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Jean-François Lemaître, Victor Ronget, Jean-Michel Gaillard. Female reproductive senescence across mammals: A high diversity of patterns modulated by life history and mating traits. *Mechanisms of Ageing and Development*, 2020, 192, pp.111377. 10.1016/j.mad.2020.111377 . hal-03453115

HAL Id: hal-03453115

<https://cnrs.hal.science/hal-03453115>

Submitted on 27 Nov 2021

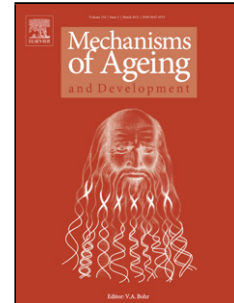
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Journal Pre-proof

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PII: S0047-6374(20)30173-1
DOI: <https://doi.org/10.1016/j.mad.2020.111377>
Reference: MAD 111377

To appear in: *Mechanisms of Ageing and Development*

Received Date: 23 June 2020
Revised Date: 15 September 2020
Accepted Date: 30 September 2020

Please cite this article as: Lemaître J-François, Ronget V, Gaillard J-Michel, Female reproductive senescence across mammals: a high diversity of patterns modulated by life history and mating traits, *Mechanisms of Ageing and Development* (2020), doi: <https://doi.org/10.1016/j.mad.2020.111377>

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Female reproductive senescence across mammals: a high diversity of patterns modulated by life history and mating traits

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Article for the special issue “*Understanding the biology of aging to better intervene*”

HIGHLIGHTS

- Reproductive senescence is widespread across mammals
- Onset and rate of reproduction are influenced by the phylogeny
- Onset and rate of reproduction vary with the species pace of life
- Promiscuous females display an earlier age at the onset of reproductive senescence
- Females that display an induced ovulation mode show an earlier at the onset of reproductive senescence

ABSTRACT

Senescence patterns are highly variable across the animal kingdom. However, while empirical evidence of actuarial senescence in vertebrates is accumulating in the wild and life history correlates of actuarial senescence are increasingly identified, both the extent and variation of reproductive senescence across species remain poorly studied. Here, we performed the first large-scale analysis of female reproductive senescence across 101 mammalian species that encompassed a wide range of Orders. We found evidence of reproductive senescence in 68.31% of the species, which demonstrates that reproductive senescence is pervasive in mammals. As expected from allometric rules, the onset of reproductive senescence occurs later and the rate of reproductive senescence decreases with increasing body mass and delayed age at first reproduction. Moreover, for a given pace of life, females displaying a high level of multiple mating and/or with induced ovulation senesce earlier than females displaying a low level of multiple mating and/or with spontaneous ovulation. These results suggest that both female mating behavior and reproductive physiology shape the diversity of reproductive senescence patterns across mammals. We propose future avenues of research regarding the role played by environmental conditions or reproductive features (e.g. type of placentation) on the evolution of reproductive senescence.

Keywords: Aging, Comparative biology, Fertility, Life-history, Reproduction

1. Introduction

From an evolutionary biology perspective, the process of senescence corresponds to a decrease in the age-specific contribution to fitness (Cohen et al., 2020; Gaillard and Lemaître, 2020; Monaghan et al., 2008). Therefore, senescence is mostly studied through a decline in demographic rates with increasing age (i.e. actuarial and reproductive senescence). Historically, senescence was thought to not show up in the wild because animals were expected to die from harsh environmental conditions or anthropogenic effects (e.g. hunting) before experiencing a decline in age-specific survival or reproductive rates (Nussey et al., 2013). Thanks to the increasing number of long-term field studies - where individuals are monitored from birth to death (Clutton-Brock & Sheldon 2010), and the subsequent demographic analyses of these populations, the view that demographic senescence does not occur in the wild has been totally revisited (Nussey et al. 2013). Yet, after pioneer descriptive studies suggesting that mortality increases in late life (e.g. Caughley, 1966), empirical evidence currently indicates that actuarial senescence is pervasive across vertebrates with determinate growth in the wild (Brunet-Rossinni and Austad, 2006; Nussey et al., 2013), whereas reproductive senescence was considered to be inexistent in the wild for a much longer period (e.g. Caughley, 1976). On the contrary, the negative effects of age on reproductive performance have been documented in laboratory rodents (e.g. Leslie and Ranson, 1940) and human populations (e.g. Tietze, 1957) for a while. The first reports of reproductive senescence in the wild only emerged in the late 70s (Coulson and Horobin, 1976; Ollason and Dunnet, 1978; Perrins and Moss, 1974; Sinclair, 1977), following the insightful work by Emlen (1970), who stated that age-specific reproductive rates should increase to a peak, then stay relatively constant during a prime-age stage (i.e. the period of adulthood between the beginning of the reproductive peak and the onset of reproductive senescence) before declining in late life.

