

Phenotypic quality influences fertility in Gombe chimpanzees

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Summary

1. Fertility is an important fitness component, but is difficult to measure in slowly reproducing, long-lived animals such as chimpanzees (*Pan troglodytes*).
2. We measured fertility and the effect of measured covariates on fertility in a 43-year sample of birth intervals of chimpanzees from the Gombe National Park, Tanzania using Cox proportional hazards regression with individual-level random effects.
3. The birth hazard declined with mothers' age at a rate of 0.84 per year following age at first reproduction. This value is somewhat stronger than previous estimates.
4. Loss of the infant that opened the birth interval increased the birth hazard 134-fold.
5. Birth intervals following the first complete birth interval were shorter than this first interval, while sex of the previous infant had no significant effect.
6. Maternal dominance rank was significant at the $P < 0.1$ level when coded as high/middle/low but was highly significant when we simply considered high rank vs. others.
7. Individual heterogeneity had a substantial impact on birth interval duration. We interpret this individual effect as a measure of phenotypic quality, controlling for the measured covariates such as dominance rank. This interpretation is supported by the correlation of individual heterogeneity scores with similar independent measures of body mass.

Key-words: chimpanzee, demography, fertility, life-history theory, phenotypic quality

Introduction

An organism's age-specific schedules of fertility and mortality are the fundamental components of fitness. A full evolutionary explication of the organism's life history requires an understanding of the patterning of reproduction through the life cycle. Moreover, practical applications, such as population projections and conservation actions, require knowledge of aggregate patterns of fertility. Understanding the contribution of individual heterogeneity to aggregate fertility schedules is essential both for interpreting aggregate analyses and ensuring accurate predictions. Individual heterogeneity is also important from an evolutionary perspective as it is individual phenotypic differences underlying age-specific fertility and survival that are the object of natural selection. In this document, we analyse long-term demographic data on the chimpanzees (*Pan troglodytes*) of Gombe National Park, Tanzania. Both the time depth and richness of the data col-

lected at Gombe make this a uniquely valuable population for understanding both age patterns of chimpanzee fertility and the contribution of individual heterogeneity to these patterns.

As in other organisms with modal singleton litters, fertility in apes depends on the interval between live births. Factors influencing birth intervals include mother's age, her parity, the survival and degree of investment in the previous offspring, access to resources, and the viability of the foetus. In humans, female fertility depends strongly on age, peaking in the 20s and declining until menopause (Wood 1994). Emery Thompson *et al.* (2007a) reported a similar trajectory in chimpanzee fertility, except that female chimpanzees have an earlier age of first reproduction, and do not have an extended post-reproductive life span. Despite an overall increase in birth intervals with age, in many primates, the interval following the first infant is often longer than subsequent infants (Koyama *et al.* 1992; Robbins *et al.* 2006). Because females resume cycling soon after the death of a nursing infant, the loss of an infant is expected to result in shorter interbirth

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intervals (Goodall 1983; Boesch 1997; Sugiyama 2004), as it does in humans (Hill & Hurtado 1996; Hossain, Phillips & Legrand 2007) and other primates (van Schaik 2000). If the infant does survive, the investment in that infant, including duration of lactation and resulting lactational amenorrhoea, may depend on the infant's sex. Supporting the predictions of Trivers & Willard (1973), some previous studies have reported that females invest more in sons by having a longer interbirth interval after the birth of a son either for all females (Nishida *et al.* 2003) or just high-ranking females (Boesch 1997). Because ovarian function is sensitive to energetics (Ellison 2003), access to resources may likewise influence interbirth interval. Factors such as resource availability, access to artificially concentrated food sources (i.e. human garbage), better habitat, smaller social groups, and higher dominance rank, each contributed to shorter interbirth intervals in baboons (Altmann & Alberts 2003). In chimpanzees, there is evidence that higher quality individual core area (Emery Thompson *et al.* 2007b) and larger community home range size (Williams *et al.* 2004) both shorten interbirth intervals. Whether high rank also shortens interbirth intervals in chimpanzees remains unclear. Pusey, Williams & Goodall (1997) found that infants born to high-ranking mothers had higher survivorship, but did not test whether female rank also affected interbirth intervals. However, the improved access to resources associated with higher rank, as measured by higher quality core areas, less time spent foraging, and higher diet quality (Murray, Eberly & Pusey 2006) may allow high-ranking females to reproduce more quickly. This idea is supported by various studies of primates and other mammals reporting increased fertility with body mass (Berube, Festa-Bianchet & Jorgenson 1999; Richard *et al.* 2000).

