

Research



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Maternal reproductive senescence shapes the fitness consequences of the parental age difference in ruffed lemurs

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In humans, pronounced age differences between parents have deleterious fitness consequences. In particular, the number of children is lower when mothers are much older than fathers. However, previous analyses failed to disentangle the influence of differential parental age *per se* from a direct age effect of each parent. In this study, we analyse the fitness consequences of both parental age and parental age differences on litter size and offspring survival in two closely related species of lemurs living in captivity. As captive lemurs do not choose their reproductive partner, we were able to measure litter size and offspring survival across breeding pairs showing a wide range of parental age differences. However, we demonstrated that the effect of the parental age difference on litter size was fully accounted for by female reproductive senescence because females mating with much younger males were old females. On the other hand, both parental age difference and female reproductive senescence influenced offspring survival. Our results emphasize the importance of teasing apart the effect of parental reproductive senescence when investigating the health and fitness consequences of parental age differences and also provide new insights for conservation programmes of endangered species.

1. Introduction

Although increasing evidence of reproductive senescence in both sexes [1,2] suggests that the interplay between mother and father age should markedly influence parental reproductive success [2], we still know very little about how the magnitude of parental age differences affects the fitness of either parents or offspring. So far, most studies of parental age differences have been performed on humans [3–5] to assess the fitness costs of the nearly ubiquitous preference of men towards women younger than themselves that is observed worldwide [6–8]. For instance, a detailed investigation of three historical Sami populations revealed a convex relationship between fecundity and parental age differences, with a maximum number of children occurring when men married women approximately 14 years younger than them [4]. Such a higher fecundity at birth when men are much older than women seems to be a common feature of human populations [3–5,9–11]. Most studies published so far only used the number of children born to measure parental reproductive success. However, from a Darwinian fitness perspective, early child survival has to be considered too [12]. To the best of our knowledge, only Helle *et al.* [4] analysed the influence of age differences between partners on a fitness metric, the lifetime reproductive success (LRS) that was measured as the number of children reaching 18 years of age. These authors reported a

convex relationship from which LRS peaked when women married men 14.6 years older than them [4]. So far, the fitness consequences of parental age differences remain unknown in species other than humans. However, many confounding factors may mitigate the relationship between differences in parental age and both parental and offspring fitness observed in humans (e.g. socioeconomic status [5]), which makes arduous any firm biological interpretation. In addition, these studies failed to disentangle the influence of differential parental age *per se* from a direct effect of the absolute age of each parent [13,14].

Reproductive senescence has now been repeatedly reported in animals [1], being most extensively studied in females [2]. Evidence of declining litter size with increasing female age initially documented in laboratory rodents [15] is now widespread across polytocous species in the wild (e.g. [16,17]). On the other hand, the effect of father age on litter size has been much less studied, although the spate of evidence for a decline in the efficiency of male's reproductive functions with increasing age suggests reproductive senescence [2,18]. Besides affecting the quantity of offspring produced per year, parental age can also have detrimental consequences on offspring health and viability, which translate into fitness costs. Nowadays, the burden of being born from old mothers has been reported in several species [2,19], especially in terms of lower offspring survival [20,21]. More recently, it has also been reported that a decline in the quantity or quality of male care with increasing age in species with parental care impairs offspring survival, independently of the maternal age (see [22] for a case study in the wandering albatross, *Diomedea exulans*). Overall, there is currently an increasing interest in the study of senescence in maternal and paternal effects [2,23], which might provide an innovative angle to shed light on the fitness consequences of parental age differences.

We performed the first analysis of the consequences of parental age differences on litter size and offspring survival in a non-human vertebrate, and we assessed how reproductive senescence in either fathers or mothers could contribute to these fitness costs. We took advantage of an exceptionally high-quality dataset of two closely related species of lemurs [24,25]: the red ruffed lemur, *Varecia rubra* and the black and white ruffed lemur, *Varecia variegata*. As with humans and other species of primates, lemurs have a slow life history [26], which leads to an expected quite weak intensity of senescence [27]. In addition, studying captive populations is particularly relevant to assess fitness consequences of parental age differences because zoological gardens pair females and males according to their degree of genetic relatedness to maximize genetic diversity but not according to age or to age differences in the breeding pair [25]. This rule allowed us to evaluate the fitness consequences of parental age differences on both parents and offspring over a wide range of age differences and independently of any mate choice tactic that could have prevented us from detecting fitness costs.

