Journal of Animal Ecology

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Maternal age at birth shapes offspring life-history trajectory across generations in long-lived Asian elephants

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Abstract

1. Advanced maternal age at birth can have pronounced consequences for offspring health, survival and reproduction. If carried over to the next generation, such fitness effects could have important implications for population dynamics and the evolution of ageing, but these remain poorly understood. While many laboratory studies have investigated maternal age effects, relatively few studies have been conducted in natural populations, and they usually only present a "snapshot" of an offspring's lifetime.

2. In the present study, we focus on how maternal age influences offspring life-history trajectories and performance in a long-lived mammal.

3. We use a multigenerational demographic dataset of semi-captive Asian elephants to investigate maternal age effects on several offspring life-history traits: condition, reproductive success, and overall survival.

4. We show that offspring born to older mothers display reduced overall survival but higher reproductive success, and reduced survival of their own progeny. Our results show evidence of a persistent effect of maternal age on fitness across generations in a long-lived mammal.

5. By highlighting transgenerational effects on the fitness of the next generation associated with maternal age, the present study helps increase our understanding of factors contributing to individual variation in ageing rates and fitness.

Introduction

Maternal age is known to affect offspring performance (Hercus & Hoffmann 2000), with important ecological and evolutionary consequences (Kirkpatrick & Lande 1989; Räsänen & Kruuk 2007). Such effects arise because an individual's phenotype can be influenced not only by its genotype and the environment in which it is raised, but also by the mother's phenotype and environment (Bernardo 1996; J Marshall & Uller 2007). In essence, these 'maternal effects' can be defined as any aspect of the mother's phenotype that affects her offspring's phenotype and influences offspring fitness (Wolf & Wade 2009), including her age - the focus of the present study. In general, maternal effects can have profound implications for several offspring traits, including growth and development, and can act as anticipatory mechanisms that pre-adapt offspring to external environmental conditions (Lindström 1999). Such effects can thus have evolutionary consequences whenever they alter phenotypes in a population.

Maternal effects can arise during embryonic development and/or offspring growth, and may stem from the mother's habitat, diet, condition, physiology, and behaviour, which may vary with her age. Aside from the maternal genotype affecting offspring development directly, maternal effects can also depend on the trade-off in energy that mothers allocate to their offspring vs. to their own survival (Cody 1966). Energy allocation into survival (Metcalfe, Bull & Mangel 2002) and reproduction (Kindsvater *et al.* 2010) also varies as a function of maternal state. For instance, numerous empirical studies have shown that reproductive performance varies throughout life (Nussey *et al.* 2013). Thus, as age is a strong predictor of individual state, maternal effects can vary throughout a mother's lifetime (Benton, St Clair & Plaistow 2008), influencing the trajectory of her offspring (Mousseau & Fox 1998). In many vertebrate species, reproductive traits increase with age, to a peak of reproduction, after which individuals display age-specific deterioration (Jones *et al.*

2014). Low reproductive success in young parents is often due to inexperience (Newton, Marquiss & Moss 1981), whereas age-related effects later in life are attributable to declining parental condition through senescence. Maternal senescence, and thus maternal age, are expected to be key drivers of maternal effects, and intense allocation into early life reproduction can lead to decreased reproduction and/or survival late in life (Kirkwood & Rose 1991; Lemaître *et al.* 2015).

The first to describe such effects in humans was Bell (1918), who found that children from older mothers had shorter lives than children from younger mothers. Since then, the influence of maternal age on offspring health and survival (known as the Lansing effect (Lansing 1947)) has been observed primarily in humans (Myrskylä & Fenelon 2012; Gillespie, Russell & Lummaa 2013), and also through experimental studies on lifespan/survival of model systems and insects. For example, maternal age in *Drosophila* species is negatively correlated to the larval viability of the progeny (Hercus & Hoffmann 2000), and has a large influence on both offspring longevity and the shape of the age-specific mortality trajectory, with older mothers generally producing shorter-lived offspring (Priest, Mackowiak & Promislow 2002). However, the ubiquity and importance of maternal age effects demonstrated in laboratory organisms has to be validated in free-living populations. Although there is a growing body of work investigating how maternal age affects offspring life history in wild study systems, both in birds (Bogdanova, Nager & Monaghan 2007; Bouwhuis *et al.* 2010; Reid *et al.* 2010; Torres, Drummond & Velando 2011; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015) and in mammals (Jones *et al.* 2005; Descamps *et al.* 2008; Nussey *et al.* 2009; Rödel, Von Holst & Kraus 2009), such studies remain scarce.

As with laboratory research carried out largely on model organisms, studies on wild systems have mainly investigated the impact of maternal age on offspring lifespan/survival. For instance, offspring that had been raised by older parents had considerably decreased weaning success in grey seals (*Halichoerus grypus)* (Bowen et al. 2006), and poorer survival in red squirrels (*Sciurius vulgaris*) (Descamps *et al.* 2008), red deer (*Cervus elaphus*) (Nussey *et al.* 2009), red-billed choughs

(*Pyrrhocorax pyrrhocorax*) (Reid *et al.* 2010), and common terns *(Sterna Hirundo)* (Bouwhuis, Vedder & Becker 2015). Maternal age effects are also observed in Soay sheep (*Ovis aries*) and in mountain gorillas (*Gorilla beringei beringei)*, though the effect is in the other direction: the offspring of young parents are less likely to survive, which could be explained by the level of maternal experience in rearing offspring (Clutton-Brock & Pemberton 2004; Jones *et al.* 2005; Robbins *et al.* 2006). There are, however fewer examples of maternal age effects on offspring traits other than survival, and results are often contradictory. For example, the effect of maternal age on offspring weight/size is not universal across taxa: older females produce larger offspring in birds (Bogdanova, Nager & Monaghan 2007) and fish (Kindsvater, Rosenthal & Alonzo 2012), whilst older female insects generally produce smaller eggs (Giron & Casas 2003), and older mothers in red deer and bison produce offspring that weigh less (Nussey *et al.* 2009).

