



# The slow ape: High infant survival and long interbirth intervals in wild orangutans

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## ABSTRACT

Orangutans (*Pongo* spp.) are reported to have extremely slow life histories, including the longest average interbirth intervals of all mammals. Such slow life history can be viable only when unavoidable mortality is kept low. Thus, orangutans' survivorship under natural conditions is expected to be extremely high. Previous estimates of orangutan life history were based on captive individuals living under very different circumstances or on small samples from wild populations. Here, we combine birth data from seven field sites, each with demographic data collection for at least 10 years (range 12–43 years) on wild orangutans to better document their life history. Using strict criteria for data inclusion, we calculated infant survival, interbirth intervals and female age at first reproduction, across species, subspecies and islands. We found an average closed interbirth interval of 7.6 years, as well as consistently very high pre-weaning survival for males and females. Female survival of 94% until age at first birth (at around age 15 years) was higher than reported for any other mammal species under natural conditions. Similarly, annual survival among parous females is very high, but longevity remains to be estimated. Current data suggest no major life history differences between Sumatran and Bornean orangutans. The high offspring survival is remarkable, noting that modern human populations seem to have reached the same level of survival only in the 20th century. The orangutans' slow life history illustrates what can be achieved if a hominoid bauplan is exposed to low unavoidable mortality. Their high survival is likely due to their arboreal and non-gregarious lifestyle, and has allowed them to maintain viable populations, despite living in low-productivity habitats. However, their slow life history also implies that orangutans are highly vulnerable to a catastrophic population crash in the face of drastic habitat change.

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## 1. Introduction

Primates, and in particular Hominoidea, are characterized by a slow life history compared to other mammals (Stearns, 2000; van Schaik and Isler, 2012). They usually produce single offspring that mature slowly, have a late age at first reproduction (AFR) and a

relatively long lifespan. All hominids basically show slow life histories regardless of living conditions (Knott, 2001). Indeed, some recent studies that compared the life histories of wild chimpanzees and nomadic human foragers (e.g., Muller and Wrangham, 2014; Blurton Jones, 2016; Wood et al., 2017) concluded that the differences were much smaller than previously estimated (Hill et al., 2001).

Such slow development and low reproductive rates are viable only when the extrinsic risk of mortality is low throughout the lifespan (Stearns, 2000). In general, pre-senescence, 'unavoidable'

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mortality is mainly attributed to predation, starvation or disease. However, at present, we can only tentatively link varying unavoidable mortality to variation in life histories among the extant great apes (Knott, 2001). The observed faster life history of gorillas compared to chimpanzees (Knott, 2001; Bronikowski et al., 2016a, b) is correlated with folivory, although why (and even whether) folivory generally speeds up life-history pace is still unclear (Janson and van Schaik, 1993; Borries et al., 2013). One would expect orangutans and chimpanzees to be most similar among the apes, given their similar female body size as well as ecological similarity as extractively foraging frugivores, even though they occupy different geographic regions (Asia versus Africa). However, available evidence suggested that orangutans have slower life histories than chimpanzees and indeed all other primates (Knott, 2001; Wich et al., 2004, 2009a; Marshall et al., 2009b). In particular, orangutans appeared to have extremely long IBIs (interbirth intervals; e.g., Galdikas and Wood, 1990; Knott, 2001; Wich et al., 2004). Even when provisioned with a steady, predictable food supply and veterinary care, captive orangutan IBIs, at around 5.5 years (Anderson et al., 2008; Shumaker et al., 2008), tend to be longer than among other apes (Knott, 2001). However, sample sizes for orangutan life-history parameters under natural conditions have remained small (Wich et al., 2004), and here we revisit this preliminary conclusion based on a more extensive dataset.

Among the suggested reasons for this especially slow life history, low forest productivity may be most relevant (Knott, 2001, 2004). Compared to African forests, the fruit production in South-east Asian forests is lower (Terborgh and van Schaik, 1987). Lower productivity may translate into lower foraging yields, which in turn may constrain reproduction and growth (Pontzer and Kamilar, 2009). Forest productivity is also less predictable in Southeast Asia, with widely spaced periods of habitat-wide high peaks, so-called ‘mast-fruiting’, and multi-year periods of variable duration with very low fruit availability (Ashton et al., 1988; van Schaik and Pfannes, 2005; Hanya et al., 2011). The latter may lead to periods of severe scarcity (Knott, 1998), potentially resulting in increased unavoidable mortality. On the other hand, it has been argued that both very slow growth (Janson and van Schaik, 1993) and an extended period of low maternal nutritional support buffer against starvation of both mothers and ecologically less competent immatures (Janson and van Schaik, 1993; van Noordwijk et al., 2013).

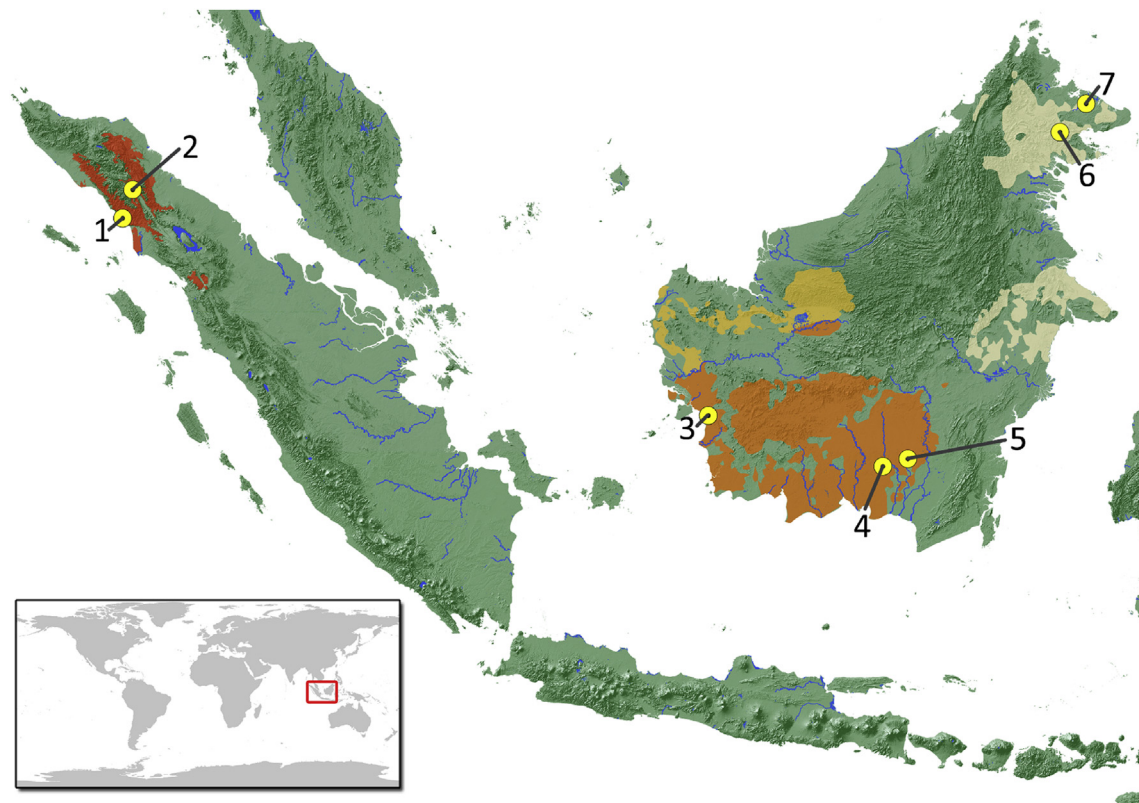
The lower food availability in Asia than Africa has also been suggested to impose a less gregarious life style on the Asian great apes (van Schaik, 1999; Wich et al., 1999). In addition, orangutans are much more arboreal than the African apes. Arboreality itself may reduce predation risk, a major source of unavoidable mortality, and therefore allow for an even slower life history, within both primates and mammals in general (van Schaik and Deaner, 2003). The combination of non-gregariousness and arboreality, in turn, may largely protect orangutans against transmission of contagious diseases, responsible for some immature deaths in chimpanzees (Kuehl et al., 2008; Hassell et al., 2017) and orphaned orangutans in rehabilitation centers (Galdikas and Ashbury, 2012; Kuze et al., 2012). It also limits exposure to soil-dwelling parasites, especially detrimental to younger animals, and transmission of primate and human diseases that were implicated as causal factors in the lower survival of orangutans at rescue centers (Mul et al., 2007; Foitova et al., 2009). Finally, arboreality may impose an additional burden on mothers who carry their offspring in the trees and need to constantly protect them against falling (e.g., Pontzer and Wrangham, 2004; Halsey et al., 2016), thus possibly further slowing down a mother's reproductive rate (Knott, 2001, 2004). For example, in human hunter-gatherers the cost of infant carrying is suggested to delay a mother's investment in a subsequent child (Blurton-Jones, 1986; Kramer, 1998).