Understanding the factors affecting interbirth intervals in apes has been hampered not only by the slow accumulation of data, but also by the use of sub-optimal statistical methods. Three problems in particular beset studies of birth interval duration. First, many studies of ape fertility exclude incomplete, or censored, birth intervals (e.g. Boesch 1997; Nishida *et al.* 2003; Sugiyama 2004; Wich *et al.* 2004; Roof *et al.* 2005). As noted by Galdikas & Wood (1990), exclusion of censored birth intervals induces a systematic downward bias in estimating the mean interval duration, a point first noted in human demography by Sheps & Menken (1973). The classic observation by Sheps and Menken is that censored intervals are, on average, longer than uncensored intervals and ignoring censored observations can introduce substantial bias into estimates of duration (see also Singer & Willett 2003). The bias introduced by ignoring censored birth intervals makes the results from a number of studies questionable. In particular, the findings of both Boesch (1997) and Nishida *et al.* (2003) that birth intervals are longer following the birth of a male infant both suffer from the exclusion of censored birth intervals in the analysis. More recent analyses of ape reproduction have used hazards models that allow the inclusion of censored observations (Littleton 2005; Emery Thompson *et al.* 2007a). Second, a number of previous studies (Galdikas & Wood 1990; Nishida *et al.* 2003;

Sugiyama 2004) have generally adopted the convention of excluding birth intervals for which the first infant dies. While such intervals certainly complicate analysis, excluding them omits valuable data in already small samples and potentially biases parameter estimates. Finally, previous studies (e.g. Galdikas & Wood 1990) have analysed data in which multiple intervals from the same mothers were present, violating the assumption of independence of the samples.

In our analysis, we adopt methods that allow us to investigate the role of covariates and use a random-effects approach that accounts for potential correlations in the birth intervals of a particular mother (Klein & Moeschberger 1997; Therneau & Grambsch 2000). In addition to affording better statistical control, the inclusion of this individual random effect proves biologically interesting in itself because it provides a potential measure of phenotypic quality. Known as 'frailty' in the statistical and human demographic literatures, this individual-level heterogeneity represents a latent propensity for individuals to experience an event such as dying, migrating, or closing a birth interval. Thus, depending on the context, high 'frailty' can be detrimental to fitness (in the case of mortality) or fitness-enhancing (in the case of fertility).

Frailty can be interpreted as a measure of general phenotypic quality in life history studies. As such, we will use the terms 'frailty' and 'phenotypic quality' interchangeably in this document.

Failure to account for population heterogeneity (both statistically and conceptually) can lead to difficulties (Vaupel & Yashin 1985). For example, despite strong predictions from life-history theory of a negative correlation between reproductive effort and survival, the two are often positively correlated when measured in natural populations (Bell 1980; Reznick 1992). This finding is a classic example of the failure to account for individual heterogeneity in studies of life-history trade-offs. While the trade-off may be real, the individuals who survive to be counted in empirical studies are typically a non-random sample of the overall population. Observations from natural populations may thus be biased by an excess of observations of individuals of high phenotypic quality. Rigorous tests of the predictions from life-history theory using field data will require that heterogeneity be controlled. Such heterogeneity can only be estimated from repeated measures on the same individuals. The multiple long-term research projects on free-ranging primates of known identity (e.g. Altmann & Alberts 2003; Fedigan, Carnegie & Jack 2008; Johnson 2003; Koyama *et al.* 1992; Lawler *et al.* 2009; Nishida *et al.* 2003; Strier *et al.* 2006a,b; Robbins *et al.* 2006) can thus potentially contribute a great deal to understand the evolution of life histories in natural populations.