2. Methods

(a) Study populations

Data were obtained from the published International Studbook for ruffed lemurs [24,25] compiling data for the majority of

V. rubra and *V. variegata* living in 322 different zoos (see the electronic supplementary material, appendix S1). The final dataset included 1721 (756 females and 965 males) and 3637 (1589 females and 2048 males) individuals from *V. rubra* and *V. variegata*, respectively, encompassing 2279 litters and 4686 offspring. Since both lemur species share the same habitat and display similar lifestyle (i.e. in terms of mating system and parental care) and life-history traits (e.g. age at first reproduction) [25,28,29], we performed all analyses on a dataset combining individuals from the two species and included the species as a fixed additive or interactive factor.

(b) Measures of litter size and offspring survival

We estimated offspring survival as the probability to reach the weaning age (i.e. 146 days for the two ruffed lemur species, [24,25]) to cover the period during which offspring mortality is mostly dependent of parents. In ruffed lemurs, litter size varies from 1 to 7 offspring.

(c) Data analyses

We analysed the influence of the parental age difference on both litter size and offspring survival. Following previous work that addressed the same question in human populations [4,5], we computed the difference in parental age as the father's age minus the mother's age (both measured in years).

In a first step, we analysed the influence of the parental age difference on litter size. We fitted generalized linear mixed effects models (package 'lme4' [30]) using a Poisson distribution with a log link. We included the identity of both mother and father as random effects to avoid any pseudo-replication problem caused by repeated measures for some individuals [31]. We then fitted a set of various models including different possible shapes for the effect of the parental age difference with or without interaction with the species effect (coded as '0' for *V. rubra* and '1' for *V. variegata*) that was included to control for possible differences between these two lemurs. The different models tested included a constant model and a set of models with the parental age difference as a covariate fitted using a linear, quadratic or threshold function. We fitted two types of threshold models: one threshold model with one slope (i.e. constant effect of the parental age difference beyond the threshold) or two slopes (i.e. the slope coefficient of the parental age difference changes after the threshold). The fit of threshold models is increasingly used when modelling senescence nowadays (e.g. [32–35]) because it allows accounting for the potential inability of quadratic models to capture reliably the full age-dependence [36].

For offspring survival, analyses were performed using generalized linear mixed effect models for binomial distribution with a logit link including mother, father and litter identities as random effects. The procedure we followed was then the same as for litter size. Moreover, we also tested the effect of the offspring sex (as a fixed factor, coded as '0' for females and '1' for males) to control for a possible difference in offspring survival between sons and daughters and included litter size as covariate to account for the expected negative relationships between offspring survival and number of offspring [37].

For both litter size and offspring survival, model selection was based on the Akaike information criterion (AIC, [38]). We also calculated the AIC weight to measure the relative likelihood of each model to be the best among the set of fitted models. When the difference of AIC between two competing models was less than 2, we retained the simplest model to satisfy parsimony rules [38]. All the analyses have been repeated with the zoo of birth included as a random effect to take into account the influence of possible differences in care and management of lemurs among zoos. As including the zoo effect did not improve the model fit (electronic supplementary material, table

Table 1. Parameter estimates from models selected to assess variation in litter size and offspring survival in relation to the parental age difference for ruffed lemur species in captivity. (Parental age difference (PAD) in a threshold model corresponds to the slope before the threshold. For random effects, the variance (Var.) and standard deviation (s.d.) are given.)

fixed effects		random effects						
	variables	β	95%CI	z value		N	Var.	s.d.
litter size (n = 2279 litters)	intercept	0.888	0.786;0.990	17.14	mother identity	600	0.00	0.00
	PAD (threshold = -4.2 years)	0.024	0.004;0.044	2.41	father identity	525	0.00	0.00
	species (<i>V. variegata</i>)	-0.075	-0.135;-0.015	-2.44				
offspring	intercept	3.052	2.435;3.669	9.69	litter identity	2256	4.81	2.19
survival (n = 4686 offspring)	litter size	-0.343	-0.505;-0.181	-4.15	mother identity	633	1.02	1.01
	PAD (threshold = +3years)	-0.058	-0.113;-0.004	-2.10	father identity	552	1.61	1.27
	species (<i>V. variegata</i>)	-0.409	-0.867;0.049	-1.75				

S1), we only reported results from models without the effect of the zoo of birth.