To date, the net effect of all these potential factors on the Asian great ape's actual life history remains unknown. The goal of this paper is to present mostly new, very carefully vetted data on orangutan life history, specifically immature survival and birth intervals, and to explain the observed differences with the other hominids, particularly chimpanzees. We combine data from seven current long-term research sites with detailed demographic records (over at least 10 years) on regularly encountered females, for two study populations of Sumatran orangutans (*Pongo abelii*: Ketambe and Suaq Balimbing) and five Bornean populations (*Pongo pygmaeus wurmbii*: Gunung Palung, Sabangau, Tuanan, and *P. p. morio*: Danum Valley and Lower Kinabatangan). Despite many years of investment, for each site the sample size for known birth dates (within a month) remains small due to the inherent challenges of studying a non-gregarious wild primate. By combining our data, we provide the best-available evidence for the orangutans' extremely long IBIs on both islands as well as their extremely low infant mortality compared with all other apes, including most humans. Published data of smaller sample sizes suggested a gradient from west to east of decreasing interbirth intervals, which was interpreted to reflect higher mortality risks due to greater periodic fruit scarcity in (east) Borneo compared to (northwestern) Sumatra (e.g., Wich et al., 2004; van Schaik et al., 2009). Our larger dataset allows us to test whether there are differences in wild orangutan interbirth intervals, infant survival, and female age at first birth and thus in their life history by (sub-) species and geographical range.

## 2. Methods

We compiled data from the long-term orangutan field sites for which regular observations over at least 10 years were available (Fig. 1, Table 1). For *P. abelii*, long-term data are available from only two sites west of the Alas river (a genetically distinct population: Nater et al., 2013), in relatively productive forests (Marshall et al., 2009a). For Bornean orangutans, data could be included only for *P. p. wurmbii* from three locations and *P. p. morio* from two sites in Sabah.

For each site we classified births (Table 2) as ‘known’ when the birth date was known to within a month (based on sightings before and after birth), ‘estimated’ when birth dates were assessed with a margin of at most three months, ‘roughly estimated’ when birth dates could be assigned with at least six months accuracy and ‘very rough estimates’ when very young and dependent infants were assessed by experienced field workers to be less than three years old at first encounter. IBIs were classified as ‘known’ when both birth dates were ‘known’, as ‘estimated’ when both were at least ‘estimated’, and as ‘roughly estimated’ when both were at least rough estimates. No IBI was assigned if one of the birth dates was unknown. Age at first reproduction was classified by the same criteria. These criteria are stricter and more accurate than those used in previous publications. Unless otherwise noted, analyses were restricted to infants of known sex, to known, estimated and roughly estimated values, and to fully wild individuals only. This final criterion served to exclude some formerly re-introduced individuals and their descendants from analyses of the data on the Ketambe population. Sex ratio among immatures was measured as the proportion of males among the infants with at least a roughly estimated birthdate. Offspring are referred to as dependent (‘infant’) when they are still seen in nipple contact with the mother multiple times per day, presumably receiving at least some milk, and having the opportunity to do this at night by sharing the mother's night nest (van Noordwijk and van Schaik, 2005; van Noordwijk et al., 2013). Accordingly, we estimated final weaning (end of lactation), which was not systematically monitored in all



**Figure 1.** Location of study sites: *Pongo abelii* in 1. Suaq Balimbing and 2. Ketambe; *P. pygmaeus wurmbii* in 3. Gunung Palung, 4. Sebangau and 5. Tuanan; and *P. p. morio* in 6. Danum Valley and 7. Lower Kinabatangan.

**Table 1**  
Data collection period per field site.

| Island                               | Site                                            | Start data | Last data  | Max. span of study in months | Coordinating researcher |
|--------------------------------------|-------------------------------------------------|------------|------------|------------------------------|-------------------------|
| <b>Sumatra: <i>Pongo abelii</i></b>  |                                                 |            |            |                              |                         |
| <i>P. abelii</i>                     | Ketambe - reintro, Aceh tenggara <sup>a/b</sup> | 1972       | June 2015  | 516                          | Sri Suci Utami Atmoko   |
|                                      | Ketambe - wild, Aceh tenggara <sup>a</sup>      | 1972       | June 2015  | 516                          | Sri Suci Utami Atmoko   |
|                                      | Suaq Balimbing, Aceh selatan <sup>a</sup>       | Jan. 1994  | Sept. 1999 | 277                          | Carel van Schaik;       |
|                                      |                                                 | Jul. 2007  | Feb. 2017  |                              | Caroline Schuppli       |
| <b>Borneo: <i>Pongo pygmaeus</i></b> |                                                 |            |            |                              |                         |
| <i>P. p. wurmbii</i>                 | Gunung Palung, West Kalimantan <sup>a</sup>     | 1994       | 2003       | 252                          | Cheryl Knott            |
|                                      |                                                 | 2008       | June 2016  |                              | Cheryl Knott            |
|                                      | Sabangau, Central Kalimantan                    | 2003       | May 2016   | 156                          | Helen Morrogh-Bernard   |
|                                      | Tuanan, Central Kalimantan                      | June 2003  | Feb. 2017  | 164                          | Maria van Noordwijk     |
| <i>P. p. morio</i>                   | KOCP-Sukau                                      | 1998       | Dec. 2016  | 221                          | Felicity Oram           |
|                                      | Danum Valley, Sabah                             | 2004       | Dec. 2016  | 149                          | Noko Kuze               |

<sup>a</sup> Monitoring interrupted for multiple years due to external circumstances.

<sup>b</sup> Data only included in [SOM Table S2](#).

