in the wild has reached a point where there are a number of high-quality longitudinal demographic datasets, in many cases representing multiple populations within species. In our discussion, we focus on these wild datasets as much as possible, referring only to captive data where they are the only data available or where they can provide meaningful insights on the range of variation.

Just as the sparsity of demographic data on great apes has constrained comparative analyses, the desire to conduct such analyses has led to the overzealous use of very limited demographic datasets. Thus, this chapter is as much about how to interpret the great ape demographic data as it is about the data themselves. Are datasets comprehensive enough to make conclusions about species differences? What sources of bias occur in great ape demography, and how important are they in different datasets? How can we best apply comparisons to human demography? Our goal is to emphasize what conclusions about interspecific variability, and the sources of that variation, can reasonably be made and what further data might be needed to address outstanding questions.

Mortality

Understanding how humans came to be so long-lived necessitates considering the evolutionary backdrop of long lifespans in our sister hominids. As a group, these species have notably lower adult mortality rates than do other primates, likely an essential precondition for slow growth, large body sizes, and other aspects of a "slow" life history (Charnov and Berrigan 1993). Great ape lifespans are so long that even the most intensively studied wild populations have not been studied long enough to capture the maximum lifespan. Several chimpanzees, all females, from the Kibale Forest in Uganda are estimated to have lived into their 60s, though their exact ages are uncertain (Hill et al. 2001; Muller and Wrangham 2014; Wood et al. 2017). Two captive chimpanzees, Cheeta (of Tarzan fame) and Little Mama (Lion Country Safari Park), are estimated to have lived nearly 80 years, but their original provenances are controversial. It can generally be concluded that only a small fraction of great apes survive past the age of 50, though they appear to be capable of exceeding 60 years in exceptional circumstances. In most wild populations, life expectancy of females exceeds that of males.

A summary of mortality data from wild populations is provided in Table 1 and Figure 1. Despite their long lifespans, wild great apes do not have reduced early life mortality compared to other primate species (Bronikowski et al. 2011). Infant mortality rates during the first year of life range from less than 10% in some populations of orangutans, western gorillas, and bonobos, to 20% or higher in some populations of chimpanzees and eastern gorillas. Infanticide plays a role in this difference, as it is more common in the latter species than in the former; orangutans and bonobos have never been reported to commit infanticide in the wild. However, infanticide is an insufficient explanation as it affects about 5.5% of mountain gorilla infants born (Robbins et al. 2013) and somewhat fewer chimpanzees (Wrangham, Wilson, and Muller 2006; Wood et al. 2017) [n.b. in both species, rates are highly variable over time, even within populations]. In Grauer's gorillas at Kahuzi-Biega, rates of first-year mortality are estimated at 20% despite a rarity of infanticide (Yamagiwa et al. 2012). Mortality rates decline after the first year in all populations studied except for the Taï community of West African chimpanzees, which has

been affected by periods of high infant and juvenile mortality from leopard predation and the Ebola virus (Boesch and Boesch-Achermann 2000). Thus, while human mortality in the first year of life falls within the range of other great apes, the rate of human survival to adulthood is considerably higher. Anywhere from 25% to over 80% of great apes in wild populations die before reaching reproductive maturity. This high sensitivity of survival in early life is particularly important for population viability and of critical concern given that many of the long-term study groups that have yielded demographic data are assumed to be relatively protected from conservation threats compared to nearby groups/populations.
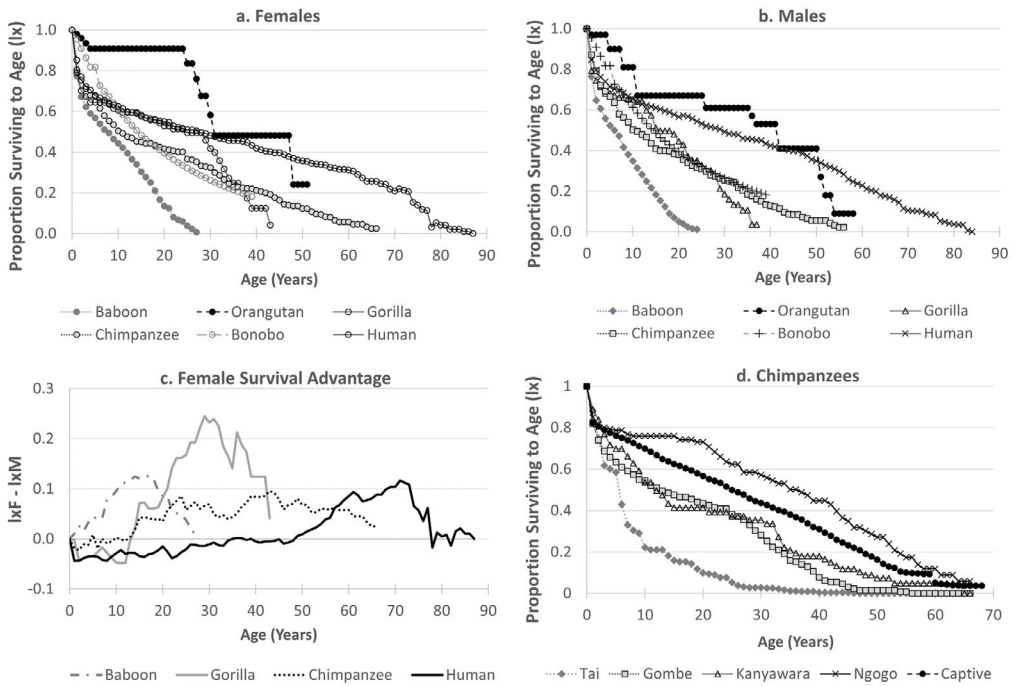

Figure 1

Fig. 1 Comparative survival data from hominid life tables, indicating proportion of individuals born surviving to age x (l_x). (a) Survivorship of females; (b) survivorship of males; (c) excess survivorship of females, calculated as female l_x − male l_x, (d) survivorship of chimpanzees (males and females combined), illustrating differences among captives and four wild populations. Baboon and human forager curves are shown for contrast. Age-specific survival/mortality were not available for bonobos past age 7 but were approximated from mortality rates by age-class and were truncated at age 40 because long-term survival is unknown. Bonobo and orangutan data excluded from sex comparison because adult mortality is based on poor samples and age estimates (see text). Human and chimpanzee curves in a, b, and c show the mean of several populations. Sources: baboons (*Papio cynocephalus*, Amboseli: Bronikowski et al. 2016a,b); orangutans (females ages 0–17, *Pongo spp.*: van Noordwijk et al. 2018; males and females aged 18+: *Pongo abelii*, Ketambe: Wich et al. 2004); mountain gorillas (*Gorilla beringei beringei*, Karisoke: Bronikowski et al. 2016a,b; wild chimpanzees (*Pan troglodytes schweinfurthii*, Gombe: Bronikowski et al. 2016a,b; Kanyawara: Muller & Wrangham 2014; Ngogo: Wood et al. 2017; *P. t. verus*, Taï: Boesch & Boesch-Achermann 2000); captive chimpanzees, averaged from United States and Europe (Dyke et al. 1995), Japan (Havercamp et al. 2019); bonobos: (Wamba: Furuichi et al. 1998); Human foragers (Ache, forest period: Hill & Hurtado 1996; Hadza: Blurton-Jones 2016; Hiwi, pre-contact: Hill et al. 2007; *n.b.* !Kung San mortality data omitted because not differentiated by sex).

Mortality in the first year of life is similar between the sexes, or slightly skewed towards females, while excess male mortality emerges in adolescence and adulthood. Prime adulthood, between the ages of approximately 15 and 30 years, is characterized by low rates of mortality, with some populations experiencing rates as low as those observed in human foraging populations (Wich et al. 2004; Muller and Wrangham 2014; Wood et al. 2017). Humans' increased longevity arises not from consistently lower mortality rates across adulthood but from a prolongation of the low mortality period. In the other great apes, mortality rates accelerate at approximately 25 years of age, while this take-off point is delayed by 20–30 years in human populations. A recent analysis of life tables in several primate species, including humans, East African chimpanzees, and mountain gorillas, concluded that there was no strong phylogenetic signal in Gompertz-derived adult mortality parameters, given that hominids fell within the continuum of other primates (Bronikowski et al. 2011). However, these data also show that hominids cluster at the low end of the continuum, with lower rates of initial mortality (i.e. mortality at onset of adulthood) and rates of aging (acceleration of age-specific mortality rate) than most other primate species.

At this point, life tables for wild apes remain sparse and may be vulnerable to stochastic variation, so caution should be used in interpreting variation among species. There are two major impediments to constructing life tables on wild great apes: age estimation and unrecognized mortality. For older individuals, who were adults when first identified by researchers, ages may be mis-estimated by 10 or more years. These oldest individuals have a relatively minor influence on the shape of survival functions, as the number of individuals whose ages are known with negligible error increases with research time. However, age estimation is a more serious problem for the dispersing sex, particularly if dispersal occurs multiple times or across a wide range of ages. Dispersal also creates the possibility for unrecognized mortality, as it may not be possible for dispersal events to be distinguished reliably from mortality events. Unrecognized mortality may also occur if rates of observation for some individuals are low. The latter is particularly a problem for identifying early infant mortality. These problems will gradually improve as researchers use genetic information to track individuals over larger study areas and monitor health and reproductive status of subjects.

Orangutans present a particular challenge, as males may experience delayed secondary sexual development, which makes it difficult to assign ages based on appearance alone (Utami et al. 2002). Sexual development is accompanied by dramatic physical changes and can occur rapidly, which also prevents researchers from recognizing an individual post-transition. Additionally, orangutan males often disperse over great distances and many remain transients for significant periods of time (van Schaik 1999; Nietlisbach et al. 2012). This creates significant uncertainty about the ages of new individuals entering the study area, as well as about the mortality status of individuals who disappear. These problems are noted by the authors of the only wild orangutan adult life table (Wich et al. 2004), which shows similar or higher survival in the wild than in captivity (Anderson et al. 2008; Wich, Shumaker, et al. 2009) or even, for early adulthood, human forager populations (Figure 1). This could be an artifact of having a small sample from a period of relative stability. Two features of the life table are cause for concern. First, the distribution of risk years exhibits distinct bulges at the author-defined age categories. For example, flanged males were assigned an age of 35 years when first encountered, thus the life table contains fourteen males aged 35 years, twice as many as were observed at age 34 and more than were observed at any age after 4 years. This could be possible if the

Ketambe study site was a particularly attractive place for flanged males to mate and feed, and thus experienced an influx, but it would then be a poor representation of the broader study population. A second concern is that Ketambe males were reported to have substantially higher survival than females. There is a general expectation for a male-bias in mortality, particularly in species experiencing strong sexual selection for male body mass and polygynous mating effort (Clutton-Brock 1991; Clinton and Le Boeuf 1993; Allman et al. 1998; Colchero et al. 2016). In captivity, male orangutans exhibit much lower survival than females (Anderson et al. 2008; Wich, Shumaker, et al. 2009). It is notable that the biases imposed by dispersal and transience are expected to be most relevant to males, thus these results should be taken with caution. Despite the limitations of this sample, it can be clearly concluded that orangutans experience low mortality rates and can achieve lifespans at least comparable to those of other great apes.

Both sexes of gorillas disperse and may occupy multiple groups over their lifetimes (Tutin 1996; Yamagiwa and Kahekwa 2001; Harcourt and Stewart 2007), thus ages can be difficult to estimate unless a large number of groups can be monitored. Since starting with three groups of mountain gorillas in the 1960s, research at Karisoke has expanded to include twenty groups, and their work provides the only published wild gorilla life table (Bronikowski et al. 2016a, 2016b). While the research centre can only study the groups of mountain gorillas ranging on the Rwandan side of the Virunga Mountains, these groups range within a fairly restricted area and are geographically isolated from most other gorilla groups (Gray et al. 2013), thus the study population comprises the majority of groups that individuals could move between, and demographic data carry a high degree of confidence. Other study sites are more constrained. For example, the Mbeli Bai site monitoring western lowland gorillas affords the opportunity to observe a large number of unhabituated groups (>60) but is limited to making long-distance observations from a platform overlooking a 12.9 ha swampy clearing (Breuer et al. 2009). Thus, little is known about the variation in mortality across gorilla populations or species.

In chimpanzees, males remain in their community for life and females disperse and reproduce within a fairly narrow age range, so age estimation is a fairly minor problem after a couple of decades of research. Accordingly, several life tables exist for chimpanzees. All but one of these life tables comprises the East African subspecies. As noted above, the West African population at Taï has had a particularly devastating recent history, reflected in mortality rates that are not viable over the long-term (Boesch and Boesch-Achermann 2000; Köndgen et al. 2008). By contrast, a recent report from East African chimpanzees in the Ngogo community describes remarkable survivorship, exceeding that of captive chimpanzees (Wood et al. 2017). This study concluded that under favourable ecological circumstances, including high food availability and relative protection from human disturbance, wild chimpanzees may experience mortality rates as low or lower than those of human hunter-gatherers until the age of about 40. There are good reasons to believe that the Ngogo community would have reduced mortality compared to other chimpanzee communities. They are relatively isolated from human settlements that can be a source of disease, and they are not hunted by humans or other predators. The Ngogo chimpanzees have access to more fruit (Potts, Watts, and Wrangham 2011) and maintain higher energy balance than the nearby Kanyawara community (Emery Thompson et al. 2009), which itself exhibits relatively high adult survival (Muller and Wrangham 2014). They may indeed exemplify the best-case scenario for wild chimpanzees, but one that would appear to generate growth rates too high to be stable over the long-term. However, these specific survival estimates

should be treated with caution due to peculiarities in the life table. For example, the survival function predicts that 20% of females ever born should live past the age of 60 years, while only 4 (in a community numbering 115 females) ever have. Unrecognized mortality is a distinct and unavoidable possibility in this sample due to the unusually large size of the community. This may occur because it takes many years to habituate and positively identify all individuals (particularly females), during which time deaths may go unrecognized. Additionally, a large number of female migration events may obscure death in early adulthood. Given the relative rarity of mortality events recorded, even a small number of unrecorded deaths could substantially alter the survival functions.

Wild bonobo life table statistics are only available for a small number of juveniles, though overall mortality rates are provided for adults and for adolescent males (Furuichi et al. 1998). These were 0.040 and 0.046 deaths/year, respectively, over an entire 20-year study, which included periods of intensive poaching. During a stable period, mortality rates dropped to approximately 2%. This initial data on adult mortality falls within the range of variation reported for other great apes, but bonobos may experience a relatively low infant mortality rate.

The range of variation in mortality among wild great apes, and even just among chimpanzees (Figure 1D), is very large, and given that long-term studies have been conducted primarily in protected areas, may represent only a fraction of the variation seen in nature. Available mortality data do not reveal a strong species signal, and instead suggest the influence of localized ecological conditions, including habitat disturbance, predation, natural disasters, poaching, and epidemic diseases. These stochastic factors, along with temporal variation in risk of infanticide (e.g., periodic male takeovers in gorillas) and intraspecific violence (e.g., intercommunity conflict in chimpanzees), mean that rates of mortality can vary dramatically even within a population over time. For example, the Taï chimpanzees experienced a 15-fold decrease in survival between earlier and later periods of study (Boesch and Boesch-Achermann 2000). Given the tremendous influence of human activities on ape populations, it may not be possible to reconstruct the patterns of mortality characteristic of these species during their evolutionary histories. This is perhaps not so different from the demographic examinations of modern human foragers (Gurven and Kaplan 2007).

After decades of research on wild great apes, there is relatively little understanding of cause-specific mortality. Even in well-monitored groups, a large number of individuals simply disappear without ever being recovered. In rainforests, decomposition and scavenging occur so rapidly that full necropsies cannot be performed even a couple of days after death. Thus, we know primarily about causes of death that have been preceded by obvious signs. For example, respiratory diseases occur in distinct outbreaks and cause readily observable signs, so individuals that disappear after coughing and sneezing can safely be assumed to have died from the disease.

Predation: As large-bodied primates, great apes are less vulnerable to predation than are other species, and large predators have in many cases been extirpated from their habitats. While rare, predation does occur and is likely to have been a low but consistent source of mortality for all great apes. Leopards are the principal non-human predator for gorillas, chimpanzees, and bonobos (Boesch and Boesch-Achermann 2000; Henschel, Abernethy, and White 2005; D'Amour, Hohmann, and Fruth 2006; Harcourt and Stewart 2007; Klailova et al. 2012). During one 4-year period, leopard predation was the primary source of mortality for West African

chimpanzees at Taï, accounting for 39% of deaths (Boesch and Boesch-Achermann 2000). Older infants and juveniles appear to be targeted most frequently (Boesch and Boesch-Achermann 2000), but adults are also attacked and consumed (Henschel, Abernethy, and White 2005). Lions have killed chimpanzees during temporary incursions into the forest (Tsukahara 1993) and likely pose a threat for chimpanzees ranging in savannah habitats, though no such attacks have been observed (Stewart and Pruetz 2013). Both tigers and clouded leopards appear to prey upon wild orangutans (Rijksen 1978), and orangutans exhibit prolonged alarm responses to predators (Lameira et al. 2013), but tigers are absent from Borneo and the high degree of arboreality in orangutans likely provides them with protection.

Poaching: Predation by humans is a persistent threat to all great ape species. Commercial poaching for bushmeat consumption is most common in western and central Africa, where it can have catastrophic impacts on great ape populations (Walsh et al. 2003; Stiles et al. 2016). Even small-scale hunting, such as for local consumption or for traditional medicine, practices that have likely persisted for much longer, can have important effects on great ape populations (Meijaard et al. 2011). For example, densities of Bornean orangutans are better predicted by distance to the nearest hunting village than by logging intensity or ecological measures of habitat quality (Marshall et al. 2006). Even where great apes are not targeted for hunting, they are vulnerable to snares and traps set for other animals (Quiatt, Reynolds, and Stokes 2002), and they are killed when perceived to be a threat to crops or the safety of local villagers.

Trauma: Non-poaching trauma accounts for a considerable number of deaths. Infanticide is common in gorillas (Robbins et al. 2007a; Breuer et al. 2010; Hassell et al. 2017) and chimpanzees (Wilson and Wrangham 2003; Townsend et al. 2007). Chimpanzees also kill mature individuals during intergroup conflicts and even within their own communities, comprising approximately 1.4 deaths/100 individuals/year (Wrangham, Wilson, and Muller 2006). One-on-one conflicts among silverback gorillas and flanged male orangutans result in severe injury and death (Meder 1994; Knott 1998b). Falls from trees can also be fatal (Boesch and Boesch-Achermann 2000).

Infectious disease: Respiratory disease, frequently of human origin, is a persistent cause of mortality in African ape populations (Leendertz et al. 2006; Williams et al. 2008; Sakamaki, Mulavwa, and Furuich 2009; Humle 2011; Spelman et al. 2013). Outbreaks spread rapidly within groups, often producing signs in nearly 100% of individuals. Single outbreaks have been known to kill 10–20% of chimpanzees in a community within a matter of weeks (Kaur et al. 2008; Köndgen et al. 2008; Negrey et al. 2019). While old chimpanzees are most likely to exhibit respiratory signs, significant mortality occurs among all age classes except juveniles (Emery Thompson et al. 2018). Multiple outbreaks of Ebola haemorrhagic fever have caused catastrophic mortality among gorillas and chimpanzees in West Africa over the past 35 years (Leroy et al. 2004; Ryan and Walsh 2011). African apes have also experienced smaller-scale outbreaks of anthrax, polio, scabies, and measles (Leendertz et al. 2006; Williams et al. 2008; Hoffmann et al. 2017). A number of viruses (e.g., simian foamy virus) and intestinal parasites (e.g., *Oesophagostomum*, *Strongyloides*), along with malaria parasites, occur persistently in wild apes, but their long-term impact on health is not yet understood (Hasegawa, Kano, and Mulavwa 1983; Landsoud-Soukate, Tutin, and Fernandez 1995; Dupain et al. 2002; Lilly, Mehlman, and Doran 2002; Liu et al. 2008; Gillespie et al. 2010; Prugnolle et al. 2010). Chronic infections may play a role in the "wasting" illness observed in some older chimpanzees (Goodall 1986; Nishida et al. 2003; Terio et al. 2011). Simian immunodeficiency virus (SIV), a retrovirus

related to HIV, occurs in some populations of chimpanzees and gorillas, but appears absent in bonobos (Santiago et al. 2002; Van Dooren et al. 2002; Van Heuverswyn et al. 2006). Among Gombe chimpanzees, the effects of SIV are not easily observed, but infected individuals have significantly reduced long-term survivorship (Keele et al. 2009). While wild orangutans are known to be infected by many of the pathogens impacting other apes (Kilbourn et al. 2003), no information is available on cause-specific mortality.

Degenerative Disease: Degenerative diseases, such as cancer, heart disease, and kidney disease, are expected to be major sources of adult mortality in long-lived species. A large number of unexplained deaths due to "old age" might suggest to be the case for great apes, but evidence of these processes has proved elusive. Heart disease is the largest cause of mortality among captive great apes (Lowenstine, McManamon, and Terio 2015; Strong et al. 2016; Laurence et al. 2017). However, atherosclerosis, arteriosclerosis, and associated coronary artery disease, the processes underlying most aging-associated cardiovascular deaths in humans, are very rare in great apes. Instead, captive great apes suffer from aortic dissections and myocardial fibrosis (Lammey et al. 2008; Varki et al. 2009; Lowenstine, McManamon, and Terio 2015). Evidence from a limited number of necropsies suggests that these or other cardiovascular processes are not significant sources of mortality in wild chimpanzees (Terio et al. 2011) or mountain gorillas (Nutter et al. 2005; Cooper 2017). Type II diabetes is rare even in well-fed captive apes (Kuhar, Bettinger, and Laudenslager 2005; Lowenstine, McManamon, and Terio 2015). Renal disease occurs in captive great apes, but its presence in the wild is unconfirmed (Lowenstine, McManamon, and Terio 2015; Strong et al. 2016). Malignant neoplasms occur but appear relatively rare in both wild and captive apes compared to humans (Lowenstine, McManamon, and Terio 2015; Laurence et al. 2017). Perhaps these would be found if more necropsies were done, but genetic evidence suggests that great apes have an increased capacity for cell apoptosis compared to humans (Arora, Mezencev, and McDonald 2012). Amyloid plaques and neuron loss have been identified in the brains of older captive great apes, but the full suite of signs of Alzheimer's disease have not (Finch and Austad 2015, Edler et al. 2020).

Growth and Development

Postnatal Growth

A key feature of primate life histories is relatively slow growth compared with other mammals. Allometric comparisons across taxa suggest that primates as a group are constrained by a rate of production — energy available for growth and/or reproduction — of about 42% that of other mammals (Charnov and Berrigan 1993). The net result is prolonged infant dependence, a slow rate of reproduction, and a delay until attainment of full adult size and reproductive maturity. Slow growth may be advantageous, allowing primates to learn complex foraging (Kaplan et al. 2000) or social skills (Joffe 1997) before they enter the adult world, or it may simply be less risky for juveniles than to assume the costs of rapid growth in competitive or unstable environments (Janson and van Schaik 1993). Alternatively, somatic growth rates may be constrained by the costs of building a large brain (Foley et al. 1991; Ross and Jones 1999). The latter has convincing, direct support for humans, who experience an unusually slow rate of early growth. Growth rates are slowest when the metabolic demands of brain growth are highest, and the subsequent adolescent growth "spurt" is delayed until the costs of the brain decline (Kuzawa et al. 2014).