Emery Thompson *et al.* (2007a) have recently published an analysis of the fertility of chimpanzees from six long-term research sites, including Gombe. They found that maternal age has a modest but significant effect on fertility. They also found that individual heterogeneity made a significant contribution to the overall variation in fertility. As this study analysed only the subset of demographic data that were available

from all six sites, Emery Thompson *et al.* (2007a) lacked the rich information available to individual long-term studies. For example, they were not able to incorporate rank, parity, or the sex of previous infant into their analysis. As a consequence, their estimate of the magnitude of individual heterogeneity may have included these effects as well as the actual variations in phenotypic quality. Research at Gombe allows us to include mother's dominance rank and the sex of previous offspring. In addition, we have other auxiliary information that may prove useful in interpreting our results, including highly detailed knowledge of individual life histories and, for a 33-year period, measures of individual body mass (Pusey *et al.* 2005). Furthermore, contextual information that arises from long-term research allows for a better understanding of outliers in aggregate analysis and other anomalous results.

Materials and methods

STUDY POPULATION

Gombe National Park is a narrow strip of land, 35 km², on the eastern shore of Lake Tanganyika, Tanzania (Goodall 1986). In 2007, it contained three communities of chimpanzees, Mitumba in the north, Kasekela in the middle and Kalande in the south (Pusey *et al.* 2007). Observations of the chimpanzees of the central community began in 1960, and details of every demographic change have been recorded since 1963 (Goodall 1983, 1986). The central community fissioned in the early 1970s, forming the Kasekela and Kahama communities. The Kahama community persisted only until 1977, however, before succumbing to a series of lethal attacks by males from the Kasekela community (Goodall 1986).

In this document, we analyse demographic data from 161 individuals of the Kasekela community up to 31 December 2007. These include infants born in the community since 1963, females present at the beginning of the study and females that immigrated after 1963. Habituated chimpanzees are readily distinguishable by trained observers, allowing straightforward determination of individual sex, vital events, etc. Ages of individuals first observed as juveniles or adults were estimated by comparison with known-aged individuals.

For the analysis of factors influencing chimpanzee fertility, we calculated birth intervals for all births (for which a live infant was observed) beyond a female's first. We used only those intervals in which the age of each infant could be assigned with an error of < 3 months (as births are typically not directly observed), reducing somewhat the sample size of usable intervals. Because two of the 119 births resulted in twins, a total of 117 usable intervals for 42 females were observed.

HAZARDS ANALYSIS

Like any time-to-event data, birth intervals are subject to censoring. To deal with the various challenges of event data, we employ hazard analysis (Klein & Moeschberger 1997; Therneau, Grambush & Pankratz 2003). The hazard represents the time-conditional rate of closure of the birth interval. Higher fertility hazards mean that birth intervals are closed more quickly and fertility is therefore higher. The key hypotheses that we are testing involve evaluating the effects of measured covariates, such as mother's age and dominance rank or the sex of her previous infant, on the duration of the birth intervals and we

employ Cox proportional hazards regression to evaluate the effects of covariates on the observed birth hazard. We used only birth intervals opened by a preceding birth for this analysis (i.e. those intervals closed by births of parity ≥ 2 since in demographic parlance a 'first birth interval' is the duration from age 0 to their first birth). Births, and consequently birth intervals, are repeated events to individual females. As such, the intervals are potentially correlated since the same female may have intervals that resemble each other because of intrinsic features such as individual constitution, the quality of their core range, etc. Such correlations can bias estimates of model coefficients and lead to the over-estimation of precision. To account for these repeated events, we employed an individual-level random effect in our hazard model (Therneau & Grambush 2000). The model for the hazard of the *i*th individual is $h_i(t) = h_0 \exp(X_i\beta + Z_i\xi)$, where h_0 is the baseline hazard, β is a vector of covariates, X_i is the *i*th row of the design matrix for the fixed effects, Z_i is the *i*th row of a design matrix for the random effects, and ξ is a vector of individual heterogeneity values. In our analysis, there is only a single random effect, mother's identity. Identity is thus the means to measure phenotypic quality through repeated events.