Importantly, most studies on maternal age-effects on wild populations present only a "snapshot" of an offspring's lifetime, and have primarily investigated the effects of maternal senescence on offspring survival to independence or first reproduction; seldom have there been studies looking at the effects of parental age over an offspring's entire lifetime. In addition, aside from those on humans (Gillespie, Russell & Lummaa 2013), only a handful of studies have been able to examine such effects over several generations at once (Bouwhuis *et al.* 2010; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). Because of this limitation, the effects of parental age on offspring performance beyond independence, and more generally on lifetime reproductive success and fitness in the next generation, are poorly understood in wild vertebrates (Rödel, Von Holst & Kraus 2009; Bouwhuis *et al.* 2010; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). Detecting these patterns requires long-term monitoring of large populations with an exact knowledge of parental age and of the lifetime fate of offspring - data that are difficult to gather in natural populations. To our knowledge, only three studies on wild birds have shown a transgenerational effect on the fitness of the next generation associated with parental age (Bouwhuis *et al.* 2010; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). However, the

results are mixed. In the great tit (*Parus major*), offspring hatched from older mothers suffer from an earlier onset, and stronger rate, of reproductive senescence later in life, but their lifetime reproductive success is unaffected by maternal age (Bouwhuis *et al.* 2010). In contrast, Schroeder *et al.* (2015) demonstrated that parental age has a negative effect on fitness in wild house sparrows (*Passer domesticus*): offspring with older parents produced fewer recruits annually when they themselves were adult than birds with younger parents. In the long-lived common tern, offspring from older parents also suffered from reduced lifetime reproductive success (Bouwhuis, Vedder & Becker 2015).

As a result, our understanding of how offspring fitness is influenced by maternal age and its evolutionary consequences is limited, especially in natural systems. Yet, such studies are essential to assess how inter-generational effects (such as the effects of delayed reproduction on offspring's fitness) will influence population dynamics (Arnold & Wade 1984; Charlesworth 1994). Moreover, the current literature is restricted to avian species (Bouwhuis *et al.* 2010; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). Thus, the extent to which maternal age at birth affects offspring trajectory across taxa and how these effects may depend on the pace of life remains unclear. Indeed, in theory, we could expect that reproductive senescence is more common in long-lived species, for which reproduction involves longer periods of offspring dependence and parents invest more in fewer offspring (Hamel *et al.* 2010; Bouwhuis *et al.* 2011). To further our understanding of how maternal age affects different aspects of offspring health and fitness, it is crucial to explore these questions in long-lived species that reproduce across several decades, and have information on different generations available.

Here, we take advantage of a large, unique multigenerational demographic dataset of semi-captive Asian elephants (*Elephas maximus*) from timber camps in Myanmar, for which maternal age and offspring life-history are known accurately (Robinson, Mar & Lummaa 2012; Lynsdale *et al.* 2017), to investigate maternal age effects on offspring life-history trajectories. The study population

is comprised of state-owned, semi-captive working Asian elephants in Myanmar (currently numbering ~2800 individuals), used in the timber industry and managed by the Myanma Timber Enterprise (MTE). Although elephants are managed as draft and transport animals by the MTE, they are more frequently described as "semi-captive" and live largely under natural conditions. To test the effects of maternal age on offspring life-history trajectories, we used demographic records and morphological data collected from the population to explore several offspring life-history traits: their morphological condition, reproductive probability, lifetime reproductive success, and juvenile/overall survival, in relation to the maternal age at offspring birth. If offspring reproductive success and survival can be used as proxies for fitness (Stearns 1992), our study may also have implications for how maternal age influences offspring fitness. We expect that offspring from older mothers could display poorer condition, a decrease in reproduction associated traits, and reduced survival.

Methods

Study population

Timber elephants inhabit forest camps distributed across Myanmar and are considered "semi-captive". The MTE imposes regulations on the daily and annual workload of elephants, which are consistent for all individuals in the study population. Although the population is "semi-captive", individuals largely experience natural conditions: 1) Elephants work in the day, but are released to the forest at night to forage naturally and interact with conspecifics, and food supplementation has been minimal historically; 2) Breeding events are natural with mating and births occurring in the forest at night, and with no reproductive management of the population; 3) Timber elephants are never culled, and numbers are not restricted or managed; and 4) Elephants benefit from bi-monthly

veterinary care, but only traditional/herbal medicines have been available for much of the study period. Records of births and deaths for individual elephants have been kept in logbooks by the MTE for over a century, who impose regulations on workload, travel distance, and working period for all animals in the population (Mar 2002).

Calves born in captivity are raised by both their biological mothers and allomothers. Allomothers are family members (grandmothers, aunts, sisters), which provide care and in some cases allosuckling for the calves (Lee 1987; Lahdenperä, Mar & Lummaa 2016). Reproductive females are given rest from mid-pregnancy (11 months into gestation) until their calf reaches its first birthday. Mothers are then used for lighter work duties until the calf reaches age four and is capable of foraging independently. Calves are separated from their mother and tamed/trained at around the age of five, at which point they are assigned a rider, name, logbook, and registration number. After taming, elephants are trained and are used for light work duties until the age of 18, at which point they enter the full workforce until retirement at 55. The MTE maintains their logbooks until the death or departure of the individual.