Comparisons across primates suggest that variation in growth is not simply a product of how long it takes to reach a particular body size, but as in humans, manifests in complex variation in the timing and speed of successive growth stages (Leigh 2001).
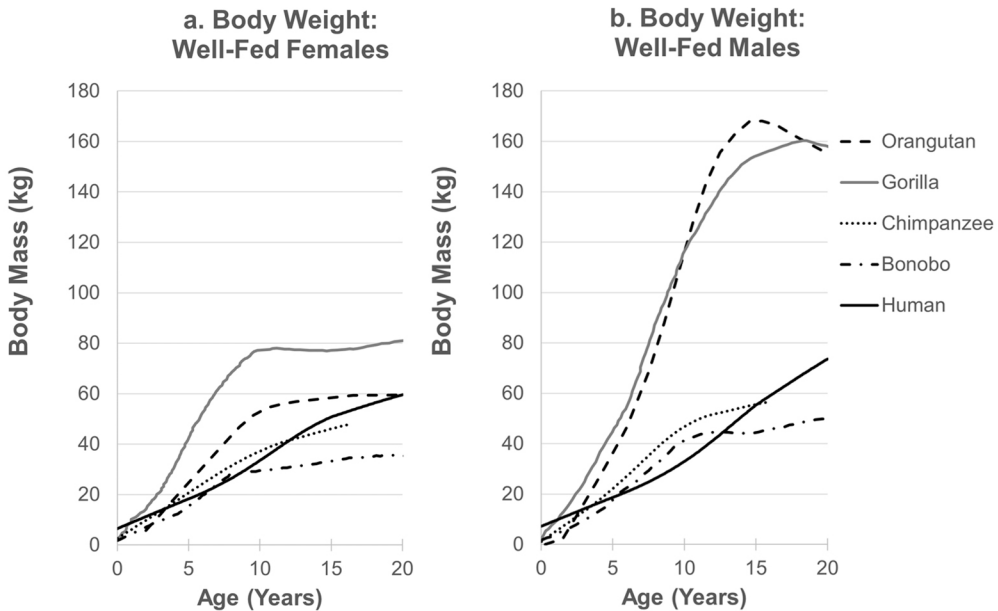

Figure 2.

Fig. 2 Comparative hominid growth. Growth in body mass among male (a) and female (b) hominids in well-fed populations, loess-smoothed data. Data sources: orangutans (*Pongo spp.*, N = 24, developmentally arrested males excluded; Fooden and Izor 1983); gorillas (*Gorilla gorilla*, N = 72F, 64M: Leigh and Shea 1996); chimpanzees (*Pan troglodytes*, N = 56F, 49M: Hamada and Udono 2002); bonobos (*P. paniscus*, N = 13F, 23M: Leigh and Shea 1996); humans (US, CDC, N >500,000: Kuczmarski et al. 2002). Where necessary, raw data acquired via WebPlotDigitizer (v. 3.9, Ankit Rohatgi).

Comparative data on growth in great apes, as in other primates, has primarily been generated from captive populations. This is important because the stable nutritional base in captivity accelerates both growth and sexual maturation and may do so differently depending on the natural diet. Captive data have other disadvantages. For example, increased fat deposition in sedentary captive colonies can lead to less robust correlations between body mass and growth in stature, and reproductive interventions can obscure the trade-off between reproduction and growth. As a general rule, differences in adult body mass among great ape species are due to differences in the rate of early growth, whereas sexual dimorphism within species results primarily from differences in the duration of growth and the magnitude of the growth spurt (Figure 2, Fooden and Izor 1983; Shea 1983; Leigh and Shea 1996). Gorilla growth rates start higher and accelerate more rapidly than either species of *Pan*, reaching peak velocities more than twice as great (Table 2). Chimpanzees grow slightly faster than bonobos during the early growth period, but chimpanzees grow for longer before reaching peak velocity. Sex differences in growth rates are minimal until adolescence, when male rates accelerate. Whereas male apes exhibit distinct adolescent growth spurts in weight, female growth spurts are notable in gorillas

and bonobos but indistinct in orangutans and chimpanzees (Leigh 1996). Growth in mass for most apes reaches an asymptote by approximately 10–15 years, except for male gorillas and orangutans who may grow for substantially longer. All of the great ape species grow faster during the early growth period than do humans and reach an earlier peak velocity. Thus, humans are exceptional both in how slowly and for how long they grow, and these characteristics are not readily explained by adult body mass (Leigh 2001).

Growth data from wild apes are sparse and differences in analytical approaches makes them difficult to compare directly to captives. Most estimates of wild body mass and length come from animals shot for museum collections, which may be a biased sample and may have errors in weight estimation. Based on the available data, the effect of captivity on adult body mass varies substantially. Orangutans are about 60% heavier, while gorillas and bonobos are of similar mass in both contexts (Table 2). Comparative growth data on living animals are available only for chimpanzees; wild chimpanzees at Gombe National Park were weighed by baiting hanging scales with food (Pusey et al. 2005). Differences in growth between Gombe and captive chimpanzees are apparent from infancy and result in an approximate 1/3 reduction in body mass (n.b., Gombe chimpanzees are small compared with other wild chimpanzees: Emery Thompson and Wrangham 2013), a difference that parallels that between human foragers and those in developed countries (Figure 3). However, wild individuals reach their full adult mass at approximately the same age as do captive individuals. Sexual dimorphism is not conspicuously enhanced with captivity for any of the great apes.

Brain growth is not well characterized in great apes. The brains of captive chimpanzees grow at a substantially lower rate than humans, and the marked difference in size is near fully realized in the first year (Leigh 2004). Growth rates subsequently decelerate rapidly such that chimpanzees complete their brain growth at about the same age, or slightly earlier (4–7 years), than do humans (5–7 years) (Herndon et al. 1999; Leigh 2004; Robson and Wood 2008; Coqueugniot and Hublin 2012; Neubauer et al. 2012). Wild mountain gorillas reach adult brain size by only age 3–4 years (McFarlin et al. 2013) The significance of adult brain mass differences among great apes is unclear. Early efforts to compare brain size across species emphasized encephalization quotients that account for body size (chimpanzees > orangutans > gorillas, Marino 1998), while recent studies suggest that absolute size (gorillas > chimpanzees = orangutans > bonobos, Table 2) is most relevant to cognition (Reader and Laland 2002). Phylogenetic analyses indicate a dissociation between brain size and body size during primate evolution (Montgomery et al. 2010). New analyses using neuronal cell counts indicate that brains of primates, including all hominids, follow a common isometric scaling pattern (Herculano-Houzel and Kaas 2011). An interesting conclusion of this work is that while human brains are extraordinary in their absolute size, sophistication, and cost, they do not actually have larger brains than expected for primates of their size (Azevedo et al. 2009; Herculano-Houzel 2012). Instead, it is the other great apes that are outliers, with the evolution of large body mass outpacing selection on the brain (Herculano-Houzel and Kaas 2011).
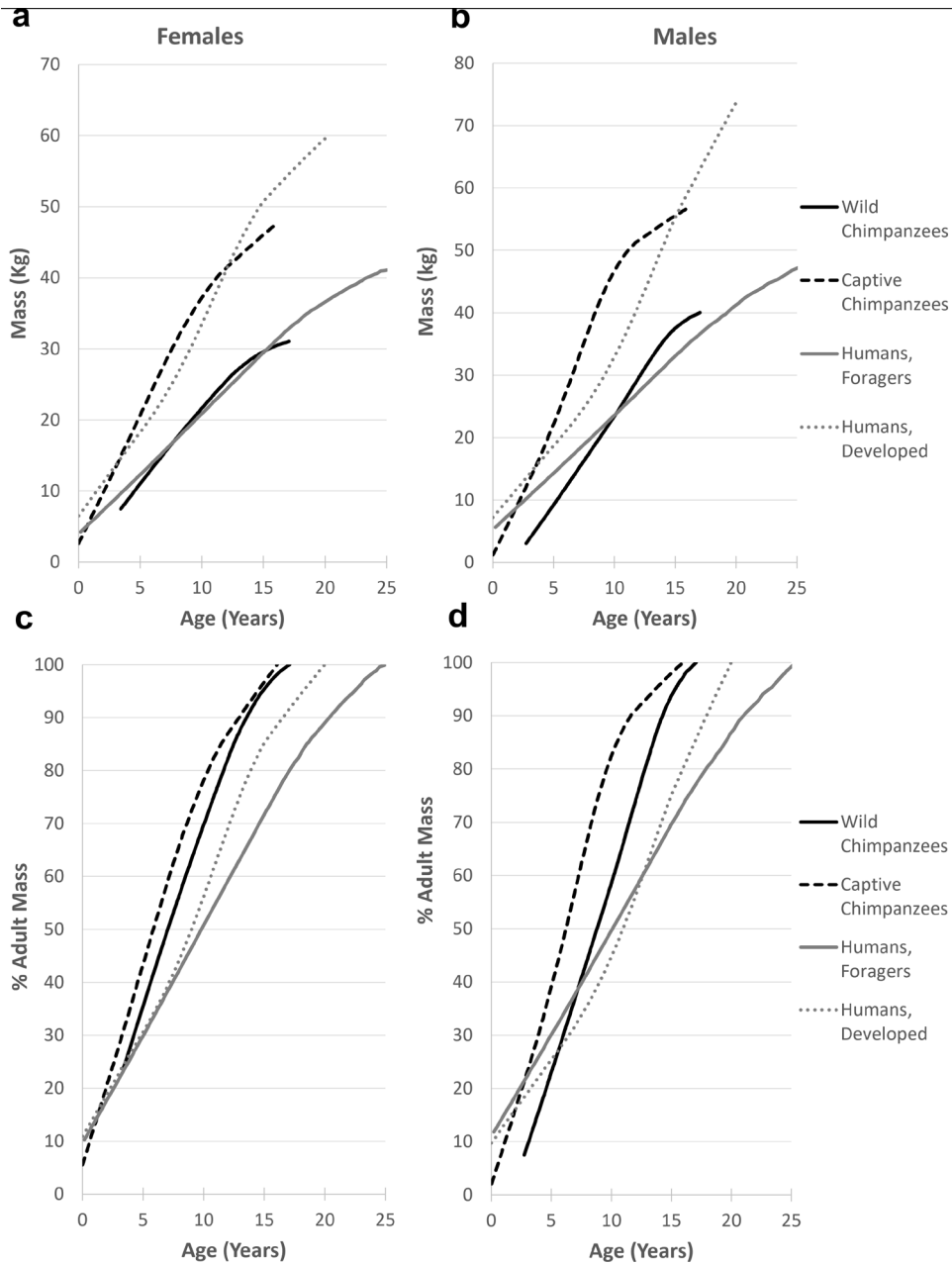
Figure 3.

Fig. 3 Growth in body mass among chimpanzees and humans under subsistence and well-fed conditions, loess smoothed data: (a,c) females, (b,d) males. Panels a, b depict absolute growth in body mass, emphasizing the intraspecific effect of energy availability. Panels c, d depict growth relative to adult body mass, emphasizing interspecific effects. Data sources: wild chimpanzees, *Pan troglodytes schweinfurthii* (Gombe, N = 26F, 31M: Pusey et al. 2005); captive chimpanzees, *P. t. verus* (Sanwa-Kagaku Kumamoto Primate Park, N = 56F, 49M: Hamada and Udono 2002); human foragers (Dobe !Kung: Howell 2010); humans, developed nation (U.S., CDC, >50,000: Kuczmarski et al. 2002). CDC data available to age 20, captive chimpanzees to age 16, !Kung and Gombe data truncated at ~95% adult weight (ages 25, 17 respectively). Where necessary, raw data acquired via WebPlotDigitizer (v. 3.9, Ankit Rohatgi).

Weaning and Nutritional Independence

While age of weaning is considered a critical developmental milestone across species, it is clear that its significance has changed in humans due to the availability of cooked or processed weaning foods and contributions to infant provisioning by fathers and alloparents. Humans consequently wean infants at a relatively young age compared to other hominids despite longer periods of nutritional dependence and maturation (Kennedy 2005). Observations from the other great apes indicate that the weaning ages correspond more clearly with the expectation of later weaning associated with slower developmental trajectories (Table 3). That is, all of the great apes nurse their infants for longer periods in the wild than do other primates. Differences among the apes correspond to later features of maturation: weaning is earliest in the Karisoke population of mountain gorillas (3.3 years) and latest in orangutans (6–8 years).

There are two major problems with defining and comparing ages of weaning in wild hominids. The first is the reliability of measurement. Nipple contact is difficult to observe and quantify, as a lot of nursing may occur out of view while high in trees or during the night. It is also not clear how well nipple contact times approximate actual milk ingestion. A second issue emerging from recent studies is that age of last nipple contact, the classic definition of weaning age, appears to be a poor indicator of relative infant development or maternal nutritional support (van Noordwijk, Kuzawa, and van Schaik 2013; Bădescu et al. 2017). In many smaller primates, the transition from exclusive maternal nutritional support to completely independent infant foraging occurs relatively rapidly at a stage of growth at which the infant's nutritional needs outstrip the mother's ability to accommodate them (Lee, Majluf, and Gordon 1991; Lee 1996). In these species, weaning is marked by overt maternal rejection and mother-infant conflict, and reliably precedes the resumption of maternal cycling, often corresponding to seasonal patterns of resource availability. For hominids, the increased energetic requirements of larger bodies and brains necessitates multiple years of lactation, including a substantial period where both mothers and infants need to contribute to meet the costs of growth (van Noordwijk, Kuzawa, and van Schaik 2013; van Noordwijk et al. 2013).

Studies of developmental processes in apes have just begun to gain traction, and these studies indicate that the multi-year lactation pattern is fundamentally different from the "classic" primate model (van Noordwijk et al. 2013). Hominid lactation comprises 3 major phases. The period of exclusive lactation lasts only a few months, with first ingestion of solid food occurring at similar ages as in other primates. Subsequently, infants continue to nurse intensively, while using supplemental foods, until their second or third year of life, at which time they undergo a marked nutritional transition to independent feeding. This transition comprises steep increases in infant time spent independently foraging (van Noordwijk et al. 2013; Matsumoto 2017; Bray et al. 2018) and decreases in time spent suckling (Clark 1977; Stewart 1988; Nowell and Fletcher 2007). The energetic relevance of these transitions has recently been confirmed using stable isotope ratios, which comprise signatures of milk ingestion or of dietary convergence by mother and infant (Reitsema 2012). For example, mother and infant chimpanzees have high divergence of carbon and nitrogen isotopes in their faeces until the infant reaches approximately 18 months and begin to converge thereafter (Bădescu et al. 2017). Dental nitrogen isotopes from deceased juvenile chimpanzees tell a similar story (Fahy et al. 2014). Urinary C-peptide of insulin levels have been used to track changes in the energetic costs of lactation for chimpanzee mothers, and these profiles also indicate a transition to a reduced load at approximately 2

years postpartum (Emery Thompson, Muller, and Wrangham 2012). This transition is most functionally equivalent to weaning in other primates, though it occurs later. However, most hominids do not fully wean until they are between 3 and 8 years old, suggesting a third stage wherein infants can provide most of their own calories but continue to use breastmilk for supplemental nutrition. It is unclear how consistently infants use breastmilk after this point, or how reliant they are on milk for survival. Dental barium isotopes from the teeth of orangutans, which have the latest weaning ages of any mammal, indicate that the pattern of milk ingestion fluctuates dramatically, with significant peaks in milk consumption during periods of food scarcity (Smith et al. 2017). Isotopic signatures of nursing disappear by about 4 years in wild chimpanzees, though infants are observed nursing for 5–6 years (Bădescu et al. 2017). Some wild chimpanzees can survive, albeit at a disadvantage, if they are weaned or even orphaned in their third year (Boesch et al. 2009; Emery Thompson et al. 2016), even though most continue to suckle for 2–4 years longer. While mountain gorilla infants can be weaned anywhere between ~2–5 years of age, final weaning age has had little impact on survival (Eckardt, Fawcett, and Fletcher 2016). Thus, for infants, whose costs of growth and competitive disadvantage make them particularly vulnerable to fluctuations in food supply (Janson and van Schaik 1993), mother's milk may not be a consistent need but an important buffer. This may help explain why mountain gorillas complete weaning substantially younger than other great apes. The low-quality herbaceous vegetation that comprises the mountain gorilla diet might seem less than ideal for infants, but it is consistently and abundantly available and requires relatively little learning of selection or processing techniques. Bamboo shoots, in particular, are soft and high in energy yield and seem to be ideal weaning foods (Grueter et al. 2014; Eckardt, Fawcett, and Fletcher 2016). On the other hand, orangutans experience the most drastic fluctuations in food supply (Conklin-Brittain, Knott, and Wrangham 2006) and continue to use supplemental nursing for the longest of any of the hominids.

The classic model of primate reproduction emphasizes the role of nursing, and consequently of weaning, as an adaptive regulator of birth spacing. As mothers are predicted to reproduce again only when their infants are sufficiently developed and capable of foraging independently, nursing itself is thought to suppress maternal reproduction. There is even a well-known mechanism for this. The hormone prolactin, produced by the mother's pituitary in response to the suckling stimulus, directly acts to suppress ovarian cycling. Under this model, infants exert considerable influence over maternal reproductive schedules, though mothers can push back by rejecting infants from the nipple at an earlier age than they might like. However, in humans it has become clear that even very intensive nursing practices may not suppress maternal cycling if the mother has abundant energy available to her (Ellison and Valeggia 2003; Valeggia and Ellison 2004; Valeggia and Ellison 2009), chiefly because the prolactin response to suckling is blunted in well-nourished mothers (Lunn et al. 1984). Instead, reproductive timing is determined by the ability of a mother to recover the energetic losses of pregnancy and lactation. While intensive breastfeeding detracts from maternal energy balance, breastfeeding alone, particularly subsequent to the introduction of supplemental foods, may not comprise a sufficient "metabolic load" to prevent the resumption of cycling (Ellison and Valeggia 2003; Valeggia and Ellison 2004). It is thus observed that many women resume cycling or even conceive while still nursing their previous infant (Gioiosa 1955; Merchant, Martorell, and Haas 1990; Moscone and Moore 1993). Similarly, weaning is not a prerequisite for the resumption

of cycling in great apes, and it appears that infants habitually suckle into their mothers' next pregnancy (orangutans: van Noordwijk et al. 2013; gorillas: Eckardt, Fawcett, and Fletcher 2016; Robbins and Robbins 2021; chimpanzees: personal observation). The final age of weaning, therefore, is determined by the mother's reproductive pattern rather than the infant's age or relative development. For example, wild chimpanzees who were forced to wean early due to a mother's pregnancy had a significant growth disadvantage relative to those whose mothers reproduced slowly (Emery Thompson et al. 2016). Thus, species variation in final weaning ages make sense in the scheme of other life history variation, but individual weaning ages may be poor indicators of development. Weaned apes are often well past the age at which they can feed themselves but well before the age when benefits of mother's milk are exhausted.

In both chimpanzees (Lonsdorf et al. 2020) and mountain gorillas (Robbins and Robbins 2021), later weaning ages have been reported male infants than for female infants. Maternal rank did not affect weaning age in the mountain gorillas. Among Gombe chimpanzees, high ranking mothers had both the earliest and latest ages of weaning (Lonsdorf et al. 2020). This pattern likely reflects two processes, one where improved condition drives faster reproduction among high-ranking females (forcing earlier weaning), and another where rank is increasing with age as fertility declines (high terminal investment).

Behavioural Development

Great apes experience many years of further growth and development after becoming nutritionally independent from their mothers. This juvenile period, defined as the interval between weaning and sexual maturity (Pagel and Harvey 1993), is greatly extended in primates compared to many other species, even after accounting for differences in adult body size (Charnov and Berrigan 1993). Skeletal, cognitive, endocrine, and sexual maturation proceed across this period. As in humans, great ape juvenility is a time of continued close proximity to mothers, frequent play, and development of foraging expertise and social relationships. The great apes also exhibit a distinct and lengthy period of adolescence, the interval between the first signs of puberty and the attainment of full adult size and adult social and breeding status. This period comprises increasing independence from the mother, initiation of sexual behaviour, slowly increasing fecundity, elaboration of secondary sexual characteristics, participation in status competition, and (depending on sex) dispersal into new groups.

Orangutans cling to their mothers almost exclusively for the first 2 years of life, and by 4 years they spend little time in direct contact with their mothers (van Noordwijk et al. 2009). They continue to spend almost all of their time within 10m of their mothers until approximately 6–8 years, and rarely associate with their mothers after age 9–10 years (van Noordwijk et al. 2009; van Adrichem et al. 2006). In Western gorillas, infants are in direct contact with mothers for 1–1.5 years and cling very rarely after approximately age 3.5 years (Nowell and Fletcher 2007). By that age, they are more apt to wander away from their mothers than are orangutans, but they continue to spend at least 50% of their time within 10m of their mothers until about age 6 years (Nowell and Fletcher 2007). Mountain gorillas reduce spatial proximity with their mothers more rapidly. They are in contact almost exclusively for the first 6 months of life, with very low rates of contact after 2 years (Fletcher 2001). Individuals begin wandering more than 5m away by age 1 and spent less than half their time within 5m by 2.5 years (Fletcher 2001). Chimpanzee infants are in contact almost exclusively until about 7–9 months (van de Rijt-Plooij and Plooij

1987). Males begin traveling in different subgroups from their mothers at about 7–8 years of age, and by ages 12–14 spend most of their time with adult males, though there is considerable variation in this (Pusey 1983, 1990a; Machanda et al. 2014). Females, who typically disperse and will not form adult relationships with other members of their natal group, continue to associate in the same subgroup as their mothers at high rates until they emigrate (Machanda et al. 2014). When individuals of either sex are in the same subgroup with their mothers, they tended to remain in close proximity (<15 m) with her until at least 10 years of age (Pusey 1983).

Though individual differences in attainment of behavioural milestones may reflect differences in growth or maturation, the difference between species likely has more to do with socioecological factors. Given their high risk of infanticide from outside males, it is somewhat surprising that mountain gorillas leave the safety of their mothers relatively early and often compared with other hominids. However, even in the first year of life, immature gorillas seek proximity with silverback males, who offer the most effective protection (Stewart 2001; Rosenbaum, Silk, and Stoinski 2011).Differences in mother-offspring distance across species covary with group cohesion — where groups as a whole exhibit tighter proximity, as in mountain gorillas, infants and juveniles spend less time in close proximity with their mothers. These differences also covary with dietary complexity, perhaps suggesting differences in the importance of staying near mothers for observational learning of foraging. In gorillas, where low-quality forage is easily acquired, infants may have less need to observe their mothers' food choices and processing behaviour. Orangutans, on the other hand, rely on a wide range of foods to buffer periods of food scarcity, and infants carefully observe their mothers in foraging contexts (Schuppli, Forss, et al. 2016; Schuppli, Meulman, et al. 2016).

Dispersal

In great apes, as in most species, one or both sexes tend to disperse from their natal groups around the time of sexual maturity, but dispersal patterns vary considerably. Dispersal is thought to serve a primary function in reducing the potential for inbreeding (Pusey 1987, 1990b). While individuals also use mate choice behaviours to avoid mating with close kin (Pusey 1980), these mechanisms can fail if a male relative is sexually coercive or if paternal kin are not well recognized (Walker et al. 2017). The diversity of dispersal patterns among great apes suggests that emigration serves additional or alternative functions, such as mitigating competition among relatives or providing access to better breeding opportunities.

Both bonobos and chimpanzees exhibit clear female-biased dispersal whereby most, but not all, females leave their natal groups around reproductive maturity, while males remain in their natal groups for life (Nishida 1979; Furuichi 1989; Eriksson et al. 2006). Female chimpanzees almost always emigrate after starting their sexual swelling cycles and having mated with males in their natal communities (Pusey 1980; Stumpf et al. 2009), and the swelling itself may serve as a kind of "passport" to facilitate acceptance by males in a new group (Nishida 1979). Most chimpanzee females emigrate between ages 10 and 15 (Emery Thompson 2013b; Wittig and Boesch 2019), while bonobos emigrate between ages 6 and 10 (Furuichi et al. 2012). Females may emigrate immediately after starting their swelling cycles or may be delayed for as much as 2 years. Dispersal timing in female chimpanzees in Kibale National Park was not predicted by gynaecological age or elevations in glucocorticoid levels, but tended to occur during periods of high diet quality, suggesting that females emigrated when they had energy to spare (Stumpf

et al. 2009). The majority of females transfer only once and do so permanently. However, female chimpanzees and bonobos may visit several communities before settling or leave their natal group temporarily and return to breed later (Pusey 1980; Goodall 1986; Furuichi et al. 2012), and rare secondary dispersal by adult female chimpanzees occurs (Nishida, Takasaki, and Takahata 1990; Emery Thompson, Newton-Fisher, and Reynolds 2006; Walker et al. 2017). In both chimpanzees and bonobos, male dispersal is rare due to hostile intergroup relations, but isolated (some temporary) male immigration events have been observed (Sugiyama 1999; Hohmann 2001; Sugiyama 2004; Furuichi et al. 2012).