Covariates included: (i) mother's age at the midpoint of the interval, (ii) loss of the infant that opened the interval before age two, (iii) mother's mid-interval dominance rank, (iv) sex of the infant that opened the interval and (v) an indicator for the first birth interval (i.e. between the first and second live birth). Mother's rank was determined for the mid-point of each interbirth interval from the pattern of submissive pant-grunts received and given (Murray *et al.* 2006). Where insufficient information on rank was available ($n = 25$ intervals), we assigned the default middle rank value, a simple form of mean-value imputation (Little & Rubin 2002). Rank codes were 1 = high, 2 = middle, 3 = low. We also used a binary rank coding that collapsed middle and low ranks into a single measure. Infant sex was coded 1 = male, -1 = female. Unsexed infants were coded as 0. This simple imputation method is conservative as it allows us to use all the data but does not bias the parameter estimates. First, birth interval was coded 1 = interval following first birth, 0 = subsequent intervals. Previous infant status was coded 1 = previous infant died before age 2, 0 = previous infant survived past age 2.

We fit all the models using the survival library for the R statistical programming language (R Development Core Team, 2008). The survival library in R uses the method of penalized likelihood to fit random-effects hazard models (Therneau *et al.* 2003). We used the Akaike's Information Criterion (AIC) as a guide to model selection (Burnham & Anderson 2002).

BODY MASS

To further test the hypothesis that frailty values represented phenotypic quality, we used data on mothers' body mass (Pusey *et al.* 2005). For seventeen of the mothers in this analysis, we have multiple measures of body mass taken more or less regularly over the period 1967–2000 (see Pusey *et al.* 2005 for details). Pusey *et al.* (2005) fit a linear mixed model to body mass data on individual chimpanzees. This model contained a number of terms to account for known sources of variability in body mass (e.g. seasonality, age, sex). While complex, the statistical strategy employed in their analysis was essentially to fit a mixed longitudinal and cross-sectional growth model for male and female chimpanzees. Chimpanzees get larger as they mature, but some do so at a faster or slower pace. The mixed longitudinal nature of the body mass data allowed Pusey *et al.* (2005) to include individual random effects, conceptually similar to our frailty scores, that measure heterogeneity otherwise unaccounted for the

Table 1. Results of the best-fitting Cox proportional hazards regression

Covariate	β	Exp(β)	SE(β)	χ^2	d.f.	P-value
Mother's age	-0.170	0.843	0.035	23.36	1	< 0.001
Previous infant died	4.904	134.85	0.657	55.45	1	< 0.001
First interval	-0.997	0.369	0.428	5.43	1	0.020
Sex previous infant	-0.195	0.822	0.157	1.55	1	0.210
Mother's rank	-1.867	0.155	0.576	10.51	1	0.001
Phenotypic quality	-	-	-	45.73	18	< 0.001

β is the coefficient, exp(β) is the exponentiated coefficient, SE(β) is the standard error of the coefficient. Coefficients that were significant at the $P < 0.05$ level are indicated in bold. Mother's rank combines middle and low rank into a single category.

measured covariates such as age, sex, season, or dominance rank. For all individuals for whom we have body mass data, we used the fitted (multiplicative) individual random effect from the growth model as the basis for a measure of body mass independent of the large annual and seasonal fluctuations in weight experienced by the Gombe chimpanzees (Pusey *et al.* 2005). While the 17 cases would have created too much missingness to make the body mass random effect a practical covariate in the Cox models, we are nonetheless able to tentatively assess the association of putative measures of individual phenotypic quality (body mass) on individual frailty. We extracted frailty scores from the Cox model described in Table 1 and correlated these with the measure of individual quality. The clear expectation is that mothers with high frailty values (i.e. those predisposed to shorter birth intervals) should have higher body mass. Consequently, all correlations were assessed as one-tailed tests.