We used logbook data to investigate how maternal age was related to offspring subsequent growth, survival, and reproduction. This dataset includes the identification number and name of each animal, their birth origin (captive-born or wild-caught), date and place of birth, mother's identification number and name (if known), year and place of capture (if wild-captured), year or age of taming, date of death or last known date alive, and cause of death. The last known date alive includes individuals who are still alive and individuals whose records may have been lost after a certain point due to logbook damage, transfer, or –in rare cases- escape of the animal. We included calves that had identification numbers and complete records for birth date, birth origin, entry date and last known date alive. We excluded calves without known mothers and calves without complete records of their mothers from our analyses. Birth dates are known precisely for captive-born individuals (72.8% of individuals included in this study), whereas the age at capture (and thus

approximate birth year) of wild-caught individuals is estimated by comparing their height and body size with captive-born elephants of known age, and through morphological assessment (Mumby *et al.* 2015a; Lahdenperä *et al.* 2018). Calf data was available for 11 regions in Myanmar (see Regions in SI-A). This demographic sample included 2437 calves (female=1205, male=1232) born to 1096 mothers (of which 134 were also grandmothers), all of which entered the population between 1911 and 2009. The oldest reproducing female in our study was 71 years old, and the mean maternal age of all calves was 31±17 years (median=30 years). Daughters' age at first reproduction varied between 8 and 31 years of age (mean=19.18 ± 4.35, median=19), and reproductive daughters produced between 1 and 9 calves during their lifetime or follow-up period (mean=2.25 ± 1.32, median=2).

In addition to demographic data, the weight (kg) and body measurements (cm) of elephants were recorded in five working camps in Myanmar. Repeated monthly measures were taken between December 2011 and October 2016 (though not every month – for details on morphological data collection, see (Mumby *et al.* 2015a), and all elephants were measured in mornings on non-work days. A total of 175 (female=101) elephants aged between 5 and 62 years with known maternal age were included in morphological analyses.

Statistical analysis

Determining confounding variables

We tested the effect of maternal (F1) age at the birth of the calf (F2) on survival, reproductive, and morphological calf traits. For all traits, we first build a 'full' model with calf (F2) traits as dependent variables, and both time-invariant and age-specific confounding variables, and we retained in the 'base' model the statistically significant fixed factors as obtained from Wald tests

(see SI-D). We then tested maternal and grandmaternal age effects by adding them to this 'base' model. The purpose of these base models was to initially reduce the dimensionality of the full models to avoid over-parameterization.

The full models included birth-order as a binomial variable (1st born vs. later born), because it is known to associate with calf traits in this population (Mar, Lahdenperä & Lummaa 2012). Inter-birth interval was included as a 5-level factor: "first-born"; "low" (i.e. interval of 2 to 4 years between two calves); "medium" (i.e. interval of 5 to 8 years); "long" (i.e. interval of birth greater than or equal to 9 years); and "unknown" (Mar, Lahdenperä & Lummaa 2012). We included the mothers' (F1) birth origin (captive-born or wild-caught) as a fixed factor. We also included an interaction between the birth origin of the mother (F1) and the number of years between the time of capture and the birth of the calf (F2) (no main effect), and an interaction between the birth origin of the mother and her age at capture from wild (no main effect) to account for the fact that for wild-caught animals only, the traumatic effects of capture may decrease with time and age (Lahdenperä *et al.* 2018). We included calf birth season (dry or monsoon season) and calf sex as binomial factors (Mumby *et al.* 2015b). For calf (F2) survival, we also included the region (SI-A) and the birth cohort (birth decade) period as fixed factors (Jackson *et al.* 2019). For calf (F2) body condition, we included the year and the season (dry or monsoon season) of measurement as factors (Mumby *et al.* 2015c). For daughter (F2) reproduction, we also included a censor variable indicating whether daughters are still alive. When testing the effect of grandmaternal (F0) age on grandcalf survival, we included calf cohort, calf sex, calf birth season, inter-birth interval, grandmothers' origin (captive or wild), and the maternal (F1) age (4 age-class term as it was retained the best-fit in analyses of maternal age) as fixed factors and calf identity as a

random factor. In all reproductive and body condition models, we included cohort, region or camp, calf identity and mother identity as random factors (See SI-C).

Dependent variables

Calf and grandcalf survival

The influence of maternal (F1) age at the birth of the calf on calf survival was explored using two response variables: survival to 5 years, corresponding to the weaning age (Mar 2002), and overall survival (longevity). We also analysed the influence of grandmother (F0) age (at the birth of the grandcalf's mother) on grandcalf survival for the same two periods. The exact age of death was not known for all calves and grandcalves in the dataset: 1379 and 201 were still alive at the end of the study, respectively. Consequently, we were able to correct for any confounding effects on survival estimates by indicating whether observations were right-censored (Gimenez *et al.* 2008). To do so, we modelled survival as a function of time to death using Accelerated Failure-Time (AFT) models fitted with the *survreg* function in the 'survival' package (Therneau, Atkinson & Ripley 2014). We used survival models to account for censored individuals. To fit models, we followed 3 steps. First, we determined which survival function at each stage in life history – Weibull, Gaussian, exponential, extreme, lognormal or loglogistic – best described the data by comparing model fit using AIC, the "Akaike Information Criterion (AIC)". For all survival analyses, we retained the lognormal distribution (See SI-B). Second, we tested the effect of potentially confounding time-invariant variables on calf survival (See SI-C, D for results). For the different calf and grandcalf survival traits, we retained the birth cohort, the inter-birth interval, calf sex and the region as fixed factor in the base model. Third, we accounted for

potential among-individual variation in survival and possible selective disappearance (via viability selection – which acts on traits and favours individuals with improved survival prospects)(Fisher 1930) using a frailty component (Vaupel, Manton & Stallard 1979). We included this as individuals differ in their age-specific mortality risk, leading to the observed distribution of longevity (corresponding to the distribution of individual mortality risk at a given age). As a result, frailer individuals are more likely to die at early ages than more robust individuals; the average risk of mortality observed at the population level decreases with increasing age. In these conditions, not accounting for individual heterogeneity in mortality risk by including a frailty component will lead to biased assessment of age-specific mortality (Vaupel & Yashin 1985). We incorporated individual frailty by entering the individual identity as a normally distributed random effect with one degree of freedom, using the function *frailty (Therneau, Atkinson & Ripley 2014)* (see SI-B for results).

