


Predictors and consequences of gestation length in wild chimpanzees

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Abstract

Objectives: Energetics are widely recognized to influence timing of birth in humans and other eutherian mammals, yet considerable variation exists in the relationship between energetic constraints and gestation length. In humans, poor nutrition and short inter-gestational intervals (IGIs) are associated with shorter gestations. In other mammals, lower energy availability is usually associated with longer gestations. We investigated the predictors of gestation length, and the impact of gestation length on offspring survival, in chimpanzees, humans' closest living relatives.

Materials and Methods: We used 50 years of demographic and behavioral data to estimate gestation lengths in the wild chimpanzees of Gombe National Park, Tanzania, and then used ecological and demographic data to explore the predictors and consequences of gestation length in our sample.

Results: Gestation lengths were shorter for females in their early 30s (relative to younger and older females), and after short IGIs. Other predictors potentially associated with maternal energetic condition and maternal investment were not associated with gestation length. We also found that shorter gestation lengths corresponded to lower offspring survival.

Discussion: Like humans, chimpanzees had shorter gestations after short IGIs, and short gestations were associated with higher offspring mortality. We consider competing explanations for the conflicting relationships between energetics and gestation length across eutherian mammals in light of these results.

KEYWORDS

chimpanzee, energetics, gestation length, life history, offspring survival

1 | INTRODUCTION

Life history theory is the study of how organisms are selected to allocate their energy throughout their lives, and how energetic trade-offs shape the timing of growth, development, reproduction, and even death (Charnov, 1991; Trivers, 1974). Every individual mammal must

survive the first life history events of gestation and birth in order to achieve any level of fitness (Brown et al., 2013). Gestation length is the least variable of female reproductive parameters, suggesting a strong evolutionary constraint on the duration of pregnancy (Gesquiere et al., 2018), and in humans, unusually short or long gestations are associated with higher offspring mortality (Hilder et al., 1998).

Anthropologists long argued that fetal head size and the shape of the maternal pelvic outlet pose an “obstetric dilemma” that places an

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upper limit on gestation length (Krogman, 1951; Rosenberg & Trevathan, 2002; Washburn, 1960), especially because newborns appear maladaptively altricial, and because mother and offspring can suffer injury or death during parturition (Wittman & Wall, 2007). The obstetric dilemma hypothesis argues that the uniquely difficult process of human birth (Wittman & Wall, 2007) is offset by selection for efficient bipedal locomotion, forcing the pelvis to remain narrow. Babies must therefore be born before their heads grow larger than the birth canal.

While obstetric constraints may place an upper limit on human gestation, more recent analyses suggest that energetic constraints are primarily responsible for the timing of human birth (Dunsworth et al., 2012). The metabolic crossover hypothesis (Ellison, 2001) argues that parturition is initiated when fetal energetic demand outpaces maternal supply. Indeed, across eutherian mammals, maternal energetic availability affects gestation length (Racey, 1981), although the direction of the relationship between maternal energy supply varies among species. In some, maternal energy restriction can lead to shorter gestation, as mothers in poor health or with limited access to resources deliver earlier as fetal energetic stress increases (Bloomfield, 2011). More commonly, maternal energy restriction appears to lead to slower fetal growth and therefore longer gestation (Racey, 1981).

Here we investigate the factors influencing gestation length, and the effect of gestation length on offspring survival, in chimpanzees, one of humans' two closest living relatives. We used over 50 years of data on sexual swellings, urinary pregnancy tests, and observed births from two habituated chimpanzee (*P. t. schweinfurthii*) communities in Gombe National Park, Tanzania, to produce the largest sample of chimpanzee gestation lengths measured in the wild. This sample permits exploration of the predictors and consequences of gestation length under natural conditions, which has not been possible with samples from captivity or more restricted samples from the wild. It therefore presents an opportunity to place human gestation in evolutionary context using data from our closest living relative.

We first investigated the effects of variables associated with maternal nutrition and energy balance on chimpanzee gestation length. Chimpanzee neonates pass easily through the birth canal (Rosenberg & Trevathan, 2002), and have slightly smaller brains at birth relative to adult female body mass than expected based on the overall primate pattern (DeSilva & Lesnik, 2008; Dunsworth et al., 2012), removing potential obstetric and nutritional constraints on longer gestation. We therefore predicted that gestation length will increase when maternal energy availability is low.

We considered several variables potentially associated with maternal condition: First, seasonal changes in diet have been identified as covariates of energetic status in wild female chimpanzees (Emery Thompson et al., 2012; Emery Thompson et al., 2009; Emery Thompson & Wrangham, 2008; Wallis, 1995). Second, high-ranking females are likely to be in better condition in Gombe (Pusey et al., 2005). Third, provisioning with bananas, which occurred during some of the study period, may have increased female energy balance (Goodall, 1986; Wilson, 2012). Finally, in chimpanzees, lactation

imposes an energetic strain that decreases as the infant matures (Bădescu et al., 2017; Emery Thompson et al., 2012), so females with longer intervals since their previous birth may have more energy available to gestate their next offspring. Alternatively, because both resumption of cycling and subsequent pregnancy are hastened by maternal energy gain (Emery Thompson & Wrangham, 2008; Emery Thompson et al., 2012), shorter inter-gestational intervals (IGIs) may instead be indicative of better maternal energetic status. We thus explored the relationship between IGI and gestation length.

We also investigated whether gestation length was influenced by variables potentially associated with maternal investment. First, maternal age could influence investment if the youngest mothers were still investing in somatic growth (Pusey et al., 2005), or via terminal investment by the oldest mothers (Pianka & Parker, 1975; Trivers, 1972; Williams, 1966). Second, female chimpanzees appear to invest more in male than female offspring at some stages of development (Bădescu et al., 2022; Murray et al., 2014), although it is not known if this investment could include gestation length.

Finally, we tested whether gestation length predicted offspring survival. In humans, unusually short and long gestations are associated with higher offspring morbidity and mortality (Hilder et al., 1998). If energy shortfalls constrain gestation lengths in chimpanzees, unusual gestation lengths should be associated with higher offspring mortality.