**Table 2**  
Classification criteria for infant birth dates and maternal stage.

| Infant birth date |                                                                                                                                  |                                                                                                                                             |
|-------------------|----------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| Class             | Accuracy                                                                                                                         | Criteria to assess birth date                                                                                                               |
| known             | within 1 month                                                                                                                   | mother known and observed before and after birth of offspring                                                                               |
| estim.            | within 3 months                                                                                                                  | mother known and observed before and after birth of offspring: "estimate"                                                                   |
| rough estim.      | within 6 months                                                                                                                  | mother known and observed before and after birth of offspring, or infant extremely young at first encounter of the mother: "rough estimate" |
| very rough estim. | within 1 year                                                                                                                    | estimated age for dependent offspring born before first encounter of mother, but estimated <3 y old: "very rough estimate"                  |
| unknown           | age & year guessed                                                                                                               | estimated age for dependent offspring born before first encounter of mother, but estimated at least 3 y old                                 |
| Maternal stage    |                                                                                                                                  |                                                                                                                                             |
| Class             | Criteria to assess maternal stage                                                                                                |                                                                                                                                             |
| young             | first offspring and <21 years - thus if first infant lost pre-weaning and second one born when <21 years, still counted as young |                                                                                                                                             |
| multiparous       |                                                                                                                                  |                                                                                                                                             |
| old               |                                                                                                                                  |                                                                                                                                             |
|                   | ≥21 years and 2nd - 4th birth                                                                                                    |                                                                                                                                             |
|                   | birth 5 or later and estimated >35 year                                                                                          |                                                                                                                                             |

populations or for all individuals, as the point in time when the immature started to sleep in its own night nest.

### 2.1. Pre-weaning mortality

Death of a known dependent offspring was assumed when the mother was seen for more than a full day without her unweaned offspring, and the immature was not later found to be alive. We measured the proportion of infants that survived at least until the birth of the younger sibling, or at least until the first offspring was completely weaned. However, in all known cases weaning preceded the birth of the next offspring. Thus our measure of pre-weaning mortality is conservative.

### 2.2. Interbirth intervals

These were calculated between live births if the first of these offspring survived at least to weaning. Right-censored IBIs (i.e., 'open', unfinished intervals in which no new infant was born yet) were calculated only when the current infant was alive at last sighting of the mother, but she had not yet given birth to her next offspring. The estimates ignore known or suspected pregnancy failures. In several cases females showed positive results on standard (locally available) human pregnancy tests, but failed to give birth to a healthy offspring. In the wild Ketambe population, two actual miscarriages with bloody tissue discharge were witnessed (Utami Atmoko pers. obs.). However, because it is impossible to systematically include such cases in all but extremely closely monitored populations, these data were not included in the analyses. Thus, as in other studies, we report IBIs between known infants only, and similarly, mortality rates for known infants only (e.g., Muller and Wrangham, 2014). Such estimates thus ignore potential perinatal mortality, which could have been missed since individuals were rarely followed every day. When a previous infant had died before weaning, we determined the interval until the next birth after the death of the unweaned offspring.

### 2.3. Maternal stage

For each birth and subsequent birth interval, mothers were classified (Table 2) based on their known reproductive histories and assessments based on visible body condition by the researchers: 'young' (when they had been known as adolescents before the birth of their first offspring and/or estimated to be <21 years old and thus having at most 1 living offspring), 'multiparous' (>21 years and 2<sup>nd</sup>–4<sup>th</sup> birth), or 'old' (birth 5 or later and estimated >35 years). The multiparous age class may include some older females whose older offspring was not recognized as such, had died or had disappeared from the study area. In particular, earlier male offspring of the older mothers may be missed, since in both orangutan species male offspring disperse before becoming reproductively active (Morrogh-Bernard et al., 2011; Arora et al., 2012; Nietlisbach et al., 2012; van Noordwijk et al., 2012). In addition, when no genetic parentage analyses were available, some earlier daughters may also not have been recognized as such and ignored in the reproductive history of the mother. Likewise, daughters of peripheral females who had settled outside the study area might have been missed. We therefore consider the assignment of females to the 'old' class as a minimum estimate.

### 2.4. Statistics

Since short intervals are more likely to be completed than longer ones within the limited duration of a study, the average or median value of completed IBIs and age at first reproduction would be

biased in favor of these shorter intervals. Therefore, we conducted survival analyses on all data (including right-censored data). To visualize IBIs, survivorship and age at first reproduction, we used the 'survival' package (Therneau, 2015a) for R (version 3.3.0, R-Core Team, 2016) to compute and plot Kaplan–Meier survival curves. To assess the probability of an event occurring in each of these three life-history parameters, we fitted Cox proportional hazard mixed-effects models to our observations on each of them, using the 'coxme' package (Therneau, 2015b).

For age at first reproduction, our initial, very strict, data-quality criteria left us with too few observations for even the simplest model to converge. Therefore, we report simple summary statistics for this life-history parameter in the Results section. For all descriptive statistics we report averages and standard deviations. IBI and survivorship could successfully be expressed as proportional hazard functions of subspecies (*P. abelii* vs. *P. p. wurmbii* vs. *P. p. morio*), infant sex, and maternal stage, while accounting for the hierarchical structure of our data by incorporating individual identity nested within study-site, nested within subspecies as random effects in the Cox models. Overall model performance was assessed by Likelihood Ratio Tests (LRT), comparing the fit of fully parameterized models to their respective null models (intercept and random structure only).

## 3. Results

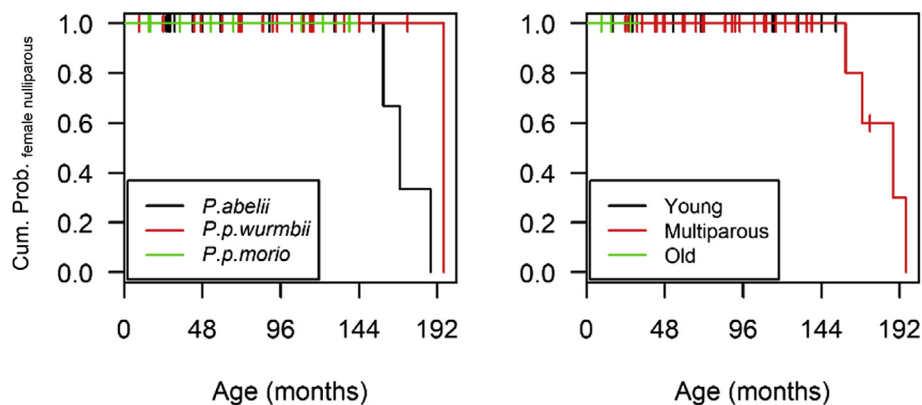
### 3.1. Age at first reproduction

Age at first reproduction (AFR) was calculated only if both the birth month of the female herself and the month in which she gave birth to a viable offspring for the first time were estimated with an accuracy of at least six months. Only four AFRs could be calculated based on these criteria, yielding an average of  $178.0 \pm 17.0$  months or 14.8 years ( $n = 3$  for Sumatra,  $n = 1$  for Borneo). If we also included very rough estimates, including females whose own birth year was estimated with a margin of >6 months (estimated when they were small, dependent immatures at first encounter with the mother – as was done in most of the previously published wild cases) AFR ranged from 152 to 196 months with an average of  $172.4 \pm 12.7$  months ( $n = 13$ ), with no apparent difference between the islands (Sumatra  $172.0 \pm 11.9$ ,  $n = 5$ ; Borneo  $172.6 \pm 13.9$ ,  $n = 8$ ; Welch's  $t$ -test:  $t_{9.74} = 0.086$ ,  $p = 0.933$ ,  $r = 0.028$ ).

A Kaplan–Meier survival analysis (Fig. 2) on all data from the seven sites, including 41 censored female ages and the four known AFRs, but excluding the very rough estimates, is consistent with a median age of first reproduction at around 14.5 years. Because sample size remains very small, no further statistics were calculated, but there was no clear difference between populations, subspecies or species (Supplementary Online Material [SOM] Table S1 for a Cox model fitted to the dataset based on less restrictive criteria of inclusion, and overview in SOM Table S5). Similarly, sample size is still too small to analyze possible other effects such as maternal age on a daughter's AFR.