Daughter (F2) reproduction

To investigate the effects of maternal (F1) age on daughter (F2) reproductive traits, we fitted generalised additive mixed models (GAMMs) to test the potential non-linear effect of maternal age. We used the function *gamm* in the 'mgcv' library (Wood 2006).

The effect of maternal (F1) age on daughter (F2) reproduction was explored in several ways. First, among daughters (F2) that reached the age of 25 (i.e. approximate age at which the reproductive peak occurred), we analysed their probability to reproduce at least once in their life (N=195, of which 121 reproduced at least once). We included the probability to reproduce at least once in life as a dependent variable with a binomial error distribution (absence of reproduction=0, 1

otherwise). We included daughters' (F2) longevity as a covariate and the birth cohort, the region and the identity of the mother (F1) as random factors.

We analysed the effect of maternal (F1) age on daughter (F2) age at first reproduction (AFR) (N=149) by including age at first reproduction as a dependent variable with a Poisson error distribution. The minimum age at first reproduction in our dataset was 8 years old, a similar age to other elephant populations (Sukumar 2006). We included daughters' longevity as a covariate, daughters' birth season as a fixed factor and the birth cohort, region and identity of the mother as random factors. AFR was assessed in daughters that reproduced at least once in their life irrespective of their lifespan or survival to 25 years, which substantially reduced the dataset (N=149). 28 daughters reproduced at least once before dying under the age of 25 years old, which explains the different sample size of 121 daughters reproducing at least once included in the analysis of reproductive probability above.

Using the same sample of females as for the AFR analysis, we also analysed the effect of maternal (F1) age on a proxy of lifetime reproductive success (referred to as LRS hereafter), defined as the number of calves (F3) produced throughout daughters' life or censored life (F2) (N=149), which was included as a dependent variable with a Gaussian distribution with a log-link function. We retained mother (F1) origin as a fixed factor and the birth cohort, the region and the identity of the mother as random factors. We also included a factor indicating whether daughters (F2) were censored or not, following Hayward *et al.* (2014). For females that we included in LRS analyses, the average lifespan of censored females was 32.4 years old, which was concurrent with the mean adult life expectancy (32.7 years old), improving our confidence in the measure of LRS.

Finally, we analysed the effect of maternal (F1) age on the age-specific variation in annual reproductive success (N=149) of daughters (F2) that reproduced at least once in their life. Annual reproductive success was scored as a binomial trait (0 = did not produce a calf in a given year of life; 1 = produced at least one calf), and analysed using GAMM models. We performed the analysis

between ages 8 and 40 years because only 17 females in our sample reproduced after 40 and mostly only once. We included the daughter's (F2) identity, the region and the birth cohort as random factors. We performed an AIC model selection where we tested an interaction between maternal age and daughter age. As above, we tested several patterns of maternal and daughters age (linear, quadratic, categories).

Calf morphology

To investigate the effect of maternal (F1) age on offspring size, we analysed 1492 measures of weight and 1772 measures of height for 175 calves. As calf age is linked to its size, we used standardised heights and weights as dependent variables, to account for multiple measures of the same individuals across their lifespans - these were obtained by dividing an individual's actual size/weight measurement by the predicted size/weight at that age, as obtained from von Bertalanffy growth curves from this population (presented in (Mumby *et al.* 2015a). Separate curves were used for males and females. For both morphological traits, we fitted models with GAMMs and included inter-birth interval as a fixed factor and the camp, the year of measurement, the birth cohort, the identity of the calf and mother as random factors. For calf height, we also included the measure season as a fixed factor.

Model selection procedure

In the next stage, we tested maternal (F1) and grandmaternal (F0) age effects on each of the dependent variables by adding these age effects into the 'base' models determined above, using several functions and testing for the most statistically competitive age-specific models. We selected the most competitive survival, reproduction and morphology models using the Akaike information criterion (AIC), considering each random effect as one parameter (Pinheiro & Bates 2000). We

retained the model with the lowest AIC as the best model. Where the difference in AIC between competing models was less than two, we retained the simplest model (Burnham & Anderson 2002). We also calculated the Akaike weight (AICw) for each model to provide the relative likelihood that the model was the best among the candidate models. We report only the results for the best models. Further details about model selection are presented in SI-E. We performed our analyses using the R software package, version 3.1.1 (R Development Core (Team 2015).

Testing maternal (F1) and grandmaternal (F0) age as predictors of calf life-history

In addition to maternal (F1) and grandmaternal (F0) age effects, we also tested an interaction between maternal/grandmaternal age and the sex of the calf to test for sex-differences in the effects of maternal age in all calf trait analyses. Of the 1096 mothers (F1), 373 were captive-born (exact age known). Grandmaternal (F0) age was taken to be the age of the grandmother at the birth of the grandcalf's mother. Age-specific variation in life-history traits such as reproduction and survival is heterogeneous, asynchronous, and potentially non-linear (Walker & Herndon 2010; Jones *et al.* 2014). Therefore, to account for non-linear relationships in age-specific life-history traits, we tested the effect of mother (and grandmother) age at birth in several ways: as linear or linear and quadratic covariates, as a smoothed function (using penalized regression splines in GAMM), and as one of three different categorical factors. The mothers and grandmothers age classes were standardised for both mother and grandmother age analyses, and were based on the largest dataset (N=2437).