2 | MATERIALS AND METHODS

2.1 | Study site

Observation of chimpanzees at Gombe began in 1960 in the central community (later called Kasekela). In 1963, a central feeding station was established which individuals visited almost daily by the mid-1960s; after 1968 the feeding regimen was adjusted in an attempt to minimize disruption to chimpanzees' natural feeding behavior, and by 1969 individuals were generally fed once every 10 days (Wrangham, 1974). Under this system, when fed, individuals generally received between one and 15 bananas (Goodall, 1986; Wrangham, 1974). All data used in the current analysis were collected after these adjustments to the provisioning system. A permanent feeding station was established in the northern Mitumba community by 1990. Provisioning in both communities was discontinued in 2000 (Wilson, 2012).

In 1973, researchers began conducting near-daily follows of focal individuals throughout the park (see Goodall, 1986; Wilson, 2012; for a complete description of data collection protocols). Habituation of the northern Mitumba community began in the mid-1980s, with reliable recognition of all individuals by 1993 and regular focal follows begun in 1994 (Goodall, 1986; Wilson, 2012). Regular focal follows are currently ongoing in both communities.

Of the 281 individuals born since the start of the Gombe study in 1960, we identified 53 for which conception and birth dates could be determined with reasonable certainty (see below). Forty-seven of these individuals were born in the Kasekela community and six in the

TABLE 1 Previous estimates of singleton gestation length in captive and wild chimpanzees

Mean	Range	Sample	Captive/wild	Source
228	204–246	42 live births	Captive	Gavan, 1952
227.8	196–248	104 live singleton births	Captive	Peacock & Rogers, 1959
231.5	192–260	40 offspring (including twins and stillbirth)	Captive	Wallis & Lemmon, 1986
233.3	231–236	3 live singleton births to nulliparous females	Captive	Shimizu et al., 2003
228	201–250	78 live singleton births	Captive	Wildman et al., 2011
228.5				(Weighted average of captive studies)
224.3	203–234	16 live singleton births	Wild	Wallis & Goodall, 1993
225.3	208–235	28 live singleton births	Wild	Wallis, 1997
227.8	209–253	47 live singleton births	Wild	This study

Note: Some individual gestations may be represented in more than one reported sample; for example, those in Gavan (1952) may also be reported by Peacock and Rogers (1959).

Abbreviation: AIC, Akaike's Information Criterion.

Mitumba community. These infants were born to 22 unique females, aged between 12.4 and 48.1 years, between 1970 and 2021.

2.2 | Measuring gestation length

To date, gestation length has only been measured in a small number of pregnancies in Gombe National Park, Tanzania (Wallis, 1997; Wallis & Goodall, 1993), likely because of the difficulty of measuring gestation length in wild chimpanzees. We summarize results from previous studies of gestation length in wild and captive chimpanzees in Table 1. Female chimpanzees do not exhibit any obvious outward cues of pregnancy, and often continue to produce sexual swellings after conception, especially during the first trimester (Boehm, 2016; Goodall, 1986; Wallis & Goodall, 1993). This makes it difficult to identify conception in long-term observations of females. Furthermore, female chimpanzees spend a great deal of time alone, especially during pregnancy (Boehm, 2016; Otali & Gilchrist, 2006; Williams et al., 2002), and tend to avoid large parties for days or weeks immediately following birth, likely to reduce the risk of infanticide (Hamai et al., 1992; Nishie & Nakamura, 2018; Pusey et al., 2008; Takahata, 1985). This “maternity leave” makes it difficult for observers to pinpoint birth dates.

Like many catarrhine primates, chimpanzees display anogenital swelling for a portion of their approximately 36-day ovarian cycle: swelling increases gradually to a sustained peak in response to rising estrogen during the follicular phase, and collapses rapidly due to the antagonistic effects of progesterone at the onset of the luteal phase (Dixson, 1983; Emery & Whitten, 2003; Goodall, 1986; Graham, 1981). Copulation is nearly exclusive to the swollen period, and previous studies have found that ovulation is most likely to occur in the final 6 days of full tumescence (Deschner et al., 2003; Emery Thompson, 2005). Field assistants record the daily swelling state of all adult females sighted using a fractional scale: 0 = no swelling; $\frac{1}{4}$, $\frac{1}{2}$, or $\frac{3}{4}$ = partial swelling, 1 = full swelling.

We primarily used records of swelling to identify conception cycles for pregnancies resulting in live births from 1970 to 2019, using only those gestations for which birthdate was known within a 7-day period. Birthdates were estimated as the midpoint between the date that the female was last seen without an infant and the date she was first seen with the infant unless there were other reasons to suggest that the birth was more recent, such as the presence of an umbilical cord. Working backwards from birth, we examined swellings that occurred within the reported range of chimpanzee gestation length, between 202 and 261 days before birth. Gestations with multiple possible conception cycles were discarded.

Like humans, pregnant chimpanzees excrete chorionic gonadotropin in their urine (Clegg & Weaver, 1972), which can be detected by commercially available human urinary pregnancy tests (UPTs; Emery Thompson, 2005). Pregnancy testing has been performed opportunistically at Gombe since 2014 (mean 26.1, range 9–53 tests per year since 2014). In three gestations in this sample, UPT results aided the identification of the conceptive cycle by allowing us to exclude cycles that occurred after a positive result.

We followed the convention established in earlier gestation studies (Graham, 1981; Wallis, 1997) and assigned conception to the last day of full swelling. We included in our analysis only those conceptions for which the day of detumescence could be identified with high certainty, when females were observed on days both before and after the recorded detumescence.

Using these criteria, we identified gestation length (last day of maximal swelling–birth date) for a total of 53 infants born in 47 singleton and three twin births. It should be noted that our sample likely misses gestations followed by stillbirths or early neonatal mortality before offspring could be observed by researchers.

We tested this sample for normality using the Shapiro–Wilk *W* test. To explore the differences between twin and singleton gestations, and between first births and subsequent births, we performed Wilcoxon rank sum tests. Finally, we used a two-sample *t* test to investigate whether gestation lengths differed during and after provisioning (see above).