### 3.2. Offspring sex ratio

Even though in the past the smaller samples from some sites seemed to indicate a biased sex ratio at birth, the current larger sample does not show either an overall bias or a difference between the islands. Among the 103 infants with known or closely estimated birth dates, the sex ratio was slightly male-biased on both islands (for Sumatra 13 f, 17 m, 1 unknown sex;  $n = 31$ ; for Borneo 33 f, 36 m, 3 unknown;  $n = 72$ ; Fischer exact tests on either the  $2 \times 3$  or  $2 \times 2$  contingency table – omitting the unknowns – are not significant:  $p = 0.928$  and  $p = 0.87$ , respectively). The sample sizes per



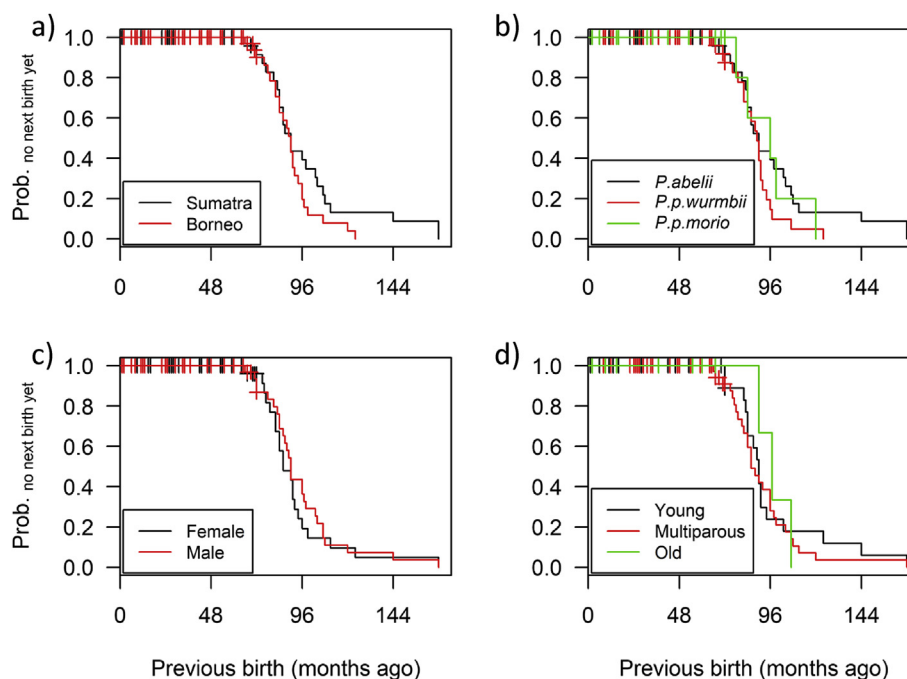
**Figure 2.** Kaplan–Meier curves for age of first reproduction (AFR),  $n = 45$  females (with birth date known within 6 months), including four females who gave birth for the first time and 41 who had not given birth by the end of the study (right-censored values). The right-hand graph shows there are too few completed AFRs to detect an effect of maternal age on her daughter's AFR.

site are still too small to test for any finer-grained geographic patterns. Young and old mothers may have more male offspring, but the differences were not significant (Fischer exact tests on either the  $2 \times 3$  or  $2 \times 2$  contingency table NS).

### 3.3. Interbirth interval after surviving infant

For the interval between live births in which the first offspring survives until weaning, the Kaplan–Meier curves and Cox proportional hazards models (Fig. 3; Table 3) show no significant differences between the islands, or subspecies (see also SOM Table S4 values per site). The mean overall IBI based on completely known intervals was  $91.5 \pm 23.7$  months or  $7.6 \pm 2$  years ( $n = 16$ ), whereas for the larger dataset, which includes estimated and roughly estimated intervals, the mean was  $93.7 \pm 21.4$  months or  $7.8 \pm 1.8$  years ( $n = 49$ ). Three females estimated to be over 45 years old, who had

successfully weaned their last offspring, apparently did not give birth to a subsequent offspring for at least 132, 168 and 180 months after the previous birth, respectively. None of the other open intervals with a reliably estimated start date was longer than 80 months and thus were all still within the range of observed closed intervals. The 'tail' in the Sumatran distribution of completed intervals seems to be longer, with three outliers of 12 years or more, suggesting exceptionally long IBIs could be more common there, although we cannot completely rule out early infant loss during this period. However, the average of the remaining Sumatran intervals ( $89.5 \pm 12.6$ ,  $n = 20$ ) was very similar to the Bornean intervals ( $89.4 \pm 13.4$ ,  $n = 26$ ; Welch's t-test:  $t_{42.24} = -0.017$ ,  $p = 0.987$ ,  $r = 0.003$ ). When the outliers are included the difference remains insignificant (Wilcoxon rank-sum test:  $W = 340$ ,  $p = 0.417$ ,  $r = -0.116$ ), and median values for Sumatra and Borneo (90.0 and 89.5 months, respectively, based on 23 vs. 26 values) were almost



**Figure 3.** Kaplan–Meier curves for interbirth intervals  $n = 99$ , with 49 completed intervals. a) Comparison between islands; b) Comparison between subspecies; c) Comparison of interbirth intervals after surviving male or female offspring; d) Comparison between females of different maternal stage. Note: Excluded from calculations were two old females without new offspring for >14 years since their last known one.

**Table 3**

Interbirth interval between live births: the Cox proportional hazards model shows no significant difference between subspecies (quadratic trend sequence *abelii-wurmbii-morio*) despite the longer 'tail' for the Sumatran orangutan (*P. abelii*). Similarly, there is no significant effect of infant sex. The (NS) quadratic trend for maternal stage indicates that multiparous females tend to have shorter interbirth intervals.

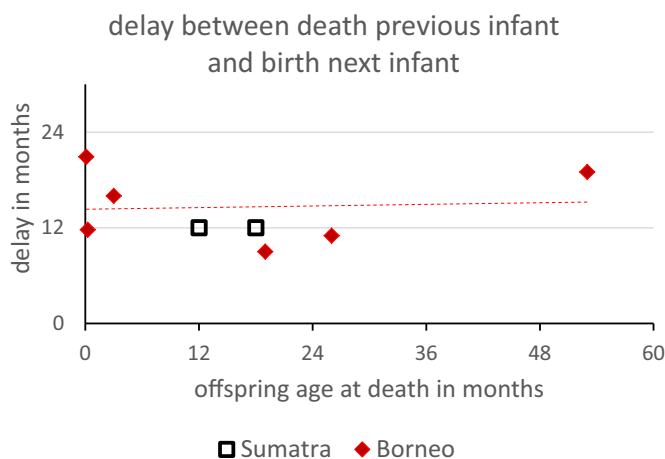
|                       | B      | se   | Hazard ratio (95% CI) | z     | p     |
|-----------------------|--------|------|-----------------------|-------|-------|
| <b>Subspecies</b>     |        |      |                       |       |       |
| Linear trend          | −0.320 | 0.76 | 0.726 (0.165–3.192)   | −0.42 | 0.670 |
| Quadratic trend       | −0.865 | 0.60 | 0.421 (0.131–1.354)   | −1.45 | 0.150 |
| <b>Infant sex</b>     |        |      |                       |       |       |
| Female                | —      | —    | —                     | —     | —     |
| Male                  | 0.140  | 0.52 | 1.151 (0.417–3.176)   | 0.27  | 0.790 |
| <b>Maternal stage</b> |        |      |                       |       |       |
| Linear trend          | −0.858 | 0.73 | 0.424 (0.101–1.771)   | −1.18 | 0.240 |
| Quadratic trend       | −0.890 | 0.49 | 0.411 (0.158–1.068)   | −1.82 | 0.068 |