Gorillas exhibit bisexual dispersal: either sex may disperse or may be philopatric (Douadi et al. 2007; Harcourt and Stewart 2007; Robbins et al. 2009). Dispersal of males appears to be dependent on breeding opportunities. Mountain gorilla males generally leave their natal groups between ages 13 and 21, after the saddles on their backs turn grey and they have reached, or nearly reached, their full adult size (Stoinski et al. 2009). They often range temporarily in bachelor groups until they are able to acquire females to establish their own groups. Some mountain gorillas remain in their natal groups by inheriting the dominant silverback position after the former silverback's death or by maturing into a position as a secondary male (Watts 2000; Robbins and Robbins 2005). In Eastern lowland gorillas, which have uni-male groups, males emigrate relatively early at 10–14 years (Yamagiwa and Kahekwa 2001). Female gorillas mature faster and leave their natal groups earlier than males: between 8–10 years in the Western species (Robbins et al. 2004), 7.5 to 15.3 years in eastern lowland gorillas (Yamagiwa and Kahekwa 2001), and approximately 8 years in mountain gorillas (Harcourt and Stewart 1978). Unlike chimpanzees, gorilla females may exhibit secondary or even tertiary dispersal, apparently to manage the risk of infanticide (Harcourt and Greenberg 2001; Stokes, Parnell, and Olejniczak 2003; Harcourt and Stewart 2007). Females may maintain kin associations by dispersing with female relatives or into groups with related individuals (Bradley, Doran-Sheehy, and Vigilant 2007).

Adult orangutans establish individual ranges, thus both sexes effectively disperse. However female orangutans can be viewed as the more philopatric sex because at least some females establish home ranges adjacent to or overlapping their mothers' and maintain friendly, albeit rare, interactions with maternal relatives (van Noordwijk et al. 2012; Ashbury et al. 2020). Males emigrate substantially farther than females (Nietlisbach et al. 2012; van Noordwijk et al. 2012), and some may continue to shift ranges throughout life (van Schaik 1999). Genetic evidence suggests that developmental arrest does not impact dispersal: even sexually-mature unflanged males are not found near related individuals (van Noordwijk et al. 2012).

Despite variation within and among great apes, as a group they depart fundamentally from the predominant pattern of male dispersal and strong female kin associations observed in cercopithecine primates. Available genetic and ethnographic evidence paint an uncertain view of sex-biased dispersal during human evolutionary history, with some studies supporting a history of female migration and others suggesting a considerably more complicated pattern (Seielstad, Minch, and Cavalli-Sforza 1998; Hammer et al. 2001; Marlowe 2004; Wilder et al. 2004; Langergraber et al. 2007). This likely emerges from high flexibility in residence patterns across human populations, including multilocality, and perhaps from different patterns of local versus long-range migration. While agriculture appears to be responsible for a recent strong

tendency for patrilocality (Marlowe 2004), the great ape data parsimoniously indicate that some degree of female dispersal would also have occurred in early hominin ancestors.

Sexual Maturation

Menstruation occurs in all great apes, but it is lighter than in humans and cannot be reliably detected in the wild. Among captive apes, menarche occurs at approximately age 8 years in orangutans, bonobos, and chimpanzees, and 6–7 in Western gorillas (Knott 2001). In female chimpanzees and bonobos, large oestrogen-dependent swellings of the anogenital region provide a conspicuous indication that ovarian cycles have begun (Dahl, Nadler, and Collins 1991). Fully tumescent swellings begin at approximately age 10–12 years in wild East African chimpanzees, after months or even years of small, sporadic swellings (Wallis 1997; Nishida et al. 2003; Stumpf et al. 2009; Walker et al. 2018). Earlier ages (8–9 years) are reported for small samples of West African chimpanzees at Bossou (Sugiyama 2004) and bonobos at Wamba (Kuroda 1989). Gorillas exhibit much smaller labial swellings that first emerge at approximately 6–8 years in wild mountain gorillas (Harcourt et al. 1980; Harcourt and Stewart 2007), but possibly not until 9–10 years in Western gorillas (Breuer et al. 2009). First cycling likely begins later in orangutans, which have no external indicators of ovulatory state, as first sexual behaviour does not occur until 10–14 years (Knott, Emery Thompson, and Wich 2009).
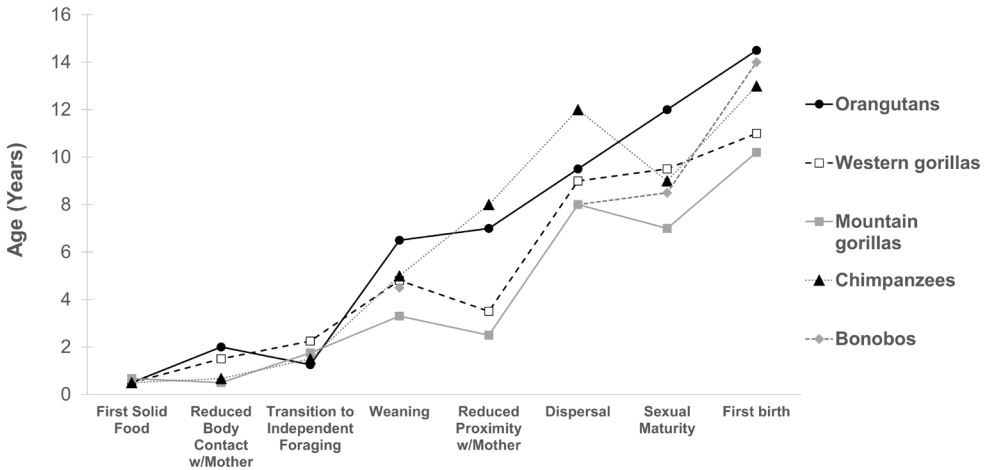
Figure 4.

Fig. 4 Maturation in hominids. Relative timing of foraging, social, and sexual development in wild great apes, showing approximate species averages for each milestone (data: see Tables 3 and 4). Note that data are missing for some events in bonobos. Mountain gorilla data shown are for Karisoke, where all milestones are available, though it should be noted that the second mountain gorilla population at Bwindi has later ages of weaning (Robbins and Robbins 2021).

Like humans, great ape females undergo substantial periods of adolescent subfecundity, defined as the interval between onset of sexual cycling and first conception (Montagu 1979). These data are difficult to acquire for individuals, as dispersal often interrupts the subfecund interval. As a result, the reports of true adolescent subfecundity based on natal individuals (approximately 1–1.5 years in mountain gorillas, 2.5 years in chimpanzees, and 4–5 years in orangutans, Knott 2001) underestimate the difference between mean age of menarche and first birth. In chimpanzees, for example, natal individuals give birth 1–2 years earlier than do immigrants (Nishida et al. 2003; Walker et al. 2018). This suggests that dispersing females may suffer a longer period of adolescent subfecundity.

Testicular enlargement occurs in wild chimpanzees at approximately 8–10 years (Goodall 1986; Pusey 1990a). First ejaculatory copulations occur at approximately age 9 years in the wild (Goodall 1986; Pusey 1990a; Sugiyama et al. 1993), compared with approximately 7 years in captivity (Marson et al. 1991). Like females, males undergo a long period of subfecundity, as sperm counts and viability increase (Marson et al. 1991). Comparable data are not available for bonobos, but puberty-associated increases in testosterone occur at the same age in captive chimpanzees and bonobos (Behringer et al. 2014). The testes of male gorillas are too small to be reliably evaluated in the wild (Harcourt 1995). The development of other adult characteristics (e.g., sagittal crest, silver hair) takes place between approximately 10 and 16 years in wild gorillas (Watts and Pusey 1993; Breuer et al. 2009). Male reproduction is typically constrained by the ability to become the dominant silverback, which occurs at a minimum age of 14 and average age of 17 (Breuer et al. 2009; Stoinski et al. 2009). Orangutan males exhibit two sexually-mature morphs (Rijksen 1978; Schürmann and van Hooff 1986; Utami et al. 2002). Some males may maintain an undeveloped ("unflanged") state, difficult to distinguish from the subadult phenotype, for up to 20 years after reaching sexual maturity. Fully "flanged" males exhibit pronounced cheek flanges, enlarged throat pouches, ropy hair, and increased body mass, and display pronounced differences in behaviour, such as in long-calling rates, activity budgets, and interactions with females (Utami Atmoko and van Hooff 2004; Knott et al. 2010). While flanged males produce higher levels of testosterone than unflanged males (Kingsley 1982; Maggioncalda, Sapolsky, and Czekala 1999), particularly if they developed early (Emery Thompson, Zhou, and Knott 2012), unflanged males are physiologically capable of siring offspring (Utami et al. 2002; Goossens et al. 2006). Given relatively late ages of first reproduction among captive orangutans compared with other great apes, it is reasonable to assume that wild orangutan males reach reproductive maturity late relative to their wild counterparts. As a general rule, great apes are similar to humans in that females exhibit outward signs of sexual maturity (e.g., sexual swellings) early in the pubertal transition and before the development of full fecundity, whereas males do not develop the physical appearance of adults until well after they are capable of siring offspring.

Figure 4 depicts the timing of behavioural development and sexual maturation across great apes. While these data indicate some consistent species differences in developmental rate, especially after weaning, they also indicate that species do not follow a consistent trajectory across modalities. For example, there is very little variation in when great apes ingest their first solid food or when they draw down their reliance on breastmilk, but greater variation in when offspring are finally weaned. While orangutans and mountain gorillas tend to fall at the upper

and lower extremes, respectively, at each time point chimpanzees deviate from the expected pattern by maintaining social cohesion with their mothers and natal groups for longer.

Female Reproduction

Fertility

First births to wild females occur at average ages of 10–12 years in gorillas, 10–14 years in chimpanzees and bonobos, and 14–16 years in orangutans (Table 4). These differences reflect an additive effect of interspecific differences in age of maturity and duration of subfecundity. In general, reproductive rates correlate with the interspecific and interpopulation variation in age of first birth (Figure 5, r = 0.696, N = 14, p = 0.006 for wild populations), with mountain gorillas exhibiting the fastest reproduction and orangutans the slowest. However, compared to the other species, most populations of chimpanzees and bonobos have faster reproductive rates than their late age of first reproduction should predict. This could, in part, reflect the costs of dispersal on delaying first reproduction in these species (Walker et al. 2018). The Bossou chimpanzee study group, where first births are known only for non-dispersing females, is an outlier for chimpanzees, but conforms to the predicted pattern for the other apes (Sugiyama and Fujita 2011).
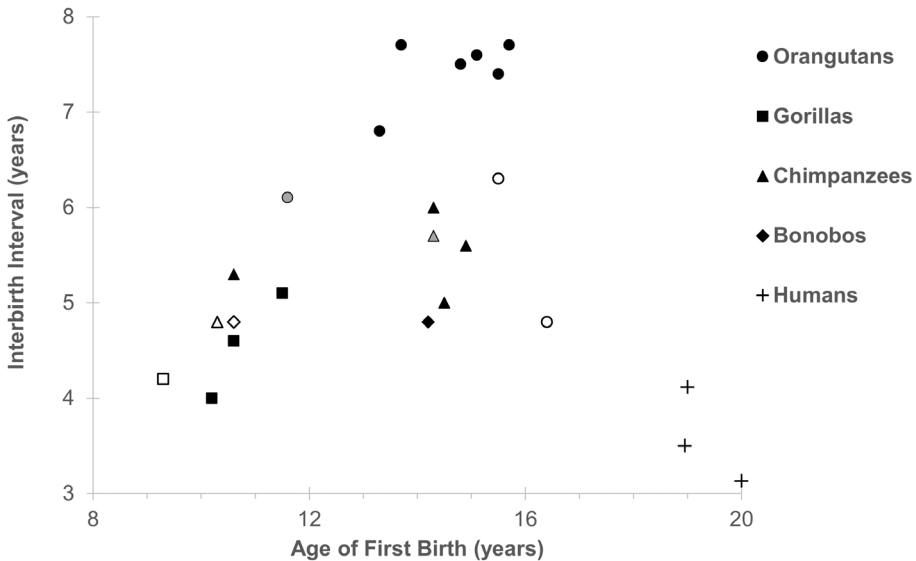

Figure 5.

Fig. 5 Relationship between the length of interbirth intervals and age of first birth in great apes, using data from Table 4. Symbol shapes according to species. Closed symbols depict wild populations, open symbols captive populations, and gray symbols free-ranging provisioned populations. Among wild populations, r = 0.696, N = 14, p = 0.006. Human data (+) shown for comparison.

Fertility data for chimpanzees is the most comprehensive and shows remarkably little interpopulation variation: for seven populations of two subspecies, average intervals between births range from 5 to 6 years. Intrapopulation variation greatly exceeds interpopulation variation (Emery Thompson 2013b), and shows broad overlap with interbirth intervals of human populations (Emery Thompson and Ellison 2017). Birth rates of wild chimpanzees peak between ages 15–25 years, an earlier and less pronounced peak than is exhibited in human forager populations (Emery Thompson, Jones, et al. 2007).

The interval between births consists of a prolonged period of postpartum amenorrhea, a shorter period of cycling to conception, and gestation. Most of the variation in interbirth intervals within and between species occurs during postpartum amenorrhea, which typically comprises 60–80% of the interbirth interval. Thus, interbirth intervals following the deaths of unweaned offspring are substantially shorter than those when the previous offspring survives (Harcourt et al. 1980; Furuichi et al. 1998; Emery Thompson, Jones, et al. 2007; Wich, de Vries, et al. 2009). However, bonobos exhibit unusually early resumption of cycling, followed by an unusually long period of cycling (Kano 1992; Furuichi and Hashimoto 2002). This pattern also has been observed in West African chimpanzees at Taï (Deschner and Boesch 2007). Since data on West African chimpanzees are available only for this one population, it is not yet clear whether this is a subspecies-typical pattern, or if they exhibit an extreme of interpopulation variation across chimpanzees. The functional significance of this difference is yet unclear, but it has been hypothesized that a longer period of cycling may reduce sexual coercion or increase the benefits of promiscuous mating (Wrangham 2002; Deschner and Boesch 2007).

Variation in fertility among chimpanzees has been attributed to temporal and interindividual variation in dietary quality and/or female energy balance (Emery Thompson 2013b), which affects occurrence of sexual cycles (Anderson, Nordheim, and Boesch 2006), ovarian hormone production (Emery Thompson, Wrangham, and Reynolds 2006; Emery Thompson, Kahlenberg, et al. 2007; Emery Thompson and Wrangham 2008; Emery Thompson, Muller, and Wrangham 2014), waiting time to conception (Emery Thompson and Wrangham 2008), and duration of postpartum amenorrhea (Emery Thompson, Muller, and Wrangham 2012). Similar effects are suggested for at least one population of wild orangutans, where ovarian hormones and conceptions peak during peaks in food availability (Knott 1999; Knott 2001; Knott, Emery Thompson, and Wich 2009). The influences of energy availability are reflected in markedly accelerated reproductive rates in captive versus wild great apes (Table 4). Interspecific variation in interbirth intervals is still evident among well-fed captive populations, so reproductive rates are likely to have a strong genetic component. However, these differences may still be long-term adaptations to feeding ecology, promoting more conservative reproductive effort in response to chronic resource instability. Mountain gorillas have the most stable food base and the shortest birth intervals, while orangutans have the most unstable food base and the longest birth intervals. Western gorillas pursue a more chimpanzee-like diet than do mountain gorillas at Karisoke, and they have correspondingly longer birth intervals. Bonobos pursue a more gorilla-like diet than do chimpanzees and have correspondingly shorter birth intervals. Early reports from orangutans proposed the reverse: longer birth intervals in Sumatran versus Bornean orangutans were suggested to result from more productive Sumatran forests, perhaps as a transition to a slower overall life history (Marshall et al. 2009; Wich et al. 2011; Skinner 2014). However, newer comprehensive analyses indicate that the birth intervals of the two species

are statistically indistinguishable (van Noordwijk et al. 2018). Captive orangutans exhibit a small but significant species difference in the opposite direction, with longer birth intervals in captive-born individuals from the Bornean species (Anderson et al. 2008). Neither captive nor wild studies detect significant differences in other demographic variables between Bornean and Sumatran orangutans, supporting a general conclusion that these species have not experienced divergence in life history evolution (Anderson et al. 2008; Knott, Emery Thompson, and Wich 2009; Wich, de Vries, et al. 2009; van Noordwijk et al. 2018).

Comparative reproduction in human populations is often estimated using completed fertility, which is the sum of all age-specific fertility rates. This statistic assumes survival to the end of the reproductive period. By this metric, completed fertility in wild chimpanzees and mountain gorillas would be approximately 8 infants per female (calculated from: Karisoke gorillas, Robbins et al. 2006; multi-site chimpanzee sample, Emery Thompson, Jones, et al. 2007), as high as many high-fertility human populations. This is clearly misleading because most wild great apes do not live through their potential fertility. If mortality is considered, each chimpanzee female born in a multi-site sample (Emery Thompson, Jones, et al. 2007) would be expected to produce 2.53 infants (a net reproductive rate of 1.27 daughters), while the net reproductive rate for the largest chimpanzee sample at Gombe is only 0.745 daughters per female (Bronikowski et al. 2016b). The net reproductive rate of mountain gorilla females at Karisoke is estimated at 1.918 daughters per female (Bronikowski et al. 2016b). Those chimpanzee and gorilla females who live long enough to reproduce at all may be expected to produce approximately 3–5 surviving offspring (Yamagiwa and Kahekwa 2001; Robbins et al. 2007a; Emery Thompson 2013b). Given that a large proportion of females do not live to reproduce at all, most great apes hover dangerously close to the replacement levels of fertility necessary for population viability.

Humans and the other great apes share derived characteristics of the reproductive system that distinguish them from many other primates (Emery Thompson 2013a, 2013b; Emery Thompson and Ellison 2017). These differences include not only the physiological systems governing the reproductive process (e.g., ovulation, pregnancy), but a generally cautious pace of reproduction in which fecundity is highly sensitive to energy availability. The unexpectedly faster rate of human reproduction may not have required major innovations in reproductive physiology but can have instead resulted largely by adaptation to enhanced energy availability for reproductive females, which is in turn a product of cognitive and social adaptations including cooking, tool use and cooperative foraging and hunting, division of labour, and food sharing (Hawkes et al. 1998; Kaplan et al. 2000; Kramer 2005; Wrangham and Carmody 2010; Reiches et al. 2009), as well as metabolic adaptations for higher energy throughput (Pontzer et al. 2016). For example, whereas male foragers increase their workload in order to provision offspring and directly supplement the energy budgets of reproductive women (Marlowe 2001), male great apes provide food for neither. Male chimpanzees have a net negative effect on the energetic status of their female associates (Emery Thompson, Muller, and Wrangham 2014), while association with males raises glucocorticoid levels of female orangutans (Kunz et al. 2020). While male gorillas protect and play with infants (Rosenbaum et al. 2018), and may even adopt orphans, infanticidal behaviour has extreme negative consequences for female reproductive success (Robbins et al. 2007b).

Female Aging and Fertility

The question of whether extended post-reproductive lifespans occur in the great apes is of central importance to evaluating hypotheses for the evolution of this feature in humans. Nevertheless, it continues to be debated whether a significant post-reproductive lifespan is a distinctly human trait (Pavelka and Fedigan 1991; Hawkes 2003; Alberts et al. 2013) or an extension of a trait common in other primates (Cohen 2004; Walker and Herndon 2008). Some of the debate hinges on the choice and definition of terms, such as "menopause", "reproductive cessation", "reproductive senescence", "post-reproductive lifespan", or "post-fertile viability". There is also some fundamental disagreement on the appropriate question. Evolutionary anthropologists are largely concerned with the occurrence and length of the post-reproductive life stage and whether it specifically evolved due to its adaptive benefits. Gerontologists are concerned with mechanistic and evolutionary processes shaping fertility decline, regardless of whether this results in reproductive cessation. Theoretical biologists have focused on whether it is a logical expectation for somatic and reproductive lifespans to be tightly linked, or if post-reproductive lifespans are and should be the norm and subject to allometric scaling (Cohen 2004). To a certain extent, these perspectives can exist simultaneously, provided that the evidence, and their interpretations are accurately understood.

A variety of processes contribute to reductions in fertility with age, but the critical constraint on reproductive lifespan in humans is the exhaustion of the lifetime supply of ovarian follicles, the specific phenomenon that results in menopause. This process is not easily detected, thus various proxies are used, including presence of menstruation (also difficult to detect in wild apes), presence of sexual swellings (only readily observed in *Pan*), and demonstrated fertility. On the one hand, evidence of continued fertility, such as from population-level analysis of age-specific fertility rates, is difficult to misconstrue. However, many analyses, particularly for cross-species comparisons, rely on inference from the interval between last reproduction and death to calculate the proportion of individuals experiencing a post-reproductive lifespan and/or the proportion of the lifespan individuals spend in the post-reproductive stage. These criteria are applied inconsistently and introduce statistical bias (Levitis and Lackey 2011). Moreover, observations of amenorrhea or infertility in a small number of older apes cannot necessarily be attributed to the menopausal process, as little is known about other sources of secondary infertility, such as foetal loss, endometriosis, hormonal imbalances, or infections in the reproductive tract. A second hurdle comes from distinguishing menopause from the natural process of reproductive senescence, which leads to longer intervals between births. For example, in the Kanyawara community of wild chimpanzees, a female estimated to be in her early 60s had experienced over 8 years of amenorrhea following her last infant but began exhibiting sexual swelling cycles in the months before her death (personal observation). The influence of ill health on fertility is also underappreciated. A cross-population study of wild chimpanzees indicated that, even in their 30s, females who were close to death exhibited reduced fertility compared with healthy females (Emery Thompson, Jones, et al. 2007).

Signs of reproductive senescence in gorillas and chimpanzees are clear and consistent with reproductive aging in humans. Cycles gradually increase in length throughout adulthood and become more irregular, ovarian hormone levels decline, and birth rates decrease (Caro et al. 1995; Atsalis et al. 2004; Atsalis and Margulis 2006; Robbins et al. 2006; Emery Thompson, Jones, et al. 2007; Lacreuse et al. 2008). Some captive apes exhibit long acyclic periods at older ages

(Atsalis and Margulis 2006). These data have been interpreted as data for perimenopause and menopause occurring prior to age 40 years in captive apes (Atsalis and Margulis 2006; Videan et al. 2006; Atsalis and Videan 2009). However, other captive facilities have reported continued menstrual cycling in nearly all individuals, suggesting the opposite — menopause is very rare (Lacreuse et al. 2008; Herndon and Lacreuse 2009). In one study of captive chimpanzees, only one of 20 females over the age of 39 years ceased cycling for longer than 12 months: she was 56 years old (Lacreuse et al. 2008).

Direct data on ovarian follicle depletion are available only for captive chimpanzees and one bonobo. In an early study of captive chimpanzees, six deceased females aged 35–48 had histological evidence of continued reproductive ability: primary follicles, recent luteal activity, and/or active endometria (Graham 1979). Two more recently histological analyses used larger samples. Based on different sample sizes and slightly different modelling approaches, one concluded that rates of follicular depletion in humans and chimpanzees were nearly indistinguishable (Jones et al. 2007), while the latter reported a faster rate of decline after age 35 years in humans, albeit with broadly overlapping confidence intervals (Cloutier, Coxworth, and Hawkes 2015). These specific conclusions should be treated with caution not only because the sample of relatively old chimpanzees is sparse but because chimpanzee follicle counts resulted from ovarian cross-sections, while human follicle counts were from whole ovaries. However, two essential points are clear. The ovaries of most (15 of 18) chimpanzee females over age 35 years (up to 49 years) had non-negligible counts of primordial follicles, suggesting continuing fertility to late ages. And, both chimpanzees and humans converge on an approximate age of follicular exhaustion near 50 years.

In humans, menopausal status can be detected by sustained, elevated levels of the gonadotropins LH and FSH and a decreased response to GnRH challenge (Wood 1994). One aged captive bonobo (the only examined, precise age unknown) exhibited menopausal ovaries and had both elevated gonadotropin levels and weak response to GnRH (Gould, Flint, and Graham 1981). The 47- and 48-year old chimpanzees in the same study responded normally to GnRH challenge and exhibited cyclic gonadotropin peaks, though they were less defined than in younger chimpanzees. A larger study of captive chimpanzees found declining LH and FSH levels among older females (Videan et al. 2006), but the significance of this pattern is unclear as it is opposite to that found in aging women. Notably, *in vivo* and post-mortem examinations of captive apes have sometimes shown structural abnormalities of the ovaries and reproductive tract that might interfere with reproductive function of some individuals independently of menopausal processes (Graham 1979; Loskutoff et al. 1991).