Once the model describing the effect of the parental age difference was selected for litter size and offspring survival, we investigated whether this result could be simply accounted for by the absolute age of one or both parents. We thus added an additive effect of father's or mother's age (using linear, quadratic or spline models or with age fitted as a categorical variable (i.e. full-age model). For the spline models, we performed generalized additive mixed effects models with the package 'gamm4' [39]. We could not include the parental age difference, the maternal age and the parental age within the same model because of the information redundancy among these covariates (i.e. mother's age = parental age difference - father's age). We compared models with and without the parental age difference based on AIC. When the effect of the parental age difference on litter size or offspring survival was accounted for by an effect of the age of one (or both) parents, the model including only the absolute age of the parents was retained.

3. Results

Among the 2279 breeding pairs, the age of the father was positively associated with the age of the mother. The slope of the relationship was lower than 1 (0.50 ± 0.01), which indicates that older females are generally paired with younger males across zoological gardens (electronic supplementary material, figure S1).

(a) Litter size

The selected model of the variation in litter size according to the parental age differences included a threshold effect of the difference between the mother's and the father's age and the species (electronic supplementary material, table S1). Mean litter size decreased at a rate of 2.4% per added year of parental age difference when the mother was older by 4.2 years or more than the father (table 1 and figure 1a). However, when the mother was younger or older by less than 4.2 years than the father, the mean litter size did not vary with the parental age difference. The pattern was the same in both species but *V. variegata* consistently had a lower mean litter size (a difference of 0.18 ± 0.05 offspring) than *V. rubra* (table 1 and figure 1a). To disentangle the effects of parental age difference from the effects of reproductive senescence in both parents, we included either maternal or

paternal age as a covariate in the model. The selected model included an effect of species and mother's age (fitted with a spline model) only and the parental age difference was not retained anymore (Δ AIC between model with a threshold effect of parental age differences and species and models with mother's age fitted with a spline model and species: 18.51, electronic supplementary material, table S2). In both *Varecia* sp., litter size increased until the mother reached 9 years of age and decreased afterwards (figure 1b).

(b) Offspring survival

The selected model for the variation in the probability for a given offspring to reach the weaning age (i.e. offspring survival) included a threshold effect of the parental age difference, the species and the litter size (electronic supplementary material, table S1). Offspring survival slightly increased when the mother was older than the father but was not influenced by the parental age difference when the mother was younger than the father by 3 years or more (table 1 and figure 2a). Overall, *V. variegata* had a lower survival than *V. rubra* (table 1 and figure 2a) and the offspring survival was negatively influenced by litter size (table 1). When we included the effects of paternal or maternal age, the selected model included a quadratic effect of maternal age in addition to the species and litter size effects (electronic supplementary material, table S2). Offspring survival increased with mother's age until 11.5 years and decreased afterwards (electronic supplementary material, table S3 and figure 2b). However, the model with the lowest AIC (electronic supplementary material, table S2) also included a weak threshold effect of the parental age difference.

4. Discussion

In ruffed lemurs, mother's age strongly influences both litter size and offspring survival. Lemur litter size slightly increases with mother's age until 9 years and then decreases steadily. Senescence in litter size has been previously documented in polytocus species [16,40,41], and matches the senescence in pregnancy rate often reported in monotocus vertebrates [1,36]. The steep decline in litter size is likely to be a direct consequence of a general depreciation of the female reproductive machinery [2,37], notably in the