57 females from 7 sites, belonging to 3 subspecies  $n_{\text{births}} = 99$ ,  $n_{\text{life-life IBI}} = 49$ ,  $\chi^2_{\text{LRT}} = 5.32$ ,  $p = 0.379$

identical. The birth interval after raising an infant to weaning seemed unaffected by offspring sex, but tended to be shorter for multiparous mothers (NS: Table 3). In some sites, conceptions appear more likely at the onset of irregularly spaced periods with superabundant fruit, leading to clustered births (e.g., Gunung Palung: Knott, 1999, 2001; Knott et al., 2009; Danum Valley: Kuze et al., unpublished data; Lower Kinabatangan: Oram, 2018). This might lead to more extremely short or long intervals, but so far this effect is not visible in the data.

#### 3.4. Interval after infant death

There were only eight cases in total to estimate the interval after the death of previous offspring until the birth of the next one (within at least a few months), which yielded an average of  $14.0 \pm 4.2$  months. Thus mothers tended to need approximately half a year to conceive again after the death of their previous, unweaned offspring (see Fig. 4: assuming an 8-months gestation: Sodaro et al., 2007). Because this interval was not affected by the age of the offspring at the time of death (Borneo only:  $r_s = -0.31$ , NS), time needed to 'recover' did not appear to be affected by the duration of their investment in the previous offspring or how close that offspring was to weaning.



**Figure 4.** Interval between death of an unweaned offspring and the next birth, in relation to the age at which the previous infant died. The linear trend for the Borneo data is indicated by a dashed line.

#### 3.5. Offspring survival

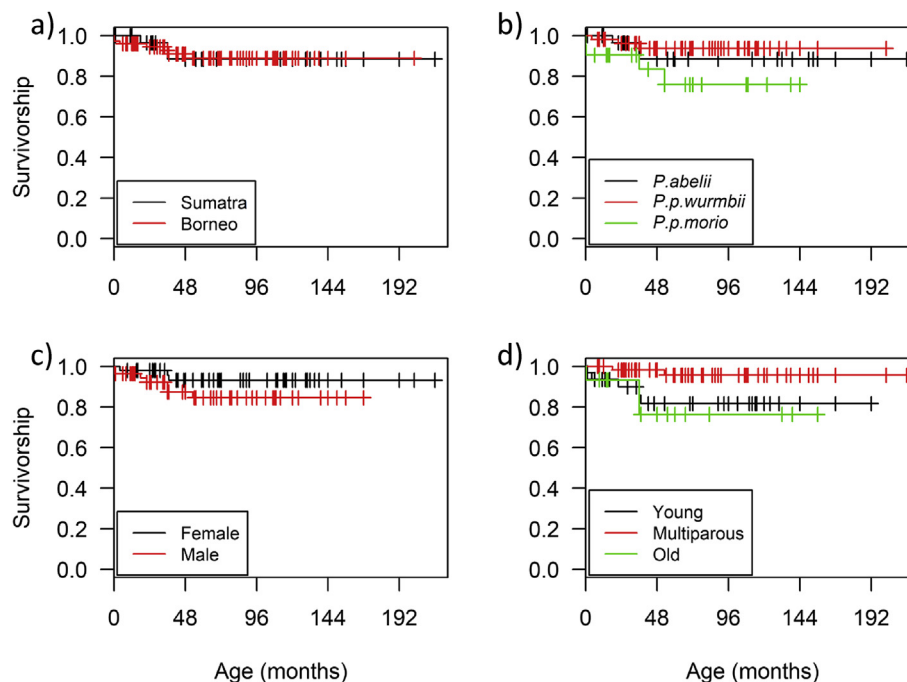
To estimate offspring survival, Kaplan–Meier survival analyses were performed including all offspring with known, estimated and roughly estimated birth dates and including those still alive at the end date of the study, or for infants, the last verified sighting of the mother (censored data). Fig. 5a shows the extremely high survivorship of infants with known birth month: 91% (combined males and females) survived to at least weaning age (see below) and even until at least 10 years of age. No deaths were reported for offspring between weaning and 15 years of age, although at least one juvenile, whose birth date could not be estimated reliably, died during the early years of study in Danum Valley (Kanamori et al., 2012). There was no statistically significant difference between Sumatra and Borneo (all sites combined) in pre-weaning survival, but pre-weaning survival in the two *P. p. morio* sites sampled in this study may have been lower (Fig. 5b; Table 4, SOM Table S5: subspecies difference). Overall there was a tendency for males to have slightly lower survival (Fig. 5c) up to age 10. Since males tend to roam widely and eventually disperse, starting at c. 10–15 years of age, the survival data beyond 10 years are more reliable for females. In our combined sample, offspring of multiparous mothers have a higher survivorship than those of young and old mothers (see methods for maternal age class criteria; Fig. 5d). However, note that survival up to 10 years for offspring of old mothers is still around 80%.

In most cases, the cause of death of an infant could not be determined (SOM Table S2). However, one early infant death (7–10 days) in the Lower Kinabatangan (Oram et al., unpublished data) was attributed to pulmonary edema. This infant had rapidly weakened between the initial sighting at 1–3 days of age to the second sighting at 6–9 days of age. This infant's experienced mother (this was her 5th known offspring – the older ones were genetically confirmed) seemed to be aware that something was not right as she spent a lot of time inspecting and repositioning the infant to try to help it nurse in ways she had not been observed doing with previous offspring, milk was noted to repeatedly leak out of the infant's mouth suggesting it could not swallow properly. This female subsequently gave birth to a healthy infant the following year.

In Danum Valley, a small but weaned immature (estimated >3 years old at first encounter – not included in current analyses) was found severely wounded a week before she succumbed to wound infection (Kanamori et al., 2012). This immature was already ranging alone after the birth of a younger sibling. The fatal wounds were consistent with an attack by a Sunda clouded leopard, *Neofelis diardi*, although it had not succeeded in killing the immature outright, despite the latter's relatively small size. Another apparent predator attack in Tuanan resulted in fatal injury to the mother but left the infant unharmed (SOM Table S2). In addition, in Kinabatangan two orangutan mothers, whose infants were playing nearby, have been observed to mob and chase a clouded leopard they had detected in the canopy (Oram unpublished data.). Male infanticide was suspected in one infant loss in Gunung Palung (Knott et al., unpublished data), but no other (suspected) cases have been reported in the wild.

#### 3.6. Comparative survival

Since ages of most adult females are not known, we cannot yet construct a complete life table. However, in all sites adult female deaths are very rare. For the Tuanan resident females (>15 years of age), for instance, only two, both estimated to be >35 years old, have disappeared (and were confirmed dead: Marzec et al., 2016) in 146 adult female years, for an average yearly mortality rate of <1.5%.



**Figure 5.** Kaplan–Meier curves for survival of immatures: a) Comparison between islands; b) Comparison between subspecies; c) Comparison of male or female offspring; d) Comparison of offspring of females of different maternal stage. 108 individuals from seven sites, belonging to three subspecies.