Results

Among the 117 interbirth intervals examined, a total of 77 were closed, for which the median interbirth interval (IBI)

was 58.5 months (range: min = 5.6, max = 109.0). Figure 1 plots the distribution of birth intervals cross-classified by observational status (censored vs. complete) and the status of the infant opening the interval (alive vs. dead). It is notable that for complete intervals for which the first infant survived, the observations tend to cluster around the mean IBI (top left panel). When intervals are censored and the first infant remains alive, there is a largely uniform distribution of IBIs which then trails off after the mean IBI. Intervals following the death of the first infant are clearly shorter, as expected, with a peak at 2 years. The best-fitting model to explain the duration of interbirth intervals included mothers' age, the first interval indicator, sex of the previous infant, loss of the previous infant, mother's rank and individual heterogeneity ($R^2 = 0.677$ out of a maximum of 0.99, LR = 127 on 22 d.f., $P < 0.001$; Table 1, Fig. 2).

Mother's age had a substantial effect on the birth hazard, reducing it by a factor of 0.843 per year after age at first birth. Loss of the infant that opened the interval had an enormous

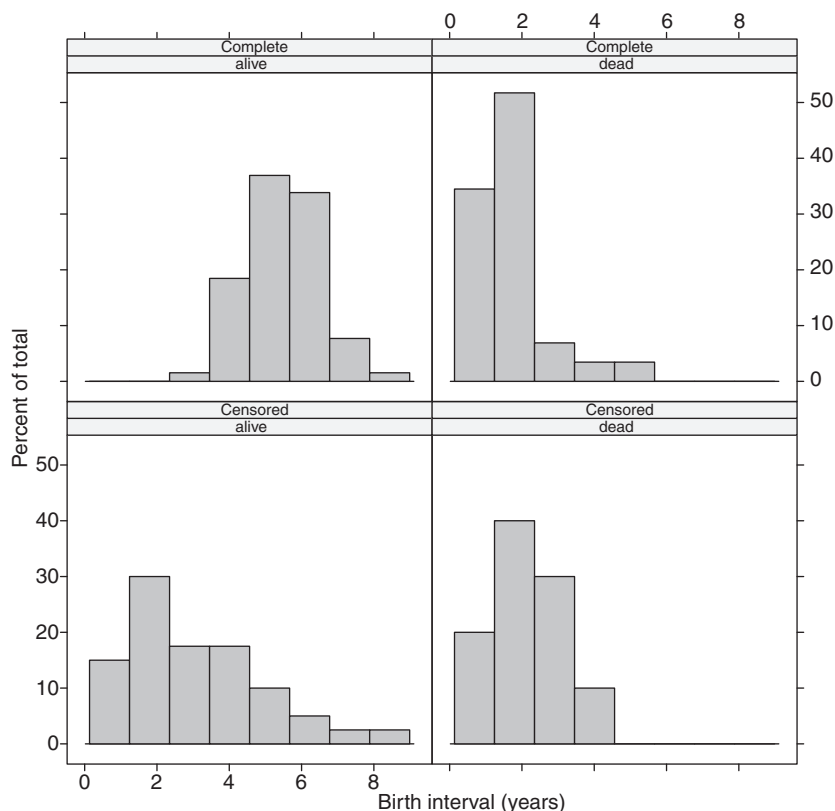


Fig. 1. Distribution of birth intervals cross-classified by observational status (censored or complete) and status of previous birth (alive or dead).

