



Maturation is prolonged and variable in female chimpanzees



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ABSTRACT

Chimpanzees are important referential models for the study of life history in hominin evolution. Age at sexual maturity and first reproduction are key life history milestones that mark the diversion of energy from growth to reproduction and are essential in comparing life history trajectories between chimpanzees and humans. Yet, accurate information on ages at these milestones in wild chimpanzees is difficult to obtain because most females transfer before breeding. Precise age at first birth is only known from a relatively small number of non-dispersing individuals. Moreover, due to small sample sizes, the degree to which age at maturation milestones varies is unknown. Here we report maturation milestones and explore sources of variance for 36 wild female chimpanzees of known age, including eight dispersing females born in Gombe National Park, Tanzania. Using Kaplan-Meier survival analysis, including censored intervals, we find an average age of 11.5 years (range 8.5–13.9) at sexual maturity and 14.9 years (range 11.1–22.1) at first birth. These values exceed previously published averages for wild chimpanzees by one or more years. Even in this larger sample, age at first birth is likely underestimated due to the disproportionate number of non-dispersing females, which, on average, give birth two years earlier than dispersing females. Model selection using Cox Proportional Hazards models shows that age at sexual maturity is delayed in females orphaned before age eight years and those born to low-ranking mothers. Age at first birth is most delayed in dispersing females and those orphaned before age eight years. These data provide improved estimates of maturation milestones in a population of wild female chimpanzees and indicate the importance of maternal factors in development.

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1. Introduction

Human life history consists of an unusual suite of characteristics including slow growth, delayed maturation, short interbirth intervals (IBI), long periods of offspring dependency, and cessation of reproduction prior to death, all of which differentiate humans from other primate taxa (Bogin and Smith, 1996; Leigh, 2001; Gurven, 2012; Alberts et al., 2013). How, why, and when a modern human-like life history pattern evolved, however, is unresolved and partly dependent on a fossil record preserving only indirect evidence. Life history patterns in the closely related extant great apes are of particular importance for understanding the origin of hominin life history. Data on chimpanzees (*Pan troglodytes*) and

bonobos (*Pan paniscus*), above all, are often used in conjunction with human data to reconstruct the life history pattern of the *Pan/Homo* last common ancestor (LCA; e.g., Robson and Wood, 2008; Gurven, 2012; Kelley and Schwartz, 2012).

Two important female maturational events used in comparative life history analysis are age at menarche and age at first birth. These signal the end of the developmental period and the diversion of energy from growth to reproduction (Stearns, 1992; Charnov and Berrigan, 1993). The ages at which these milestones are reached are used to compare the length of the developmental period between species, and reviews comparing the age at first birth for chimpanzees and humans variously report that human ages exceed those of chimpanzees by 38–80% (or five to eight years; Schultz, 1969; Bogin, 1997; Robson and Wood, 2008; Gurven, 2012; Kelley and Schwartz, 2012). These data are often interpreted as being indicative of a lengthening of the developmental period in humans after the *Pan/*

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Homo split. However, a number of factors complicate the determination of maturational milestones in chimpanzees and bonobos for use in these comparisons. First, accumulating a sufficient sample size of known aged females requires the continuous observation of numerous females, from birth until ages of up to 25 years, to encompass the full range of variability in the age of first birth in chimpanzees and bonobos (and even longer for humans). Such records exist for some captive individuals, and several long-term studies of wild chimpanzees have now surpassed this length. Nevertheless, because most of these field studies have focused on only one social group, the number of known aged females reaching menarche is still small and no records of known aged bonobos have been published. The problem of sample size is greatly exacerbated for the determination of age at first birth in wild groups because of the dispersal patterns of *Pan* species (Kano, 1992; Tutin, 1994). In social primates, it is common for the members of one sex or the other to leave their natal group before breeding, at least partly as a mechanism to avoid inbreeding (Pusey and Packer, 1987). Unlike many primates, where males leave but females remain in their natal group, the common pattern in chimpanzees and bonobos is for females to leave their natal community around menarche and settle in new communities before breeding (Pusey, 1979; Kano, 1992; Boesch and Boesch-Achermann, 2000; Nishida et al., 2003; Reynolds, 2005; Kahlenberg et al., 2008; Langergraber et al., 2009). This means that unless more than one community is under observation, which is rarely the case, the majority of known aged females is lost to follow-up. However, across chimpanzee sites, some females remain and breed in their natal community for life. This proportion varies considerably from ~50% in the Kasekela community of Gombe National Park to less than 10% in most other studied communities (Pusey and Schroepfer-Walker, 2013). The small number of non-dispersing female chimpanzees at a few sites is, currently, the only source of data for accurate information on age at first birth in wild *Pan* populations.