First, following (Mar, Lahdenperä & Lummaa 2012) and (Lahdenperä, Mar & Lummaa 2016), we use a 4-level factor (ages 9-21/22-28/29-37/38-71), using the quartiles of the maternal age distribution. Second, we used a 5-level factor (ages 9-21/22-28/29-37/38-49/50-71), which was the same as the 4-level factor, but with the fourth level divided in two to distinguish the oldest mothers in the population, in order to determine whether these oldest mothers were driving the age effect. We did not include grandmaternal effects using the 5-level factor because the oldest grandmaternal

age-class contained only 7 grandmothers and 15 calves. Third, we used the 4-level factor to build a 2-level factor (ages 9-28/29-71 for maternal age, 9-28/29-61 for grandmaternal age).

Disentangling the within- and between- maternal age differences on calf survival and daughters' LRS

When investigating maternal (F1) age-related variation in life history traits, one important challenge is to disentangle the within- and between- individual maternal age differences. Indeed, if selective disappearance occurred in this population, low quality individuals would die younger, and the oldest age class would be composed of a non-random subset of the best quality mothers producing long-lived calves with high reproductive performance (Vaupel, Manton & Stallard 1979; Van de Pol & Wright 2009). We thus tested for a selective disappearance effect on calf survival (F2) and daughters' LRS (F2). To do so, we used the method of Van de Pol and Wright (2009), including both the mean age per mother (F1) (between-maternal age effects) and the deviation value from the mean age of mothers (within-maternal age effects) in the base model of overall calf survival (F2) and daughters' LRS (F2) (see SI-D and SI-J for details).

Results

Influence of maternal (F1) age on calf survival

The mean life expectancy of female and male calves at birth (life expectancy including juvenile stages) in our sample was 19.5 and 11.6 years in our dataset, respectively. The mean life expectancies for adults (>11 years – start of reproduction) in our sample were 32.7 and 24.9 years

old for females and males, respectively. We first examined how maternal age was related to variation in calf survival in juveniles and across lifespan.

Maternal (F1) age did not significantly influence calf survival up to five years of age (weaning) in the full sample (see SI-E), but calf survival of both sexes to five years decreased linearly with maternal age when only calves from captive-born mothers were included (72% of the total sample, $\beta= 0.981 \pm 0.007$, these results are based on the captive subset not an interaction between maternal age and birth origin). Maternal age did, however, have a significant influence on overall calf survival across all ages in both sexes (See SI-E). F2-individuals born to older mothers aged between 38 and 71 years old showed a significant reduction in survival of 33% (Event time ratio=0.679, SE [0.596; 0.773]) when compared to those born to young mothers aged between 9 and 21 years old (Fig. 1a). Calves from mothers aged between 22-28 years old displayed a similar reduction in survival (Event time ratio: 0.688 [0.609; 0.778]). The survival of calves born to mothers between 29 and 37 years was also lower than those born to mothers between 9 and 21, but the relationship was not significant (Event time ratio: 0.820 [0.724; 0.928]). We observed a linear selective disappearance of poor-quality mothers, which influenced maternal age effects on overall calf survival ($\beta_{between}=-0.02\pm0.01$, p=0.04, see SI-J).

Influence of grandmaternal (F0) age on grandcalf survival

When accounting for maternal (F1) age, grandmaternal (F0) age (at the birth of the grandcalf's mother) did not influence grandcalf survival to age five, but it did influence overall grandcalf survival in both sexes (SI-E). The most competitive model included grandmaternal age as a 2-level factor (above and below 30 years old, the median grandmother age). Grandcalf survival decreased by 19% (Event time ratio: 0.812[0.694; 0.949], Fig. 1b, SI-E) for grandmothers aged between 30 and 61 years old at the birth of

their daughter when compared to those born from young grandmothers (between 11 and 29).

Influence of maternal (F1) age on daughter (F2) reproduction

We found that daughters' LRS (F2) showed a positive quadratic relationship with maternal age (F1); the LRS of daughters (F2) declined with increased maternal age until 37 years ($\beta=-0.366\pm0.125$), and then increased again for daughters from mothers older than 37 ($\beta=0.299\pm0.157$; Fig. 2). We did not observe any selective disappearance of poor-quality mothers on daughters' (F2) LRS ($\beta_{between}=-0.0007 \pm 0.02$, p=0.98, see SI-J). Because we found that maternal (F1) age affected daughter (F2) survival (see above), we also tested the effect of maternal (F1) age on daughter (F2) LRS, correcting for differences in daughter (F2) longevity. When correcting for longevity, maternal age did not significantly influence daughter LRS ($\beta= 0.002 \pm 0.004$, see SI for model selection), suggesting that the effect of maternal age on daughter LRS was mainly driven by differences in daughter longevity rather than their fertility. This was further supported by the absence of a significant relationship between maternal age and either daughters' reproductive probability or age at first reproduction (see SI-E for model selection). Moreover, maternal age did not influence the age-specific variation in daughters' annual reproductive success ($\beta= -0.0002\pm0.005$, see SI-I).

Influence of maternal (F1) age on calf morphology

Overall calf body mass showed a positive quadratic effect with maternal age. Calf body mass decreased by 7.8% as a function of maternal age at birth for mothers up to 30 years old, and increased thereafter by 18.6% (N=175, $\beta=-0.014\pm0.005$, $\beta^2 = 0.0002\pm0.00005$; Fig. 3). Calf body height, however, did not change with maternal age (N=175, $\beta =$

0.00006±0.0003), suggesting that maternal age influenced offspring body condition but not offspring overall size.