Relevant data from the wild are limited to observed births. Among Sumatran orangutans at Suaq Balimbing, interbirth intervals (N = 14) did not increase with age, and the three oldest females had recent births (at ages 38, 38, and 41–50 years: Wich et al. 2004). An analysis of 38 years of demographic data from the mountain gorilla population in the Virungas found that birth rates declined moderately in older age groups, but births to females in their late 30s and early 40s were observed (Robbins et al. 2006). As many as 25% females had terminal birth intervals that exceeded expectation, but the post-reproductive lifespan was trivial, approximately 1–3% of the total lifespan. Birth rates aggregated across six populations of chimpanzees also exhibited a clear pattern of reproductive senescence; interbirth intervals increased with age, but there was evidence for continued reproductive ability in females in their late 40s and even

early 50s (Emery Thompson, Jones, et al. 2007). Birth rates declined to zero at approximately the same age that survivorship reached zero. Taken together, these data suggest that great apes experience a senescent process that can culminate in menopause in some individuals during the 5th or 6th decade of life, but that even in favourable conditions, few individuals live to see this transition. Post-reproductive viability in the great apes would appear to be too rare and too brief to have been a target for selection.

Comparisons across mammals indicates that as maximum lifespan increases, the duration of fertility fails to keep pace, suggesting that the "shelf-life" of oocytes is constrained (Huber and Fieder 2018). In accordance, the great ape data is consistent with the conclusion that the age of last reproduction has been largely conserved during human evolution, such that menopause is primarily the result of extended human lifespan (Hawkes 2003).

The great ape data suggest that the attraction of human men to young women (Buss 1989; Kenrick and Keefe 1992) is a derived feature linked to long-term pair bonding. Whereas men seeking marriage partners may be concerned with the years of fertility remaining, great ape males can be expected to allocate reproductive effort according to a female's likelihood of bearing offspring in the immediate future, as well as her probability of successfully rearing them. In the absence of a long post-reproductive period, aging chimpanzee females not only retain their attractiveness, they actually become more attractive to males, earning more solicitations and inciting more vigorous male competition than younger females (Muller, Emery Thompson, and Wrangham 2006). In most nonhuman primates, young females are less attractive mates (Anderson 1986). Lengthy sub-fecund periods of nulliparous females may deter males from expending mating effort on them. In both chimpanzees and gorillas, females also experience a particularly long interval between first and second births (Jones et al. 2010; Robbins et al. 2006), perhaps because early reproductive effort competes with the last years their own growth. Additionally, older mothers are expected to produce higher quality offspring due to prior maternal experience, increased access to resources, and/or stronger social ties. Like many other primates, first-born mountain gorilla infants have significantly higher mortality than later-born infants (Robbins et al. 2006). This is not true of chimpanzees, despite the low rank of primiparous mothers, perhaps because primiparous mothers are more solicitous of their infants (Stanton et al. 2014). Because birth rates decline at later ages, chimpanzees born to older mothers receive longer periods of investment and experience less sibling competition, positively impacting their growth (Emery Thompson et al. 2016). On the other hand, without a prolonged post-reproductive period, older ape mothers pose a higher risk of orphaning dependent infants.

Male Reproduction

In the wild, chimpanzee males are capable of siring offspring by the age of 9 years (Langergraber et al. 2012). According to genetic paternity analyses, males achieve a peak in paternity between ages 16 and 25 years (Newton-Fisher 2004; Boesch et al. 2006; Wroblewski et al. 2009; Muller et al. 2020) and appear to be capable of successful reproduction into at least their mid-forties or early fifties, though the ages of some of the oldest fathers may be overestimated. As rank influences paternity in all populations studied, the age distribution of paternities is influenced in part by the ages that males can achieve high rank. However, males who were unusually young or old when siring their offspring did not do so because they were high-ranking, but in

spite of being low-ranking (Wroblewski et al. 2009). Individual males are known to have sired up to 7 offspring, and some have sired offspring over periods of at least 16 years (Wroblewski et al. 2009). In addition to dominance rank, male reproductive success can be influenced by the formation of coalitions with other males (Gilby et al. 2013) and the use of coercive aggression against females (Feldblum et al. 2014).

Mountain gorilla males are known to have sired offspring between the ages of approximately 9 and 25 years, with a mean paternal age of 19 years at Karisoke (Bradley et al. 2005; Nsubuga et al. 2008). With the assumption that they sired all offspring born during their tenures, dominant silverbacks (N=22) sired an average of 7.2 (range 0–27) offspring that survived to weaning (Robbins et al. 2014). This is a slight overestimate, as dominant silverbacks actually sire only 71–85% of those offspring born in multimale groups (Bradley et al. 2005; Nsubuga et al. 2008). Due to higher infant mortality, shorter tenure lengths, and smaller harems, silverback harem leaders in the western gorilla population at Kahuzi-Biega produce only approximately 2 infants that survive to weaning (Breuer et al. 2010). The fertility rate of an average male should be lower if not all males are able to become dominant. Male body size and competitive strength can impact reproductive success by increasing harem size and tenure length (Caillaud et al. 2008; Breuer et al. 2010). In multimale groups, mountain gorilla males are reported to improve their paternity success by behaving affiliatively with infants, even those they have not sired (Rosenbaum et al. 2018).

The occurrence of male bimaturism, and the dispersal of males over long distances, hinders estimates of fertility parameters for wild male orangutans. Males succeed at siring offspring when both flanged and unflanged (Utami et al. 2002; Goossens et al. 2006). One successful male is known to have sired at least 3 offspring over the course of 19 years (Utami et al. 2002).

Data on the ages of sires are not available for bonobos. A recent study indicates high reproductive skew compared with chimpanzees, with one bonobo male siring at least 9 offspring over a 12-year period (Surbeck et al. 2017). In addition to dominance rank, the presence of a male's mother improves reproductive success (Surbeck et al. 2019). Mothers provide agonistic support to males and facilitate their proximity to fecundable females (Surbeck, Mundry, and Hohmann 2011).

The most obvious feature that distinguishes human male fertility from that of great apes is the extent to which men are constrained by marriage in most societies. Depending on marital practices within a population, men may experience delays to the age of first reproduction, economic or cultural constraints on polygyny, and fertility rates that are interdependent with their wives'. Additionally, the ways in which males compete differs between the great apes, who rely largely on aggressive competition, and humans for whom economic resources and social prestige may be better predictors of reproductive success (Gurven, Kaplan, and Gutierrez 2006; von Rueden, Gurven, and Kaplan 2010). As the latter peak relatively later in life than physical prowess, human males can be predicted to experience later ages of paternity than their great ape counterparts (Muller et al. 2020). Nevertheless, recent evidence suggests that male chimpanzees in some communities can leverage coalitionary support to maintain high rank long past their physical prime (Watts 2018), potentially extending reproductive tenures.

Conclusions

Demographic data from the great apes provide an essential comparison for understanding the nature of human life history evolution. Historically, these comparisons have relied on small numbers of individuals in captivity or rough estimates from the wild. As this review reveals, there are still many gaps where we lack comprehensive, ecologically-valid data on great ape life history parameters. This is not for lack of effort. Great ape researchers face enormous hurdles, some owing to the elusive habits of the species themselves, and some to chronic problems of civil unrest, epidemic disease, and other conservation threats in the areas they inhabit. Yet, these problems place a premium on high-quality demographic data that can be used to evaluate the impacts of human disturbance on long-term population sustainability.

Mountain gorilla research at Karisoke and chimpanzee research at Gombe, Kibale, and other younger field sites have generated high-quality datasets on fertility and mortality and will yield more detailed and precise data as their study durations approach and surpass the lifespans of the animals they study. An exciting new wave of research has produced increasingly detailed analysis of behavioural development in infants and juveniles. New and newly-reopened field sites are beginning to build datasets for poorly-studied species, such as western lowland gorillas and bonobos. Researchers are now in the process of using modern techniques of parallel-laser photogrammetry, genetic analysis, endocrinology, immunology, and stable isotope analysis to generate detailed data on body growth, infant nutrition, health, and population structure. The next ten to twenty years will be a critical period of coalescence for great ape life history studies.

By combining what we do know about great apes from the wild and captivity, some broad conclusions are possible. In general, orangutans exhibit characteristics of a conspicuously slower life history than the other great apes, characterized by a later age of sexual maturity, later ages of weaning, longer interbirth intervals, and higher survivorship. Mountain gorillas, at least in one of the two populations, exhibit the inverse suite of characteristics indicative of a faster life history schedule. The other species fall in the middle, with bonobos and western gorillas exhibiting reproductive characteristics at the faster end of the range of variation exhibited in chimpanzees. Considerable intraspecific variation is evident but poorly estimated as some species are well-studied in only one locality.

The pace of reproductive events is notable because it does not indicate a strong correspondence to body mass within this clade. Classic models of life history predict, with the support of ample comparative evidence, that larger body mass will correspond with a slow life history because it takes longer to grow larger, and body mass confers a survival advantage (Harvey and Clutton-Brock 1985; Read and Harvey 1989; Charnov 1991). Gorillas would then be predicted to be the slowest, and chimpanzees and bonobos the fastest. Furthermore, body growth studies suggest that among the great apes, larger body mass (except for the males of highly dimorphic species) is not associated with a longer growth period. We suggest that while large body size is essential to understanding the evolution of slow life histories in the hominids as a clade, variation within this group of closely-related species may stem from more specific adaptations to feeding ecology. Importantly, we may expect selection on body mass and selection on life history strategies to move along different axes in response to different features of the environment. Generally, growing too large is disadvantageous for apes due to the costs of travel, particularly when patchily-distributed fruit resources require ranging over large areas (Isbell et al. 1999; Key and Ross 1999). Indeed, flanged male orangutans appear to suffer

high costs of travel, and modify their behaviour (and perhaps their developmental strategies) accordingly (Mitani 1989; Utami Atmoko and van Hooff 2004; Knott and Emery Thompson 2013). However, large body mass in gorillas confers a nutritional advantage for processing large amounts of herbaceous material (Gaulin 1979; Watts 1996; Müller et al. 2013). These resources pose low ecological risk to mothers and infants, as they are widespread and continuously available (Watts 1998). Orangutans, by contrast, experience the highest ecological risk, posed by dramatic and unpredictable fluctuations in fruit availability (Knott 1998a; Harrison, Morrogh-Bernard, and Chivers 2010; Vogel et al. 2012). Such conditions certainly constrain fertility in the short term, but may have additionally selected for a highly risk-adverse reproductive schedule with extended infant dependence on maternal nutritional support (van Noordwijk and van Schaik 2005; Knott, Emery Thompson, and Wich 2009; Smith et al. 2017). Thus, when we consider humans alongside the apes, we have no reason to invoke strong allometric constraints and can expect that the dramatic differences in resource quality and stability effected by technological and social adaptations (Hawkes et al. 1998; Kaplan et al. 2000; Carmody and Wrangham 2009) will have been critical to shaping our life histories (Emery Thompson and Ellison 2017). However, the reduction of ecological constraints has been replaced by strong internal constraints of a greatly enlarged brain (Aiello and Wheeler 1995; Kuzawa et al. 2014).

Over and above the progress on generating demographic statistics on great apes, researchers are gaining important insights into the dynamics of life history variation. This includes close study of the role of energy availability in interindividual and interpopulation variation in fertility, and perhaps mortality. Additionally, rapid progress has been made in understanding the dynamics of infant nutritional development and birth spacing. These types of examinations have revealed important differences in life history processes between hominids and other primates that have the potential to transform our approach to human life history evolution (Knott 2001; Emery Thompson 2013b; van Noordwijk, Kuzawa, and van Schaik 2013; van Noordwijk et al. 2013; Emery Thompson and Ellison 2017). With this in mind, there is a critical need for detailed data on the natural causes of mortality in all of the great apes to better understand the factors that constrain lifespan. Finally, as datasets improve, an essential future goal will be to model the influence of variance in particular life history parameters on reproductive success. Together, these approaches may allow us to assess the vulnerability of different life history features to selection during the evolution of the human species.

Acknowledgments

Tables 1–4 (Comparative mortality and survival data for wild great apes, Comparative growth data for great apes, Weaning and nutritional development in wild great apes, and Reproductive parameters of wild and captive great apes) are available online at https://doi.org/10.11647/OBP.0251#resources

References[1]

Aiello, Leslie C., and Peter Wheeler. 1995. 'The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution', *Current Anthropology*, 36.2: pp. 199–221, https://www.doi.org/10.1086/204350

Alberts, Susan C., Jeanne Altmann, Diane K. Brockman, Marina Cords, Linda M. Fedigan, Anne Pusey, Tara S. Stoinski, Karen B. Strier, William F. Morris, and Anne M. Bronikowski. 2013. 'Reproductive aging patterns in primates reveal that humans are distinct', *Proceedings of the National Academy of Sciences*, 110.33: pp. 13440–45, https://www.doi.org/10.1073/pnas.1311857110

Allman, John M., Aaron Rosin, Roshan Kumar, and Andrea Hasenstaub. 1998. 'Parenting and survival in anthropoid primates: caretakers live longer', *Proceedings of the National Academy of Science USA*, 95.12: pp. 6866–69, https://www.doi.org/10.1073/pnas.95.12.6866

Anderson, Connie M. 1986. 'Female age: male preference and reproductive success in primates', *International Journal of Primatology*, 7.3: pp. 305–25. https://doi.org/10.1007/bf02736394

Anderson, Dean P., Erik V. Nordheim, and Christophe Boesch. 2006. 'Environmental factors influencing the seasonality of estrus in chimpanzees', *Primates*, 47: pp. 43–50, https://www.doi.org/10.1007/s10329-005-0143-y

Anderson, Holly B., Melissa Emery Thompson, Cheryl D. Knott, and Lori Perkins. 2008. 'Fertility and mortality patterns of captive Bornean and Sumatran orangutans: is there a species difference in life history?', *Journal of Human Evolution*, 54.1: pp. 34–42, https://www.doi.org/10.1016/j.jhevol.2007.05.014

Ardito, G. 1976. 'Check-list of the data on the gestation length of primates', *Journal of Human Evolution*, 5.2: pp. 213–22. https://doi.org/10.1016/0047-2484(76)90023-3

Arora, Gaurav, Roman Mezencev, and John F. McDonald. 2012. 'Human cells display reduced apoptotic function relative to chimpanzee cells', *Public Library of Science ONE*, 7: p. e46182, https://www.doi.org/10.1371/journal.pone.0046182

Ashbury, Alison M., Erik P. Willems, Sri Suci Utami Atmoko, Fajar Saputra, Carel P. van Schaik, and Maria A. van Noordwijk. 2020. 'Home range establishment and the mechanisms of philopatry among female Bornean orangutans (Pongo pygmaeus wurmbii) at Tuanan', *Behavioural ecology and Sociobiology*, 74: p. 42, https://www.doi.org/10.1007/s00265-020-2818-1

Atsalis, Sylvia, and Susan W. Margulis. 2006. 'Sexual and hormonal cycles in geriatric *Gorilla gorilla gorilla*', *International Journal of Primatology*, 27: pp. 1663–87, https://www.doi.org/10.1007/s10764-006-9097-1

Atsalis, Sylvia, Susan W. Margulis, Astrid Bellem, and Nadja Wielebnowski. 2004. 'Sexual behavior and hormonal estrus cycles in captive aged lowland gorillas (*Gorilla gorilla*)', *American Journal of Primatology*, 62.2: pp. 123–32, https://www.doi.org/10.1002/ajp.20010

Atsalis, Sylvia, and Elaine Videan. 2009. 'Reproductive aging in captive and wild common chimpanzees: factors influencing the rate of follicular depletion', *American Journal of Primatology*, 71.4: pp. 271–82, https://www.doi.org/10.1002/ajp.20650

Azevedo, Frederico A. C., Ludmila R. B. Carvalho, Lea T. Grinberg, José Marcelo Farfel, Renata E. L. Ferretti, Renata E. P. Leite, Wilson Jacob Filho, Roberto Lent, and Suzana Herculano-Houzel. 2009. 'Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain', *The Journal of Comparative Neurology*, 513.5: pp. 532–41, https://www.doi.org/10.1002/cne.21974

Bădescu, Iulia, M. Anne Katzenberg, David P. Watts, and Daniel W. Sellen. 2017. 'A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees', *American Journal of Physical Anthropology*, 162.2: pp. 285–99, https://www.doi.org/10.1002/ajpa.23116

---

[1]   Note this chapter has been posted on the Open Science Framework website since 06/09/2019, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

Beck, Benjamin B. 1982. 'Fertility in North American male lowland gorillas', *American Journal of Primatology*, 3.Suppl. 1: pp. 7–11, https://www.doi.org/10.1002/ajp.1350030505

Behringer, Verena, Tobias Deschner, Caroline Deimel, Jereon M. G. Stevens, and Gottfried Hohmann. 2014. 'Age-related changes in urinary testosterone levels suggest differences in puberty onset and divergent life history strategies in bonobos and chimpanzees', *Hormones and Behavior*, 66.3: pp. 525–33, https://www.doi.org/10.1016/j.yhbeh.2014.07.011

Bellem, Astrid C., Steven L. Monfort, and Karen L. Goodrowe. 1995. 'Monitoring reproductive development, menstrual cyclicity, and pregnancy in the lowland gorilla (*Gorilla gorilla*) by enzyme immunoassay', *Journal of Zoo and Wildlife Medicine*, 26.1: pp. 24–31. https://www.jstor.org/stable/20095432

Boesch, Christophe, and Hedwige Boesch-Achermann. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution* (Oxford: Oxford: University Press).

Boesch, Christophe, Camile Bole, Nadin Eckhardt, and Hedwige Boesch. 2009. 'Altruism in forest chimpanzees: the case of adoption', *Public Library of Science ONE*, 5: p. e8901, https://www.doi.org/10.1371/journal.pone.0008901

Boesch, Christophe, Gregoire Kohou, Honora Nene, and Linda Vigilant. 2006. 'Male competition and paternity in wild chimpanzees of the Taï Forest', *American Journal of Physical Anthropology*, 130.1: pp. 103–15, https://www.doi.org/10.1002/ajpa.20341

Bradley, Brenda J., Diane M. Doran-Sheehy, and Linda Vigilant. 2007. 'Potential for female kin associations in wild western gorillas despite female dispersal', *Proceedings of the Royal Society of London B: Biological Sciences*, 274.1622: pp. 2179–85, https://www.doi.org/10.1098/rspb.2007.0407

Bradley, Brenda J., Martha M. Robbins, Elizabeth A. Williamson, H. Dieter Steklis, Netzin Gerald Steklis, Nadin Eckhardt, Christophe Boesch, and Linda Vigilant. 2005. 'Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups', *Proceedings of the National Academy of Sciences USA*, 102.26: pp. 9418–23, https://www.doi.org/10.1073/pnas.0502019102

Bray, Joel, Melissa Emery Thompson, Martin N. Muller, Richard W. Wrangham, and Zarin P. Machanda. 2018. 'The ontogeny of feeding in wild chimpanzees (*Pan troglodytes schweinfurthii)',* *American Journal of Physical Anthropology*, 165: pp. 34–46.

Breuer, Thomas, Mireille Breuer-Ndoundou Hockemba, Claudia Olejniczak, Richard J. Parnell, and Emma J. Stokes. 2009. 'Physical maturation, life-history classes and age estimates of free-ranging western gorillas — Insights from Mbeli Bai, Republic of Congo', *American Journal of Primatology*, 71.2: pp. 106–19, https://www.doi.org/10.1002/ajp.20628

Breuer, Thomas, Andrew M. Robbins, Claudia Olejniczak, Richard J. Parnell, Emma J. Stokes, and Martha M. Robbins. 2010. 'Variance in the male reproductive success of western gorillas: acquiring females is just the beginning', *Behavioural ecology and Sociobiology*, 64: pp. 515–28, https://www.doi.org/10.1007/s00265-009-0867-6

Brewer-Marsden, Stella, David Marsden, and Melissa Emery Thompson. 2006. 'Demographic and female life history parameters of free-ranging chimpanzees at the Chimpanzee Rehabilitation Project, River Gambia National Park', *International Journal of Primatology*, 27: pp. 391–410, https://www.doi.org/10.1007/s10764-006-9029-0

Bronikowski, Anne M., Jeanne Altmann, Diane K. Brockman, Marina Cords, Linda Fedigan, Anne Pusey, Tara Stoinski, William F. Morris, Karen B. Strier, and Susan C. Alberts. 2011. 'Aging in the natural world: comparative data reveal similar mortality patterns across primates', *Science*, 331.6022: pp. 1325–28, https://www.doi.org/10.1126/science.1201571

Bronikowski, Anne M., Marina Cords, Susan C. Alberts, Jeanne Altmann, Diane K. Brockman, Linda M. Fedigan, Anne Pusey, Tara Stoinski, Karen B. Strier, and William F. Morris. 2016a. 'Data from: Female and male life tables for seven wild primate species', in Dryad Data Repository, https://www.doi.org/10.5061/dryad.v28t5

—. 2016b. 'Female and male life tables for seven wild primate species', *Scientific Data*, 3: p. 160006, https://www.doi.org/10.1038/sdata.2016.6

Buss, David M. 1989. 'Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures', *Behavioral and Brain Sciences*, 12.1: pp. 1–14. https://doi.org/10.1017/s0140525x00023992

Caillaud, Damien, Florence Levréro, Sylvain Gatti, Nelly Ménard, and Michel Raymond. 2008. 'Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas', *American Journal of Physical Anthropology*, 135.4: pp. 379–88, https://www.doi.org/10.1002/ajpa.20754

Carmody, Rachel N., and Richard W. Wrangham. 2009. 'The energetic significance of cooking', *Journal of Human Evolution*, 57.4: pp. 379–91, https://www.doi.org/10.1016/j.jhevol.2009.02.011

Caro, T. M., D. W. Sellen, A. Parish, R. Frank, D. M. Brown, Eckart Voland, and M. Borgerhoff Mulder. 1995. 'Termination of reproduction in nonhuman and human female primates', *International Journal of Primatology*, 16: pp. 205–20, https://www.doi.org/10.1007/BF02735478

Charnov, Eric L. 1991. 'Evolution of life history variation among female mammals', *Proceedings of the National Academy of Science USA*, 88.4: pp. 1134–37, https://www.doi.org/10.1073/pnas.88.4.1134

Charnov, Eric L., and David Berrigan. 1993. 'Why do female primates have such long lifespans and so few babies? Or life in the slow lane', *Evolutionary Anthropology: Issues, News, and Reviews*, 1.6: pp. 191–94, https://www.doi.org/10.1002/evan.1360010604

Clark, C. B. 1977. 'A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania', in *Primate Bio-Social Development: Biological, Social and Ecological Determinants*, ed. by S. Chevalier-Skolnikoff and F. Poirier (New York: Garland Press), pp. 235–60.

Clinton, Walter L., and Burney J. Le Boeuf. 1993. 'Sexual selection's effects on male life history and the pattern of male mortality', *Ecology*, 74.6: pp. 1884–92, https://www.doi.org/10.2307/1939945

Cloutier, Christina T, James E. Coxworth, and Kristen Hawkes. 2015. 'Age-related decline in ovarian follicle stocks differ between chimpanzees (*Pan troglodytes*) and humans', *AGE*, 37.1: p. 10. https://doi.org/10.1007/s11357-015-9746-4

Clutton-Brock, Tim H. 1991. 'The evolution of sex differences and the consequences of polygyny in mammals', in *The Development and Integration of Behavior* (Cambridge: Cambridge University Press), pp. 229–53.