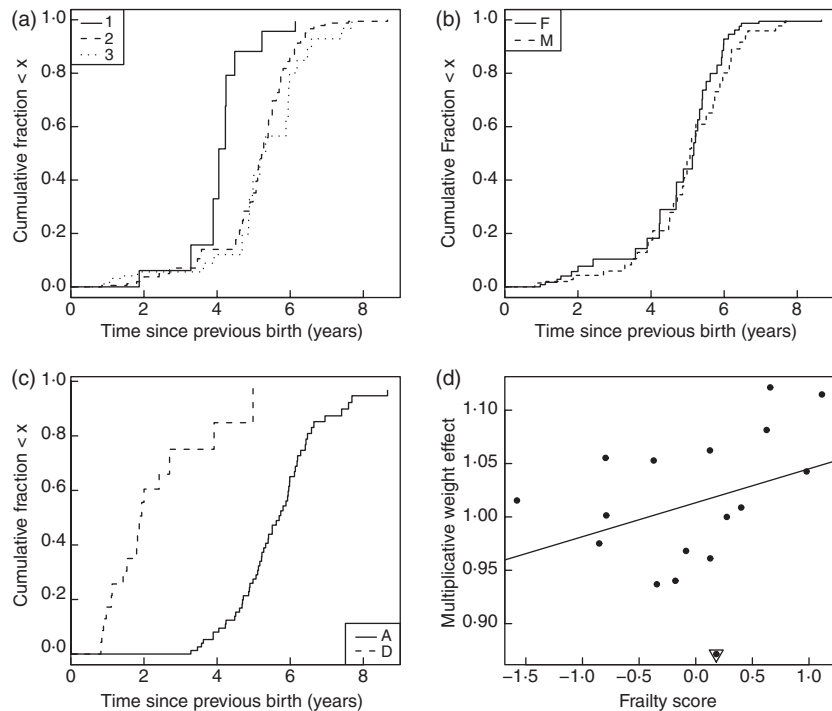


Fig. 2. (a) Cumulative event plot for births stratified by mother's dominance rank (1 = high, 2 = middle, 3 = low), (b) sex of previous infant, and (c) loss of previous infant (A = alive, D = dead). (d) Bivariate correlation between multiplicative weight effect from Pusey *et al.* (2005) and phenotypic quality measured by the frailty score of the Cox model. The point surrounded by the open triangle represents Flo. When Flo is excluded from the analysis, the correlation is significant at the $P < 0.05$ level (see main text).

effect on the birth hazard, increasing it by a factor of 134. Intervals following first birth were longer than subsequent intervals. Sex of previous infant did not have a statistically significant coefficient but the model including this term had lower AIC score than the model excluding it (Table 2). Mother's rank had an effect that was significant at the $0.1 > P > 0.05$ level, where low rank led to a 57.5% lower hazard for closing the birth interval, when full ranks were used. However, inspection of Fig. 2a led us to re-code dominance rank into a binary variable, corresponding to high rank and not high rank. Including this binary rank improved the model fit substantially and the final model reflects this

Table 2. Models and AIC values

Model	AIC	Δ
Age, previous infant death, first interval, binary rank, sex of previous infant	398.19	–
Age, previous infant death, binary rank, sex of previous infant	401.03	2.84
Age, previous infant death, first interval, rank, sex of previous infant	404.04	5.86
Age, previous infant death, rank, sex of previous infant	404.14	5.95
Age, previous infant death, first interval, binary rank	429.91	31.72
Age, previous infant death, first interval, rank	433.30	35.11
Age, previous infant death, first interval, sex of previous infant	489.84	91.65
Age, previous infant death, first interval	552.98	154.79

AIC, Akaike's Information Criterion. Δ represents the difference between the specified and best-fitting model. All models contain frailty as the data contain repeated measures.

dominance coding. When we consider only high ranking females against all others, the effect of rank is sizeable, with high ranking having a sixfold increase in the rate of closing IBIs.

Phenotypic quality, as measured by the individual random effect, had a considerable impact on the model fit ($\chi^2 = 45.73$, d.f. = 18, $P < 0.001$). This result is consistent with previous observations that the Gombe females appear to have characteristic birth intervals, regardless of their age (Goodall 1983). This result means that the birth intervals in our sample contain structured heterogeneity not captured in the measured covariates, which can be attributed to individual differences.

For the 17 females from whom data on body mass were available, individual heterogeneity and body mass were significantly correlated but only at the $0.1 > P < 0.05$ level ($r = 0.339$, $t = 1.396$, d.f. = 15, $P = 0.091$), providing weak support for the hypothesis that the individual heterogeneity scores measure some aspect of phenotypic quality. The bivariate plot of the multiplicative weight effect against frailty (Fig. 2d) shows that one individual, Flo, is an outlier. When we remove her, we find there to be a significant correlation at the $P < 0.05$ level ($r = 0.455$, $t = 1.91$, d.f. = 14, $P = 0.038$). We should note that body mass and rank are correlated, but rank was included in the Cox model from which we derive our heterogeneity estimates. This means that individual heterogeneity is correlated with body mass independently of rank.