Empirical evidence of reproductive senescence from wild populations of vertebrates is now compelling (Nussey et al., 2013). So far, these case studies have been almost entirely performed on females (but see Lemaître and Gaillard, 2017 for a review of evidence in males), simply because accurate paternity assignments in the wild require the use of molecular tools. Age-specific declines in a wide array of traits reflecting female reproductive success have been documented, such as breeding proportions (e.g. Photopoulou et al., 2017), birth rates (e.g. Lee et al., 2016), number of offspring produced at birth (e.g. Sparkman et al., 2017) or at the end of parental care (i.e. at weaning or fledgling, e.g. Thorley et al., 2020), and

offspring survival (e.g. Karniski et al., 2018). Interestingly, it has been suggested that female reproductive senescence patterns can markedly differ across species (Baudisch and Stott, 2019; Jones et al., 2014), even between closely related species. For instance, a population-level comparison of reproductive senescence in terms of breeding success across three albatross species has revealed that the age at the onset of reproductive senescence was much earlier in the wandering albatross (*Diomedea exulans*) than in both the black-browed albatross (*Thalassarche melanophris*) and the grey-headed albatross (*Thalassarche chrysostoma*) (Froy et al., 2017). Likewise, the southern fulmar (*Fulmarus glacialisoides*) showed clear evidence of senescence in breeding success, whereas the snow petrel (*Pagodroma nivea*) did not (Berman et al., 2009). Despite these reports of contrasted patterns of age-specific decline in reproductive performance with increasing age, there has been so far no attempt to quantify the occurrence and the variation in reproductive senescence across a wide range of species, or to identify the ecological and biological factors underlying the diversity of patterns. This contrasts with the increasing number of comparative analyses that focused on actuarial senescence (Bronikowski et al., 2011; Lemaître et al., 2020c; Péron et al., 2019b; Ricklefs, 1998, 2006; Ricklefs and Scheuerlein, 2001), which have notably revealed that life-history strategies (e.g. Garratt et al., 2013; Ricklefs, 2010) and environmental conditions (Colchero et al., 2019; Lemaître et al., 2013; Tidière et al., 2016) modulate both the onset and the rate of actuarial senescence. So far, most comparative analyses of age-specific reproductive data in mammals have focused on the evolution of post-reproductive lifespan (e.g. Alberts et al., 2013; Cohen, 2004; Ellis et al., 2018) and did not investigate among-species differences in the onset or rate of reproductive senescence. Only Jones and colleagues (2008) analyzed interspecific differences in female reproductive senescence patterns (i.e. measured as the age-specific decline in the number of recruited offspring) across 19 species of birds and mammals. They found that the rate of reproductive senescence decreased with increasing generation time, a reliable measure of the species position along the slow-fast continuum (Gaillard et al., 2005). Thus, slow-living species had a lower rate of reproductive senescence than fast-living species (Jones et al., 2008; see also Gaillard et al., 2016).

The aim of this work is twofold. First, we assess whether female reproductive senescence is the rule rather than the exception across mammals by accurately quantifying reproductive senescence using a large sample of mammalian species that display a high diversity of lifestyles and life history strategies. This first step allowed quantifying among-species variation in both the onset and the rate of reproductive senescence. Second, we investigate the role of several ecological, biological and life history traits in shaping the

diversity of reproductive senescence patterns observed across mammalian females. Among these factors, we focus on the role played by the phylogeny, the species position along the slow-fast continuum, the mating behavior and the ovulation mode.

Following comparative analyses of many life history traits (e.g. Kamilar and Cooper, 2013; Wootton, 1987), notably the rate of actuarial senescence (e.g. Lemaître et al., 2020b), we expected closely related species to share more similar reproductive senescence patterns than distant species across the phylogeny. We also expected the onset and the rate of senescence to occur earlier and to increase, respectively, with increasingly fast-living life history as a direct consequence of the covariation among all biological times (i.e. life history traits expressed in time units that positively covary across species, see Gaillard et al., 2016; Ronget and Gaillard, 2020). Moreover, we investigated whether the number of mating partners and the ovulation mode influenced the timing and intensity of reproductive senescence. In most mammals, females generally copulate with more than one male during a given reproductive event (Gomendio et al., 1998; Hayssen and Orr, 2017; Soulsbury, 2010). The propensity of females to mate repeatedly within a reproductive event increases from monogamous species to polyandrous or polygynandrous species, which is considered as a way to increase fitness through genetic benefits (e.g. increased genetic diversity among offspring, Jennions and Petrie, 2000; Stockley, 2003). However, multiple mating promotes sperm competition (i.e. when sperm from two or more males compete to fertilize a given set of ova, Parker, 1970), which in turn can lead to intense sexual conflicts between sexes (Stockley, 1997). Physiological and subsequent fertility costs associated to these sexual conflicts have been widely documented (see Arnqvist and Rowe, 2005; Stockley, 1997 for reviews) and might increase with female age. Thus, the risk of contracting infectious diseases increases steadily with age in species displaying high levels of multiple mating (Nunn et al., 2014) and the negative consequences of such infections in terms of female fertility are likely to be amplified at old ages due to the progressive (and taxonomically widespread) decline in immune performance throughout the lifetime (Peters et al., 2019). We thus tested whether the degree of multiple mating by females leads to an earlier and/or steeper reproductive senescence. We also investigated whether the ovulation mode influences mammalian reproductive senescence. Ovulation is a physiological process governed by complex interactions between hormonal levels and external cues (e.g. photoperiod, mating) (Hayssen and Orr, 2017). Mammalian females are typically divided between spontaneous and induced ovulators (Soulsbury and Iossa, 2010). When spontaneous, ovulation is mostly triggered by endogenous hormonal changes, whereas with induced ovulation, the mating event triggers a

physiological cascade that leads to ovulation. Comparative analyses performed so far have revealed that the intensity of sperm competition is stronger in species with spontaneous ovulation (Iossa et al., 2008; Soulsbury and Iossa, 2010). Since sperm competition can be associated with long-term aging costs in females, including a decline in age-specific physiological performance and fertility in females (Lemaître et al., 2020a; Stockley, 1997), we expect females from species with spontaneous ovulation to suffer from an earlier and/or steeper reproductive senescence than females from species with induced ovulation.