Discussion

The present study on semi-captive Asian elephants shows evidence for effects of maternal age on a comprehensive range of demographic and morphological traits in a long-lived species. We find maternal (F1) age effects on offspring (F2) body weight, on overall offspring (F2) survival and LRS; and grandmaternal (F0) age effects on grandoffspring survival. In detail, we observe a decline of overall offspring survival with increasing maternal age, which is consistent with existing literature on how maternal age influences lifespan across taxa (Descamps *et al.* 2008; Nussey *et al.* 2009; Bouwhuis *et al.* 2010; Reid *et al.* 2010; Torres, Drummond & Velando 2011; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). We also show that maternal (F1) age exerted positive quadratic effects on offspring (F2) LRS. Daughters (F2) from younger and older mothers (F1) displayed higher LRS than daughters born to middle-aged mothers, in contrast to previous studies in other taxa, which found lower LRS in offspring born to older mothers (Rödel, Von Holst & Kraus 2009; Torres, Drummond & Velando 2011; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). There are different non-mutually exclusive processes that may explain the pattern we observe. First, middle-aged mothers, who produce daughters with lower LRS, are at the peak of both their annual reproductive rate (Hayward *et al.* 2014) and their working activity (Mar 2002), and may therefore be able to invest less into each offspring born at this time, producing lower quality daughters with lower LRS. This hypothesis is supported by the similar pattern we see on offspring body condition: offspring from younger and older mothers are heavier than offspring born to middle-aged mothers. Second, the higher LRS detected in daughters (F2) born to older mothers (F1) might be attributed to

the selective disappearance of low quality individuals that older mothers might produce. Given our finding that overall survival is lower in calves born to older mothers, it is possible that the putative low quality offspring produced by older mothers die before being able to produce offspring of their own. Thus only high quality offspring with high LRS would remain in the population. Even though there was no effect of mothers' viability selection when assessing how maternal age influences daughters' LRS; we found such an effect when assessing how maternal age influences calves' survival in the considerably bigger dataset, which supports the above hypothesis. Interestingly, when correcting for longevity, maternal age no longer affected daughter LRS. This suggests that the effect of maternal (F1) age on daughters' LRS (F2) is mainly driven by the influence of maternal age on daughter (F2) longevity (but not their fertility; see SI-G), thus supporting the idea that low quality daughters born to older mothers would die before being able to reproduce. Notably, even though daughters (F1/F2) born to older mothers (F0/F1) display higher LRS, there is a reduction in survival associated with the progeny of these females (F1/F2), with grandmaternal (F0) age negatively influencing grandoffspring survival rates.

Our findings are likely to have evolutionary implications and reveal the hidden consequences of late-life reproduction. Identifying maternal age as a parameter influencing offspring body condition, reproduction (mediated by longevity), and overall survival, suggests that there are long-term maternal age effects on offspring's phenotype in this population. Thus maternal age might be a factor underlying variation in ageing rates in this semi-captive population. As LRS in long-lived species is predominantly determined by longevity (Clutton-Brock 1988), including closely related African elephants (Lee *et al.* 2016), our observed patterns of maternal age effects could reveal an evolutionary strategy of older mothers aiming to favour calf reproduction and condition, and therefore greater indirect fitness, instead of calf longevity. Indeed, calves from older mothers might increase their reproductive performance by producing more offspring (resulting in the observed pattern of higher LRS) thus maximising their own fitness and the indirect fitness of their mothers, but at the cost of their own longevity.

Nonetheless, to understand the evolutionary consequences of maternal age effects in our study population, we need to disentangle what constitutes an outcome of life-history strategy versus the workload imposed on the elephants. Even though our study system is a working population, variation in life-history traits in calves born to mothers of different ages are unlikely to be the sole result of differences in workload across ages for several reasons. First, pregnant females and mothers with calves under the age of one year old are relieved of any workload, reducing the likelihood of immediate workload impacts on calves. Second, the workload of an individual elephant is also determined by other factors in addition to age, such as health, general capability, and climate, meaning age-specific workload may not be a fully reliable indicator of actual workload (Mar 2002). Third, while there are potentially differences in workload for young mothers under the age of 18, the majority of births in younger age classes are to mothers over the age of 18 and already in the full working population (age 18-55). In the maternal age category between 9 and 21 years of age, approximately 60% of all calves born are to mothers over 18 (peak in reproduction at age 19-20 years, see Hayward *et al.* (2014)), Fig.H1 in SI-H), and 80% to mothers over 16 (which are used for transport and lighter carrying work). Thus, maternal age effects are unlikely to be the result of age-specific workload alone and represent more general patterns of life-history in this species. Instead, we propose that detrimental maternal age effects could be exacerbated by the negative influence of workload.

Our results may be influenced by three factors that we are currently unable to investigate further. First, matings in our study population take place naturally in the forest with both captive and wild bulls, preventing us from having information on male LRS, and our LRS data is thus limited to females. Given the sexual dimorphism observed in this species, we have to keep in mind that the maternal age effects we observe on female LRS might differ in males. Second, we cannot exclude paternal effects as an additional influence on offspring life-history trajectory, either interplaying with maternal effects or operating independently. Finally, the grandmaternal age effect suggests that we cannot exclude that the effect of maternal age might be partly due the effect of grandmaternal age.