A second problem concerns the treatment of right-censored data in calculating mean ages at menarche or first birth. In any prospective study, there will always be females for whom the interval between birth and the maturation milestone is completed (closed) and those in which the interval is still open (right-censored); that is, they have not yet experienced the milestone at the end of the study, or they were lost to follow-up through death or emigration. Failure to include right-censored intervals in calculations of the mean length of intervals introduces a systematic downward bias (Sheps and Menken, 1972; Galdikas and Wood, 1990; Jones et al., 2010), which will be particularly marked in studies of short duration with many right-censored intervals. Although techniques of survival analysis exist that handle right-censoring, the published data on chimpanzee age at menarche and first birth are based only on closed intervals. Because human datasets generally have larger samples sizes and are more likely to be retrospective, the proportion of intervals that are right-censored is much smaller. Thus, comparisons of published figures for the two species are likely to amplify the differences between them.

A third issue to take into account in choosing appropriate data for species comparisons is the extent and causes of variability in developmental rates and, hence, the age at which reproductive milestones are reached. It is well known from studies of non-human mammals (e.g., ring-tailed lemurs [Parga and Lessnau, 2005], long-tailed macaques [van Noordwijk and van Schaik, 1999], baboons [Bronikowski et al., 2002], chimpanzees [Tutin, 1994]) that rates of development are often greatly accelerated in captive, compared to wild, populations; an effect that is thought to be largely the result of access to a high quality, predictable diet (Sadler, 1969; Lee and Kappeler, 2003). An analogous pattern is also found in humans maturing in industrial societies compared to

those maturing in resource-limited societies (Bentley, 1999). For this reason, it is important to compare populations experiencing similar conditions in studies of life history evolution and, accordingly, in recent reviews, data from wild chimpanzee populations have been compared to data from modern hunter-gatherer and foraging populations (Robson and Wood, 2008; Gurven, 2012). More generally, measurement of the magnitude of variation in age at sexual maturity and examination of the factors influencing inter- and intra-population variability are important considerations when selecting the appropriate metrics for species comparisons and for understanding the selective forces in life history evolution.

Accurate data are available from a small number of female chimpanzees in Gombe National Park, Tanzania (Wallis, 1997), Mahale National Park, Tanzania (Nishida et al., 2003; Nakamura, 2015), the Kanyawara community in Kibale National Park, Uganda (Stumpf et al., 2009), and Bossou, Guinea (Sugiyama, 2004), where non-dispersing known aged females have been observed to sexual maturity, emigration, or first birth (summarized in Table 1). While studies are currently underway, little is known about maturation milestones in bonobos and values reported to date are derived from a small number of females with estimated ages. Nevertheless, the published data show little difference from wild chimpanzees except for the age at emigration (Furuichi, 1989; Kuroda, 1989; Table 1). Reported ages at first birth for non-dispersing female chimpanzees (~13 years) are undoubtedly low compared to the ages at which emigrants give birth. When assigning ages to immigrant females, based on the average age at emigration of known aged females and general body size and condition of immigrating individuals, researchers at Tai National Park, Ivory Coast, and Mahale estimated that immigrants give birth closer to age 14 years (Boesch and Boesch-Achermann, 2000; Nishida et al., 2003; Table 1). In Mahale, the difference in age at first birth in non-dispersing and dispersing females is estimated to exceed one year (Nishida et al., 2003), though this difference diminished when more data became available (Nakamura, 2015).

The timing of life history events varies, not only between species, but also between and within populations. Extensive investigation of human growth rates and the onset of reproduction reveals tremendous variation among traditional societies (Walker et al., 2006). Typically, humans raised under better environmental conditions (i.e., in areas of high food availability) grow faster and experience menarche and first birth earlier (Hill and Hurtado, 1996; Bentley, 1999), however, in some cases, accelerated maturation may also be associated with poor conditions and high mortality (Walker et al., 2006). This phenomenon has been best studied among modern humans, but non-human primates are subject to similar variation. In baboons, females mature faster in periods with more rainfall and when group size is smaller and competition is presumably alleviated (Altmann and Alberts, 2003; Charpentier et al., 2008). Maternal effects, especially dominance rank, also affect maturation rates in some primates. For example, in many cercopithecoid species (both in the wild and captivity), daughters born to higher ranking mothers tend to give birth earlier than those born to lower ranking mothers (Harcourt, 1987; Ellis, 1995; Pusey, 2012). In many primates, infants born to nulliparous mothers suffer high mortality due to a combination of factors including small maternal size, inexperience, and poor resource access (Bercovitch et al., 1998; Setchell et al., 2002; Pusey, 2012). In savannah baboons, first born infants are smaller than later born infants, a disadvantage that leads to a delay in age at sexual maturity (Altmann and Alberts, 2005). Overall, in female baboons, maternal and kin effects explain most of the variance in age at maturity (Charpentier et al., 2008).

Maturation milestones in chimpanzees are expected to be similarly affected by environmental and social conditions, but limited sample sizes have impeded such analyses. Nevertheless, substantial variation in maturation milestones and reproductive

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