2.3 | Predictors of gestation length

To determine the predictors of gestation length, we used a model comparison approach. The three pairs of twins had significantly shorter gestations than did singleton offspring (Wilcoxon rank sum test, $W = 282$, $p < 0.0001$); while this provided anecdotal support for the importance of energy for gestation length, due to the increased energetic demand imposed by two fetuses, we excluded the six twins in the sample from the analysis of predictors of gestation length (but not from the survival analyses; see below). We also excluded six primiparous births from this analysis, as it was impossible to calculate intergestational intervals for these offspring (see below). This resulted in a sample of 41 offspring with known gestation lengths among 20 individual mothers.

We calculated several predictor terms potentially related to maternal condition. First, season should influence food abundance and therefore the energy available to females for gestation, with more food available during the wet season, inferred from larger party sizes and weight gain in Gombe (Goodall, 1986; Murray et al., 2006; Pusey et al., 2005; Wrangham, 1977; Wallis, 1995) and measured via urinary c-peptides in the Kanyawara population in Kibale National Park, Uganda (Emery Thompson et al., 2012; Emery Thompson et al., 2009; Emery Thompson & Wrangham, 2008). We therefore calculated two measures of *wet season overlap* for each gestation. Because nutritional deprivation around conception is associated with shorter gestations in humans and sheep (Bloomfield, 2011), we calculated the percentage of the first trimester (lasting 76 days) of each pregnancy that fell during the rainy season, here defined as October 16 to May 15 (Pusey et al., 2005).

In addition, in human pregnancies, energetic cost is greatest in the third trimester: average maternal energetic investment escalates from 375 kJ/day in the first trimester to 1200 kJ/day in the second trimester and 1950 kJ/day in the third trimester (Butte & King, 2005). Therefore, we also calculated *wet season overlap* as the percentage of the third trimester (the final 76 days of each pregnancy) that fell during the Gombe rainy season.

Second, because higher-ranking females in Gombe have access to higher-quality foods and tend to be heavier than lower-ranking females (Murray et al., 2006, 2007; Pusey et al., 2005), we calculated female rank scores using submissive pant-grunt vocalizations with unambiguous actor and recipient, as well as targeted aggression events with unambiguous aggressor and recipient, from August, 1969 to December, 2015 (Foerster et al., 2016). Because the youngest maternal age at conception in our sample was 12.4, we only included pant-grunt and aggression data in our Elo score calculations between females of at least 12 years of age. The resulting dataset contained 995 female–female pant-grunts and 200 decided female–female aggression events among 47 females (mean 50.8 agonistic interactions, range three to 290 agonistic interactions per female). We used a modification of the Elo score method (Neumann et al., 2011) that uses maximum likelihood fitting to optimize entry scores and the scaling parameter k in the Elo score formula (Foerster et al., 2016), implemented in the *EloOptimized* package in R (Feldblum et al., 2019). Data

were available to calculate Elo score at conception for 40 of the 53 offspring in the overall sample (all born in Kasekela), so analyses involving maternal Elo score were restricted to this subsample (see Data S1).

Third, we included a measure to account for the possible influence of provisioning on gestation. Because the additional nutrition supplied by occasional provisioning could have influenced gestation, we included a binary variable in our full model to indicate whether the offspring was born before the year 2001, when provisioning ended (22 of 41 gestations in the sample began after provisioning ended).

Fourth, we calculated intergestational interval (IGI) for each parous female in the sample. This was the period in years between the birth of parous females' preceding infant and the conception date of the sampled gestation. IGIs ranged from 0.25 to 7.01 years, with a median of 4.07 years. Among the 47 births to multiparous mothers, IGIs following the death of the previous offspring were considerably shorter (IGI following surviving infant: $n = 32$, median = 4.63 years, range 2.67–7.01 years; IGI following death of previous infant: $n = 15$, median = 1.29 years, range = 0.25–4.32 years). As explained above, analyses including IGI as a fixed effect were restricted to gestations in multiparous females. As noted above, lactation imposes an energetic strain that decreases as the infant matures (Bădescu et al., 2017; Emery Thompson et al., 2012). A typical chimpanzee interbirth interval is characterized by a period of lactational amenorrhea lasting approximately 2–5 years, with variation among populations (Deschner & Boesch, 2007). The recovery of pre-pregnancy levels of energy availability is associated with the end of amenorrhea and the resumption of cycling (Emery Thompson et al., 2012), and energetic factors are further hypothesized to influence the number of cycles a female exhibits before conception (Deschner & Boesch, 2007; Wrangham, 2002). If an accelerated return to cycling and pregnancy reduces the opportunity for energetic recovery between pregnancies, females with shorter intervals between pregnancies are likely to have lower energy availability at the time of conception than those with longer intervals. On the other hand, because resumption of cycling requires a sustained period of energetic gain (Emery Thompson et al., 2012), and because waiting time to conception is reduced during periods of better feeding conditions (Emery Thompson & Wrangham, 2008), females with shorter IGIs may instead be in better energetic condition.

Because early offspring death is often followed by a short interbirth interval (current data; Jones et al., 2010), we also included an indicator variable for offspring death preceding subsequent conception. Eleven of the 41 gestations in the multiparous singleton gestation sample were preceded by the death of the previous offspring. Although the mean gestation length following the loss of the previous offspring was slightly lower (226.2 days following infant loss versus 229.0 days with a surviving older sibling), the distributions of gestation lengths in the two groups overlapped considerably (two sample t -test, $t = 0.78$, $p = 0.45$).

Next, we calculated several variables that could potentially contribute to longitudinal changes to gestation length. First, maternal age is associated with multiple components of female fertility in

chimpanzees and other primates (Campos et al., 2022; Jones et al., 2010). In humans, older females tend to have longer gestations (Jukic et al., 2013). In chimpanzees, female rank increases with age (Foerster et al., 2016), conferring social and energetic benefits (Foerster et al., 2015; Jones et al., 2010; Kahlenberg et al., 2008; Murray et al., 2006, 2007; Pusey et al., 1997; Pusey et al., 2005; Riedel et al., 2011; Walker et al., 2018; Wittig & Boesch, 2003). Exploratory analysis indicated a possible quadratic relationship between maternal age and gestation length, so we scaled and centered the maternal age variable and included both maternal age and squared maternal age in our full model. Second, to test for a trend in gestation lengths across successive births within females, we included the birth order of each gestation based on the number of prior known, live births to that female.