Cohen, Alan A. 2004. 'Female post-reproductive lifespan: a general mammalian trait', *Biological Reviews*, 79.4: pp. 733–50, https://www.doi.org/10.1017/s1464793103006432

Colchero, Fernando, Roland Rau, Owen R. Jones, Julia A. Barthold, Dalia A. Conde, Adam Lenart, Laszlo Nemeth, Alexander Scheuerlein, Jonas Schoeley, Catalina Torres, Virginia Zarulli, Jeanne Altmann, Diane K. Brockman, Anne M. Bronikowski, Linda M. Fedigan, Anne E. Pusey, Tara S. Stoinski, Karen B. Strier, Annette Baudisch, Susan C. Alberts, and James W. Vaupel. 2016. 'The emergence of longevous populations', *Proceedings of the National Academy of Sciences USA*, 113.48: p. E7681-E90, https://www.doi.org/10.1073/pnas.1612191113

Cole, Megan F, Averill Cantwell, Joshua Rukundo, Lilly Ajarova, Sofia Fernandez-Navarro, Rebeca Atencia, and Alexandra G Rosati. 2020. 'Healthy cardiovascular biomarkers across the lifespan in wild-born chimpanzees (*Pan troglodytes)*', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375.1811: p. 20190609. https://doi.org/10.1098/rstb.2019.0609

Conklin-Brittain, Nancy Lou, Cheryl D. Knott, and Richard W. Wrangham. 2006. 'Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison', in *Feeding Ecology in Apes and Other Primates*, ed. by Gottfried Hohman, Martha M. Robbins and Christophe Boesch (Cambridge: Cambridge University Press), pp. 445–71.

Coolidge, Harold J. 1936. 'Zoological results of the George Vanderbilt African Expedition of 1934. Part IV: Notes on four gorillas from the Sanga River region', *Proceedings of the Academy of Natural Sciences of Philadelphia*, 88: pp. 479–501. NO DOI FOUND

Coolidge, Harold J., and Brian T. Shea. 1982. 'External body dimensions of *Pan paniscus* and *Pan troglodytes* chimpanzees', *Primates*, 23: pp. 245–51, https://www.doi.org/10.1007/bf02381164

Cooper, John E. 2017. 'Infectious disease and host responses', in *Gorilla Pathology and Health: With a Catalogue of Preserved Materials*, ed. by John E. Cooper and Gordon Hull (San Diego, CA: Academic Press), pp. 19–32. https://www.doi.org/10.1016/b978-0-12-802039-5.00003-2

Coqueugniot, Hélène, and Jean-Jacques Hublin. 2012. 'Age-related changes of digital endocranial volume during human ontogeny: Results from an osteological reference collection', *American Journal of Physical Anthropology*, 147.2: 312–18, https://doi.org/10.1002/ajpa.21655

Courtenay, Jackie, and Gigi Santow. 1989. 'Mortality of wild and captive chimpanzees', *Folia Primatologica*, 52.3–4: pp. 167–77, https://www.doi.org/10.1159/000156395

D'Amour, Danielle E., Gottfried Hohmann, and Barbara Fruth. 2006. 'Evidence of leopard predation on bonobos (*Pan paniscus*)', *Folia Primatologica*, 77.3: pp. 212–17, https://www.doi.org/10.1159/000091230

Dahl, Jeremy F., Ronald D. Nadler, and Delwood C. Collins. 1991. 'Monitoring the ovarian cycles of *Pan troglodytes* and *P. paniscus*: a comparative approach', *American Journal of Primatology*, 24.3–4: pp. 195–209, https://www.doi.org/10.1002/ajp.1350240306

de Lathouwers, M., and Linda van Elsacker. 2005. 'Reproductive parameters of female *Pan paniscus* and *P. troglodytes*: quality versus quantity', *International Journal of Primatology*, 26: pp. 55–71, https://www.doi.org/10.1007/s10764-005-0723-0

Deschner, Tobias, and Christophe Boesch. 2007. 'Can the patterns of sexual swelling cycles in female Taï chimpanzees by explained by the cost-of-sexual-attractiveness hypothesis?', *International Journal of Primatology*, 28: pp. 389–406, https://www.doi.org/10.1007/s10764-007-9120-1

Dettwyler, Katherine A. 1995. 'A time to wean: the hominid blueprint for the natural age of weaning in modern human populations', in *Breastfeeding: Biocultural Perspectives*, ed. by Patricia Stuart Macadam and Katherine A. Dettwyler (Hawthorne, NY: Aldine de Gruyter), pp. 39–73.

Dixson, Alan F, and Robert Denis Martin. 1981. *The Natural History of the Gorilla* (New York: Columbia University Press).

Douadi, Mélanie I., Sylvain Gatti, Florence Levrero, Gaetan Duhamel, Magdalena Bermejo, Dominique Vallet, Nelly Menard, and Eric J. Petit. 2007. 'Sex-biased dispersal in western lowland gorillas (*Gorilla gorilla gorilla*)', *Molecular Ecology*, 16.11: pp. 2247–59, https://www.doi.org/10.1111/j.1365-294x.2007.03286.x

Dupain, Jef, Linda Van Elsacker, Carlos Nell, Paola Garcia, Francisco Ponce, and Michael A. Huffman. 2002. 'New evidence for leaf swallowing and *Oesophagostomum* infection in bonobos (*Pan paniscus*)', *International Journal of Primatology*, 23.5: pp. 1053–62. https://doi.org/10.1023/a:1019697915897

Durrleman, Stanley, Xavier Pennec, Alain Trouvé, Nicholas Ayache, and José Braga. 2012. 'Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration', *Journal of Human Evolution*, 62.1: pp. 74–88, https://www.doi.org/10.1016/j.jhevol.2011.10.004

Eckardt, Winnie, Katie Fawcett, and Alison W. Fletcher. 2016. 'Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): influential factors', *Behavioural ecology and Sociobiology*, 70: pp. 493–507, https://www.doi.org/10.1007/s00265-016-2066-6

Edler, Melissa K., Emily L. Munger, Richard S. Meindle, William D. Hopkins, John J. Ely, Joseph M. Erwin, Elliot J. Mufson, Patrick R. Hof, Chet C. Sherwood, and Mary Ann Raghanti. 2020. 'Neuron loss associated with age but not Alzheimer's disease pathology in the chimpanzee brain', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375.1811: p. 20190619. https://doi.org/10.1098/rstb.2019.0619

Ellison, Peter T., and Claudia R. Valeggia. 2003. 'C-peptide levels and the duration of lactational amenorrhea', *Fertility and Sterility*, 80.5: pp. 1279–80, https://www.doi.org/10.1016/s0015-0282(03)02158-7

Ely, John J., Brent Dye, William I. Frels, Jo Fritz, Pascal Gagneux, Henry H. Khun, William M. Switzer, and D. Rick Lee. 2005. 'Subspecies composition and founder contribution of the captive US chimpanzee (*Pan troglodytes*) population', *American Journal of Primatology*, 67.2: pp. 223–41, https://www.doi.org/10.1002/ajp.20179

Emery Thompson, Melissa. 2005. 'Endocrinology and ecology of wild female chimpanzee reproduction', PhD Dissertation, Harvard University.

—. 2013a. 'Comparative reproductive energetics of human and nonhuman primates', *Annual Review of Anthropology*, 42.1: pp. 287–304. https://doi.org/10.1146/annurev-anthro-092412-155530

—. 2013b. 'Reproductive ecology of female chimpanzees', *American Journal of Primatology*, 75.3: pp. 222–37, https://www.doi.org/10.1002/ajp.22084

Emery Thompson, Melissa, and Peter T. Ellison. 2017. 'Fertility and fecundity', in *Chimpanzees and Human Evolution*, ed. by Martin N. Muller, Richard W. Wrangham and David Pilbeam (Cambridge, MA: Harvard University Press), pp. 217–58.

Emery Thompson, Melissa, James H. Jones, Anne E. Pusey, Stella Brewer-Marsden, Jane Goodall, David Marsden, Tetsuro Matsuzawa, Toshisada Nishida, Vernon Reynolds, and Yukimaru Sugiyama. 2007. 'Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause', *Current Biology*, 17.24: pp. 2150–56, https://www.doi.org/10.1016/j.cub.2007.11.033

Emery Thompson, Melissa, Sonya M. Kahlenberg, Ian C. Gilby, and Richard W. Wrangham. 2007. 'Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park', *Animal Behaviour*, 73.3: pp. 501–12, https://www.doi.org/10.1016/j.anbehav.2006.09.007

Emery Thompson, Melissa, Zarin P. Machanda, Erik J. Scully, Drew K. Enigk, Emily Otali, Martin N. Muller, Tony G. Goldberg, Colin A. Chapman, and Richard W. Wrangham. 2018. 'Risk factors for respiratory illness in a community of wild chimpanzees (*Pan troglodytes schweinfurthii)*', *Royal Society Open Science*, 5.9: p. 180840. https://doi.org/10.1098/rsos.180840

Emery Thompson, Melissa, Zarin P. Machanda, Sarah Phillips-Garcia, Emily Otali, Martin N. Muller, and Richard W. Wrangham. 2017. 'Longitudinal changes in diet and reproduction among wild chimpanzees at Kanyawara, Kibale National Park', *American Journal of Physical Anthropology*, S64: p. 173.

Emery Thompson, Melissa, Martin N. Muller, Zarin P. Machanda, Emily Otali, and Richard W. Wrangham. 2020. 'The Kibale Chimpanzee Project: Over thirty years of research, conservation, and change', *Biological Conservation*, 252: p. 108857. https://doi.org/10.1016/j.biocon.2020.108857

Emery Thompson, Melissa, Martin N. Muller, Kris Sabbi, Zarin P. Machanda, Emily Otali, and Richard W. Wrangham. 2016. 'Faster reproductive rates trade off against offspring growth in wild chimpanzees', *Proceedings of the National Academy of Science USA*, 113.28: pp. 7780–85, https://www.doi.org/10.1073/pnas.1522168113

Emery Thompson, Melissa, Martin N. Muller, and Richard W. Wrangham. 2012. 'The energetics of lactation and the return to fecundity in wild chimpanzees', *Behavioural ecology*, 23.6: pp. 1234–41, https://www.doi.org/10.1093/beheco/ars107

—. 2014. 'Male chimpanzees compromise the foraging success of their mates in Kibale National Park, Uganda', *Behavioural ecology and Sociobiology*, 68: pp. 1973–83, https://www.doi.org/10.1007/s00265-014-1803-y

Emery Thompson, Melissa, Martin N. Muller, Richard W. Wrangham, Jeremiah S. Lwanga, and Kevin B. Potts. 2009. 'Urinary C-peptide tracks seasonal and individual variation in energy balance in wild chimpanzees', *Hormones and Behavior*, 55.2: pp. 299–305, https://www.doi.org/10.1016/j.yhbeh.2008.11.005

Emery Thompson, Melissa, Nicholas E. Newton-Fisher, and Vernon Reynolds. 2006. 'Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda', *International Journal of Primatology*, 27: pp. 1601–17, https://www.doi.org/10.1007/s10764-006-9098-0

Emery Thompson, Melissa, and Richard Wrangham. 2013. '*Pan troglodytes* robust chimpanzee (common chimpanzee)', in *Mammals of Africa*, ed. by D. C. D. Happold, Jonathon Kingdon and Thomas M. Butynski (New York: Bloomsbury Publishing), pp. 55–64.

Emery Thompson, Melissa, and Richard W. Wrangham. 2008. 'Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda', *American Journal of Physical Anthropology*, 135.2: pp. 171–81, https://www.doi.org/10.1002/ajpa.20718

Emery Thompson, Melissa, Richard W. Wrangham, and Vernon Reynolds. 2006. 'Urinary estrone conjugates and reproductive parameters in Kibale (Kanyawara) and Budongo (Sonso) chimpanzees', in *Primates of Western Uganda*, ed. by Nicholas E. Newton-Fisher, Hugh Notman, Vernon Reynolds and James Paterson (New York: Springer), pp. 227–46, https://www.doi.org/10.1007/978-0-387-33505-6_13

Emery Thompson, Melissa, Amy Zhou, and Cheryl D. Knott. 2012. 'Low testosterone correlates with delayed development in male orangutans', *Public Library of Science ONE*, 7: p. e47282, https://www.doi.org/10.1371/journal.pone.0047282

Eriksson, Jonas, Heike Siedel, Dieter Lukas, Manfred Kayser, Axel Erler, Chie Hashimoto, Gottfried Hohmann, Christophe Boesch, and Linda Vigilant. 2006. 'Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus)*', *Molecular Ecology*, 15.4: pp. 939–49, https://www.doi.org/10.1111/j.1365-294x.2006.02845.x

Fahy, Geraldine E., Michael P. Richards, Benjamin T. Fuller, Tobias Deschner, Jean-Jacques Hublin, and Christophe Boesch. 2014. 'Stable nitrogen isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild chimpanzees (*Pan troglodytes)*', *American Journal of Physical Anthropology*, 153.4: pp. 635–42, https://www.doi.org/10.1002/ajpa.22464

Feldblum, Joseph T., Emily E. Wroblewski, Rebecca S. Rudicell, Beatrice H. Hahn, Thais Paiva, Mine Cetinkaya-Rundel, Anne E. Pusey, and Ian C. Gilby. 2014. 'Sexually coercive male chimpanzees sire more offspring', *Current Biology*, 24.23: pp. 2855–60. https://doi.org/10.1016/j.cub.2014.10.039

Finch, Caleb E., and Steven N. Austad. 2015. 'Commentary: is Alzheimer's disease uniquely human?', *Neurobiology of Aging*, 36.2: pp. 553–55, https://www.doi.org/10.1016/j.neurobiolaging.2014.10.025

Fletcher, Alison. 2001. 'Development of infant independence from the mother in wild mountain gorillas', in *Mountain Gorillas: Three Decades of Research at Karisoke*, ed. by Martha M. Robbins, Pascal Sicotte and Kelly J. Stewart (New York: Cambridge University Press), pp. 153–82, https://www.doi.org/10.1017/cbo9780511661631.007

Foley, Robert A., Phyllis C. Lee, E. M. Widdowson, C. D. Knight, and J. H. P. Jonxis. 1991. 'Ecology and energetics of encephalization in hominid evolution', *Philosophical Transactions: Biological Sciences*, 334.1270: pp. 223–32, https://www.doi.org/10.1098/rstb.1991.0111

Fooden, Jack, and Robert J. Izor. 1983. 'Growth curves, dental emergence norms, and supplementary morphological observations in known-age captive orangutans', *American Journal of Primatology*, 5.4: pp. 285–301, https://www.doi.org/10.1002/ajp.1350050402

Furuichi, Takeshi. 1989. 'Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire', *International Journal of Primatology*, 10: pp. 173–97, https://www.doi.org/10.1007/bf02735199

Furuichi, Takeshi, and Chie Hashimoto. 2002. 'Why female bonobos have a lower copulation rate during estrus than chimpanzees', in *Behavioural Diversity in Chimpanzees and Bonobos*, ed. by Christophe Boesch, Gottfried Hohmann and Linda F. Marchant (Cambridge: Cambridge University Press), pp. 156–67.

Furuichi, Takeshi, Gen'ichi Idani, Hiroshi Ihobe, Suehisa Kuroda, Koji Kitamura, Akio Mori, Tomoo Enomoto, Naobi Okayasu, Chie Hashimoto, and Takayoshi Kano. 1998. 'Population dynamics of wild bonobos (*Pan paniscus*) at Wamba', *International Journal of Primatology*, 19.6: pp. 1029–43. https://doi.org/10.1023/a:1020326304074

Furuichi, Takeshi, Gen'ichi Idani, Hiroshi Ihobe, Chie Hashimoto, Yasuko Tashiro, Tetsuya Sakamaki, Mbangi N. Mulavwa, Kumugo Yangozene, and Suehisa Kuroda. 2012. 'Long-term studies on wild bonobos at Wamba, Luo Scientific Reserve, D. R. Congo: towards the understanding of female life history in a male-philopatric species', in *Long-Term Field Studies of Primates*, ed. by Peter M. Kappeler and David P. Watts (Berlin, Heidelberg: Springer), pp. 413–33, https://www.doi.org/10.1007/978-3-642-22514-7_18

Galbany, Jordi, Didier Abavandimwe, Meagan Vakiener, Winnie Eckardt, Antoine Mudakikwa, Felix Ndagijimana, Tara S. Stoinski, and Shannon C. McFarlin. 2017. 'Body growth and life history in wild mountain gorillas (*Gorilla beringei beringei*) from Volcanoes National Park, Rwanda', *American Journal of Physical Anthropology*, 163.3: pp. 570–90. https://doi.org/10.1002/ajpa.23232

Galdikas, Birute M. F. 1981. 'Orangutan reproduction in the wild', in Charles E. Graham (ed.), *Reproductive Biology of the Great Apes: Comparative and Biomedical Perspectives* (Academic Press, New York), pp. 281–300.

Galdikas, Birute M. F., and J. W. Wood. 1990. 'Birth spacing patterns in humans and apes', *American Journal of Physical Anthropology*, 83.2: 185–91. https://doi.org/10.1002/ajpa.1330830207

Gaulin, Steven J. C. 1979. 'A Jarman/Bell model of primate feeding niches', *Human Ecology*, 7.1: pp. 1–20. https://doi.org/10.1007/bf00889349

Gavan, James A. 1953. 'Growth and development of the chimpanzee: a longitudinal and comparative study', *Human Biology*, 25: pp. 93–143.

—. 1971. 'Longitudinal, postnatal growth in chimpanzee', in Goeffrey Howard Bourne (ed.), *The Chimpanzee, Vol. 4: Behavior, Growth, and Pathology of Chimpanzees* (Karger, Basel), pp. 46–102.

Gilby, Ian C., Lauren J. N. Brent, Emily E. Wroblewski, Rebecca S. Rudicell, Beatrice H. Hahn, Jane Goodall, and Anne E. Pusey. 2013. 'Fitness benefits of coalitionary aggression in male chimpanzees', *Behavioural ecology and Sociobiology*, 67.3: pp. 373–81. https://doi.org/10.1007/s00265-012-1457-6

Gillespie, Thomas R., Elizabeth V. Lonsdorf, Elizabeth P. Canfield, Derek J. Meyer, Yvonne Nadler, Jane Raphael, Anne E. Pusey, Joel Pond, John Pauley, and Titus Mlengeya. 2010. 'Demographic and ecological effects on patterns of parasitism in eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania', *American Journal of Physical Anthropology*, 143.4: pp. 534–44. https://www.doi.org/10.1002/ajpa.21348

Gioiosa, Rose. 1955. 'Incidence of pregnancy during lactation in 500 cases', *American Journal of Obstetrics and Gynecology*, 70.1: pp. 162–74. http://dx.doi.org/10.1016/0002-9378(55)90300-8

Goodall, Jane. 1986. *The Chimpanzees of Gombe: Patterns of Behavior* (Belknap Press of Harvard University Press).

Goossens, B., J. M. Setchell, S. S. James, S. M. Funk, L. Chikhi, A. Abulani, M. Ancrenaz, I. Lackman-Ancrenaz, and M. W. Bruford. 2006. 'Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus)*', *Molecular Ecology*, 15.9: pp. 2577–88. https://doi.org/10.1111/j.1365-294x.2006.02952.x

Gould, Kenneth G., Marcha Flint, and C. E. Graham. 1981. 'Chimpanzee reproductive senescence: a possible model for evolution of the menopause', *Maturitas*, 3.2: pp. 157–66. https://doi.org/10.1016/0378-5122(81)90007-4

Graham, Charles E. 1979. 'Reproductive function in aged female chimpanzees', *American Journal of Physical Anthropology*, 50.3: pp. 291–300. https://doi.org/10.1002/ajpa.1330500302

Gray, Maryke, Justin Roy, Linda Vigilant, Katie Fawcett, Augustin Basabose, Mike Cranfield, Prosper Uwingeli, Innocent Mburanumwe, Edwin Kagoda, and Martha M. Robbins. 2013. 'Genetic census reveals increased but uneven growth of a critically endangered mountain gorilla population', *Biological Conservation*, 158: pp. 230–38. https://www.doi.org/10.1016/j.biocon.2012.09.018

Groves, Colin P., and Kenhelm W. Stott Jr. 1979. 'Systematic relationships of gorillas from Kahuzi, Tshiaberimu and Kayonza', *Folia Primatologica*, 32.3: pp. 161–79. https://doi.org/10.1159/000155910

Grueter, Cyril C., Tobias Deschner, Verena Behringer, Katie Fawcett, and Martha M. Robbins. 2014. 'Socioecological correlates of energy balance using urinary C-peptide measurements in wild female mountain gorillas', *Physiology and Behavior*, 127: pp. 13–19. https://www.doi.org/10.1016/j.physbeh.2014.01.009

Gurven, Michael, and Hillard Kaplan. 2007. 'Longevity among hunter- gatherers: A cross-cultural examination', *Population and Development Review*, 33.2: pp. 321–65. https://www.doi.org/10.1111/j.1728-4457.2007.00171.x

Gurven, Michael, Hillard Kaplan, and Maguin Gutierrez. 2006. 'How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span', *Journal of Human Evolution*, 51.5: pp. 454–70. https://www.doi.org/10.1016/j.jhevol.2006.05.003

Hamada, Yuzuru, and Toshifumi Udono. 2002. 'Longitudinal analysis of length growth in the chimpanzee (*Pan troglodytes)*', *American Journal of Physical Anthropology*, 118.3: pp. 268–84. https://doi.org/10.1002/ajpa.10078

Hammer, Michael F, Tatiana M Karafet, Alan J Redd, Hamdi Jarjanazi, Silvana Santachiara-Benerecetti, Himla Soodyall, and Stephen L Zegura. 2001. 'Hierarchical patterns of global human Y-chromosome diversity', *Molecular Biology and Evolution*, 18.7: pp. 1189–203. https://doi.org/10.1093/oxfordjournals.molbev.a003906

Harcourt, A. H., and J. Greenberg. 2001. 'Do gorilla females join males to avoid infanticide? A quantitative model', *Animal Behaviour*, 62.5: pp. 905–15. https://www.doi.org/10.1006/anbe.2001.1835

Harcourt, Alexander H. 1995. 'Sexual selection and sperm competition in primates: What are male genitalia good for?', *Evolutionary Anthropology: Issues, News, and Reviews*, 4.4: pp. 121–29. https://www.doi.org/10.1002/evan.1360040404

Harcourt, Alexander H., Dian Fossey, Kelly J. Stewart, and David P. Watts. 1980. 'Reproduction in wild gorillas and some comparisons with the chimpanzee', *Journal of Reproduction and Fertility*, Suppl. 28: pp. 59–70. https://pubmed.ncbi.nlm.nih.gov/6934312/

Harcourt, Alexander H., and Kelly J. Stewart. 1978. 'Sexual behavior of wild mountain gorillas', in D. J. Chivers and J. Herberts (eds.), *Recent Advances in Primatology* (Academic Press, London), pp. 611–12.

—. 2007. *Gorilla Society: Conflict, Compromise, and Cooperation between the Sexes* (University of Chicago Press: Chicago).

Harrison, Mark E., and Andrew J. Marshall. 2011. 'Strategies for the use of fallback foods in apes', *International Journal of Primatology*, 32: pp. 531–65. https://www.doi.org/10.1007/s10764-010-9487-2

Harrison, Mark E., Helen C. Morrogh-Bernard, and David J. Chivers. 2010. 'Orangutan energetics and the influence of fruit availability in the nonmasting peat-swamp forest of Sabangau, Indonesian Borneo', *International Journal of Primatology*, 31: pp. 585–607. https://www.doi.org/10.1007/s10764-010-9415-5

Harvey, NC. 1997. 'Gestation, parturition, interbirth intervals, and lactational recovery in bonobos', *The Care and Management of Bonobos in Captive Environments*: 6.1–6.11.