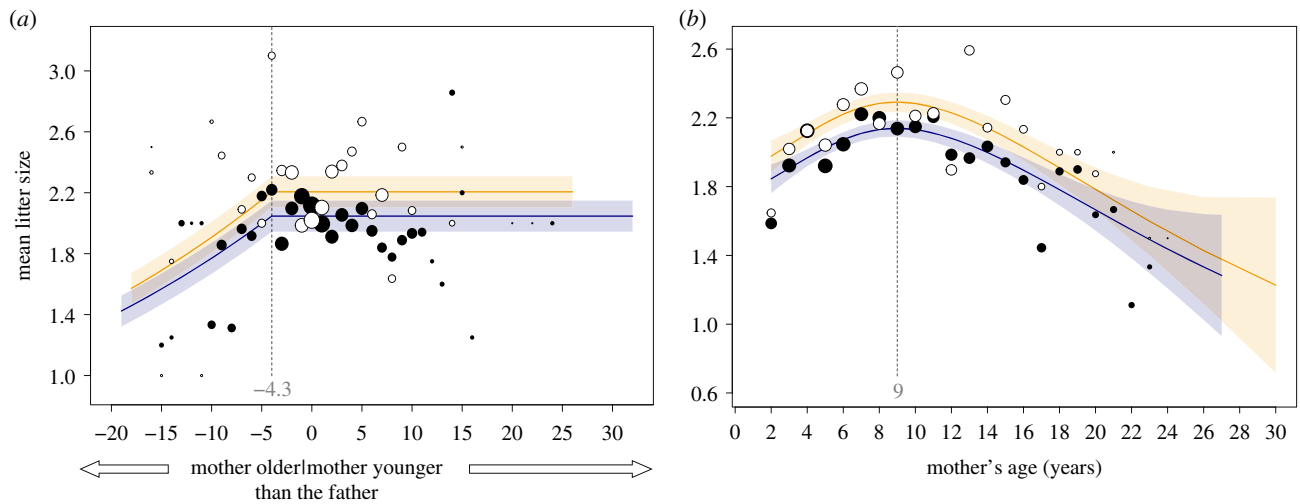


Figure 1. Relationship between litter size and (a) the parental age difference (PAD, computed as father's age minus mother's age) or (b) the mother's age for *V. rubra* (open circles, orange (light grey) line) and *V. variegata* (full circles, blue (dark grey) line), along with the 95% confidence interval ($n = 2279$ litters). Points size is proportional to the sample size. PAD negatively influences litter size only when the mother is of the same age or older than the father; the PAD has no influence when the mother is younger than the father. The effect of PAD is only due to the maternal age effect with a maximum of litter size reached around 9 years of age and a decline afterwards, which indicates reproductive senescence. (Online version in colour.)

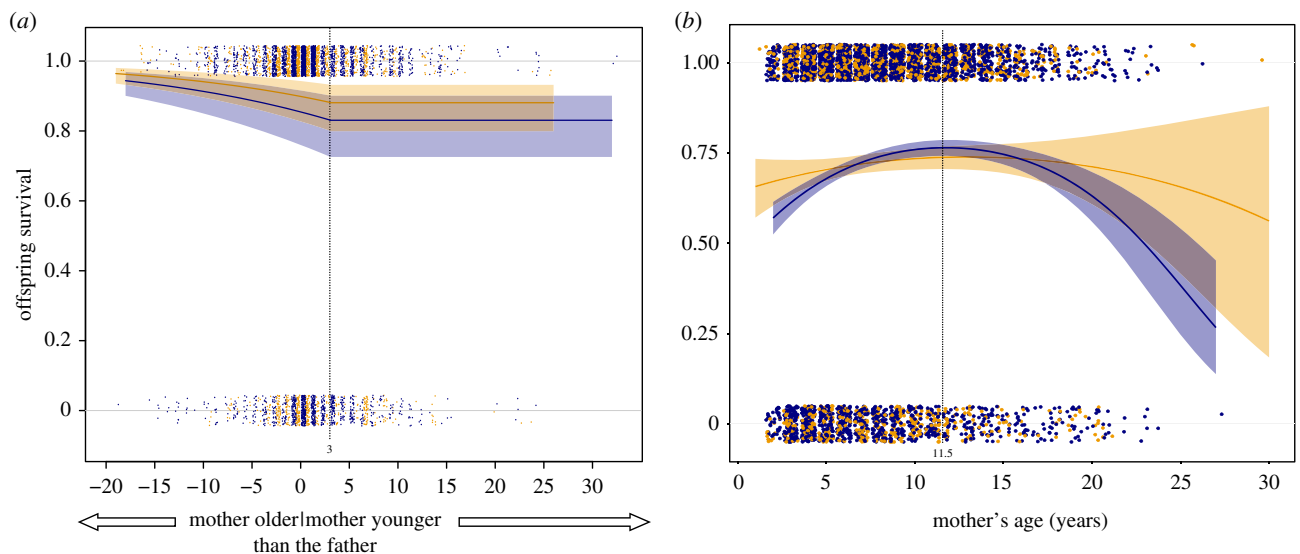


Figure 2. Relationship between offspring survival and (a) the parental age difference (PAD, computed as father's age minus mother age) or the mother age (b) for *V. rubra* (open circles, orange (light grey) line) and *V. variegata* (full circles, blue (dark grey) line), along with the 95% confidence interval ($n = 4686$ offspring). PAD positively influences offspring survival only when the mother is of the same age or older than the father; the PAD has no influence when the mother is younger than the father. Moreover, maternal age influences (quadratic effect) offspring survival, with a maximum survival when mothers are about 11.5 years of age and a decline afterwards, which indicates reproductive senescence. (Online version in colour.)