Finally, we included offspring sex as a predictor variable. Our sample included 23 male offspring, 17 female offspring, and 1 offspring for which researchers were unable to assign sex before it disappeared. We followed convention from Jones et al. (2010), and coded male offspring as 1, female offspring as -1 , and offspring of unknown sex as 0. This approach maximizes sample size while avoiding introducing bias in parameter estimates (Jones et al., 2010).

To check for sampling bias, we compared the distribution of our predictor variables with the distributions of those variables among the full set of Gombe births (Table S1). Distributions of all predictor terms in our current sample corresponded closely to those in the overall Gombe population, suggesting our sample was representative of the larger population according to our predictors of interest.

We used a model comparison procedure to determine the best set of factors for predicting gestation length in our sample. We started by constructing a linear mixed model with gestation length as the outcome variable and maternal age and squared maternal age, first and third trimester wet season percentages, infant sex, IGI, and the indicator variable for previous offspring death as predictor variables. We also included maternal identity as a random effect. All analyses were conducted in R version 4.0.5 (R Core Team, 2021).

We then calculated variance inflation factors (VIFs) to test for multicollinearity among predictor variables in the full model (Fox & Monette, 1992; Fox & Weisberg, 2018). Maternal age and birth order both had VIF values of 7.0, suggesting problematic multicollinearity, and were highly correlated in the sample (Pearson correlation = 0.87). Additionally, the first and third trimester wet season percentage terms had VIF values of 3.5 and 3.4, respectively, suggesting modest concern for multicollinearity, unsurprising given their nonindependence. Finally, IGI had a VIF of 4.1, but this value fell below 2.7 when excluding either maternal age or birth order.

We then compared models including combinations of our predictor variables using the dredge function in MuMIn version 1.43.17 (Barton, 2020). Because of concerns with multicollinearity (see above), we excluded models from the comparison set that (1) included both maternal age and birth order, and/or (2) included both first and third trimester wet season percentages. We also excluded models that (3) included squared maternal age but did not include the first order maternal age term. We compared models using Akaike's Information

Criterion corrected for small sample size (AICc). We included models within six AICc points of the best-supported model in the comparison set (Harrison et al., 2018).

Because adding a nuisance (i.e., completely random) parameter to a model will tend to result in a Δ AIC value of two, excluding models from the model comparison set that differ from a better-supported model by the addition of a single parameter can improve inference and parameter estimation (Arnold, 2010; Richards et al., 2011). We therefore excluded such "nested" models from our comparison set. We then calculated model-averaged parameter estimates based on Akaike weights across the full set of best models (Burnham & Anderson, 1998).

Finally, human mothers show marked heterogeneity in gestation length, with individual women tending to give birth at consistent gestational ages (Jukic et al., 2013); to determine whether chimpanzees showed similar within-individual consistency in gestation length, we used the function *r.squaredGLMM* in the R package MuMIn to determine the percentage of model variance explained by individual random effects (as well as fixed effects) in our best model.

Because maternal dominance rank is associated with shorter intervals between births (Jones et al., 2010) and could also influence energy availability via access to resources (Murray et al., 2006, 2007; Pusey et al., 2005), we ran a second model comparison procedure using a reduced data set including only multiparous singleton births with known maternal rank at conception (full details are reported in the Data S1).

2.4 | Offspring survival

We again used a model comparison procedure with Cox proportional hazards models to assess whether gestation length was associated with offspring survival. We began with a data set of 53 total offspring from 22 unique mothers. We excluded seven offspring that died in their first year for reasons unlikely to be related to the timing of their births (i.e. deaths caused by infanticide or infant kidnapping; Lonsdorf, Wilson, et al., 2020). After these exclusions, only two pairs of twins remained in the sample. Given that twins have unusually short gestations (see below) and higher mortality (Seal et al., 1985), we excluded the remaining twin pairs from the data to ensure that they were not driving the relationship between gestation length and offspring survival.

To facilitate comparison of effect sizes, we centered and scaled gestation lengths by Z transformation. In humans, offspring survival is highest after median gestation lengths, with lower survivorship among unusually short and long gestations (Hilder et al., 1998). Therefore, to capture potential nonlinear effects of gestation length on survival, we also included a squared gestation length term. Other, more complicated nonlinear relationships between gestation length and survival, such as threshold effects, would likely require a larger dataset to detect, and therefore cannot be ruled out by the current analysis. As before, we included centered and scaled maternal age, as well as squared (centered and scaled) maternal age to account for potential

nonlinear effects of maternal age on offspring survival. Because birth order may affect offspring survival (Pusey, 2012), we also included a binary term to indicate whether each offspring was a particular female's first-born offspring or not. Finally, because maternal death is a strong predictor of offspring mortality, especially when offspring are still in the dependent stage when they are orphaned, we included a term to indicate orphan status; that is, whether their mother died before they turned five, the average age of weaning in Gombe; (Lonsdorf, Stanton, et al., 2020; Van de Rijt-Plooij & Plooij, 1987).

Two females in the sample disappeared from their communities at ages 11.3 and 11.4, respectively. These departures fall within the range of emigration ages observed at Gombe (Walker et al., 2018), making it likely that these females emigrated rather than died. We therefore treated these two females as right-censored, leading to a total of 24 right-censored individuals of the 42 in the sample.

We then constructed a Cox proportional hazard model with offspring longevity as the outcome variable, the predictor terms described above, and a frailty term for maternal identity, using the `coxph` function in the `survival` package in R (version 3.2-10; Therneau, 2021). We used the `cox.zph` function to assess the proportional hazard assumptions of the terms in the model (Grambsch & Therneau, 1994). The test indicated that the orphan status term did not meet proportional hazard assumptions ($p < 0.01$). Further inspection of the data revealed that three of the 42 offspring in the sample were orphaned, all before age two, and all three died within 8 days of their mother's death. Therefore, given the limited value of these individuals for determining the effects of other predictor terms, and to meet model assumptions, we excluded these three offspring from the sample.