Harvey, Paul H., and Tim H. Clutton-Brock. 1985. 'Life history variation in primates', *Evolution*, 39.3: PP. 559–81. https://www.doi.org/10.2307/2408653

Hasegawa, Hideo, Takayoshi Kano, and Mbangi Mulavwa. 1983. 'A parasitological survey on the feces of pygmy chimpanzees, Pan paniscus, at Wamba, Zaïre', *Primates*, 24: pp. 419–23. https://www.doi.org/10.1007/bf02381986

Hassell, James M., Dawn Zimmerman, Michael R. Cranfield, Kirsten Gilardi, Antoine Mudakikwa, Jan Ramer, Elisabeth Nyirakaragire, and Linda J. Lowenstine. 2017. 'Morbidity and mortality in infant mountain gorillas (*Gorilla beringei beringei*): A 46-year retrospective review', *American Journal of Primatology*, 79.10: p. e22686. https://doi.org/10.1002/ajp.22686

Havercamp, Kristin, Koshiro Watanuki, Masaki Tomonaga, Tetsuro Matsuzawa, and Satoshi Hirata. 2019. 'Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018', *Primates*, 60: pp. 525–35. https://www.doi.org/10.1007/s10329-019-00755-8

Hawkes, Kristen. 2003. 'Grandmothers and the evolution of human longevity', *American Journal of Human Biology*, 15.3: pp. 380–400. https://www.doi.org/10.1002/ajhb.10156

Hawkes, Kristen, J. F. O'Connell, Nicholas G. Blurton-Jones, H. Alvarez, and Eric L. Charnov. 1998. 'Grandmothering, menopause, and the evolution of human life histories', *Proceedings of the National Academy of Science USA*, 95.3: pp. 1336–39. https://doi.org/10.1073/pnas.95.3.1336

Henschel, P., K. A. Abernethy, and L. J. T. White. 2005. 'Leopard food habits in the Lopé National Park, Gabon, Central Africa', *African Journal of Ecology*, 43.1: pp. 21–28. https://www.doi.org/10.1111/j.1365-2028.2004.00518.x

Herculano-Houzel, Suzana. 2012. 'The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost', *Proceedings of the National Academy of Sciences*, 109.Supplement 1: pp. 10661–68. https://doi.org/10.1073/pnas.1201895109

Herculano-Houzel, Suzana, and Jon H. Kaas. 2011. 'Gorilla and orangutan brains conform to the primate cellular scaling rules: implications for human evolution', *Brain, Behavior and Evolution*, 77.1: pp. 33–44. https://www.doi.org/10.1159/000322729

Herndon, James G., and Agnes Lacreuse. 2009. 'Commentary: "Reproductive aging in captive and wild common chimpanzees: factors influencing the rate of follicular depletion," by S. Atsalis and E. Videan, American

Journal of Primatology 71, 271–82 (2009)', *American Journal of Primatology*, 71.11: pp. 1–2. https://www.doi.org/10.1002/ajp.20724

Herndon, James G., Johannes Tigges, Daniel C. Anderson, Sherry A. Klumpp, and Harold M. McClure. 1999. 'Brain weight throughout the life span of the chimpanzee', *The Journal of Comparative Neurology*, 409.4: pp. 567–72. https://www.doi.org/10.1002/(sici)1096-9861(19990712)409:4<567::aid-cne4>3.0.co;2-j

Hill, Kim, Christophe Boesch, Jane Goodall, Anne Pusey, Jennifer Williams, and Richard Wrangham. 2001. 'Mortality rates among wild chimpanzees', *Journal of Human Evolution*, 40.5: pp. 437–50. https://www.doi.org/10.1006/jhev.2001.0469

Hoffmann, Constanze, Fee Zimmermann, Roman Biek, Hjalmar Kuehl, Kathrin Nowak, Roger Mundry, Anthony Agbor, Samuel Angedakin, Mimi Arandjelovic, Anja Blankenburg, Gregory Brazolla, Katherine Corogenes, Emmanuel Couacy-Hymann, Tobias Deschner, Paula Dieguez, Karsten Dierks, Ariane Düx, Susann Dupke, Henk Eshuis, Pierre Formenty, Yisa Ginath Yuh, Annemarie Goedmakers, Jan F. Gogarten, Anne-Céline Granjon, Scott McGraw, Roland Grunow, John Hart, Sorrel Jones, Jessica Junker, John Kiang, Kevin Langergraber, Juan Lapuente, Kevin Lee, Siv Aina Leendertz, Floraine Léguillon, Vera Leinert, Therese Löhrich, Sergio Marrocoli, Kerstin Mätz-Rensing, Amelia Meier, Kevin Merkel, Sonja Metzger, Mizuki Murai, Svenja Niedorf, Hélène De Nys, Andreas Sachse, Joost van Schijndel, Ulla Thiesen, Els Ton, Doris Wu, Lothar H. Wieler, Christophe Boesch, Silke R. Klee, Roman M. Wittig, Sébastien Calvignac-Spencer, and Fabian H. Leendertz. 2017. 'Persistent anthrax as a major driver of wildlife mortality in a tropical rainforest', *Nature*, 548: pp. 82–86. https://www.doi.org/10.1038/nature23309

Hohmann, Gottfried. 2001. 'Association and social interactions between strangers and residents in bonobos (*Pan paniscus)*', *Primates*, 42: pp. 91–99. https://www.doi.org/10.1007/bf02640692

Howell, Nancy. 2010. *Life histories of the Dobe! Kung: Food, Fatness, and Well-Being over the Life Span* (Univ of California Press).

Huber, Susanne, and Martin Fieder. 2018. 'Evidence for a maximum "shelf-life" of oocytes in mammals suggests that human menopause may be an implication of meiotic arrest', *Scientific reports*, 8.1: p. 14099. https://doi.org/10.1038/s41598-018-32502-2

Humle, Tatyana. 2011. 'The 2003 epidemic of a flu-like respiratory disease at Bossou', in, *The Chimpanzees of Bossou and Nimba* (Springer), pp. 325–33. https://www.doi.org/10.1007/978-4-431-53921-6_33

Isbell, Lynne A., Jill D. Pruetz, Bernard Musyoka Nzuma, and Truman P. Young. 1999. 'Comparing measures of travel distances in primates: methodological considerations and socioecological implications', *American Journal of Primatology*, 48.2: pp. 87–98. https://doi.org/10.1002/(sici)1098-2345(1999)48:2%3C87::aid-ajp1%3E3.0.co;2-g

Janson, Charles H., and Carel P. van Schaik. 1993. 'Ecological risk aversion in juvenile primates: slow and steady wins the race', in Michael E. Pereira and Lynn A. Fairbanks (eds.), *Juvenile Primates: Life History, Development, and Behavior* (University of Chicago Press: Chicago, IL), pp. 57–74.

Joffe, Tracey H. 1997. 'Social pressures have selected for an extended juvenile period in primates', *Journal of Human Evolution*, 32.6: pp. 593–605. http://dx.doi.org/10.1006/jhev.1997.0140

Jones, James Holland, Michael L Wilson, Carson M. Murray, and Anne Pusey. 2010. 'Phenotypic quality influences fertility in Gombe chimpanzees', *Journal of animal ecology*, 79: 1262–69. NO DOI FOUND

Jones, K. P., L. C. Walker, D. Anderson, A. Lacreuse, S. L. Robson, and K. Hawkes. 2007. 'Depletion of ovarian follicles with age in chimpanzees: similarities to humans', *Biology of Reproduction*, 77.2: pp. 247–51. https://www.doi.org/10.1095/biolreprod.106.059634

Jungers, William L., and Randall L. Susman. 1984. 'Body size and skeletal allometry in African apes', in Randall L. Susman (ed.), *The Pygmy Chimpanzee* (Plenum Press, New York).

Kano, Takayoshi. 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology* (Stanford University Press, Stanford).

Kaplan, Hillard, Kim R. Hill, Jane B. Lancaster, and A. Magdalena Hurtado. 2000. 'A theory of human life history evolution: diet, intelligence, and longevity', *Evolutionary Anthropology*, 9.4: pp. 156–84. https://doi.org/10.1002/1520-6505(2000)9:4%3C156::aid-evan5%3E3.0.co;2-7

Kaur, Taranjit, Jatinder Singh, Suxiang Tong, Charles Humphrey, Donna Clevenger, Wendy Tan, Brian Szekely, Yuhuan Wang, Yan Li, Epaphras Alex Muse, Mieko Kiyono, Shunkichi Hanamura, Eiji Inoue, Michio Nakamura, Michael A. Huffman, Baoming Jiang, and Toshisada Nishida. 2008. 'Descriptive epidemiology of fatal respiratory outbreaks and detection of a human-related metapneumovirus in wild chimpanzees (*Pan troglodytes*) at Mahale Mountains National Park, Western Tanzania', *American Journal of Primatology*, 70.8: pp. 755–65. https://www.doi.org/10.1002/ajp.20565

Keele, Brandon F., James Holland Jones, Karen A. Terio, Jacob D. Estes, Rebecca S. Rudicell, Michael L. Wilson, Yingying Li, Gerald H. Learn, T. Mark Beasley, and Joann Schumacher-Stankey. 2009. 'Increased mortality and AIDS-like immunopathology in wild chimpanzees infected with SIVcpz', *Nature*, 460: pp. 515–19. https://www.doi.org/10.1038/nature08200

Kennedy, Gail E. 2005. 'From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context', *Journal of Human Evolution*, 48.2: pp. 123–45. https://www.doi.org/10.1016/j.jhevol.2004.09.005

Kenrick, Douglas T, and Richard C Keefe. 1992. 'Age preferences in mates reflect sex differences in human reproductive strategies', *Behavioral and Brain Sciences*, 15.1: pp. 75–91. https://doi.org/10.1017/s0140525x00067595

Key, Catherine, and Caroline Ross. 1999. 'Sex differences in energy expenditure in non–human primates', *Proceedings of the Royal Society of London B: Biological Sciences*, 266.1437: pp. 2479–85. https://doi.org/10.1098/rspb.1999.0949

Kilbourn, Annelisa M., William B. Karesh, Nathan D. Wolfe, Edwin J. Bosi, Robert A. Cook, and Mahedi Andau. 2003. 'Health evaluation of free-ranging and semi-captive orangutans (*Pongo pygmaeus pygmaeus*) in Sabah, Malaysia', *Journal of Wildlife Diseases*, 39.1: pp. 73–83. https://www.doi.org/10.7589/0090-3558-39.1.73

Kingsley, S. 1982. 'Causes of non-breeding and the development of secondary sexual characteristics in the male orang-utan: a hormonal study', in L. E. M. de Boer (ed.), *The Orang-Utan, Its Biology and Conservation* (W. Junk: The Hague), pp. 215–29.

Klailova, M., C. Casanova, P. Henschel, P. Lee, F. Rovero, and A. Todd. 2012. 'Non-human predator interactions with wild great apes in Africa and the use of camera traps to study their dynamics', *Folia Primatologica*, 83.3–6: pp. 312–28. https://www.doi.org/10.1159/000342143

Knott, Cheryl D. 1998a. 'Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability', *International Journal of Primatology*, 19.6: pp. 1061–79. https://doi.org/10.1023/a:1020330404983

—. 1999. 'Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability. PhD Dissertation', Harvard University. https://cherylknott.files.wordpress.com/2011/06/knott-1999-thesis.pdf

Knott, Cheryl D. 1998b. 'Orangutans in the wild', *National Geographic*, August: pp. 30–57.

—. 2001. 'Female reproductive ecology of the apes: implications for human evolution', in, *Reproductive Ecology and Human Evolution*, pp. 429–63.

—. 2005. 'Energetic responses to food availability in the great apes: implications for hominid evolution', in Diane K. Brockman and Carel P. van Schaik (eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (Cambridge University Press, Cambridge), pp. 351–78.

Knott, Cheryl D., M. Emery Thompson, and Serge A. Wich. 2009. 'The ecology of female reproduction in wild orangutans', in Serge A. Wich, Sri Suci Utami Atmoko, Tatang Mitra-Setia and Carel P. van Schaik (eds.), *Orangutans: Geographic Variation in Behavioural ecology and Conservation*. (Oxford University Press: New York, NY), pp. 171–88.

Knott, Cheryl D., and Melissa Emery Thompson. 2013. 'Male bi-maturism and the costs of reproduction in wild Bornean orangutans', *American Journal of Physical Anthropology Supplement*, 150: pp. 170–70.

Knott, Cheryl D., Melissa Emery Thompson, Rebecca M. Stumpf, and Matthew H. McIntyre. 2010. 'Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion', *Proceedings of the Royal Society of London B: Biological Sciences*, 277.1678: pp. 105–13. https://www.doi.org/10.1098/rspb.2009.1552

Köndgen, Sophie, Hjalmar Kühl, Paul K. N'Goran, Peter D. Walsh, Svenja Schenk, Nancy Ernst, Roman Biek, Pierre Formenty, Kerstin Mätz-Rensing, Brunhilde Schweiger, Sandra Junglen, Heinz Ellerbrok, Andreas Nitsche, Thomas Briese, W. Ian Lipkin, Georg Pauli, Christophe Boesch, and Fabian H. Leendertz. 2008. 'Pandemic human viruses cause decline of endangered great apes', *Current Biology*, 18.4: pp. 260–64. https://www.doi.org/10.1016/j.cub.2008.01.012

Kramer, Karen L. 2005. 'Children's help and the pace of reproduction: cooperative breeding in humans', *Evolutionary Anthropology: Issues, News, and Reviews*, 14.6: pp. 224–37. https://doi.org/10.1002/evan.20082

Kuczmarski, R J, C L Ogden, S S Guo, L M Grummer-Strawn, K M Flegal, Zuguo Mei, Rong Wei, Lester R Curtin, Alex F Roche, and Clifford L Johnson. 2002. '2000 CDC growth charts for the United States: data from the National Health Examination Surveys and the National Health and Nutrition Examination Surveys', *National Center for Health Statistics, Vital Health Stat*, 11. https://pubmed.ncbi.nlm.nih.gov/12043359/

Kuhar, Chris W., Tamara L. Bettinger, and Mark L. Laudenslager. 2005. 'Salivary cortisol and behaviour in an all-male group of western lowland gorillas (*Gorilla g. gorilla)', Animal Welfare*, 14.3: pp. 187–93. https://doi.org/10.1017/s0962728600029341

Kunz, Julia A., Guilhem J. Duvot, Maria A. van Noordwijk, Erik P. Willems, Manuela Townsend, Neneng Mardianah, Sri Suci Utami Atmoko, Erin R. Vogel, Taufiq Purna Nugraha, Michael Heistermann, Muhammad Agil, Tony Weingrill, and Carel P. van Schaik. 2020. 'The cost of associating with males for Bornean and Sumatran female orangutans: a hidden form of sexual conflict?', *Behavioural ecology and Sociobiology*, 75: p. 6. https://www.doi.org/10.1007/s00265-020-02948-4

Kuroda, Suehisa. 1989. 'Developmental retardation and behavioral characteristics of pygmy chimpanzees', in Paul G. Heltne and Linda A. Marquardt (eds.), *Understanding Chimpanzees* (Harvard University Press, Cambridge), pp. 184–93.

Kuzawa, Christopher W., Harry T. Chugani, Lawrence I. Grossman, Leonard Lipovich, Otto Muzik, Patrick R. Hof, Derek E. Wildman, Chet C. Sherwood, William R. Leonard, and Nicholas Lange. 2014. 'Metabolic costs and evolutionary implications of human brain development', *Proceedings of the National Academy of Sciences*, 111.36: pp. 13010–15. https://www.doi.org/10.1073/pnas.1323099111

Kuze, Noko, Symphorosa Sipangkui, Titol Peter Malim, Henry Bernard, Laurentius N Ambu, and Shiro Kohshima. 2008. 'Reproductive parameters over a 37-year period of free-ranging female Borneo orangutans at Sepilok Orangutan Rehabilitation Centre', *Primates*, 49: pp. 126–34. https://www.doi.org/10.1007/s10329-008-0080-7

Lacreuse, Agnès, Lakshmi Chennareddi, Kenneth G. Gould, Kristen Hawkes, Sameera R. Wijayawardana, Jian Chen, Kirk A. Easley, and James G. Herndon. 2008. 'Menstrual cycles continue into advanced old age in the common chimpanzee (*Pan troglodytes)', Biology of Reproduction*, 79.3: pp. 407–12. https://www.doi.org/10.1095/biolreprod.108.068494

Lameira, Adriano R., Han de Vries, Madeleine E. Hardus, Cedric P. A. Hall, Tatang Mitra-Setia, Berry M. Spruijt, Arik Kershenbaum, Elisabeth H. M. Sterck, Maria van Noordwijk, Carel van Schaik, and Serge A. Wich. 2013. 'Predator guild does not influence orangutan alarm call rates and combinations', *Behavioural ecology and Sociobiology*, 67: pp. 519–28. https://www.doi.org/10.1007/s00265-012-1471-8

Lammey, Michael L., D. Rick Lee, John J. Ely, and Meg M Sleeper. 2008. 'Sudden cardiac death in 13 captive chimpanzees (*Pan troglodytes)', Journal of Medical Primatology*, 37: pp. 39–43. https://doi.org/10.1111/j.1600-0684.2007.00260.x

Landsoud-Soukate, J, CEG Tutin, and M Fernandez. 1995. 'Intestinal parasites of sympatric gorillas and chimpanzees in the Lope Reserve, Gabon', *Annals of Tropical Medicine & Parasitology*, 89.1: pp. 73–79. https://doi.org/10.1080/00034983.1995.11812931

Langergraber, Kevin E, Kay Prüfer, Carolyn Rowney, Christophe Boesch, Catherine Crockford, Katie Fawcett, Eiji Inoue, Miho Inoue-Muruyama, John C Mitani, and Martin N Muller. 2012. 'Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution', *Proceedings of the National Academy of Sciences*, 109.39: pp. 15716–21. https://doi.org/10.1073/pnas.1211740109

Langergraber, Kevin E., Heike Siedel, John C. Mitani, Richard W. Wrangham, Vernon Reynolds, Kevin Hunt, and Linda Vigilant. 2007. 'The genetic signature of sex-biased migration in patrilocal chimpanzees and humans', *PloS one*, 2: p. e973. https://www.doi.org/10.1371/journal.pone.0000973

Laurence, Hannah, Shyamesh Kumar, Michael A Owston, Robert E Lanford, Gene B Hubbard, and Edward J Dick Jr. 2017. 'Natural mortality and cause of death analysis of the captive chimpanzee (*Pan troglodytes*): A 35-year review', *Journal of Medical Primatology*, 46.3: pp. 106–15. https://doi.org/10.1111/jmp.12267

Lee, Phyllis C. 1996. 'The meanings of weaning: growth, lactation, and life history', *Evolutionary Anthropology Issues News and Reviews*, 5.3: pp. 87–98. https://www.doi.org/10.1002/(sici)1520-6505(1996)5:3<87::aid-evan4>3.0.co;2-t

Lee, Phyllis C., Patricia Majluf, and Iain J. Gordon. 1991. 'Growth, weaning and maternal investment from a comparative perspective', *Journal of Zoology*, 225.1: pp. 99–114. https://www.doi.org/10.1111/j.1469-7998.1991.tb03804.x

Leendertz, Fabian H., Georg Pauli, Kerstin Maetz-Rensing, Wayne Boardman, Charles Nunn, Heinz Ellerbrok, Siv Aina Jensen, Sandra Junglen, and Boesch Christophe. 2006. 'Pathogens as drivers of population declines: The importance of systematic monitoring in great apes and other threatened mammals', *Biological Conservation*, 131.2: pp. 325–37. https://www.doi.org/10.1016/j.biocon.2006.05.002

Leigh, Steven R. 1996. 'Evolution of human growth spurts', *American Journal of Physical Anthropology*, 101.4: pp. 455–74. https://www.doi.org/10.1002/(sici)1096-8644(199612)101:4<455::aid-ajpa2>3.3.co;2-6

—. 2001. 'Evolution of human growth', *Evolutionary Anthropology*, 10.6: pp. 223–36. https://www.doi.org/10.1002/evan.20002

—. 2004. 'Brain growth, life history, and cognition in primate and human evolution', *American Journal of Primatology*, 62.3: pp. 139–64. https://www.doi.org/10.1002/ajp.20012

Leigh, Steven R., and Brian T. Shea. 1995. 'Ontogeny and the evolution of adult body size dimorphism in apes', *American Journal of Primatology*, 36.1: pp. 37–60. https://www.doi.org/10.1002/ajp.1350360104

—. 1996. 'Ontogeny of body size variation in African apes', *American Journal of Physical Anthropology*, 99.1: pp. 43–65. https://www.doi.org/10.1002/(sici)1096-8644(199601)99:1<43::aid-ajpa3>3.0.co;2-0

Leroy, Eric M., Pierre Rouquet, Pierre Formenty, Sandrine Souquiere, Annelisa Kilbourne, Jean-Marc Froment, Magdalena Bermejo, Sheilag Smit, William Karesh, Robert Swanepoel, Sherif R. Zaki, and Pierre E. Rollin. 2004. 'Multiple Ebola virus transmission events and rapid decline of central African wildlife', *Science*, 303.5656: pp. 387–90. https://www.doi.org/10.1126/science.1092528

Levitis, Daniel A., and Laurie Bingaman Lackey. 2011. 'A measure for describing and comparing postreproductive life span as a population trait', *Methods in Ecology and Evolution*, 2.5: pp. 446–53. https://www.doi.org/10.1111/j.2041-210X.2011.00095.x

Lilly, Alecia A, Patrick T Mehlman, and Diane Doran. 2002. 'Intestinal parasites in gorillas, chimpanzees, and humans at Mondika research site, Dzanga-Ndoki National Park, Central African Republic', *International Journal of Primatology*, 23.3: pp. 555–73. https://doi.org/10.1023/a:1014969617036

Littleton, Judith. 2005. 'Fifty years of chimpanzee demography at Taronga Park Zoo', *American Journal of Primatology*, 67.3: pp. 281–98. https://www.doi.org/10.1002/ajp.20185

Liu, Weimin, Michael Worobey, Yingying Li, Brandon F. Keele, Frederic Bibollet-Ruche, Yuanyuan Guo, Paul A. Goepfert, Mario L. Santiago, Jean-Bosco N. Ndjango, and Cecile Neel. 2008. 'Molecular ecology and natural history of simian foamy virus infection in wild-living chimpanzees', *PLoS Pathogens*, 4: p. e1000097. https://www.doi.org/10.1371/journal.ppat.1000097

Lonsdorf, Elizabeth V, Margaret A Stanton, Anne E Pusey, and Carson M Murray. 2020. 'Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania', *American Journal of Physical Anthropology*, 171.3: pp. 419–29. https://doi.org/10.1002/ajpa.23986

Loskutoff, Naida M., Sheri L. Huntress, J. Michael Putman, Bill Yee, Todd R. Bowsher, Richard R. Chacon, Paul P. Calle, Richard C. Cambre, Gregory F. Rosen, and Duane C. Kraemer. 1991. 'Stimulation of ovarian activity for oocyte recovery in nonreproductive gorilllas (*Gorilla gorilla gorilla)*', *Journal of Zoo and Wildlife Medicine*. 22.1: pp. 32–41. https://www.jstor.org/stable/20095116

Lowenstine, L. J., R. McManamon, and K. A. Terio. 2015. 'Comparative pathology of aging great apes', *Veterinary Pathology*, 53.2: pp. 250–76. https://www.doi.org/10.1177/0300985815612154

Lunn, Peter G., Steven Austin, Andrew M. Prentice, and Roger G. Whitehead. 1984. 'The effect of improved nutrition on plasma prolactin concentrations and postpartum infertility in lactating Gambian women', *American Journal of Clinical Nutrition*, 39.2: pp. 227–35. https://doi.org/10.1093/ajcn/39.2.227

Mace, Georgina M. 1988. 'The genetic and demographic status of the western lowland gorilla (*Gorilla g. gorilla*) in captivity', *Journal of Zoology*, 216.4: pp. 629–54. https://doi.org/10.1111/j.1469-7998.1988.tb02462.x

Machanda, Zarin P., Melissa Emery Thompson, Martin N. Muller, and Richard W. Wrangham. 2014. 'Sex differences in the development of long-term association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii)*', *American Journal of Physical Anthropology*, 153: pp. 173.