number of mature follicles at old ages [42]. The strong negative effect of female chronological age on litter size might be strengthened by an enhanced lifespan of lemurs in captivity. However, ruffed lemurs have a slow pace of life and the gain of longevity provided by a protected environment should not be particularly pronounced [43]. Our findings show that not accounting for the effect of maternal age might lead to spurious conclusions when analysing the effect of parental age difference. In our study, an absence of control for maternal age would have wrongly led to conclude that parental age difference negatively influences litter size when the mother is 4.2 years older than the father.

The resulting effect of litter size contrasts with the analyses performed on offspring survival. From the offspring's point of view, a survival cost tends to show up when mothers

are slightly older or younger than their partners. Juveniles born from fathers older than mothers might have a poorer health, independently of both the father's absolute age and the magnitude of the parental age difference. Although several studies performed in humans have revealed that children born from fathers older than mothers can suffer from some specific health issues (e.g. autism [44]), there is so far no overall assessment of parental age differences on offspring condition. We emphasize the need of further studies to investigate the effect of parental age differences on offspring survival. This would constitute a first step to decipher the complex interaction between mother's and father's age on offspring health. However, the effect of the parental age difference on offspring survival almost vanished when controlling for parental age. Offspring survival steadily

decreased when mothers were older than 11.5 years, which might involve a decreased quantity or quality of care provided to the offspring [2]. Milk quality and quantity may decrease with increasing female age, which could negatively impact offspring survival as infants reach about 70% of their average adult body mass within their four first months of life [45]. Then, the increase of offspring survival for females of captive ruffed lemurs between 2 and 11 years of age may be related to experience gained by the mother (e.g. [46] in mammals, [47] in birds) while the decrease of offspring survival may be related to a decrease of milk quality when the mother ages. This argument has been proposed to explain the similar reproductive pattern reported in females of wild Milne Edwards' sifaka involving a decrease of infant survival when females were older than 18 years of age [48].

The absence of any effect of father chronological age on litter size or offspring survival suggests that male reproductive senescence is absent in ruffed lemurs, at least under captive conditions. In that context, a decline in ejaculate quality with increasing age appears unlikely and contrasts with results reported in the abundant literature in humans [18]. While repeated measures of ejaculate quality are scarce in wild populations of mammals [2], a few studies have revealed senescence in testes size [49,50], a robust proxy of sperm production. This suggests that the probabilities of fertilizing one or more female might be impaired at old ages, especially in promiscuous species who are under strong selection for an elevated sperm production (e.g. [51] for primate species). Captive environment might explain the absence of a father age effect because the intensity of sperm competition [52] is likely to be artificially reduced (i.e. females in oestrus are generally paired with only one male). Therefore, even if males suffer from senescence in sperm quantity, they might still provide enough viable sperm to fertilize the female oocytes.

Our findings might also have consequences in terms of conservation and management. The two lemur species we studied are highly threatened in the wild as a direct consequence of both hunting [53] and loss of favourable habitats [54]. In that context, the reintroduction of captive-bred individuals is now seen as a powerful way to reinforce or re-establish natural populations of lemurs (see [55] for a case study of the golden lion tamarin, *Leontopithecus rosalia*). Bringing a specific attention to the age of the parents before setting any breeding pair and, for the specific case of ruffed lemurs, avoiding pairs with old females, would maximize the reproductive success of individuals living in captivity. We hope that our findings will stimulate similar investigations across a wide range of vertebrate species. We propose that the age range of optimal parental age differences is shaped by the sex-specific patterns of reproductive senescence. Since the timing and the intensity of both male and female reproductive senescence vary a lot across species [2,36], an assessment of the optimal range of parental age differences in terms of reproductive success might be highly beneficial for conservation programmes.

Data accessibility. Data used in this study have been already published in Whipple [24,25].

Authors' contributions. M.T., J.M.G. and J.F.L. conceived the study. M.T., M.W., G.D. and A.S. compiled the dataset. M.T., X.T. and A.D. analysed the data. M.T. and J.F.L. wrote the first draft of the paper and then received input from all authors. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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