2. Material and methods

2.1. Data collection

Age-specific reproductive data for females were extracted from an unpublished database (entitled ‘Malddaba’) built and managed by VR, JFL and JMG, and currently under development. This database contains sex- and age-specific demographic data for wild populations of mammals gathered from published life tables or extracted from graphs (using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>)) over the past few years. We focused mainly on reporting the m_x series, defined as number of daughters alive at birth that are produced by a female of age x . For each study we collected the mean m_x value at each age, as well as corresponding sample size. In some studies, the sample size was not directly reported but the information on the age distribution of females was provided. In those cases, we extracted the age distribution and used the number of females expected to be alive at age x as the sample size of the m_x series. When m_x series were not available, we reported either the age-specific litter size or the age-specific pregnancy (or birth) rates with the sample sizes (i.e. in monotocous species, the m_x is equivalent to the birth rates divided by 2 when assuming a balanced sex ratio at birth). Only one population per species was considered in this study. When age-specific reproductive parameters were available for several populations of the same species, we selected the one based on the best data quality and with the largest sample size (see *Supplementary datasets* for the full list of populations included in our comparative analysis).

Based on the accuracy of the methods used to assign the age of the individuals, we distinguished two main categories of studies. The first type of study (i.e. longitudinal data) corresponds to age-specific reproductive estimates obtained from the long-term monitoring of individuals marked at birth or early in life when age can be accurately identified. In the second type of studies (i.e. cross-sectional data), age is generally estimated through indirect

methods (e.g. tooth wear) and subject to uncertainty. These cross-sectional data correspond to age-specific reproductive rates obtained from a single assessment of individual reproductive status using individuals either controlled alive in the population or recovered as dead in the field. In cross-sectional studies performed from dead recoveries, the count of embryos or placental scars often provide estimates of the litter size (e.g. Lieury et al., 2017). Sampled populations were also classified as hunted vs. non-hunted according to the information reported in the original publication. Finally, we used the age-specific reproductive data provided in the life tables to recover the age at first reproduction. We limited our research to wild or semi-captive (i.e. where individuals can freely reproduce) mammalian populations. However, we observed that this selection did not allow including small (and fast) mammalian species, which is easily explained by the lack of long-term field studies for such species. Therefore, to avoid any bias in our interpretation of the diversity of reproductive senescence patterns across mammals, we included in our dataset age-specific reproductive rates gathered in three captive populations of rodents, all belonging to the Cricetidae family (Field vole, *Microtus agrestis*, Orkney vole, *Microtus arvalis* and Tundra vole, *Microtus oeconomus*). At the end of our literature survey, we gathered age-specific reproductive data for 101 mammalian species (including 52 longitudinal studies and 49 cross-sectional studies) encompassing a wide diversity of mammalian Orders (Figure 1). Carnivora and Cetartiodactyla were the most represented Orders (35.6% and 27.7% of the species, respectively) followed by Rodentia and the Primates (16.8% and 11.8% of the species, respectively).

When possible, we extracted data on female body mass from the population where we retrieved age-specific reproductive data. When this information was lacking, we looked for female adult body mass from other populations. In mammals, there is widespread evidence that testes mass (relative to body mass) is a reliable indicator of the level of multiple mating that is experienced by females during a given reproductive event (Harcourt et al., 1995; Lemaître et al., 2009; Ramm et al., 2005; Soulsbury, 2010). Indeed, multiple mating promotes sperm competition among males, which in turn selects for large testes (Parker, 2016). We thus used published reviews to compile data on combined adult testes mass and the corresponding adult male body mass (e.g. Lüpold, 2013). Data on ovulation mode were retrieved from Soulsbury (2010) and Soulsbury and Iossa (2010). All data and associated references are provided in the *Supplementary datasets*.

2.2. Measures of reproductive senescence

In living organisms, age-specific fertility is predicted to “rise with age to a peak, which may occur at almost any age depending on the sort of organism considered, and then fall” (Emlen 1970). When looking at age-specific variation in reproductive rates across mammals, this prediction is most likely verified but also associated with substantial variation across species in the strength of the initial increase, the form of the reproductive pattern near the peak of reproduction and the strength of the decrease. For instance, in the bighorn sheep (*Ovis canadensis*), three distinct phases are observed (Figure 2). First, the reproduction rate steadily increases with age from 2 to 4 years of age and then slightly increases during the prime-age stage between 4 and 12 years of age when the reproduction rate peaks and then reproductive senescence begins to occur (i.e. fertility is decreasing with increasing age from 12 years of age onwards). Although many mammalian species display this three-phase pattern, there is still a lot of variation. For instance, the prime-age stage associated with high and constant reproductive rates is not consistently observed. Reproductive rates can slightly but consistently increase (such as in Bighorn sheep, Figure 2) or decrease during this prime-age stage or this plateau phase can simply not exist when reproductive senescence occurs for instance right after the age at first reproduction (e.g. in Short-finned pilot whale, *Globicephala macrorhynchus*, Kasuya and Marsh, 1984). Lastly, reproductive senescence has not been detected in all mammal species studied so far (e.g. Northern elephant seal, *Mirounga angustirostris*, Le Boeuf and Laws, 1994).