Maggioncalda, Anne N., Robert M. Sapolsky, and Nancy M. Czekala. 1999. 'Reproductive hormone profiles in captive male orangutans: implications for understanding developmental arrest', *American Journal of Physical Anthropology*, 109.1: pp. 19–32. https://www.doi.org/10.1002/(sici)1096-8644(199905)109:1<19::aid-ajpa3>3.0.co;2-3

Manguette, Marie L., Andrew M. Robbins, Thomas Breuer, Emma J. Stokes, Richard J. Parnell, and Martha M. Robbins. 2019. 'Intersexual conflict influences female reproductive success in a female-dispersing primate', *Behavioural ecology and Sociobiology*, 73: 118. https://www.doi.org/10.1007/s00265-019-2727-3

Marino, Lori. 1998. 'A comparison of encephalization between odontocete cetaceans and anthropoid primates', *Brain, Behavior and Evolution*, 51.4: pp. 230–38. https://doi.org/10.1159/000006540

Markham, Rosemary J. 1990. 'Breeding orangutans at Perth Zoo: twenty years of appropriate husbandry', *Zoo Biology*, 9.2: pp. 171–82. https://doi.org/10.1002/zoo.1430090212

Marlowe, Frank. 2001. 'Male contribution to diet and female reproductive success among foragers', *Current Anthropology*, 42.5: pp. 755–60. https://doi.org/10.1086/323820

Marlowe, Frank W. 2004. 'Marital residence among foragers', *Current Anthropology*, 45.2: pp. 277–84. https://doi.org/10.1086/382256

Marshall, Andrew J., Marc Ancrenaz, Francis Q. Brearley, Gabriella M. Fredriksson, Nilofer Ghaffar, Matt Heydon, Simon J. Husson, Mark Leighton, Kim R. McConkey, and Helen C. Morrogh-Bernard. 2009. 'The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans', *Orangutans: Geographic variation in behavioural ecology and conservation. Oxford University Press, Oxford*: pp. 97–117.

Marshall, Andrew J., Nardiyono, Linda M. Engström, Bhayu Pamungkas, Jhon Palapa, Erik Meijaard, and Scott A. Stanley. 2006. 'The blowgun is mightier than the chainsaw in determining population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan', *Biological Conservation*, 129.4: pp. 566–78. http://dx.doi.org/10.1016/j.biocon.2005.11.025

Marson, Jocelyne, Sylvain Meuris, Robert W. Cooper, and Pierre Jouannet. 1991. 'Puberty in the male chimpanzee: progressive maturation of semen characteristics', *Biology of Reproduction*, 44.3: pp. 448–55. https://www.doi.org/10.1095/biolreprod44.3.448

Martin, D. E., Charles E. Graham, and Kenneth G. Gould. 1978. 'Successful artificial insemination in the chimpanzee', *Symposia of the Zoological Society of London*, 43: pp. 249–60.

Marvan, R., J. M. G. Stevens, A. D. Roeder, I. Mazura, M. W. Bruford, and J. R. De Ruiter. 2006. 'Male dominance rank, mating and reproductive success in captive bonobos (*Pan paniscus)*', *Folia Primatologica*, 77.5: pp. 364–76. https://www.doi.org/10.1159/000093702

Matsumoto, Takuya. 2017. 'Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact', *American Journal of Physical Anthropology*. 163.2: pp. 356–66. https://www.doi.org/10.1002/ajpa.23212

McFarlin, Shannon C., Sarah K. Barks, Matthew W. Tocheri, Jason S. Massey, Amandine B. Eriksen, Katie A. Fawcett, Tara S. Stoinski, Patrick R. Hof, Timothy G. Bromage, and Antoine Mudakikwa. 2013. 'Early brain growth cessation in wild Virunga mountain gorillas (*Gorilla beringei beringei)*', *American Journal of Primatology*, 75.5: pp. 450–63. https://www.doi.org/10.1002/ajp.22100

Meder, A. 1994. 'Causes of death and diseases of gorillas in the wild', *Gorilla Journal*, 9: pp. 3–4. NO DOI FOUND

Meijaard, Erik, Damayanti Buchori, Yokyok Hadiprakarsa, Sri Suci Utami-Atmoko, Anton Nurcahyo, Albertus Tjiu, Didik Prasetyo, Lenny Christie, Marc Ancrenaz, and Firman Abadi. 2011. 'Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia', *Public Library of Science ONE*, 6: p. e27491. https://www.doi.org/10.1371/journal.pone.0027491

Merchant, Kathleen, Reynaldo Martorell, and Jere Haas. 1990. 'Maternal and fetal responses to the stresses of lactation concurrent with pregnancy and of short recuperative intervals', *American Journal of Clinical Nutrition*, 52.2: pp. 280–88. https://doi.org/10.1093/ajcn/52.2.280

Mitani, John C. 1989. 'Orangutan activity budgets: monthly variations and the effects of body size, parturition, and sociality', *American Journal of Primatology*, 18.2: pp. 87–100. https://doi.org/10.1002/ajp.1350180203

Montagu, M. F. Ashley. 1979. *The Reproductive Development of the Female: A Study in the Comparative Physiology of the Adolescent Organism* (PSG Publishing Co., Inc, Littleton).

Montgomery, Stephen H., Isabella Capellini, Robert A. Barton, and Nicholas I. Mundy. 2010. 'Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*', *BMC Biology*, 8: p. 9. https://www.doi.org/10.1186/1741-7007-8-9

Morbeck, Mary Ellen, and Adrienne L. Zihlman. 1989. 'Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania', *Primates*, 30.3: pp. 369–82. https://doi.org/10.1007/bf02381260

Moscone, Sherrill R., and Mary Jane Moore. 1993. 'Breastfeeding during pregnancy', *Journal of Human Lactation*, 9.2: pp. 83–88. https://www.doi.org/10.1177/089033449300900219

Müller, Dennis W. H., Daryl Codron, Carlo Meloro, Adam Munn, Angela Schwarm, Jürgen Hummel, and Marcus Clauss. 2013. 'Assessing the Jarman–Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores', *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 164.1: pp. 129–40. https://www.doi.org/10.1016/j.cbpa.2012.09.018

Muller, Martin N, Nicholas G Blurton Jones, Fernando Colchero, M Emery Thompson, Drew K Enigk, Joseph T Feldblum, Beatrice H Hahn, Kevin E Langergraber, Erik J Scully, Linda Vigilant, Kara K Walker, Richard W Wrangham, Emily E Wroblewski, and Anne E Pusey. 2020. 'Sexual dimorphism in chimpanzee (*Pan troglodytes schweinfurhii*) and human age-specific fertility', *Journal of Human Evolution*, 144: p. 102795. https://doi.org/10.1016/j.jhevol.2020.102795

Muller, Martin N, Melissa Emery Thompson, and Richard W Wrangham. 2006. 'Male chimpanzees prefer mating with old females', *Current Biology*, 16.22: pp. 2234–38. https://doi.org/10.1016/j.cub.2006.09.042

Muller, Martin N., and Richard W. Wrangham. 2014. 'Mortality rates among Kanyawara chimpanzees', *Journal of Human Evolutebion*, 66: pp. 107–14. https://www.doi.org/10.1016/j.jhevol.2013.10.004

Nakamura, Michio. 2015. 'Demography of the M group', in Michio Nakamura, Kazuhiko Hosaka, Noriko Itoh and Koichiro Zamma (eds.), *Mahale Chimpanzees: 50 Years of Research* (Cambridge University Press: New York, NY), pp. 82–93.

Negrey, Jacob D, Rachna B Reddy, Erik J Scully, Sarah Phillips-Garcia, Leah Owens, Kevin E Langergraber, John Mitani, Melissa Emery Thompson, Richard W Wrangham, Martin N Muller, Emily Otali, Zarin P Machanda, David Hyeroba, Kristine A Grindle, Tressa S. Pappas, Ann C. Palmenberg, James E. Gern, and Tony L Goldberg. 2019. 'Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin', *Emerging Microbes and Infections*, 8.1: pp. 139–49. https://doi.org/10.1080/22221751.2018.1563456

Neubauer, Simon, Philipp Gunz, Uta Schwarz, Jean-Jacques Hublin, and Christophe Boesch. 2012. 'Brief communication: endocranial volumes in an ontogenetic sample of chimpanzees from the Taï Forest National Park, Ivory Coast', *American Journal of Physical Anthropology*, 147.2: pp. 319–25. https://www.doi.org/10.1002/ajpa.21641

Newton-Fisher, Nicholas E. 2004. 'Hierarchy and social status in Budongo chimpanzees', *Primates*, 45: pp. 81–87. https://www.doi.org/10.1007/s10329-003-0064-6

Nietlisbach, P., N. Arora, A. Nater, B. Goossens, C. P. van Schaik, and M. Krützen. 2012. 'Heavily male-biased long-distance dispersal of orang-utans (genus: *Pongo*), as revealed by Y-chromosomal and mitochondrial genetic markers', *Mol Ecol*, 21.13: pp. 3173–86. https://www.doi.org/10.1111/j.1365-294X.2012.05539.x

Nishida, Toshisada. 1979. 'The social structure of chimpanzees of the Mahale Mountains', in David A. Hamburg and E. R. McCown (eds.), *Perspectives on Human Evolution, Vol. V: The Great Apes* (Benjamin/Cummings Publishing Co, San Francisco),

—. 1990. *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies* (University of Tokyo Press, Tokyo).

Nishida, Toshisada, Nadia Corp, Miya Hamai, Toshikazu Hasegawa, Mariko Hiraiwa-Hasegawa, Kazuhiko Hosaka, Kevin D. Hunt, Noriko Itoh, Kenji Kawanaka, Akiko Matsumoto-Oda, John C. Mitani, Michio Nakamura, Koshi Norikoshi, Tetsuya Sakamaki, Linda Turner, Shigeo Uehara, and Koichiro Zamma. 2003. 'Demography, female life history, and reproductive profiles among the chimpanzees of Mahale', *American Journal of Primatology*, 59.3: pp. 99–121. https://www.doi.org/10.1002/ajp.10068

Nishida, Toshisada, H. Takasaki, and Yukio Takahata. 1990. 'Demography and reproductive profiles', in Toshisada Nishida (ed.), *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies* (University of Tokyo Press, Tokyo), pp. 63–98.

Nowell, Angela A., and Alison W. Fletcher. 2007. 'Development of independence from the mother in *Gorilla gorilla gorilla*', *International Journal of Primatology*, 28: pp. 441–55. https://www.doi.org/10.1007/s10764-007-9128-6

—. 2008. 'The development of feeding behaviour in wild western lowland gorillas (*Gorilla gorilla gorilla*)', *Behaviour*, 145.2: pp. 171–93. https://doi.org/10.1163/156853907783244747

Nsubuga, Anthony M, Martha M Robbins, Christophe Boesch, and Linda Vigilant. 2008. 'Patterns of paternity and group fission in wild multimale mountain gorilla groups', *American Journal of Physical Anthropology*, 135.3: pp. 263–74. https://www.doi.org/10.1002/ajpa.20740

Nsubuga, Anthony M., Jason Holzman, Leona G. Chemnick, and Oliver A. Ryder. 2010. 'The cryptic genetic structure of the North American captive gorilla population', *Conservation Genetics*, 11: pp. 161–72. https://www.doi.org/10.1007/s10592-009-0015-x

Nutter, F. B., C. A. Whittier, Mike R. Cranfield, and L. J. Lowenstine. 2005. 'Causes of death for mountain gorillas (*Gorilla beringei beringei* and *Gorilla beringei* undecided) from 1968–2004: an aid to conservation programs', *Proceedings of the Wildlife Disease Association International Conference, Cairns, Queensland, Australia*: pp. 200–01.

Pagel, Mark, and Paul H. Harvey. 1993. 'Evolution of the juvenile period in mammals', in, *Juvenile Primates: Life History, Development, and Behavior* (Oxford University Press, New York), pp. 28–37.

Pavelka, Mary S. M., and Linda Marie Fedigan. 1991. 'Menopause: a comparative life history perspective', *American Journal of Physical Anthropology*, 34.S13: pp. 13–38. https://www.doi.org/10.1002/ajpa.1330340604

Pontzer, Herman, Mary H. Brown, David A. Raichlen, Holly Dunsworth, Brian Hare, Kara Walker, Amy Luke, Lara R. Dugas, Ramon Durazo-Arvizu, Dale Schoeller, Jacob Plange-Rhule, Pascal Bovet, Terrence E. Forrester, Estelle V. Lambert, Melissa Emery Thompson, Robert W. Shumaker, and Stephen R. Ross. 2016. 'Metabolic acceleration and the evolution of human brain size and life history', *Nature*, 533: pp. 390–92. https://www.doi.org/10.1038/nature17654

Pontzer, Herman, David A. Raichlen, Robert W. Shumaker, Cara Ocobock, and Serge A. Wich. 2010. 'Metabolic adaptation for low energy throughput in orangutans', *Proceedings of the National Academy of Sciences*, 107.32: pp. 14048–52. https://www.doi.org/10.1073/pnas.1001031107

Potts, Kevin B., David P. Watts, and Richard W. Wrangham. 2011. 'Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda', *International Journal of Primatology*, 32: pp. 669–90. https://www.doi.org/10.1007/s10764-011-9494-y

Prugnolle, Franck, Patrick Durand, Cécile Neel, Benjamin Ollomo, Francisco J. Ayala, Céline Arnathau, Lucie Etienne, Eitel Mpoudi-Ngole, Dieudonné Nkoghe, and Eric Leroy. 2010. 'African great apes are natural

hosts of multiple related malaria species, including *Plasmodium falciparum*', *Proceedings of the National Academy of Sciences*, 107.4: pp. 1458–63. https://www.doi.org/10.1073/pnas.0914440107

Pusey, Anne E. 1983. 'Mother-offspring relationships in chimpanzees after weaning', *Animal Behaviour*, 31.2: pp. 363–77. https://www.doi.org/10.1016/s0003-3472(83)80055-4

—. 1990a. 'Behavioural changes at adolescence in chimpanzees', *Behaviour*, 115.3–4: pp. 203–46. https://doi.org/10.1163/156853990x00581

Pusey, Anne E. 1980. 'Inbreeding avoidance in chimpanzees', *Animal Behaviour*, 28.2: pp. 543–52. https://www.doi.org/10.1016/s0003-3472(80)80063-7

—. 1987. 'Sex-biased dispersal and inbreeding avoidance in birds and mammals', *Trends in Ecology & Evolution*, 2.10: pp. 295–99. https://www.doi.org/10.1016/0169-5347(87)90081-4

—. 1990b. 'Mechanisms of inbreeding avoidance in nonhuman primates', in Jay R. Feierman (ed.), *Pedophilia: Biosocial Dimensions* (Springer-Verlag, Inc, New York), pp. 201–20.

Pusey, Anne E., Gary W. Oehlert, Jennifer M. Williams, and Jane Goodall. 2005. 'Influence of ecological and social factors on body mass of wild chimpanzees', *International Journal of Primatology*, 26: pp. 3–31. https://www.doi.org/10.1007/s10764-005-0721-2

Quiatt, D, V Reynolds, and EJ Stokes. 2002. 'Snare injuries to chimpanzees (*Pan troglodytes*) at 10 study sites in east and west Africa', *African Journal of Ecology*, 40.3: pp. 303–05. https://doi.org/10.1046/j.1365-2028.2002.00356.x

Read, A. F., and P. H. Harvey. 1989. 'Life history differences among the eutherian radiations', *Journal of Zoology*, 219.2: pp. 329–53. https://www.doi.org/10.1111/j.1469-7998.1989.tb02584.x

Reader, Simon M., and Kevin N. Laland. 2002. 'Social intelligence, innovation, and enhanced brain size in primates', *Proceedings of the National Academy of Sciences*, 99.7: pp. 4436–41. https://www.doi.org/10.1073/pnas.062041299

Reiches, Meredith W., Peter T. Ellison, Susan F. Lipson, Katherine C. Sharrock, Eliza Gardiner, and Laura G. Duncan. 2009. 'Pooled energy budget and human life history', *American Journal of Human Biology*, 21.4: pp. 421–29. https://www.doi.org/10.1002/ajhb.20906

Reinartz, Gay E., Ellen J. Ingmanson, and Hilde Vervaecke. 2013. '*Pan paniscus* Gracile chimpanzee (bonobo, pygmy chimpanzee)', in D. C. D. Happold, Jonathon Kingdon and Thomas M. Butynski (eds.), *Mammals of Africa* (Bloomsbury Publishing: New York), pp. 64–69.

Reitsema, Laurie J. 2012. 'Introducing fecal stable isotope analysis in primate weaning studies', *American Journal of Primatology*, 74.10: pp. 926–39. https://www.doi.org/10.1002/ajp.22045

Remis, Melissa J. 2003. 'Are gorillas vacuum cleaners of the forest floor? The roles of body size, habitat, and food preferences on dietary flexibility and nutrition', in A. B. Taylor and Michele L. Goldsmith (eds.), *Gorilla biology: A multidisciplinary perspective* (Cambridge University Press: New York), pp. 385–404. https://www.doi.org/10.1017/cbo9780511542558.017

Rijksen, H. D. 1978. *A Field Study on Sumatran Orang-utans* (Pongo pygmaeus abelli, *Lesson 1827): Ecology, Behaviour and Conservation* (Veenman & Zonen, Wageningen, Netherlands).

Robbins, Andrew M., Maryke Gray, Augustin Basabose, Prosper Uwingeli, Innocent Mburanumwe, Edwin Kagoda, and Martha M. Robbins. 2013. 'Impact of male infanticide on the social structure of mountain gorillas', *Public Library of Science ONE*, 8: p. e78256. https://www.doi.org/10.1371/journal.pone.0078256

Robbins, Andrew M., Maryke Gray, Prosper Uwingeli, Innocent Mburanumwe, Edwin Kagoda, and Martha M. Robbins. 2014. 'Variance in the reproductive success of dominant male mountain gorillas', *Primates*, 55: pp. 489–99. https://www.doi.org/10.1007/s10329-014-0426-2

Robbins, Andrew M., and Martha M. Robbins. 2005. 'Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*)', *Behavioural ecology and Sociobiology*, 58: pp. 295–309. https://www.doi.org/10.1007/s00265-005-0917-7

Robbins, Andrew M., Martha M. Robbins, Netzin Gerald-Steklis, and H. Dieter Steklis. 2006. 'Age-related patterns of reproductive success among female mountain gorillas', *American Journal of Physical Anthropology*, 131.4: pp. 511–21. https://www.doi.org/10.1002/ajpa.20474

Robbins, Andrew M., Tara S. Stoinski, Katie A. Fawcett, and Martha M. Robbins. 2009. 'Socioecological influences on the dispersal of female mountain gorillas — evidence of a second folivore paradox', *Behavioural ecology and Sociobiology*, 63: pp. 477–89. https://www.doi.org/10.1007/s00265-008-0679-0

Robbins, Martha M., Magdelena Bermejo, Chloé Cipolletta, Florence Magliocca, Richard J. Parnell, and Emma Stokes. 2004. 'Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla)*', *American Journal of Primatology*, 64.2: pp. 145–59. https://www.doi.org/10.1002/ajp.20069

Robbins, Martha M., and Andrew M. Robbins. 2021. 'Variability of weaning age in mountain gorillas (*Gorilla beringei beringei)*', *American Journal of Physical Anthropology*, 174.4: pp. 776–84. https://www.doi.org/10.1002/ajpa.24237

Robbins, Martha M., Andrew M. Robbins, Netzin Gerald-Steklis, and H. Dieter Steklis. 2007a. 'Female reproductive success of the Virunga mountain gorillas: comparisons with the socioecological model', *Behavioural ecology and Sociobiology*, 61: pp. 919–31.

Robbins, Martha, Andrew M Robbins, Netzin Gerald-Steklis, and H Dieter Steklis. 2007b. 'Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei)*', *Behavioural ecology and Sociobiology*, 61: pp. 919–31. https://www.doi.org/10.1007/s00265-006-0321-y

Robson, Shannen L., and Bernard Wood. 2008. 'Hominin life history: reconstruction and evolution', *Journal of Anatomy*, 212.4: pp. 394–425. https://www.doi.org/10.1111/j.1469-7580.2008.00867.x

Rosenbaum, S., J. B. Silk, and T. S. Stoinski. 2011. 'Male–immature relationships in multi-male groups of mountain gorillas (*Gorilla beringei beringei)*', *American Journal of Primatology*, 73.4: pp. 356–65. https://www.doi.org/10.1002/ajp.20905

Rosenbaum, Stacy, Linda Vigilant, Christopher W Kuzawa, and Tara S Stoinski. 2018. 'Caring for infants is associated with increased reproductive success for male mountain gorillas', *Scientific reports*, 8.1: p. 15223. https://doi.org/10.1038/s41598-018-33380-4

Ross, Caroline, and Kate E. Jones. 1999. 'Socioecology and the evolution of primate reproductive rates', in Phyllis C Lee (ed.), *Comparative primate socioecology* (Cambridge University Press: New York), pp. 73–110.

Ryan, Sadie J., and Peter D. Walsh. 2011. 'Consequences of non-intervention for infectious disease in African great apes', *Public Library of Science ONE*, 6: p. e29030. https://www.doi.org/10.1371/journal.pone.0029030

Sakamaki, Tetsuya, Mbangi Mulavwa, and Takeshi Furuich. 2009. 'Flu-like epidemics in wild bonobos (*Pan paniscus*) at Wamba, the Luo Scientific Reserve, Democratic Republic of Congo', *Pan Africa News*, 16.1: pp. 1–4. https://doi.org/10.5134/143503

Santiago, Mario L., Cynthia M. Rodenburg, Shadrack Kamenya, Frederic Bibollet-Ruche, Feng Gao, Elizabeth Bailes, Sreelatha Meleth, Seng-Jaw Soong, J. Michael Kilby, Zina Moldoveanu, Babette Fahey, Martin N. Muller, Ahidjo Ayouba, Eric Nerrienet, Harold M. McClure, Jonathan L. Heeney, Anne E. Pusey, D. Anthony Collins, Christophe Boesch, Richard W. Wrangham, Jane Goodall, Paul M. Sharp, George M. Shaw, and Beatrice H. Hahn. 2002. 'SIVcpz in wild chimpanzees', *Science*, 295.5554: p. 465. https://doi.org/10.1126/science.295.5554.465

Sarmiento, Esteban E., Thomas M. Butynski, and Jan Kalina. 1996. 'Gorillas of Bwindi-Impenetrable Forest and the Virunga Volcanoes: Taxonomic implications of morphological and ecological differences', *American Journal of Primatology*, 40.1: pp. 1–21. https://www.doi.org/10.1002/(SICI)1098-2345(1996)40:1<1::AID-AJP1>3.0.CO;2-1

Schaller, George B. 1963. *The Mountain Gorilla: Ecology and Behavior* (University of Chicago Press: Chicago, IL).