**Table 4**

Cox proportional hazards model of offspring survival. The subspecies quadratic trend is based on sequence *abelii-wurmbii-morio*, suggesting somewhat higher survival for *wurmbii* than either *abelii* or *morio*. Similarly, offspring of multiparous females have higher survival than either young or old mothers. No significant difference between males and female infants in survivorship.

|                       | B     | se   | Hazard ratio (95% CI) | z    | p     |
|-----------------------|-------|------|-----------------------|------|-------|
| <b>Subspecies</b>     |       |      |                       |      |       |
| Linear trend          | 1.101 | 0.61 | 3.006 (0.910–9.930)   | 1.81 | 0.071 |
| Quadratic trend       | 1.198 | 0.60 | 3.314 (1.018–10.785)  | 1.99 | 0.047 |
| <b>Infant sex</b>     |       |      |                       |      |       |
| Female                | –     | –    | –                     | –    | –     |
| Male                  | 1.384 | 0.77 | 3.990 (0.853–18.648)  | 1.76 | 0.079 |
| <b>Maternal stage</b> |       |      |                       |      |       |
| Linear trend          | 0.031 | 0.53 | 1.031 (0.364–2.920)   | 0.06 | 0.950 |
| Quadratic trend       | 1.796 | 0.70 | 6.027 (1.520–23.905)  | 2.56 | 0.011 |

108 individuals from 7 sites, belonging to 3 subspecies  $n_{\text{individuals}} = 108$ ,  $n_{\text{deaths}} = 10$ ,  $\chi^2_{\text{LRT}} = 14.21$ ,  $p = 0.014$

Our data from the seven sites do allow for a comparison of female survival from birth up to 15–18 years of age with data on captive orangutans (Wich et al., 2009a), wild chimpanzees (Kanyawara: Muller and Wrangham, 2014; Ngogo: Wood et al., 2017), wild gorillas (Bronikowski et al., 2016b), and traditional human societies (Hadza: Blurton-Jones, 2016; combined survival up to 15 years in 13 small-scale human societies: Walker et al., 2006) (Fig. 6; Table 5). We also added the female survival data of the current human female population of Switzerland (Human Life-Table Database, <http://www.lifetable.de>; see also SOM Table S3). Actually, the Swiss girls fall within the 95%-CI of wild orangutan females, so although survival of the former is higher, this difference is not statistically significant given the uncertainty around our estimate for wild orangutans. To broaden the perspective, we also included the survival data for female Amboseli elephants (Lee et al., 2011), which have a similarly slow life history, with IBIs (4–5 years) in the same range as chimpanzees (Moss and Lee, 2011). Even though early elephant survival rates are higher than all

chimpanzees and hunter-gatherer populations (Fig. 6), they still have lower immature survival values than wild orangutans in our sample.

## 4. Discussion

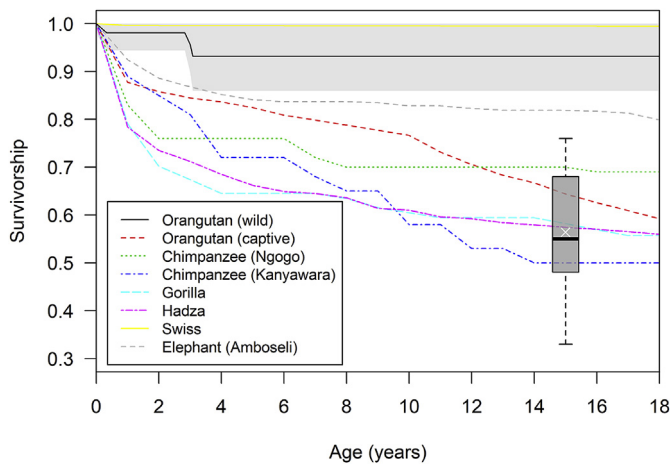
### 4.1. Orangutan life history

Despite several decades of field research, only a few orangutan females are known from birth to their AFR. The average AFR of 14.8 years for the four known cases is only half a year higher than when an additional nine females, with (mostly very roughly) estimated ages, are included: 14.3 years. Thus, earlier estimates of AFR at 14–15 years of age (Knott, 2001) were confirmed in our combined dataset. Studies covering at least 20 consecutive years will be

**Table 5**

Orangutan female life-table (0–18 years).

| Age (years) | Enter | Censored | Dead | At Risk | $q_x$  | $p_x$  | $l_x$  |
|-------------|-------|----------|------|---------|--------|--------|--------|
| 0–1         | 52    | 1        | 1    | 51      | 0.0196 | 0.9804 | 1.0000 |
| 1–2         | 50    | 3        | 1    | 47      | 0.0213 | 0.9787 | 0.9804 |
| 2–3         | 46    | 6        | 1    | 40      | 0.0250 | 0.9750 | 0.9595 |
| 3–4         | 39    | 5        | 1    | 34      | 0.0294 | 0.9706 | 0.9355 |
| 4–5         | 33    | 3        | 0    | 30      | 0.0000 | 1.0000 | 0.9080 |
| 5–6         | 30    | 6        | 0    | 24      | 0.0000 | 1.0000 | 0.9080 |
| 6–7         | 24    | 0        | 0    | 24      | 0.0000 | 1.0000 | 0.9080 |
| 7–8         | 24    | 4        | 0    | 20      | 0.0000 | 1.0000 | 0.9080 |
| 8–9         | 20    | 1        | 0    | 19      | 0.0000 | 1.0000 | 0.9080 |
| 9–10        | 19    | 6        | 0    | 13      | 0.0000 | 1.0000 | 0.9080 |
| 10–11       | 13    | 4        | 0    | 9       | 0.0000 | 1.0000 | 0.9080 |
| 11–12       | 9     | 3        | 0    | 6       | 0.0000 | 1.0000 | 0.9080 |
| 12–13       | 6     | 1        | 0    | 5       | 0.0000 | 1.0000 | 0.9080 |
| 13–14       | 5     | 2        | 0    | 3       | 0.0000 | 1.0000 | 0.9080 |
| 14–15       | 3     | 0        | 0    | 3       | 0.0000 | 1.0000 | 0.9080 |
| 15–16       | 3     | 1        | 0    | 2       | 0.0000 | 1.0000 | 0.9080 |
| 16–17       | 2     | 1        | 0    | 1       | 0.0000 | 1.0000 | 0.9080 |
| 17–18       | 1     | 1        | 0    | 0       | 0.0000 | 1.0000 | 0.9080 |



**Figure 6.** Comparative survival until 18 years among female great apes and modern human populations. The box plot with median (bar) and mean (x) values at 15 years is based on the average survivorship in 13 small-scale societies taken from Walker et al. (2006). The orangutan curve is surrounded by its confidence limits.

Sources: orangutan (wild) - this study; orangutan (captive) - Wich et al., 2009a; Swiss population - Schweizerische Bundesamt für Statistik, 2017; Hadza - Blurton-Jones, 2016; Ngogo chimpanzees - Wood et al., 2017; Kanyawara chimpanzees - Muller and Wrangham, 2014; gorilla - Bronikowski et al., 2016a, b.

needed to test whether there are systematic differences between populations, or what conditions affect relatively early or late AFRs.