To identify the different phases of age-specific variation in reproductive rates and estimate when possible both the age at the onset of reproductive senescence and the rate of reproductive senescence, we modeled age-specific changes of reproductive rates using segmented models from the R-package *segmented* (Muggeo, 2017). We acknowledge that this approach is not necessarily the most accurate to model age-specific variation in a reproductive trait for each species included in our dataset. However, our goal was to assess at the large scale of mammalian species the existence of reproductive senescence using a standardized method, and when present to estimate both the age at the onset of reproductive senescence and the rate of reproductive senescence. To account for the diversity of age-specific trajectories of reproductive rates, we fitted four models of variation in reproductive rates: a constant model with age, a linear model with age, a model with one threshold age including two linear segments (i.e. one before and one after the threshold age) and a model with 2 threshold ages including 3 linear segments (i.e. one before the first age threshold, one between the two age thresholds, and one after the second age threshold).

Models were fitted by weighting the age-specific reproductive trait by sample size. Standard deviation of the reproductive trait was not used because it was not reported in most cases contrary to sample size. Aggregated mean values per age were used for the model fitting and, as we did not have access to the raw individual data in most cases, we had to make an assumption about the distribution of the mean reproductive trait. Following the central limit theorem, we considered each mean trait value to be normally distributed because individual reproductive traits studied here were either binomial or Poisson distributed. All models were fitted between the age at first reproduction and the last age reported in the study. For three species (Crabeater seal, *Lobodon carcinophagus*; Leopard, *Panthera pardus*; Western Jumping Mouse, *Zapus princeps*) we set the reproductive trait to 0 one year before the age at first reproduction to anchor the models and help reach numeric convergence. For each species, the most parsimonious model was selected using the Akaike Information Criterion (AIC). We calculated AIC weights (AIC_w) to assess the relative likelihood that a given model was the best among all the three fitted models (Burnham and Anderson, 2002). We selected the model with the lowest AIC. To account for the propensity of AIC to retain a too complex model (Link and Barker, 2006), when the difference in AIC (denoted ΔAIC) of two competing models was less than two units, we retained the simplest model in accordance with parsimony rules, except in two species (Alpine marmot, *Marmota marmota* and Wolf, *Canis lupus*) for which the original studies reported statistical evidence of reproductive senescence using threshold models (i.e. Berger et al., 2015, Stahler et al., 2013). In both cases, we retained the model including senescence and checked that our estimates of the age at the onset of reproductive senescence matched those provided in the original sources. Depending on the model selected, we used a pre-defined procedure to assess the occurrence of reproductive senescence (see *Appendix B* for detailed procedure).

2.3. Statistical analyses of the factors influencing reproductive senescence

To avoid any statistical issue due to phylogenetic inertia (Felsenstein, 1985), all the following analyses involved phylogenetically controlled models. We used Phylogenetic Generalized Least-Squares models (PGLS), with a variance-covariance matrix extracted using the R-package *ape* (Paradis et al., 2004). The strength of the phylogenetic signal on the error structure of each model was assessed with the Pagel's λ (Pagel, 1999, henceforth called ' λ '), which is incorporated into the analysis to control for the phylogenetic dependence among species (Symonds and Blomberg, 2014). Here, λ was estimated with maximum likelihood by using the PGLS command from the R-package *caper* (Orme et al., 2013). In most cases, λ

varies between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the phylogeny; similarity among species scales proportionally to their shared evolutionary time following a Brownian motion model; Pagel, 1999). As it is not possible to estimate λ for binary data, we used the D statistic for this specific analysis (Fritz and Purvis, 2010), which we estimated with the R-package *caper* (Orme et al., 2013). The D statistic is equal to 1 if the trait of interest has a phylogenetically random distribution across the species included in the phylogeny and to 0 if its evolution follows a Brownian motion model (Fritz and Purvis, 2010). For all the phylogenetically-controlled analyses, data were linked to a super-tree of extant mammals that provides information on both topology and branch length (Bininda-Emonds et al., 2008, 2007). To identify factors shaping the interspecific variation in both the onset and the rate of reproductive senescence, our statistical analyses were run in the following four steps.