Schuppli, Caroline, Sofia I. F. Forss, Ellen J. M. Meulman, Nicole Zweifel, Kevin C. Lee, Evasari Rukmana, Erin R. Vogel, Maria A. van Noordwijk, and Carel P. van Schaik. 2016. 'Development of foraging skills in two orangutan populations: needing to learn or needing to grow?', *Frontiers in Zoology*, 13: p. 43. https://www.doi.org/10.1186/s12983-016-0178-5

Schuppli, Caroline, Ellen J. M. Meulman, Sofia I. F. Forss, Fikty Aprilinayati, Maria A. van Noordwijk, and Carel P. van Schaik. 2016. 'Observational social learning and socially induced practice of routine skills in immature wild orang-utans', *Animal Behaviour*, 119: pp. 87–98. https://www.doi.org/10.1016/j.anbehav.2016.06.014

Schürmann, Chris L., and Jan Aram van Hooff. 1986. 'Reproductive strategies of the orang-utan: new data and a reconsideration of existing sociosexual models', *International Journal of Primatology*, 7: pp. 265–87. https://www.doi.org/10.1007/bf02736392

Seielstad, Mark T., Eric Minch, and Luigi Luca Cavalli-Sforza. 1998. 'Genetic evidence for a higher female migration rate in humans', *Nature Genetics*, 20.3: pp. 278–80. https://doi.org/10.1038/3088

Shea, Brian T. 1983. 'Allometry and heterochrony in the African apes', *American Journal of Physical Anthropology*, 62.3: pp. 275–89. https://www.doi.org/10.1002/ajpa.1330620307

Shimizu, Keiko, Chisato Douke, Shiho Fujita, Tetsuro Matsuzawa, Masaki Tomonaga, Masayuki Tanaka, Kiyoaki Matsubayashi, and Motoharu Hayashi. 2003. 'Urinary steroids, FSH and CG measurements for monitoring the ovarian cycle and pregnancy in the chimpanzee', *Journal of Medical Primatology*, 32.1: pp. 15–22. https://doi.org/10.1034/j.1600-0684.2003.01039.x

Sievert, Judy, William B. Karesh, and Violet Sunde. 1991. 'Reproductive intervals in captive female western lowland gorillas with a comparison to wild mountain gorillas', *American Journal of Primatology*, 24.3–4: pp. 227–34. https://doi.org/10.1002/ajp.1350240308

Skinner, Mark F. 2014. 'Variation in perikymata counts between repetitive episodes of linear enamel hypoplasia among orangutans from Sumatra and Borneo', *American Journal of Physical Anthropology*, 154.1: pp. 125–39. https://www.doi.org/10.1002/ajpa.22485

Smith, Richard J., and William L. Jungers. 1997. 'Body mass in comparative primatology', *Journal of Human Evolution*, 32.6: pp. 523–59. https://www.doi.org/10.1006/jhev.1996.0122

Smith, Richard J., and Steven R. Leigh. 1998. 'Sexual dimorphism in primate neonatal biomass', *Journal of Human Evolution*, 34.2: pp. 173–201. https://www.doi.org/10.1006/jhev.1997.0190

Smith, Tanya M., Christine Austin, Katie Hinde, Erin R. Vogel, and Manish Arora. 2017. 'Cyclical nursing patterns in wild orangutans', *Science Advances*, 3.5: p. e1601517. https://www.doi.org/10.1126/sciadv.1601517

Spelman, Lucy H., Kirsten V. K. Gilardi, Magdalena Lukasik-Braum, Jean-Felix Kinani, Elisabeth Nyirakaragire, Linda J. Lowenstine, and Michael R. Cranfield. 2013. 'Respiratory disease in mountain gorillas (*Gorilla beringei beringei*) in Rwanda, 1990–2010: outbreaks, clinical course, and medical management', *Journal of Zoo and Wildlife Medicine*, 44.4: pp. 1027–35. https://doi.org/10.1638/2013-0014r.1

Stanton, Margaret A, Elizabeth V Lonsdorf, Anne E Pusey, Jane Goodall, and Carson M Murray. 2014. 'Maternal behavior by birth order in wild chimpanzees (*Pan troglodytes*) increased investment by first-time mothers', *Current Anthropology*, 55.4: pp. 483–89. https://doi.org/10.1086/677053

Stewart, Fiona A., and Jill D. Pruetz. 2013. 'Do chimpanzee nests serve an anti-predatory function?', *American Journal of Primatology*, 75.6: pp. 593–604. https://www.doi.org/10.1002/ajp.22138

Stewart, Kelly J. 2001. 'Social relationships of immature gorillas and silverbacks', *Mountain gorillas: Three decades of research at Karisoke*: pp. 183–213. https://www.doi.org/10.1017/cbo9780511661631.008

Stewart, Kelly J. 1988. 'Suckling and lactational anoestrus in wild gorillas (*Gorilla gorilla*)', *Journal of Reproduction and Fertility*, 83.2: pp. 627–34. https://www.doi.org/10.1530/jrf.0.0830627

Stiles, Daniel, Ian Redmond, Doug Cress, Christian Nellemann, and Rannveig Knutsdatter Formo. 2016. 'Stolen apes* The illicit trade in chimpanzees, gorillas, bonobos, and orangutans', *The Environment in Anthropology: A Reader in Ecology, Culture, and Sustainable Living*: pp. 359–61.

Stoinski, Tara S., Veronica Vecellio, Theogene Ngaboyamahina, Felix Ndagijimana, Stacy Rosenbaum, and Kathryn A. Fawcett. 2009. 'Proximate factors influencing dispersal decisions in male mountain gorillas, *Gorilla beringei beringei*', *Animal Behaviour*, 77.5: pp. 1155–64. http://dx.doi.org/10.1016/j.anbehav.2008.12.030

Stokes, Emma J., Richard J. Parnell, and Claudia Olejniczak. 2003. 'Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*),' *Behavioural ecology and Sociobiology*, 54: pp. 329–39. https://www.doi.org/10.1007/s00265-003-0630-3

Strong, Victoria J., Douglas Grindlay, Sharon Redrobe, Malcolm Cobb, and Kate White. 2016. 'A systematic review of the literature relating to captive great ape morbidity and mortality', *Journal of Zoo and Wildlife Medicine*, 47.3: pp. 697–710. https://www.doi.org/10.1638/2015-0240.1

Stumpf, R. M., M. Emery Thompson, M. N. Muller, and R. W. Wrangham. 2009. 'The context of female dispersal in Kanyawara chimpanzees', *Behaviour*, 146.4–5: pp. 629–56. https://www.doi.org/10.1163/156853909x413853

Sugiyama, Yukimaru. 1999. 'Socioecological factors of male chimpanzee migration at Bossou, Guinea', *Primates*, 40: pp. 61–68. https://www.doi.org/10.1007/bf02557702

—. 2004. 'Demographic parameters and life history of chimpanzees at Bossou, Guinea', *American Journal of Physical Anthropology*, 124.2: pp. 154–65. https://www.doi.org/10.1002/ajpa.10345

Sugiyama, Yukimaru, and Shiho Fujita. 2011. 'The demography and reproductive parameters of Bossou chimpanzees', in Tetsuro Matsuzawa, Tatyana Humle and Yukimaru Sugiyama (eds.), *The Chimpanzees of Bossou and Nimba* (Springer: Tokyo), pp. 23–34.

Sugiyama, Yukimaru, Sakie Kawamoto, Osamu Takenaka, Kiyonori Kumazaki, and Norikatsu Miwa. 1993. 'Paternity discrimination and inter-group relationships of chimpanzees at Bossou', *Primates*, 34: pp. 545–52. https://www.doi.org/10.1007/bf02382665

Surbeck, Martin, Christophe Boesch, Melissa Emery Thompson, Takeshi Furuichi, Barbara Fruth, Gottfried Hohmann, Shintaro Ishizuka, Zarin Machanda, Martin Muller, Anne Pusey, Tetsuya Sakamaki, Nahoko Tokuyama, Kara Walker, Richae Wrangham, Emily Wroblewski, Klaus Zuberbuehler, Linda Vigilant, and Kevin Langergraber. 2019. 'Males with a mother living in their community have higher reproductive success in bonobos but not chimpanzees', *Current Biology*, 29.10: pp. R354-55. https://doi.org/10.1016/j.cub.2019.03.040

Surbeck, Martin, Kevin E. Langergraber, Barbara Fruth, Linda Vigilant, and Gottfried Hohmann. 2017. 'Male reproductive skew is higher in bonobos than chimpanzees', *Current Biology*, 27.13: pp. R640-R41. https://www.doi.org/10.1016/j.cub.2017.05.039

Surbeck, Martin, Roger Mundry, and Gottfried Hohmann. 2011. 'Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*),' *Proceedings of the Royal Society of London B: Biological Sciences*, 278.1705: pp. 590–98. https://doi.org/10.1098/rspb.2010.1572

Taylor, Andrea B., and Carel P. van Schaik. 2007. 'Variation in brain size and ecology in Pongo', *Journal of Human Evolution*, 52.1: pp. 59–71. https://doi.org/10.1016/j.jhevol.2006.07.010

Terio, Karen A., Michael J. Kinsel, Jane Raphael, Titus Mlengeya, Iddi Lipende, Claire A. Kirchhoff, Baraka Gilagiza, Michael L. Wilson, Shadrack Kamenya, and Jacob D. Estes. 2011. 'Pathologic lesions in chimpanzees (*Pan trogylodytes schweinfurthii*) from Gombe National Park, Tanzania, 2004–2010', *Journal of Zoo and Wildlife Medicine*, 42.4: pp. 597–607. https://www.doi.org/10.1638/2010-0237.1

Thompson-Handler, Nancy. 1990. 'The pygmy chimpanzee: sociosexual behavior, reproductive biology and life history patterns', Yale University.

Tilson, R., U. S. Seal, K. Soemarna, W. Ramano, E. Sumardja, S. Poniran, Carel P. van Schaik, Mark Leighton, H. Rijksen, and A. A. Eudey. 1993. "Orangutan population and habitat viability analysis report', In *Orangutan Population and Habitat Viability Analysis Workshop*. Medan, Indonesia.

Townsend, Simon W., Katie E. Slocombe, Melissa Emery Thompson, and Klaus Zuberbühler. 2007. 'Female-led infanticide in wild chimpanzees', *Current Biology*, 17.10: pp. R355-R56. https://www.doi.org/10.1016/j.cub.2007.03.020

Tsukahara, Takahiro. 1993. 'Lions eat chimpanzees: The first evidence of predation by lions on wild chimpanzees', *American Journal of Primatology*, 29.1: pp. 1–11. https://www.doi.org/10.1002/ajp.1350290102

Tutin, Caroline E. G. 1996. 'Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon', in Linda F. Marchant, Toshisada Nishida and William C. McGrew (eds.), *Great Ape Societies* (Cambridge University Press: Cambridge), pp. 58–70. https://www.doi.org/10.1017/CBO9780511752414.007

Uehara, Shigeo, and Toshisada Nishida. 1987. 'Body weights of wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania', *American Journal of Physical Anthropology*, 72.3: pp. 315–21. https://www.doi.org/10.1002/ajpa.1330720305

Utami Atmoko, Suci, and Jan A. R. A. M. van Hooff. 2004. 'Alternative male reproductive strategies: male bimaturism in orangutans', in P. M. Kappeler and C. P. van Schaik (eds.), *Sexual Selection in Primates: New and Comparative Perspectives* (Cambridge University Press: Cambridge), pp. 196–207. https://www.doi.org/10.1017/cbo9780511542459.013

Utami, Sri Suci, Benoit Goossens, Michael W. Bruford, Jan R. de Ruiter, and Jan A. R. A. M. van Hooff. 2002. 'Male bimaturism and reproductive success in Sumatran orangutans', *Behavioural ecology*, 13.5: pp. 643–52. https://www.doi.org/10.1093/beheco/13.5.643

Valeggia, Claudia, and Peter T. Ellison. 2009. 'Interactions between metabolic and reproductive functions in the resumption of postpartum fecundity', *American Journal of Human Biology*, 21.4: pp. 559–66. https://www.doi.org/10.1002/ajhb.20907

Valeggia, Claudia R., and Peter T. Ellison. 2004. 'Lactational amenorrhoea in well-nourished Toba women of Formosa, Argentina', *Journal of Biosocial Science*, 36.5: pp. 573–95. https://doi.org/10.1017/s0021932003006382

van Adrichem, Gijsbertus G. J., Sri Suci Utami, Serge A. Wich, Jan A. R. A. M. van Hooff, and Elisabeth H. M. Sterck. 2006. 'The development of wild immature Sumatran orangutans (*Pongo abelii*) at Ketambe', *Primates*, 47: pp. 300–09. https://www.doi.org/10.1007/s10329-006-0193-9

van de Rijt-Plooij, Hedwig H. C., and Frans X. Plooij. 1987. 'Growing independence, conflict and learning in mother-infant relations in free-ranging chimpanzees', *Behaviour*, 101.1–3: pp. 1–86. https://www.doi.org/10.1163/156853987x00378

Van Dooren, Sonia, William M. Switzer, Walid Heneine, Patrick Goubau, Ernst Verschoor, Bharat Parekh, Walter De Meurichy, Chris Furley, Marc Van Ranst, and Anne-Mieke Vandamme. 2002. 'Lack of evidence for infection with simian immunodeficiency virus in bonobos', *AIDS research and human retroviruses*, 18.3: pp. 213–16. https://www.doi.org/10.1089/08892220252781275

Van Heuverswyn, Fran, Yingying Li, Cecile Neel, Elizabeth Bailes, Brandon F Keele, Weimin Liu, Severin Loul, Christelle Butel, Florian Liegeois, and Yanga Bienvenue. 2006. 'Human immunodeficiency viruses: SIV infection in wild gorillas', *Nature*, 444.7116: pp. 164–64. https://doi.org/10.1038/444164a

van Noordwijk, M. A., Simone E. B. Sauren, Nuzuar, Ahbam Abulani, H. C. Morrogh-Bernard, S. S. Utami Atmoko, and C. P. van Schaik. 2009. 'Development of independence: Sumatran and Bornean orangutans compared', in S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia and C. P. van Schaik (eds.), *Orangutans: Geographic Variation in Behavioural ecology and Conservation* (Oxford University Press: New York), pp. 189–203. https://www.doi.org/10.1093/acprof:oso/9780199213276.003.0012

van Noordwijk, M. A., and Carel P. van Schaik. 2005. 'The development of ecological competence in Sumatran orangutans', *American Journal of Physical Anthropology*, 127: 79–94.

van Noordwijk, Maria A., Natasha Arora, Erik P. Willems, Lynda P. Dunkel, Rahmalia N. Amda, Neneng Mardianah, Corinne Ackermann, Michael Krützen, and Carel P. van Schaik. 2012. 'Female philopatry and its social benefits among Bornean orangutans', *Behavioural ecology and Sociobiology*, 66: pp. 823–34. https://www.doi.org/10.1007/s00265-012-1330-7

van Noordwijk, Maria A., Christopher W. Kuzawa, and Carel P. van Schaik. 2013. 'The evolution of the patterning of human lactation: A comparative perspective', *Evolutionary Anthropology: Issues, News, and Reviews*, 22.5: pp. 202–12. https://www.doi.org/10.1002/evan.21368

van Noordwijk, Maria A., S. Suci Utami Atmoko, Cheryl D. Knott, Noko Kuze, Helen C. Morrogh-Bernard, Felicity Oram, Caroline Schuppli, Carel P. van Schaik, and Erik P. Willems. 2018. 'The slow ape: High infant survival and long interbirth intervals in wild orangutans', *Journal of Human Evolution*, 125: pp. 38–49. https://www.doi.org/10.1016/j.jhevol.2018.09.004

van Noordwijk, Maria A., Erik P. Willems, Sri Suci Utami Atmoko, Christopher W. Kuzawa, and Carel P. van Schaik. 2013. 'Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*)', *Behavioural ecology and Sociobiology*, 67: pp. 805–14. https://www.doi.org/10.1007/s00265-013-1504-y

van Schaik, Carel P. 1999. 'The socioecology of fission-fusion sociality in orangutans', *Primates*, 40: pp. 69–86. https://www.doi.org/10.1007/bf02557703

Varki, Nissi, D. Anderson, James G. Herndon, Tho Pham, Christopher J. Gregg, Monica Cheriyan, J. Murphy, Elizabeth Strobert, Jo Fritz, James G. Else, and Ajit Varki. 2009. 'Heart disease is common in humans and chimpanzees, but is caused by different pathological processes', *Evolution Applications*, 2.1: pp. 101–12. https://www.doi.org/10.1111/j.1752-4571.2008.00064.x

Videan, E., Jo Fritz, C. Heward, and J. Murphy. 2006. 'The effects of aging on hormone and reproductive cycles in female chimpanzees (*Pan troglodytes*)', *Comparative Medicine*, 56.4: pp. 291–99. https://pubmed.ncbi.nlm.nih.gov/16941957/

Vogel, Erin R., Cheryl D. Knott, Brooke E. Crowley, Melissa D. Blakely, Michael D. Larsen, and Nathaniel J. Dominy. 2012. 'Bornean orangutans on the brink of protein bankruptcy', *Biology Letters*, 8.3: pp. 333–36. https://www.doi.org/10.1098/rsbl.2011.1040

von Rueden, Christopher, Michael Gurven, and Hillard Kaplan. 2010. 'Why do men seek status? Fitness payoffs to dominance and prestige', *Proceedings of the Royal Society B: Biological Sciences*. 278.1715. https://www.doi.org/10.1098/rspb.2010.2145

Walker, Kara K, Christopher S Walker, Jane Goodall, and Anne E Pusey. 2018. 'Maturation is prolonged and variable in female chimpanzees', *Journal of Human Evolution*, 114: pp. 131–40. https://doi.org/10.1016/j.jhevol.2017.10.010

Walker, Kara K., Rebecca S. Rudicell, Yingying Li, Beatrice H. Hahn, Emily Wroblewski, and Anne E. Pusey. 2017. 'Chimpanzees breed with genetically dissimilar mates', *Royal Society Open Science*, 4.1. https://www.doi.org/10.1098/rsos.160422

Walker, Margaret L., and James G. Herndon. 2008. 'Menopause in nonhuman primates?', *Biology of Reproduction*, 79.3: pp. 398–406. https://www.doi.org/10.1095/biolreprod.108.068536

Wallis, Janette. 1997. 'A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park', *Journal of Reproduction and Fertility*, 109.2: pp. 297–307. https://www.doi.org/10.1530/jrf.0.1090297

Walsh, Peter D., Kate A. Abernethy, Magdalena Bermejo, Rene Beyers, Pauwel De Wachter, Marc Ella Akou, Bas Huijbregts, Daniel Idiata Mambounga, Andrew Kamdem Toham, Annelisa M. Kilbourn, Sally A. Lahm, Stefanie Latour, Fiona Maisels, Christian Mbina, Yves Mihindou, Sosthene Ndong Obiang, Ernestine Ntsame Effa, Malcolm P. Starkey, Paul Telfer, Marc Thibault, Caroline E. G. Tutin, Lee J. T. White, and David S. Wilkie. 2003. 'Catastrophic ape decline in western equatorial Africa', *Nature*, 422: pp. 611–14. https://www.doi.org/10.1038/nature01566

Watts, David P. 1996. 'Comparative socio-ecology of gorillas', in William C. McGrew, Linda F. Marchant and Toshisada Nishida (eds.), *Great ape societies* (Cambridge University Press: Cambridge), pp. 16–28.

—. 2018. 'Male dominance relationships in an extremely large chimpanzee community at Ngogo, Kibale National Park, Uganda', *Behaviour*, 155.13–15: pp. 969–1009. https://doi.org/10.1163/1568539x-00003517

Watts, David P. 1985. 'Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*)', *American Journal of Primatology*, 8.1: pp. 1–10. https://www.doi.org/10.1002/ajp.1350080102

—. 1998. 'Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*)', *International Journal of Primatology*, 19: pp. 929–48. https://link.springer.com/article/10.1023/A:1020366018187

—. 2000. 'Causes and consequences of variation in male mountain gorilla life histories and group membership', in Peter M. Kappeler (ed.), *Primate Males* (Cambridge University Press: Cambridge), pp. 169–80.

Watts, David P., and Anne E. Pusey. 1993. 'Behavior of juvenile and adolescent great apes', in M. E. Pereira (ed.), *Juvenile Primates: Life History, Development, and Behavior* (Oxford University Press, New York).

Wich, S. A., H. de Vries, Marc Ancrenaz, Lori Perkins, R. Shumaker, A. Suzuki, and Carel P. van Schaik. 2009. 'Orangutan life history variation', in Serge A. Wich, Sri Suci Utami, T. Mitra Setia and Carel P. van Schaik (eds.), *Orangutans: Ecology, Evolution, Behaviour and Conservation* (Oxford University Press).

Wich, S. A., R. W. Shumaker, L. Perkins, and H. de Vries. 2009. 'Captive and wild orangutan (*Pongo sp.*) survivorship: a comparison and the influence of management', *American Journal of Primatology*, 71.8: pp. 680–86. https://www.doi.org/10.1002/ajp.20704

Wich, S. A., S. S. Utami-Atmoko, T. Mitra Setia, H. D. Rijksen, C. Schurmann, Jan Aram van Hooff, and Carel P. van Schaik. 2004. 'Life history of wild Sumatran orangutans (*Pongo abelii)*', *Journal of Human Evolution*, 47.6: pp. 385–98. https://www.doi.org/10.1016/j.jhevol.2004.08.006

Wich, Serge A., Erin R. Vogel, Michael D. Larsen, Gabriella Fredriksson, Mark Leighton, Carey P. Yeager, Francis Q. Brearley, Carel P. van Schaik, and Andrew J. Marshall. 2011. 'Forest fruit production is higher on Sumatra than on Borneo', *Public Library of Science ONE*, 6: p. e21278. https://www.doi.org/10.1371/journal.pone.0021278

Wilder, Jason A, Sarah B Kingan, Zahra Mobasher, Maya Metni Pilkington, and Michael F Hammer. 2004. 'Global patterns of human mitochondrial DNA and Y-chromosome structure are not influenced by higher migration rates of females versus males', *Nature Genetics*, 36.10: pp. 1122–25. https://doi.org/10.1038/ng1428

Williams, J. M., E. V. Lonsdorf, M. L. Wilson, J. Schumacher-Stankey, J. Goodall, and A. E. Pusey. 2008. 'Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania', *American Journal of Primatology*, 70.8: pp. 766–77. https://www.doi.org/10.1002/ajp.20573

Williamson, E. A., and Thomas M Butynski. 2013a. '*Gorilla beringei* Eastern gorilla', in D. C. D. Happold, Jonathon Kingdon and Thomas M. Butynski (eds.), *Mammals of Africa* (Bloomsbury Publishing: New York), pp. 45–53.

Williamson, E. A., and Thomas M. Butynski. 2013b. '*Gorilla gorilla* Western gorilla', in D. C. D. Happold, Jonathon Kingdon and Thomas M. Butynski (eds.), *Mammals of Africa* (Bloomsbury Publishing: New York), pp. 39–45.

Wilson, Michael L., and Richard W. Wrangham. 2003. 'Intergroup relations in chimpanzees', *Annual Review of Anthropology*, 32.1: pp. 363–92. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Wittig, Roman, and Christophe Boesch. 2019. 'Demography and life history of five chimpanzee communities in Taï National Park', in Christophe Boesch, Roman Wittig, Catherine Crockford, Linda Vigilant, Tobias Deschner and Fabian Leendertz (eds.), *The chimpanzees of the Taï forest: 40 years of research* (Cambridge University Press: Cambridge, UK), pp. 125–40.

Wood, Brian M., David P. Watts, J. C. Mitani, and Kevin E. Langergraber. 2017. 'Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers', *Journal of Human Evolution*, 105: pp. 41–56. https://www.doi.org/10.1016/j.jhevol.2017.01.003

Wood, James W. 1994. *Dynamics of Human Reproduction: Biology, Biometry, Demography* (Aldine de Gruyter, New York).

Wrangham, Richard, and Rachel Carmody. 2010. 'Human adaptation to the control of fire', *Evolutionary Anthropology: Issues, News, and Reviews*, 19.5: pp. 187–99. https://www.doi.org/10.1002/evan.20275

Wrangham, Richard W. 2002. 'The cost of sexual attraction: is there a trade-off in female *Pan* between sex appeal and received coercion?' in Christophe Boesch, Gottfried Hohmann and Linda F Marchant (eds.), *Behavioural diversity in chimpanzees and bonobos* (Cambridge University Press), pp. 204–15.

Wrangham, Richard W., Michael L. Wilson, and Martin N. Muller. 2006. 'Comparative rates of violence in chimpanzees and humans', *Primates*, 47.1: pp. 14–26. https://doi.org/10.1007/s10329-005-0140-1

Wright, Edward, Jordi Galbany, Shannon C. McFarlin, Eric Ndayishimiye, Tara S. Stoinski, and Martha M. Robbins. 2020. 'Dominance rank but not body size influences female reproductive success in mountain gorillas', *PloS one*, 15: p. e0233235. https://www.doi.org/10.1371/journal.pone.0233235

Wroblewski, Emily E., Carson M. Murray, Brandon F. Keele, Joann C. Schumaker-Stankey, Beatrice H. Hahn, and Anne E. Pusey. 2009. 'Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*', *Animal Behaviour*, 77.4: pp. 873–85. https://doi.org/10.1016/j.anbehav.2008.12.014

Yamagiwa, J., and John Kahekwa. 2001. 'Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide', in Martha M. Robbins, Pascal Sicotte and Kelly J. Stewart (eds.), *Mountain gorillas: Three decades of research at Karisoke* (Cambridge University Press, Cambridge), pp. 89–122.

Yamagiwa, Juichi, Augustin Kanyunyi Basabose, John Kahekwa, Dominique Bikaba, Chieko Ando, Miki Matsubara, Nobusuke Iwasaki, and David S Sprague. 2012. 'Long-term research on Grauer's gorillas in Kahuzi-Biega National Park, DRC: life history, foraging strategies, and ecological differentiation from sympatric chimpanzees', in, *Long-term field studies of primates* (Springer), pp. 385–412.

Yapuncich, Gabriel S., Aleah Bowie, Raphaël Belais, Steven E. Churchill, and Christopher S. Walker. 2020. 'Predicting body mass of bonobos (*Pan paniscus*) with human-based morphometric equations', *American Journal of Primatology*, 82.2: p. e23088. https://www.doi.org/10.1002/ajp.23088

Yerkes, Robert M. 1943. *Chimpanzees: A Laboratory Colony* (Yale University Press, New Haven).