Our dataset on IBIs with a median of 7.5 years confirms the long mean interbirth interval reported based on earlier, smaller samples (Galdikas and Wood, 1990; Knott, 2001; Wich et al., 2004). Pregnancy failure affects IBIs, and we recorded multiple cases of suspected pregnancy, based on human pregnancy tests and/or labial swelling (which appear within weeks of conception: Sodaro et al., 2007). For example, in 20% (three of 15) of the suspected pregnancies in Tuanan, the female was later seen before the expected due date but no longer pregnant and receiving renewed male sexual interest. In addition, two miscarriages of bloody tissue without the shape of a full-term infant were witnessed in Ketambe, and in most other sites pregnancy failure was suspected at least once. Early pregnancy loss is a common phenomenon in humans as well (10–20% after the first month of gestation: Avalos et al., 2012) and often related to fetal abnormalities. The frequency in orangutans appears to be in the same range, but early fetal loss and later miscarriage are hard to document under field conditions. There is little indication that pregnancy failures were due to poor condition (cf. Brockman and van Schaik, 2005). For example, in Tuanan, all three females known to be pregnant before the onset of the long period of Kalimantan-wide haze due to fires in 2015, subsequently gave birth to healthy infants.

Interbirth interval estimates are systematically overestimated when early infant mortality is missed. Since many females in this dataset were seen irregularly and certainly not on a monthly basis, this possibility must be examined. Reassuringly, among the known births the calculated mortality during the first three months was very low (only two in 66 known births and 0 in 38 births with estimated birth dates and 1–3 months of age), suggesting early mortality is quite low, and thus our estimates are largely unbiased. Hassell et al. (2017) found that in wild mountain gorillas early infant mortality attributable to fetal and developmental problems is around 10% of all mortality up to 3.5 years. However, even if we assume a similar value for early mortality in orangutans, i.e., if we had missed an extra 10% of early infant mortality in our field data because observations were intermittent, the infant survival rate would still be considerably higher in the orangutan sample than reported for any other apes or pre-industrial human populations.

In our compilation of data on life history parameters we found not only a very high infant survival rate (94% for female and 87% for male infants up to weaning), but we also did not record any mortality among females known since weaning until AFR across all sites, and only one instance in the larger sample of known individuals. Similarly, males have high survival rates during their early post-weaning years, after which their disappearance from the study sites may be due to dispersal rather than death. We did not find evidence for increased mortality around or following weaning (as in some chimpanzee populations: Hill et al., 2001), suggesting offspring have sufficient ecological competence at the time of weaning (van Noordwijk and van Schaik, 2005; Schuppli et al., 2016).

Earlier studies suggested (west-) Sumatran orangutans (*P. abelii*) have an even slower life history than the Bornean orangutans (*P. pygmaeus*), with the population of *P. p. morio* having the fastest life history (Wich et al., 2004; van Schaik et al., 2009). In our larger dataset, although still small compared to other primate species, we found no evidence for systematic differences in interbirth intervals between the study populations. This was true for all other life history parameters as well, with the possible exception of slightly higher infant mortality in *P. p. morio*. This lack of life history differences between Sumatran and Bornean orangutans was also reported in studies of captive orangutans that either found no inter-island difference in IBI, AFR or infant mortality (Cocks, 2007b; b; Anderson et al., 2008; Wich et al., 2009a) or the opposite of the early wild data (Anderson et al., 2008).

Adult female life tables cannot be constructed yet, but available evidence (Wich et al., 2004; Marshall et al., 2009b; Tuanan data) suggests adult female yearly mortality rate during most of the lifespan is <2%. Longevity remains unknown, but is likely to be more than 50 years, although very old females appear to range less widely and become more solitary, at least at Tuanan (van Noordwijk et al., unpublished data). Indeed, we found that middle-aged (multiparous) females tended to have shorter interbirth intervals and had higher infant survival than either primiparous or old females. This pattern mirrors that found in many other species (van Noordwijk and van Schaik, 1999; Lee et al., 2016; Bronikowski et al., 2016a).

In sum, current evidence suggests an age at first reproduction of nearly 15 years, infant survival until weaning of around 90% and a mean IBI of around 7.6 years for all wild orangutans. Clearly, more detailed comparisons at the population level are warranted, but we should not expect these taxon-level averages to change much in the future.

#### 4.2. Causes of mortality

All unweaned offspring that disappeared were assumed dead, but the cause was usually not established (SOM Table S2) because bodies were rarely found. In most cases, the infant looked healthy when last sighted shortly before disappearance. Since mothers usually conceived again within half a year from when their pre-weaned offspring had died, malnourishment or poor maternal condition was an unlikely cause in most cases reported here. Respiratory or other contagious diseases are often associated with both infant and adult mortality in the more gregarious and terrestrial chimpanzees (Kuehl et al., 2008; Wood et al., 2017) and gorillas (Hassell et al., 2017), but there is no evidence for this in wild orangutans.

Predation, though rare, is not absent (see SOM Table S2). The observed case of mobbing of a clouded leopard in Kinabatangan (Oram, unpublished data) was very similar to witnessed mobbing by other arboreal primates (e.g., gibbons and langurs: Wilcox et al., 2016). This suggests that clouded leopards are an important threat

for immatures; indeed, they are known to kill orangutans in rescue sites (Rijksen, 1978; Phillipps and Phillipps, 2016). Even though male infanticide is a frequent cause of early death in chimpanzees and gorillas (overview in Palombit, 2012; Hassell et al., 2017), we know of only one suspected case of infanticide in wild orangutans (Knott et al., unpublished data) and one known case in captivity (Mallinson, 1984). Although it is generally assumed that male orangutans, especially in Borneo will not consistently benefit from infanticide (Beaudrot et al., 2009; van Schaik, 2016), females were found to conceive within six months after the loss of their infant on average (Fig. 4), so males might derive a fitness benefit from killing infants.

Unlike in chimpanzees and gorillas (Hassell et al., 2017; Wood et al., 2017), by elimination, we suggest that the most likely cause of death for pre-weaning orangutans may well be accidents, such as falls from the canopy either during social interactions, solitary play or travel. Although such falls were frequently observed, we do not have hard evidence so far on fatal outcomes. Similarly, in our comparison with the species with the next lowest infant mortality, African elephants, 'accidents' are recorded as a major cause of death of young calves, in addition to mortality due to poor nutrition and predation (Moss and Lee, 2011), whereas disease does not seem to play a major role. In this long-lived species, living in matrilineal herds, the protection provided by maternal relatives contributes to the calves' early high survival.

In conclusion, wild orangutans appear to have largely eliminated contagious disease and starvation, and strongly reduced predation and, probably, infanticide as causes of immature mortality, leaving accidents as the most common, albeit still rare, cause.

#### 4.3. Plasticity versus maladaptation

Studies of reproductive ecology suggest that in primates, including humans and chimpanzees, higher energy availability leads to earlier AFR and shorter IBIs (Ellison et al., 1993; Knott, 2001; Emery Thompson, 2013). Orangutans likewise speed up growth and reproduction when food is more reliably available (Knott et al., 2009). Provisioned rehabilitant orangutans on both islands are reported to give birth several years earlier than wild ones (Galdikas and Ashbury, 2012; Kuze et al., 2012). Mothers in captivity tend to have IBIs two years shorter (Cocks, 2007a; b; Anderson et al., 2008) than the median IBI of 7.5 years (this study) found for wild orangutans, even when the previous offspring was housed continuously with its mother (Shumaker et al., 2008). Both earlier AFR and shorter IBIs suggest a strong effect of physical condition and health, and possibly social (and management) conditions, on these reproductive parameters (Knott, 2001). This suggests high plasticity in the rate of development and reproduction in orangutans.