First, we tested whether the probability to detect reproductive senescence was influenced by the sample size (i.e. total number of reproductive records in the population; log-transformed in the analysis), the hunting status of the population, the type of data (i.e. longitudinal vs. cross-sectional) or the age at first reproduction (to control for the pace of life). For this, we ran phylogenetically controlled logistic regressions with the presence or absence of reproductive senescence using the R-package *phylolm* (Ives and Garland, 2010). To identify the best models of the onset and of the rate of reproductive senescence, we performed a model selection procedure using AIC (see above for a description of the procedure). Second, we estimated the phylogenetic signal in both the onset and the rate of reproductive senescence (see Kamilar and Cooper, 2013 for a similar approach). Third, we focused on all the candidate factors for the whole set of species displaying reproductive senescence ($N = 69$ species). We thus tested whether the onset of reproductive senescence and the rate of reproductive senescence were influenced by both the age at first reproduction and the female body mass (entered as covariates). We also included potential confounding factors such as data quality (entered as a two-level categorical data: longitudinal vs. cross-sectional data) and the hunting status of the population (entered as a two-level categorical data: hunted vs. non-hunted population). As expected, the age at first reproduction was positively associated with the female body mass (slope of 0.20 ± 0.04 , $R^2 = 0.31$, $\lambda = 0.83$, on a log-log scale, *Appendix C* - Figure S1). However, we kept both variables in our model selection procedure because the Pearson coefficient of correlation between the age at first reproduction and female body mass ($r = 0.56$) was below the threshold of 0.7 indicating statistical issues due to a collinearity among predictor variables (Dormann et al., 2013). In addition, to get

estimates of the rate of reproductive senescence independently of the onset of reproductive senescence (slope between rate and onset of reproductive senescence of -0.81 ± 0.22 , $R^2 = 0.17$, $\lambda = 0.87$, Figure 3), we included the age at the onset of reproductive senescence among our set of covariates in the pool of models seeking to explain interspecific variation in the rate of reproductive senescence. To identify the best models of the onset and of the rate of reproductive senescence, we performed a model selection procedure using the AIC (see above). Fourth, we tested on a subset of species ($N = 54$) for an effect of relative testes mass on both the onset and the rate of reproductive senescence. For these analyses, we added as covariates both testes mass and male body mass (Freckleton et al., 2002; Gage and Freckleton, 2003) to the factors found to influence reproductive senescence traits in the previous analyses, and we then updated the model selection. Fifth, we analyzed the influence of the ovulation mode (i.e. spontaneous vs. induced ovulation) using another subset of species ($N = 40$). We followed the exact same procedure by adding the ovulation mode (as a categorical variable) to the previously identified set of factors influencing reproductive senescence and by running model selection, for the onset and the rate of reproductive senescence, respectively. For all the statistical analyses, the onset of reproductive senescence, the rate of reproductive senescence, the age at first reproduction, testes mass and both female and male body mass were log-transformed. All PGLS models were performed with R 4.0.0 (R Core Development Team) using the packages *ape* (Paradis et al., 2004) and *caper* (Orme et al., 2013). Unless otherwise stated, parameter estimates are given as \pm one standard error.

3. Results

3.1. Occurrence of female reproductive senescence across mammalian species

Reproductive senescence was detected in 68.31 % of the species (69 out of 101 species). The probability to detect senescence was moderately influenced by the phylogeny ($D = 0.61$). When looking at the different traits that putatively had an influence on the probability to detect senescence, the selected model contains the data quality, the hunting status and the sample size (*Appendix C*, Table S1; Table 1a). As we could expect, reproductive senescence was more often detected in longitudinal studies (80.77 %, 42 out of 52 studies) than in cross-sectional studies (55.10 %, 27 out of 49 studies) and the probability to detect reproductive senescence increased with the sample size (slope of 0.36 ± 0.15 , Table 1a, *Appendix C* - Figure S2). When the sample size was large (> 80 individuals), the probability to detect reproductive senescence was above 0.5 (computed on the entire dataset). Reproductive

senescence was also more often detected in non-hunted populations (73.41 %, 58 out of 79 populations) than in hunted populations (50 %, 11 out of 22 populations).

3.2. Factors modulating female reproductive senescence

The age at the onset of senescence was strongly influenced by the phylogeny ($\lambda=0.96$, 95% CI [0.88, 0.99]). Species that displayed a late age at the onset of reproductive senescence were typically long-lived mammals (e.g. Proboscidae), which could confound the effect of the phylogeny (Figure 1). To disentangle these effects, we scaled the age at the onset of reproductive senescence by the age of the oldest individual sampled in the population. The influence of the phylogeny on the standardized age at the onset of reproductive senescence was still statistically significant but lower than the one previously observed for the *absolute* age at the onset of reproductive senescence ($\lambda=0.66$, 95% CI [0.22, 0.88]; Figure 1). Three cetaceans known to display extended periods of post-reproductive lifespan (see Péron et al., 2019a) showed very early *relative* ages at the onset of reproductive senescence (i.e. onset located at 11.5%, 24.5% and 35.4% of the lifespan for *G. macrorhynchus*, *O. orca* and *P. crassidens*, respectively). Interestingly, when applying our statistical procedure to study reproductive senescence in human populations (see *Appendix D* for an illustration), which display the longest post-reproductive life ever reported in mammals, we noted a possible association between an early onset of reproductive senescence and the existence of an extended period of post-reproductive lifespan.