More broadly, we cannot exclude a potential influence of allomaternal care in general: other close female relatives are more likely to be available (i.e. alive) and more influential to provide allo-care, especially for the early life reproducers (Lahdenperä, Mar & Lummaa 2016), which could for instance explain the higher calf survival in young mothers. However, our current dataset does not permit us to disentangle these effects. Nonetheless, if grandoffspring survival rates can be used as a proxy for individual fitness (Clutton-Brock 1988), our findings suggest that there is a transgenerational reduction of fitness associated with increased maternal age. We show a persistent effect of maternal age on fitness across generations for the first time (to our knowledge) in a free-living mammalian population.

Our results raise a key question: how are maternal age effects transferred to the offspring? Although identifying the proximate mechanisms linking maternal age effects across generations is crucial, the physiological mechanisms that potentially underlie these responses are poorly understood. One molecular mechanism by which maternal age could alter the physiology and phenotype of offspring is through epigenetic modifications such as DNA methylation, histone modifications, or small RNA transmission (Bonduriansky, Crean & Day 2012). A study in humans has shown that increased maternal age was associated with reduced methylation at four adjacent CpGs in one gene in newborns (Markunas *et al.* 2016), thus providing evidence from a long-lived mammal that maternal age could affect offspring health and phenotype through epigenetic mechanisms. Such epigenetic marks could have pleiotropic effects, being beneficial early in life to pre-adapt offspring to external environmental conditions, but being detrimental later in life, and thus might explain why they are not reset. Telomere shortening is another potential candidate for mediating maternal age effects. Telomeres are known to shorten with age both at the organism level (Hall *et al.* 2004) and in oocytes (Kalmbach *et al.* 2013); short telomeres are linked with reduced lifespan (Wilbourn *et al.* 2018). Evidence also indicates that telomere length is heritable in several taxa (see Reichert *et al.* (2015) for an overview). Offspring of older mothers could therefore display shorter telomeres (Asghar *et al.* 2015), which might potentially be associated with reduced fitness (Pauliny *et al.* 2006)

and lifespan (Wilbourn *et al.* 2018). A third explanation could be related to mitochondrial function, which is known to decline during ageing (Bratic & Larsson 2013; Hebert *et al.* 2015). In addition, mitochondria are maternally inherited (Giles *et al.* 1980), and mitochondrial function seems a likely candidate to mediate the effects of maternal age on offspring phenotype (Shama *et al.* 2016). Given our limited understanding of the mechanistic base underlying maternal effects in any species, future studies should focus on this question if we are to fully assess the evolution of maternal effects and their role in population dynamics.

Irrespective of the potential mechanisms involved in mediating transgenerational effects, and more specifically maternal age effects, our study underlines the effects of maternal age at conception on offspring survival and fitness across generations. Our data adds to the small, but growing, number of studies investigating transgenerational effects on the fitness of the next generation associated with parental age in free-living populations (Bouwhuis *et al.* 2010; Bouwhuis, Vedder & Becker 2015; Schroeder *et al.* 2015). By highlighting a substantial fitness cost of late reproduction (i.e. negative influence of grandmaternal age on grandoffspring survival rates, despite higher LRS of daughters born to older mothers), our results help increase our understanding of the factors (here, maternal age) that contribute to the variation in ageing rates and fitness among individuals. Thus, maternal age effects appear to be transmitted across generations, supporting the idea that such effects may play a fundamental role in the evolution of ageing (Priest, Mackowiak & Promislow 2002; Bouwhuis *et al.* 2010), and are important evolutionary agents.

Acknowledgements

This study adheres to the ethical guidelines of the University of Turku. All methods were performed in accordance with the Horizon2020 guidelines.

Author Contributions

Data accessibility

Data from this study have been deposited in Dryad: http://doi.org/10.5061/dryad.k47bn07 (Reichert et al 2019).

Funding

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Figures and figures captions