After excluding orphans from the sample, a second test suggested that infant sex may also fail to meet the proportional hazards assumption ($p = 0.063$). Inspection of the data suggested that this was because only two of 15 females in the sample died, both before age five. We therefore included infant sex as a stratification factor rather than a regressor. This approach precludes the estimation of effect size for the stratified variable but removes the problem of non-proportionality (Therneau & Grambsch, 2000). This also required that we exclude the one offspring of unknown sex to avoid a stratification factor with a single observation, leaving 38 total offspring in the sample.

Next, we fit a mixed effects Cox model with the remaining terms, using the `coxme` function in the `coxme` package, with maternal identity specified as a random effect (version 2.2-16; Therneau, 2020). We then conducted model comparisons to find the best set of terms for predicting offspring survival using the `dredge` function in the `MuMIn` package in R, using AICc as our selection criterion. We excluded models from the comparison set that included squared maternal age or squared gestation length, but not their corresponding first order effects. As before, we used the nesting rule (Arnold, 2010; Richards et al., 2011) to exclude models from the top model set that differ from better-supported models by the addition of a single term, and considered models within six AICc points of the best-supported model in our top model set.

We ran two additional analyses on slightly different data sets to check for potential confounds. First, to ensure that our inclusion criteria did not influence model results, and because postnatal energetic status could theoretically influence maternal ability to resist infanticidal attacks, we repeated the model comparison procedure without excluding (1) the seven infants that died in infancy due to kidnapping or infanticide, or (2) the twin births (see Data S1).

Second, we conducted an additional model comparison procedure with a restricted dataset to investigate potential interactions between gestation length and maternal rank at conception (full details are reported in the Data S1).

Finally, because of the surprisingly dramatic differences in survivorship between first-born and subsequent offspring, and between male and female offspring in the current sample (see below), we ran an additional survival analysis using 172 offspring of known sex and birth order in Gombe.

3 | RESULTS

3.1 | Measuring gestation length

Our sample of 47 singleton gestations was normally distributed (Shapiro-Wilk W test: $W = 0.97$, $p = 0.54$). Gestation ranged from 209 to 253 days among singleton births, with a mean of 227.8 days ($n = 47$; $SD = 9.18$) and a coefficient of variation of 4.1%. Twin gestations ranged from 198 to 203 days, with a mean of 200.7 days ($n = 3$; $SD = 2.25$). Gestations of twin births were significantly shorter than those of singleton births (Wilcoxon rank sum test: $W = 282$, $p < 0.0001$).

Among singleton births, gestation for the six first births ranged from 218 to 231 days (mean = 224.8 days, $SD = 4.96$ days), while gestation for the 41 births to parous mothers ranged from 209 to 253 days (mean = 228.2, $SD = 9.82$ days). We did not find evidence that gestation length differed among first births and subsequent births (Wilcoxon rank sum test: $W = 147.5$, $p = 0.4436$).

The 23 singleton births that occurred during provisioning had a mean duration of 227.4 ($SD = 10.8$) days, while the 24 that occurred after provisioning had a mean duration of 228.2 ($SD = 8.1$) days. We did not find evidence that gestation lengths differed between these periods (two-sample t -test: $t = 0.31$, $p = 0.76$).

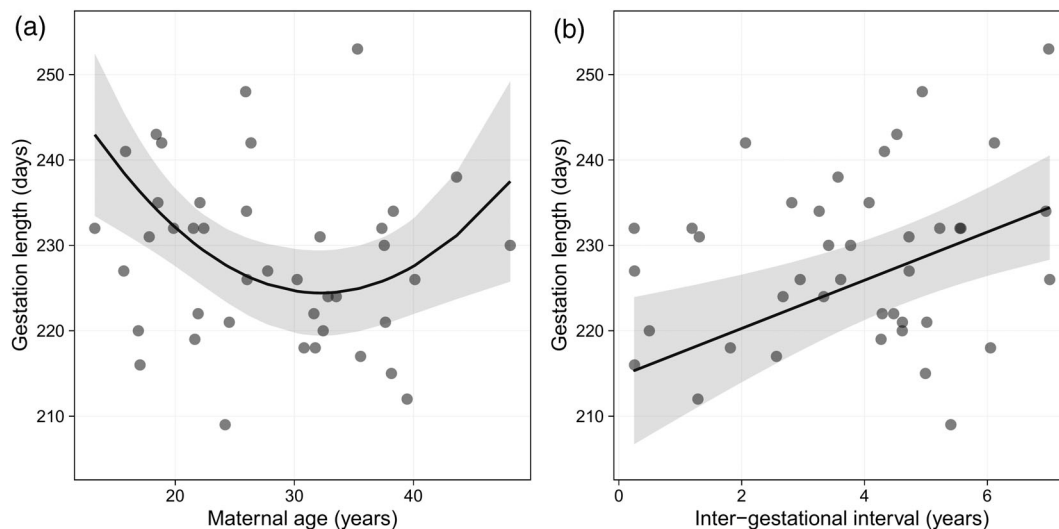
3.2 | Predictors of gestation length

Only one of our variables related to maternal condition was associated with gestation length. We found that longer IGIs were followed by longer gestation periods. Four models were within six AICc points of the best model. IGI was present in models accounting for 89% of total model weight, while the best model (accounting for 50% of total model weight) also contained maternal age and squared maternal age (Table 2). Using model-averaged estimates, a one standard deviation (about 1.9 years) increase in IGI corresponded to a four-day increase

TABLE 2 Parameter estimates and model fit statistics for the best models for predicting gestation length for multiparous births

Model	Intercept	Maternal age	Maternal age ²	IGI	3rd trimester wet season pct	df	AICc	ΔAICc	Weight
1	226.419	−5.788	4.223	5.283		6	306.221	0	0.5
2	225.997			3.069	5.863	5	307.848	1.628	0.222
3	228.836			2.773		4	308.452	2.231	0.164
4	228.639					3	309.171	2.95	0.114
Avg.	226.976	−2.895	2.112	3.777	1.299				

Note: ΔAICc shows the difference in corrected AIC score between each model and the best-fitting model, with lower AICc values indicating better fit. IGI indicates inter-gestational interval, and models including IGI account for 89% of total model weight. Avg. indicates model averaged parameter estimates. Abbreviations: AIC, Akaike's Information Criterion; IGI, inter-gestational interval.