The selected model of among-species variation in the age at the onset of reproductive senescence included both age at first reproduction (slope of 0.45 ± 0.12) and body mass (slope of 0.10 ± 0.04) (Table 1b, *Appendix C* - Table S2A). As expected from the existence of both time and allometric constraints on overall life histories, the onset of reproductive senescence increased with both age at first reproduction and female body mass (Figure 4a, 4b). Once scaled, the effect of the age at first reproduction was stronger than the effect of body mass (slope of 0.40 ± 0.11 vs. 0.26 ± 0.12), with an effect 1.54 times stronger. Although not retained in the selected model, data quality and hunting status were also included in the model with the lowest AIC value (*Appendix C* - Table S2A) suggesting that, for a given age at first reproduction and a given body mass, the age at the onset of reproductive senescence tends to be later in populations monitored longitudinally and hunted (Table 1c, *Appendix C* - Figure S3).

We then analyzed the effect of testes mass (relative to body mass) on the onset of reproductive senescence. The selected model only included the age at first reproduction

(Appendix C - Table S2B) but the model with the lowest AIC value included an additional negative effect of relative testes mass on the onset of reproductive senescence (slope of -0.12 ± 0.07 , Table 1d). For a given age at first reproduction, females with high levels of multiple mating (i.e. species where males carry large testes relative to body mass) tend to show an earlier age at the onset of reproductive senescence (Figure 5). Finally, the onset of reproductive senescence was earlier in species with induced ovulation than in species with spontaneous ovulation (Figure 6). Indeed, the selected model included both the age at first reproduction and the ovulation mode (Appendix C - Table S2C, Table 1e). Moreover, the effect of the ovulation mode remained statistically significant when the relative testes mass was added to the model (Table 1e). Interestingly, when considering this model, the effect of testes mass (controlled for body mass) was also statistically significant (Table 1f).

Similar to the onset of reproductive senescence, the rate of senescence was strongly influenced by the phylogeny ($\lambda=0.94$, 95% CI [0.84, 0.99], Appendix C - Figure S4). The retained model explaining variation in the rate of reproductive senescence across mammalian species included both the age at first reproduction and female body mass (Table S3A), as expected from both time and allometric constraints. Thus, the rate of senescence decreased with increasing age at first reproduction and female body mass (Table 1g, Figure 2c, 2d). However, contrary to what was observed for the age at the onset of reproductive senescence, the effect of body mass on the rate of reproductive senescence was 1.48 times stronger than the effect of the age at first reproduction once both traits were scaled (slope of -0.83 ± 0.22 vs. -0.56 ± 0.20). Here, we can notice that the onset of reproductive senescence was not retained in the selected model (Appendix C Table S3A), which highlights that the three biological times included in the analysis positively covaried, with the age at first reproduction being more closely associated to the rate of reproductive senescence than the age at the onset of reproductive senescence. Subsequent analyses did not reveal any detectable influence of either relative testes mass or ovulation mode on the rate of reproductive senescence (Appendix C - Table S3B, S3C). Importantly, when we restricted our analyses to species for which age-specific reproductive data are based on m_x series, all results were qualitatively unchanged (Appendix C - Table S3D).

4. Discussion

The widespread occurrence of reproductive senescence in mammalian females

Our comparative analysis provides firm evidence that reproductive senescence is widespread across mammals in the wild. More specifically, we found support for an age-specific decline

in reproductive performance in more than two-third (68.3%) of the species included in our analysis, and at least four lines of evidence suggest that we currently underestimate its occurrence.

First, the ability to detect reproductive senescence was much higher when analyzing age-specific reproductive traits from longitudinal trajectories rather than cross-sectional data. A higher accuracy in age assessment of longitudinal data compared to cross-sectional data is most likely to be involved. For instance, while longitudinal studies are performed from known-aged individuals (generally marked near birth or within the early life period), cross-sectional data rely on age estimates most often based on tooth wear, which varies in reliability among species (Hamlin et al., 2000). This difference in the quality of the age estimation thus likely explains our results.

Second, the probability to detect reproductive senescence increased with sample size (i.e. the number of reproductive records per species). Therefore, the absence of reproductive senescence in e.g. Sea Otter (*Enhydra lutris*) or Orangutan (*Pongo pygmaeus*) might simply be a direct consequence of low sample size ($N = 36$ and $N = 58$ for which the probability to detect senescence was only 0.40 and 0.46, respectively; see *Appendix C* - Figure S2). This shows that we faced a lack of statistical power to detect a statistically significant decline in reproductive performance in late life in some hunted populations (e.g. racoon dog, *Nyctereutes procyonydes*, Helle and Kauhala, 1993). It is also noteworthy that sample size also influenced the shape we identified for the reproductive senescence patterns because the number of segments (from 1 to 3) increased with the sample size (*Appendix C* - Table S5).

Third, we might have failed to detect reproductive senescence in some of the species due to discrepancies between our approach and the approaches used in the original studies. To compare reproductive senescence across mammalian species, we had to apply a standardized approach to estimate parameters of reproductive senescence across all species, which has led to some differences in the data themselves (aggregated data per age in our study vs. individual data in the original study) and also in the way data were analyzed. For instance, in Columbian ground squirrels (*Spermophilus columbianus*), Broussard and colleagues (Broussard et al., 2003) detected reproductive senescence by comparing two groups of females (2-5 years old vs. 6-9 years old), whereas we did not detect reproductive senescence by analyzing the full age-dependent reproductive trajectory. Despite these constraints the species-specific estimates we reported for the onset of reproductive senescence closely matched the information provided in the original source (*Appendix A*, Table S2).