Figure 1. Variation in **a)** observed overall calf survival and, **b)** observed overall grandcalf survival as a function of maternal (the most competitive model included age as a 4-level factor, using the quartiles of maternal age distribution to retain a balanced sample between age categories) and grandmaternal age (the most competitive model included grandmaternal age as a 2-level factor), respectively. The horizontal line within the box indicates the median, boundaries of the box indicate the 25th- and 75th-percentiles, and the whiskers indicate the highest and lowest values of the results. The survival estimates were generated correcting for significant confounding factors: Cohort, sex, region for maternal age and cohort, sex, interval of birth, region for grandmaternal age. Calves are from captive- and wild born-mothers.
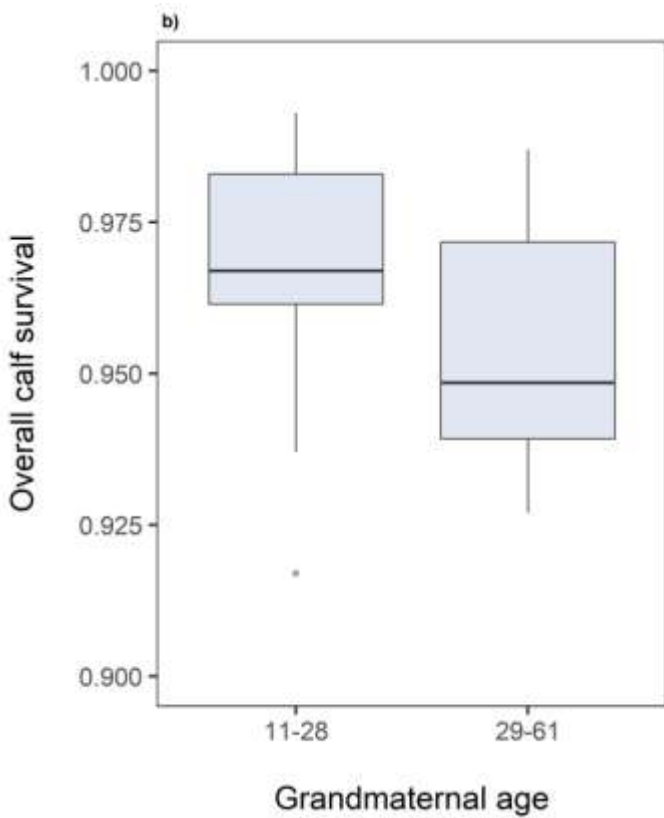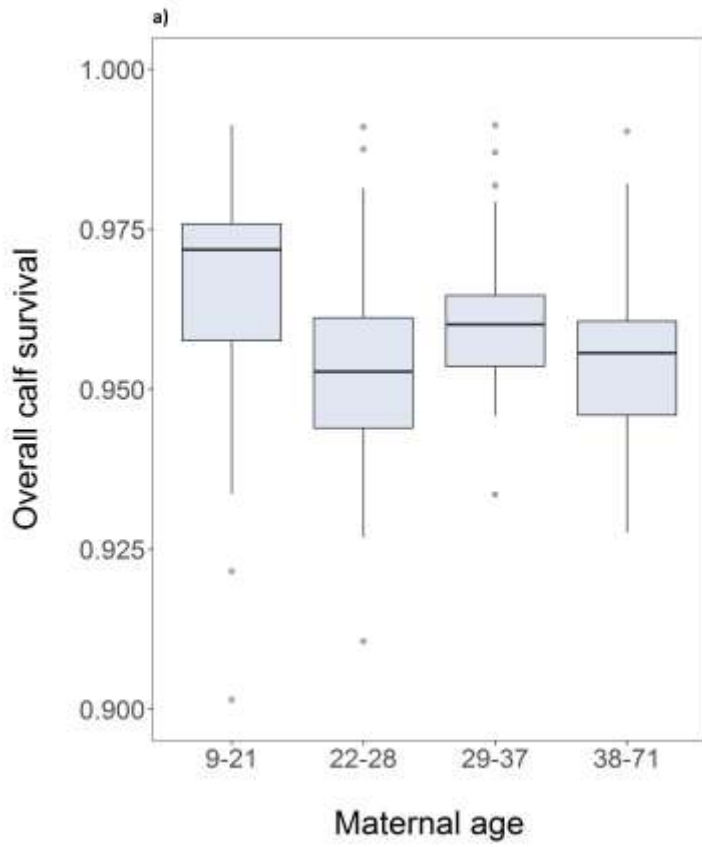
Figure 2. Variation in daughters' LRS (number of calves produced throughout life) as a function of maternal age (included age as a 4-level factor, using the quartiles of maternal age distribution), correcting for significant confounding factors: mother origin. Black points indicate raw LRS values and standard error bars for each maternal age class, blue squares indicate model predicted values and confidence intervals.
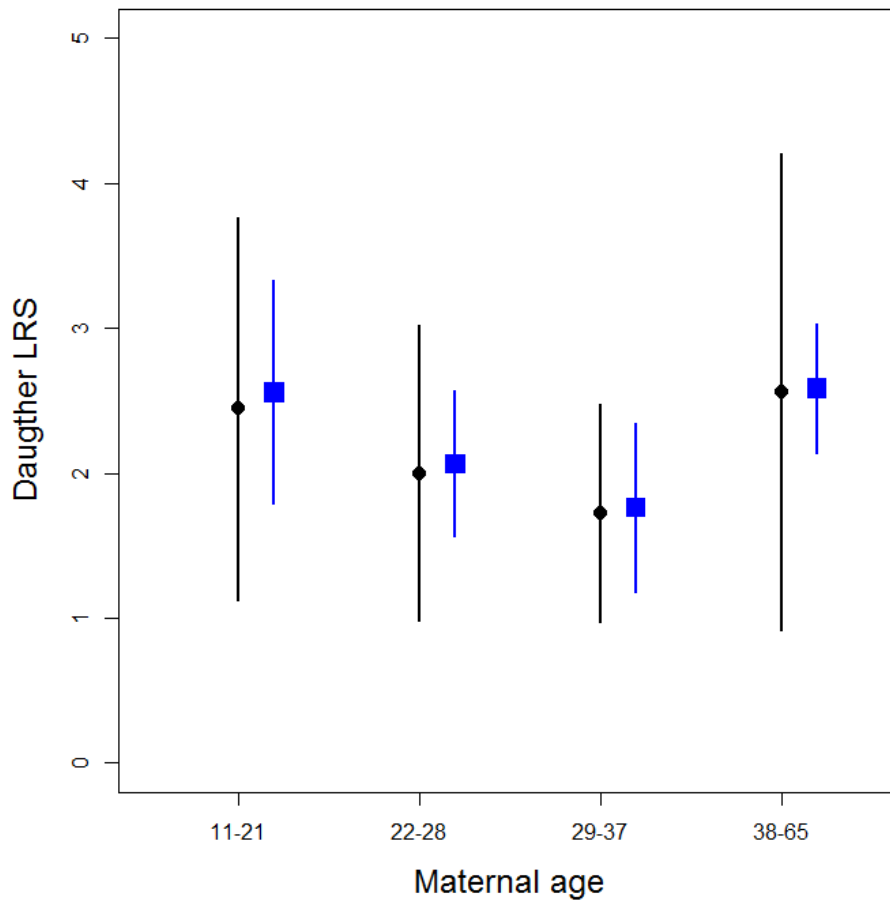
Figure 3. Variation in standardised calf body weight as a function of maternal age (included as a continuous quadratic term), correcting for significant confounding factors: interval of birth. Filled black circles represent mean standardised body mass per age and standard error bars. Open grey circles represent raw standardised observed body mass data. Blue solid line represents the prediction from the best model. Blue dashed lines correspond to confidence intervals.