**FIGURE 1** Predicted gestation lengths based on the best-supported gestation length model. (a) Shows predicted gestation length by maternal age, and (b) shows predicted gestation length by inter-gestational interval. Points show raw data

in gestation length (Figure 1). In addition, maternal age had a quadratic relationship with gestation length, with females in their early 30s having shorter gestations than both younger and older females (Figure 1).

None of the other measures related to maternal energy status were associated with gestation length. The first trimester rainy season term did not appear in any of the best models, and the third trimester rainy season term appeared in only one of the best models, accounting for only 22% of total model weight. Furthermore, the provisioning term did not appear in any of the best models (Table 2). We also found no evidence that the relationship between IGI and gestation length was mediated by maternal rank at conception (Table S2). Finally, although IGIs were shorter following the death of an infant (see above), the term indicating the death of a female's previous infant was not present in any of the best models, suggesting that IGI was a better predictor of subsequent gestation length than the loss of a dependent offspring.

The fixed effects in the best model accounted for 25% of the total variance, while the random intercepts accounted for a further 37% of variance. However, the latter statistic could be artificially inflated because the sample included only one observed pregnancy for 10 of 20 mothers. We therefore re-ran the best model, restricting

the sample to the 31 gestations among the 10 females with multiple recorded gestations. The direction and magnitude of estimated effects remained largely unchanged, and using the restricted data set, fixed effects accounted for 30% of the model variance, while random intercepts accounted for a further 25% of model variance.

3.3 | Offspring survival

Even after excluding twin births from the survival analysis, short gestations were associated with lower offspring survival in our sample. Five models were within six AICc points of the best model for predicting offspring survival (Table 3). Gestation length was present in models accounting for 77% of total model weight, with longer gestation length associated with lower risk of mortality (Figure 2). In addition, firstborn status was present in models accounting for 70% of total model weight, with firstborn offspring having increased risk of mortality. Two models in the best model set contained the maternal age term, with the maternal age effect capturing a similar longitudinal change to offspring survivorship, with higher mortality among offspring of the youngest females.

TABLE 3 Parameter estimates and model fit statistics for the best models for predicting offspring survival using the data set that excludes offspring that died from infanticide or kidnapping, as well as twin births. All models are stratified by infant sex

Model	Firstborn	Gestation length	Maternal age	Maternal age ²	df	AICc	ΔAICc	Weight
1	2.235	-0.429			2	68.155	0	0.467
2	2.241				1	69.555	1.4	0.232
3		-0.586	-0.734	0.597	3	70.453	2.298	0.148
4		-0.479	-0.570		2	71.49	3.335	0.088
5		-0.393			1	72.101	3.946	0.065
Avg.	1.564	-0.355	-0.159	0.088				

Note: ΔAICc shows the difference in corrected AIC score between each model and the best-fitting model, with lower AICc values indicating better fit. Gestation length is present in models accounting for 77% of total model weight. Avg. indicates model averaged parameter estimates.

Abbreviation: AIC, Akaike's Information Criterion.

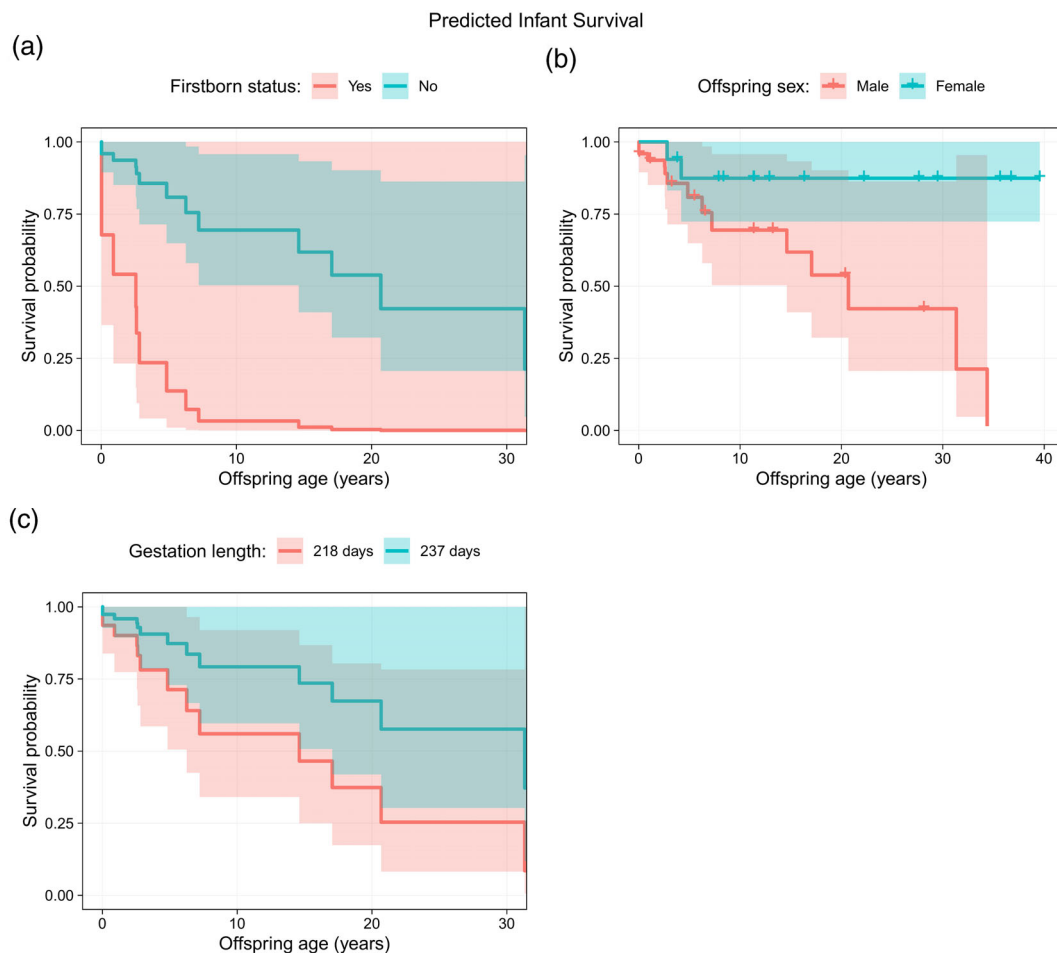


FIGURE 2 Infant survival curves from best-supported model predicting infant survival using the data set that excludes offspring that died from infanticide or kidnapping, as well as twin births. (a) Shows predicted survival based on infant firstborn status, (b) shows survival by offspring sex, and (c) shows predicted survival by gestation length; 218 and 237 days represent the mean gestation length ± 1 standard deviation among singleton births. (+) signs in (b) indicate right-censored individuals. (a) and (c) show predicted survival in the male stratum.