Lastly, there is now widespread evidence that the senescence process is asynchronous among traits (Gaillard and Lemaître, 2017; Promislow et al., 2006). For instance, some immune traits drop sharply with increasing age, while others remain quite constant throughout life (Cheynel et al., 2017). Interestingly, the asynchrony in senescence patterns can also occur among traits within the single reproductive function (Lemaître and Gaillard, 2017). Let compare for instance reproductive senescence in Alpine marmot (*Marmota marmota*) and Soay sheep (*Ovis aries*). In marmots, female litter size decreases with increasing age but offspring mass stays constant with maternal age (Berger et al., 2015b), whereas the opposite is observed in Soay sheep (Hayward et al., 2013). Our analysis mostly focused on the m_x values but we cannot exclude that species in which we did not detect reproductive senescence display age-specific decline in at least another reproductive trait. For instance, a recent meta-analysis demonstrated that a decreasing offspring survival with increasing maternal age is widespread in mammals (Ivimey-Cook and Moorad, 2020).

Overall, current evidence suggests that reproductive senescence is - similarly to actuarial senescence - the rule rather than the exception in mammals. Nevertheless, the shape of reproductive senescence (here depicted by the variable number of segments included in the selected model, *Appendix A*, Table S1) as well as its timing (i.e. age at the onset of reproductive senescence) and intensity (i.e. rate of reproductive senescence) display a high diversity across mammalian species.

The influence of life history, mating behavior and ovulation mode on reproductive senescence

As predicted, we found that both the onset and the rate of reproductive senescence were tightly associated with the age at first reproduction. In absence of data required to estimate generation time, the age at first reproduction constitutes the most reliable proxy of the species position along the slow-fast continuum (Gaillard et al., 2005). As previously acknowledged by Jones et al. (2008), slow species show a later age at reproductive senescence and a lower rate of reproductive senescence compared to fast species. The species ranking according to the pattern of covariation in biological times is the most recognized axis of variation across mammalian species (Gaillard et al., 2016; Stearns, 1983). Since both the onset and the rate of reproductive senescence can be expressed in time units (years and years⁻¹, respectively), these two metrics are logically aligned with the other biological times (e.g. generation time, age at first reproduction, lifespan or gestation length). Moreover, as several life history traits measured in time units are known to be strongly influenced by phylogeny (e.g. Capellini et al., 2008 for the sleep duration; Wootton, 1987 for the age at first reproduction, Lemaître et

al. 2020b for adult lifespan), it is not so surprising that both the onset and the rate of reproductive senescence also depend on the species taxonomic position. When the onsets of reproductive senescence are scaled by the maximum lifespan recorded in the focal populations, (i.e. standardized for the species pace of life), the influence of the phylogeny was unsurprisingly strongly reduced.

Once controlled for the species-specific pace of life, we found that traits associated with female mating behavior and physiology influenced the timing of reproductive senescence. Interestingly, the rate of reproductive senescence was not detectably influenced by mating patterns, which adds to the growing evidence that both the onset and the rate of senescence have to be investigated simultaneously when it comes to identify factors influencing senescence patterns. Contrary, to our expectations, the onset of reproductive senescence was earlier in species with induced ovulation than in those with spontaneous ovulation. This might seem surprising at first glance because the intensity of sperm competition (and its possible deleterious consequences for females) are known to be higher in presence of spontaneous ovulation (Iossa et al., 2008; Soulsbury and Iossa, 2010). Yet, two hypotheses can be proposed to explain this unexpected result. First, in many species with induced ovulation, males bear keratinized spines on the surface of the penis (e.g. Dixson, 1991 common marmoset *Callithrix jacchus*; Lemaître et al., 2012 in bank voles, *Myodes glareolus*), which could be involved in the induction of ovulation during the mating (Parag et al., 2006; Stoddart and Milligan, 1979). The density of spines on the male genitalia can in some species be high, with spines being particularly sharp (Orr and Brennan, 2016; Parag et al., 2006; Stockley, 2002). On the long run, repeated injuries caused by spines to the female reproductive tract likely impair female's reproductive condition and might be responsible for the earlier age at the onset of reproductive senescence we reported for these species. While this hypothesis clearly deserves further consideration from studies performed both within and across species, it might not be the whole story, as some species with spontaneous ovulation can also bear spines (e.g. in some primates, see Stockley, 2002). Another (non-mutually exclusive) explanation is that the efficiency of the neuro-endocrinological pathway regulating the relationship between mating and ovulation (reviewed in Bakker and Baum, 2000) decreases with increasing age. So far, the ageing of many physiological functions governing female reproduction has been described in human and laboratory rodents (vom Saal et al., 1994). However, whether neuronal mechanisms controlling the cascade of physiological responses (e.g. release of reproductive hormones by the hypothalamic–pituitary–gonadal axis)

following mating in species with induced ovulation are particularly prone to senesce is currently unknown.