Discussion

In the best-fitting model, mother's age, loss of the previous infant, the first interval indicator, a binary measure of

dominance rank (high vs. not) and individual heterogeneity had statistically significant effects on birth hazard. Including sex of the previous infant improved the model substantially (AIC = 398 vs. 429, Table 2), but its individual coefficient was not in itself statistically significant at the $P < 0.05$ level.

The effect of mother's age is consistent with the findings of Emery Thompson *et al.* (2007a) who analysed a larger, more heterogeneous sample of chimpanzee birth intervals from a variety of chimpanzee research sites (including Gombe). Unlike Emery Thompson *et al.*, we were able to include a number of other measured covariates in our model and the inclusion of these covariates probably allows a less biased estimate of the effect of reproductive senescence on chimpanzee fertility. Our results suggest that reproductive senescence is greater in the Gombe chimpanzees than reported by Emery Thompson *et al.* This may result from our ability to control for other covariates. However, Gombe is also the most seasonal sites included in Emery Thompson's sample and it is possible that the overall rate of senescence is higher at Gombe, reflecting the harsher environment. Such a pattern would be consistent with the cost-of-reproduction being paid in a condition-dependent manner (Jones 2005). Also consistent with many previous studies of primates (van Schaik 2000), infant death dramatically shortened interbirth intervals. Consistent with the findings of Robbins *et al.* (2006) in gorillas and various other primates, intervals for parity greater than two were shorter than the interval following the first birth, suggesting that primiparous females pay a greater cost of reproduction (Bercovitch *et al.* 1998).

In contrast to previous studies (Boesch 1997; Nishida *et al.* 2003), we found no significant increase in the length of the birth interval when the first birth in the interval was male once the effects of individual heterogeneity, rank, and loss of previous infant are accounted for. Figure 2b illustrates the negligible effect of sex of the previous infant on the birth hazard. To maximize comparability with previous studies, we also tested for differences limiting analysis to complete intervals in which the first infant survived. Using a linear mixed model, we detected no significant coefficient on either sex of previous infant or its interaction with rank ($n = 56$, $t = -0.990$, $P = 0.79$; $t = 1.188$, $P = 0.22$). We think that the most parsimonious explanation for this different outcome is the failure of previous studies to control for heterogeneity and account for censoring.

A number of previous studies of primates (e.g. *Macaca fascicularis*: van Noordwijk & van Schaik (1999); *Papio anubis*: Packer, Collins & Eberly (2000); *Papio cynocephalus*: Altmann & Alberts (2003); *Gorilla beringei*: Robbins *et al.* (2006)) showed a relationship between dominance rank and fertility, though this is not universally true (e.g. *Macaca radiata*: Silk (1990); *Cebus capucinus*: Fedigan *et al.* (2008)). Our results show that mother's dominance rank did not have a significant effect on the birth hazard at the $P < 0.05$ level when it was coded as high-middle-low. However, Fig. 2a suggests that high rank does actually confer higher fertility, while middle rank does not shorten IBIs relative to low rank. As a result, we re-coded mother's rank and found that high rank

conferred substantial benefits in terms of shortening the IBIs. The lack of a clear statistically significant positive relationship between mother's rank and birth interval at lower ranks may arise because of correlations between mother's rank and phenotypic quality. Clearly, phenotypic quality plays a role in an individual female's dominance rank. Rank is difficult to measure in female chimpanzees and as a categorical variable, it is quite a blunt measure. Phenotypic quality presumably captures some of the rank effect – thereby masking it in the Cox regressions – but also measures other factors not captured by categorical rank measures. Alternatively, it is possible that the imputed middle-ranks diminished any real effect on birth interval between middle and low-ranking females. That is, some females whose rank was actually low were coded as middle-ranking because not enough dyadic interactions with other females involving them were observed. Some high-ranking females have extremely short IBIs, and this, combined with differential infant survival (Pusey *et al.* 1997), helps account for substantial rank-associated differences in reproductive success.