We also found no evidence that the negative effects of shorter gestation were mitigated among offspring of high-ranking females (Table S4), and results did not change when including twins and victims of infanticide or kidnapping in the analysis (Table S3). Finally, in the larger sample of 172 offspring, the mortality effect of firstborn status was modest and nonsignificant.

Furthermore, while male offspring had higher mortality than did female offspring, this effect was again more modest than in the smaller gestation lengths sample (Figure S1). This suggests that the dramatic firstborn effect in our gestation sample (Table 3) was the result of the small number of firstborn offspring in the sample.

4 | DISCUSSION

Using the largest available sample of gestations in wild chimpanzees, we found that the average singleton gestation was 227.8 days, 2 days longer than the previous estimate for wild chimpanzees in the same population (Wallis, 1997). The mean gestation falls within the range of previous estimates from both captive and wild populations (Nissen & Yerkes, 1943; Shimizu et al., 2003; Wallis & Lemmon, 1986; Wildman et al., 2011; Wallis & Goodall, 1993; Wallis, 1997; Yerkes & Elder, 1937; Table 1).

Variation in gestation lengths in the current sample was also consistent with that reported in previous studies. Gestation length among singleton births varied between 209 and 253 days, with a coefficient of variation of 4.1%. The coefficient of variation was in line with those reported in other mammal species, including humans (Jukic et al., 2013; Kiltie, 1982; Martin, 1992; Martin, 2007). We also found evidence of considerable interindividual differences on gestation length, consistent with the pattern observed in humans (Jukic et al., 2013). Nevertheless, this supports the idea that, as in other mammals, gestation lengths in chimpanzees are less variable than other components of the interbirth interval (e.g., Campos et al., 2022; Jones et al., 2010), and thus that gestation length is more likely to have fitness consequences for females via its influence on offspring survival than via its influence on reproductive rates (Gesquiere et al., 2018).

Each of the three twin gestations fell below the singleton range, with an average length of just 201 days. This is consistent with earlier reports from chimpanzees (Peacock & Rogers, 1959; Wallis, 1997) and humans, where as many as 50% of twin births occur before 37 weeks of gestation (Soucie et al., 2006). However, 64% of individual twins die within a year of birth, even in captivity (Seal et al., 1985). Across wild chimpanzee populations, only one pair of twins, included in this sample, is known to have survived to adulthood.

We explored several factors that may produce variation in gestation length. Notably, female chimpanzees in our sample with shorter IGIs had shorter pregnancies. This effect appeared to be independent of the effect of maternal rank on gestation in a reduced sample. Using model averaging, our models predicted that a one-standard-deviation (about 1.9-year) increase in IGI corresponded to a four-day increase in gestation. Therefore, a female with the longest IGI in our sample would be expected to have a gestation approximately 13 days longer than a female with the shortest IGI in our sample. Average interbirth interval for chimpanzees is over 5 years when infants survive (Emery Thompson et al., 2007; Nishida et al., 2003; Wallis, 1997), and resumption of cycling following lactational amenorrhea seems to be related to energy availability. Among chimpanzees in Kanyawara, females typically exhibit their first postpartum cycles after a period of sustained energy gain lasting 4–6 months (Emery Thompson et al., 2012). Age at weaning in the Gombe population is highly variable (Lonsdorf, Wilson, et al., 2020) but tends to occur between 4 and 6 years of age. However, the amount of breastmilk in the diet decreases steadily after just 1 year (Bădescu et al., 2017). Females who have recently given birth and been lactating intensively may be

more energetically stressed than those whose previous infant was gestated years earlier and has since been weaned, even if they have recovered sufficiently to conceive, potentially impacting gestation length.

On the other hand, as noted above, short IGIs could instead reflect good female condition and the ability to conceive quickly. However, this would be somewhat puzzling given the relationship between gestation length and offspring mortality in our sample. Offspring mortality was higher after shorter gestations, even when excluding twins, which have both unusually short gestations and lower survivorship in our study population. These results conform to earlier findings: in humans, gestation length is strongly associated with offspring mortality and morbidity, including low birthweight and health problems later in life, such as cardiovascular disease and even cancer (Alexander et al., 1996; Callaghan et al., 2006; Gladstone et al., 2011; Risnes et al., 2011). Human twin- and triplet-gestations are particularly likely to end in preterm birth, and mortality for these infants is elevated relative to singletons (Kahn et al., 2003). Among captive chimpanzees, gestations with normal outcomes—live births where mothers successfully cared for their infants—were on average 4 days longer than those that resulted in pathological outcomes like maternal abandonment and stillbirth (Dahl, 1999).

In non-human primates, too, low birthweight and early life adversity are often good predictors of later growth and survival (Altmann & Alberts, 2005; Holekamp & Strauss, 2020; Lee et al., 2020; Tung et al., 2016). Large-for-age juvenile baboons tend to remain larger than their cohort throughout development, have higher survivorship and mature earlier (Altmann & Alberts, 2005). Similarly, rhesus macaque infants with lower body weights were less likely to survive in a semi-wild population (Lee et al., 2020). Unfortunately, because birth weight data are unavailable in our study population, we were unable to determine whether the short gestations in our study yielded infants with low birthweights, nor whether short gestation and low birthweight may exert dependent or independent effects on mortality. Therefore, the energetic implications of short IGIs must remain speculative.