Among mothers in rehabilitation centers, infant mortality (at 18–61%) was found to be much higher than in the wild, which was attributed to poor mothering skills, increased rates of disease transmission in high-density release sites with fixed feeding locations (Kuze et al., 2012), and high parasite prevalence accompanying high use of the ground around the feeding sites (Foitova et al., 2009). However, infant mortality rate in zoo-housed orangutans is similarly high (Cocks, 2007b). Thus, despite nutritional advantages, veterinary care and freedom from predation in captivity and rescue centers, infant mortality is much lower in the wild (Fig. 6).

Although mean survivorship has generally increased significantly for orangutans in captivity since 1965, and some individuals are known to be over 50 years old, median survival of captive-born maternally raised Sumatran (*P. abelii*) females was calculated to be only 24.6 years (based on international studbook data since 1986: Wich et al., 2009b). In another comprehensive captive study, the

age at last reproduction was found to be 41 years (Shumaker et al., 2008). To date, good longevity and life time reproductive records of wild orangutans are still scarce, but in all populations under long-term observation in this study, females in their mid-to-late 30s are well documented and at least some females are known to be reproducing well into their mid-to-late 40s.

The discrepancy between reproductive parameters, such as AFR and IBI, under natural vs. 'human-enhanced' conditions suggests a shift in resource allocation when an individual grows up without experiencing scarcity. However, there are indications that plasticity allowing accelerated maturation (early AFR) and increased reproductive rate (shorter IBIs) involves a life-history tradeoff. The relatively high infant mortality reported in rescue centers and zoos holds especially for second-generation primiparous mothers with very early AFR (<12 years old) (Cocks, 2007b; Galdikas and Ashbury, 2012). Moreover, zoo-housed females with shorter IBIs tend to die at a younger age (Cocks, 2007b). All this suggests that the observed response to superabundant food conditions is actually maladaptive. Apparently, such conditions are so far outside the natural range in extent and duration that natural selection did not need to cap the open-ended response to improved conditions. Similar negative consequences of deviations from the average life history pattern have also been reported for other long-lived species with slow life history (e.g., red deer: Nussey et al., 2006, elephants: Hayward et al., 2014; and humans: King, 2003; Hayward et al., 2015). This finding has obvious and important implications for captive management.

#### 4.4. Orangutans and chimpanzees compared

The new results on both orangutans and chimpanzees (Muller and Wrangham, 2014; Wood et al., 2017) suggest similar life-history variables, but with a consistent difference: orangutans are slower. Orangutan IBIs are longer (7.5 years versus 5–6 years: Watts, 2012), indicating higher reproductive effort. AFR is later at 14.8 years, especially when compared with the chimpanzee females that breed in their natal community (c. 13.5 years; Walker et al., 2018). Although this is not the modal situation in chimpanzees, it is actually the more meaningful comparison of growth and development with the female-philopatric orangutan because delays due to dispersal do not reflect unconstrained energetic allocation. Finally, the very high adult female survival in orangutans (this study, see also Wich et al., 2004) relative to most chimpanzee populations (Muller and Wrangham, 2014; Wood et al., 2017) is consistent with delayed senescence in orangutans. Thus, orangutans are simply slower than chimpanzees.

This slowdown in orangutan life history is consistent with the rarity of observed disease or predation in wild populations, since it suggests that conservative growth, development and reproduction could actually pay off in improved survival. The very conservative reproductive investment may reflect the need to deal with fluctuating food abundance (Knott, 2001), including multiple periods of food scarcity during the years of extended lactational effort (van Noordwijk et al., 2013). The arboreal lifestyle limits opportunities for fat storage to buffer fluctuations in food intake (Heldstab et al., 2017), which further contributes to the risk of maternal energy depletion in orangutans (Knott, 2001; Knott et al., 2009). The slowdown also enables the hypometabolism found in orangutans (Pontzer et al., 2016). The extreme conservatism in growth may explain the remarkable near-absence of any starvation-induced mortality, even during extended periods with extremely low food abundance. If conceptions are more likely during increasing fruit abundance, one may expect a strong influence of food scarcity on maternal condition and thus infant survival. Yet, mortality rates were equally low at sites that experience irregular mast-fruiting

and sites with less extreme variation and higher fruit abundance, e.g., Suaq Balimbing. In addition, even during the extended period of fruit scarcity in Tuanan following the fires and Kalimantan-wide severe haze for c. three months in 2015 (unpublished data), no known immatures were lost and three infants born during the post-haze scarcity period all survived at least their first year of life.

Overall, then, the chimpanzee is the faster ape because it is more terrestrial and more gregarious. The orangutan's extreme arboreality and low gregariousness protects it from the threats of predation and spread of contagious diseases that affect the more terrestrial hominids. Because terrestriality is obviously a derived trait in great apes, given its morphology adapted to below-branch arboreal locomotion (Thorpe and Crompton, 2006), the orangutan may actually reflect the ancestral great ape state. This speculation is supported by the remarkably slow life history of the relatively very small, but exclusively arboreal gibbons, with IBIs of c. 3.5 years and an AFR of 11 years (Reichard and Barelli, 2008), in the gorilla range.

#### 4.5. Implications for human evolution

Orangutan life history illustrates how the basic hominoid bauplan can give rise to extremely slow life histories when conditions enable very low unavoidable mortality. Paradoxically, low habitat productivity may have enforced a near-solitary lifestyle, which in combination with arboreality, allows orangutans to largely avoid both predation and contagious diseases. In contrast, most likely, modern humans only reached similar or higher survival probabilities than female orangutans in the 20th century (SOM Table S3). Even though pre-contact hunter gatherer populations may have suffered much lower mortality due to disease (Curven and Kaplan, 2007), all current populations represented in Fig. 6 fall outside the confidence limits for orangutans from c. six months of age onward.

Although ape longevity remains only crudely estimated, we can now see why humans differ from the basic hominoid pattern. First, extensive allomaternal care allowed for shortened IBIs (Knott, 2001; Robson et al., 2006; Kramer and Ellison, 2010; van Schaik, 2016). Second, weaponry and cooperative defense reduced unavoidable mortality due to predation, despite a fully terrestrial lifestyle, allowing longevity to be maximized (Isler and van Schaik, 2012). Third, very low densities (Kelly, 2013) ensured low mortality due to infectious disease (Black, 1975). Finally, development slowed down due to the strong increase in brain size and the resulting competition for energy during development (Isler and van Schaik, 2012; Kuzawa et al., 2014).

#### 4.6. Concluding remarks

Before getting overly optimistic about the orangutans' ability to survive in low-productivity forest thanks to their extremely slow life history, it should be remembered that our long-term study sites are situated in some of the best remaining larger forest areas, despite a selective logging history in some sites, and border areas with increasing disturbance for most sites. Orangutans living in smaller remnant forest patches are unlikely to achieve these high survival rates found in larger and rather undisturbed forests. Their exceptionally slow life history leaves orangutans vulnerable to unfettered anthropogenic change (such as hunting and habitat loss due to land conversion; Marshall et al., 2009b), which may affect health and infant and maternal survival. Such effects could result in catastrophic population crashes, but the ability of adults to endure periods of starvation (perhaps especially in Borneo: Vogel et al., 2012) may mean these crashes are not numerically visible until it is too late.

The data presented here are still modest, especially with respect to longevity. The big differences in reproductive timing between

wild and captive orangutans illustrate that it is important to collect long-term data on natural populations to gain an understanding of their life history (Borries et al., 2013). This should further increase our motivation to protect and enable healthy populations of great apes to survive in their natural habitats.

#### Declarations of interest

None.

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## Supplementary Online Material

Supplementary online material related to this article can be found at <https://doi.org/10.1016/j.jhevol.2018.09.004>.

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