The inclusion of frailty had a considerable impact on the model fit. This result means that the birth intervals in our sample contain structured heterogeneity not captured in the measured covariates that can be attributed to individual differences. Two hypotheses can explain this result. First, measurable differences in the quality of female core areas exist (Murray *et al.* 2006) and these may lead to different reproductive rates. Second, females may simply differ constitutionally from each other. Our ability to test the effect of core area quality was constrained by limited data. The available core area quality measurements were conducted in 2004 and it is clear from satellite images and other evidence that the forest composition has changed significantly over time at Gombe (Pusey *et al.* 2007). Nonetheless we attempted to include core area quality in the model by estimating core area quality for each interbirth interval for all females for whom detailed ranging data were available, using the 2004 measurements of density and size of key food trees. This halved the sample size and the model failed to converge.

One important way that females differ constitutionally from each other is in their body mass. The multiplicative body mass effect (Pusey *et al.* 2005), which provides an measure of individual mass controlling for known sources of variation, was significantly correlated with frailty in the small sample of females for which we have body mass measures (Fig. 2d). Body size has also been suggested to be a proxy measure for phenotypic quality in other species. Berube *et al.* (1999) suggest that the weak positive correlation between early and late fertility among bighorn sheep ewes (*Ovis canadensis*) was mediated by body mass. Large ewes live longer and reproduce more successfully. Similarly, Beauplet & Guinet (2007) found that subarctic fur seal (*Arctocephalus tropicalis*) of higher quality, as determined by a frailty measure (Beauplet *et al.* 2006), had greater body mass. The body mass difference between mothers of high quality vs. those of lower quality accounted for the differential ability of high-quality mothers to provision pups. Pelletier *et al.* (2007) found that

body mass in Soay sheep accounted for up to 20% of the observed population growth. The correlation between our measures of individual heterogeneity in fertility and body mass suggest that mass is indeed a measure of phenotypic quality among chimpanzees as well. Both Hill & Hurtado (1996) and Sear, Allal & Mace (2004) have found evidence for a positive (though sometimes curvilinear) effect of body size on human reproductive success.

One individual, Flo, was a substantial outlier in the bivariate plot of multiplicative weight effect vs. individual heterogeneity (Fig. 2d). Flo was already old (estimated age of 43) when the study began (Goodall 1986). Skeletal measurements show that she was a large framed individual (Zilhman, Morbeck & Goodall 1990) and when she and a small number of other chimpanzees were first weighed in 1967 she was heavier than the other two adult females. However, most of the measurements that contributed to her multiplicative weight effect were made in the years 1970–1972 just before she died when, despite her high dominance rank, she had already become extremely emaciated with worn teeth that made feeding very difficult (Pusey *et al.* 2005). Thus, the measurement in Fig. 2d does not accurately reflect her body mass over most of her life. The Cox model indicates that there is moderate reproductive senescence in the Gombe chimpanzees. Nonetheless, both Flo and her eldest daughter Fifi had births well into their forties. Flo thus appears to be the exception that proves the rule: Flo probably survived to a very old age because of high phenotypic quality and because she survived so long, most of the body mass measurements of her were low. If Flo did not have high phenotypic quality, she probably would not have lived to even be measured.

Our results indicate that fertility is a function of phenotypic quality. Understanding the ontogeny of phenotypic quality is now a fundamental open question. For example, to what degree, if any, is phenotypic quality heritable in chimpanzees? To what extent does it depend on non-heritable ontogenetic factors like maternal effects, early events, or birth seasonality (McLoughlin *et al.* 2007; Becker *et al.* 2008; Lang, Iverson & Bowen 2009)? To make predictions about aggregate patterns of fertility or the fertility-mediated fitness consequences of dominance, for example, we will need to better understand the ontogeny of differences in phenotypic quality. Shared frailty models (e.g. Cam *et al.* 2002) offer a promising if conceptually and technically demanding possibility to answering such fundamental questions in evolutionary ecology.

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