On the other hand, several results were inconsistent with an energetic explanation for gestation lengths. The two largest studies of gestation length in captivity reported mean gestation lengths for live, singleton births that were remarkably similar to our estimate here (228 days and 227.8 days, respectively; Peacock & Rogers, 1959; Wildman et al., 2011), suggesting that average gestation lengths do not differ substantially between wild and captive populations of chimpanzees. The similarity of mean gestation lengths between captive and wild populations is not consistent with the hypothesis that maternal condition mediates gestation length, as captive chimpanzees are not subject to energetic shortfalls as are their wild counterparts. Furthermore, other factors associated with energetic condition did not predict gestation length in our sample. We did not find evidence that maternal rank at conception predicted gestation length (in a reduced sample), nor did we find evidence of an effect of provisioning on gestation, likely because provisioning occurred only infrequently (Wrangham, 1974). We also did not find evidence that the proportion

of the first or third trimesters that fell during the rainy season had any relationship with gestation length. Measurements of body mass from Gombe show that chimpanzees are heavier in the wet than in the dry season, likely due to the increased availability of ripe fruit during these months (Pusey et al., 2005), yet neither early- or late-pregnancy exposure to this period of improved condition was associated with longer gestations. Because season is only a rough proxy for food availability, more detailed phenology data may reveal more about the effects of early- or late-pregnancy nutritional deprivation on chimpanzee gestation length.

How do these predictors of chimpanzee gestation length compare to those in other animals? In most nonhuman mammals, individual females tend to have *longer* gestations in the face of lower-quality habitats and reduced rainfall in the wild, and experimentally-reduced provisioning in captivity (Langurs, *Semnopithecus entellus*: Borries et al., 2001; rhesus macaques, *Macaca mulatta*: Riopelle & Hale, 1975; yellow baboons: Gesquiere et al., 2018; Silk, 1986; other mammals, reviewed in Racey, 1981). On the other hand, in humans, nutritional stress, particularly around conception and during the first trimester, is consistently associated with shorter gestations (reviewed in: Bloomfield, 2011; Ellison, 2003). Maternal weight at the time of conception is positively associated with gestation length, and good maternal nutrition around conception decreases the risks of preterm delivery and low birthweight (Bloomfield, 2011; Ramakrishnan et al., 2012). Furthermore, a meta-analysis found support for relationships between unusually short inter-pregnancy intervals (IPI) and both preterm birth and low birthweight (Wendt et al., 2012), suggesting that maternal energetic supply has not fully recovered after unusually short IPIs—even though conception is possible.

Though rare, this pattern has also been reported in other mammals. Captive sheep experiencing experimentally reduced nutrition around conception suffered higher rates of preterm birth (Bloomfield et al., 2003), and one study found that wild yellow baboons (*Papio cynocephalus*) living in lower-quality habitat had shorter gestation lengths (although another proxy of nutritional status had the opposite relationship with gestation lengths, as noted above; Gesquiere et al., 2018).

Thus, previous work suggests that humans may possess an unusual relationship between gestation and nutritional stress relative to other mammals, perhaps because human neonates have unusually large brains as a proportion of adult female body mass relative to other primates (DeSilva & Lesnik, 2008; Dunsworth et al., 2012). Our analysis finds that chimpanzee gestation resembles that of humans in at least one respect: chimpanzee gestations are shorter following shorter IGIs.

This effect may be dictated by the timing of energetic restriction: In humans, gestation length is shorter following energy shortfalls around conception and early pregnancy, but shortfalls during the third trimester have little effect on the length of gestation (Bloomfield, 2011). In contrast, studies of other mammals reporting longer gestation in response to energy shortfalls rely on measures of energy availability over the entire period of gestation or those that apply to the end of gestation (Borries et al., 2001; Gesquiere

et al., 2018; Riopelle & Hale, 1975; Silk et al., 1993). Therefore, additional studies of gestation length focusing on energy shortfalls during the periconceptive period and first trimester are required to better understand the drivers of gestation length across eutherian mammals, and to determine whether humans and chimpanzees share a derived response to energy restriction relative to a broader mammalian pattern.

While female chimpanzees appear to invest more in male than female offspring at some stages of development (Bădescu et al., 2022; Murray et al., 2014), we did not find evidence that gestation length differed by offspring sex. We did, however, find that gestation lengths among parous females changed predictably over female lifetimes, independent of the effect of IGI. Females in their early 30s had the shortest gestations, while younger and older females had longer gestations. This differs from the pattern reported in female baboons, which have *shorter* gestations among old and young females (Gesquiere et al., 2018), and from other mammal species that did not have a quadratic relationship between age and gestation length (e.g., rhesus macaques: Silk et al., 1993; reindeer, *Rangifer tarandus*: Mysterud et al., 2009). Longer gestations among the youngest mothers could reflect the fact that these females may still be investing in somatic growth (Pusey et al., 2005), while longer gestations among older females could indicate terminal investment by older mothers (Pianka & Parker, 1975; Trivers, 1972; Williams, 1966), but further work is required to understand why gestation length varies with maternal age.

Taken together, we find that IGIs and maternal age are associated with gestation length in wild chimpanzees, and that gestation length could be a target of selection due to its effect on offspring survival. More work is needed to establish whether short IGIs can indeed be energetically costly for female chimpanzees despite having sufficient energy gain to conceive again. Further, more comparative work is required to determine whether energy shortfalls in early gestation have similar effects across mammals. While it is difficult to pinpoint conception and birth in wild primates, collecting these data in other chimpanzee populations and other great ape species will help build a more detailed picture of the selective pressures that have shaped pregnancy and birth in our own human lineage.

AUTHOR CONTRIBUTIONS

Joseph T. Feldblum: Conceptualization (equal); formal analysis (lead); visualization (lead); writing – original draft (supporting); writing – review and editing (equal). **Emily E. Boehm:** Conceptualization (lead); formal analysis (supporting); writing – original draft (lead); writing – review and editing (equal). **Kara K. Walker:** Conceptualization (supporting); writing – review and editing (equal). **Anne E. Pusey:** Conceptualization (supporting); data curation (lead); funding acquisition (lead); supervision (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code to reproduce the analyses in this manuscript can be found at <https://github.com/jtfeld/gestationlength> and are permanently archived at <https://zenodo.org/record/5555095> (Feldblum et al., 2022).

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