We also found that - independently of the ovulation mode - species where females mate multiply with different males during a given reproductive bout (i.e. when male's relative testes mass is high) also suffer from an earlier onset of reproductive senescence. This contrasts with a previous comparative analysis that revealed that females displaying such behavior do not pay any costs in terms of reduced lifespan or strengthened actuarial senescence (Lemaître and Gaillard, 2013). Overall, this suggests that the physiological costs associated with multiple mating in females are paid in terms of reproductive senescence rather than actuarial senescence. A few hypotheses can be elaborated to explain this link. For instance, evidence that infectious diseases negatively impact reproductive success is increasing (e.g. Nguyen et al., 2015; Pioz et al., 2008). The increased risk of contracting sexually transmitted diseases throughout life in promiscuous females (Nunn et al., 2014) might compromise reproductive performance in late life. In addition, mammalian females might also suffer from the repeated exposure to the male seminal fluid. Such deleterious consequences have been reported in *Drosophila melanogaster*, for which some specific seminal fluid proteins influence various aspects of female reproductive physiology, notably receptivity (see Chapman, 2001 for a review). The composition of the seminal fluid is also complex in mammals (Poiani, 2006) and can impact female reproductive physiology (e.g. by inducing ovulation in some camelids, see Ratto et al., 2010). However, whether male seminal fluid proteins are associated with long-term deleterious effects on female reproductive success is yet to be investigated and constitutes one promising avenue of research.

Future directions

We provide a first evidence of the high diversity of reproductive senescence patterns across mammals in the wild and identify key biological and behavioral factors that shape this diversity. Yet, we are only scratching the surface of the reproductive senescence conundrum and we point out below some of the most promising avenues for future research in this area.

We found a huge diversity of reproductive senescence patterns across mammalian species. Nevertheless, whether this interspecific variation translates to high variation among populations within a given species remains unknown. Indeed, while there is now compelling evidence that environmental conditions modulate age-specific survival patterns, as individuals in captivity have longer lifespan and similar or later onset of actuarial senescence than their wild conspecifics (Tidière et al. 2016), similar large-scale comparative studies are lacking for

reproductive senescence. Empirical studies have revealed that the amount of resources available in the environment positively influences the female reproductive output (e.g. Persson, 2005). However, as females age, their ability to maintain large home range (e.g. Froy et al., 2018 in Soay sheep, *Ovis aries* and red deer, *Cervus elaphus*), to acquire resources (e.g. MacNulty et al., 2009 in wolves) or to eat and digest food (e.g. Gaillard et al. 2015 for a study on tooth wear in ruminants) are impaired, which ultimately decreases the efficiency of food provisioning to their progeny during the energy-demanding period of maternal care (Gittleman and Thompson, 1988; Clutton-Brock et al. 1989; see also below) and thereby jeopardizes their reproductive success. However, whether the quality and quantity of resources available in the environment mitigate the reproductive ageing cost of these functional declines remains to be investigated. Moreover, following a resource-based allocation trade-off, a high reproductive effort during early life can be paid in terms of increased reproductive senescence (Douhard et al., 2020; Lemaître et al., 2015; Nussey et al., 2006). For instance, it has been suggested that the early onset of reproductive senescence reported in domestic mammals might be due to the strong artificial selection for a high reproductive effort during early life in domestic animals (Myerud et al., 2002 for sheep, Grange et al. 2009 for horses, *Equus caballus*). Alternatively, whether these costs are rather induced by a mismatch with environmental conditions remains unknown. In that context, comparing mammalian populations facing contrasted environmental conditions would allow assessing whether some species simply escape reproductive senescence or whether particularly good environmental conditions prevent reproductive senescence to occur.

While we found that female mating behavior, ovulation mode, allometry and pace of life all shape reproductive senescence, many other biological factors are likely to influence either its onset or its rate. It is beyond the scope to list all of them but we can emphasize two aspects we consider as being particularly promising: the cost of lactation and the type of placentation. In mammals, the lactation period constitutes the most energy-demanding part of the reproductive cycle (Clutton-Brock et al., 1989) and to produce high quality milk in sufficient quantity, females need to increase their food intake. Interestingly, the magnitude of this extra food intake varies substantially across species (see Douhard et al., 2016; Hayssen and Orr, 2017 for reviews), and the energy intake required by lactating females can sometimes be two- or threefold that required during the non-breeding period (see Speakman, 2008 for some striking examples in rodents and insectivores). The physiological costs associated to lactation are diverse and well-documented, ranging from organ remodeling (e.g. increased size of liver, pancreas and mammary glands) to a risk of hyperthermia or bone loss

(due to the need to transfer calcium to the offspring) (Dufour and Sauter, 2002; Jasienska, 2013; Speakman, 2008). On the contrary, much less is known on the long-term fitness costs of lactation, notably in terms of ageing. We hypothesize that the repeated physiologically costly periods of lactation should translate into an earlier/and or stronger reproductive senescence. Moreover, such costs are likely to be buffered or exacerbated by the quality of the environment, which in turn might constitute selective pressures towards specific reproductive tactics. For instance, the harsh environmental conditions faced by female white-tailed deer (*Odocoileus virginianus*) in Minnesota (i.e. severe winters and wolf predation) might explain their relatively low allocation to reproduction throughout their lives, a tactic that might ultimately minimize reproductive senescence as reported by DelGuidice and colleagues (DelGuidice et al., 2007) in this population. Another interesting feature of the mammalian reproductive machinery is the structure of the placenta that can influence the amount of nutrients transferred by the mother to the fetus(es). Indeed, the morphology of the placenta is highly variable across species, notably in its degree of invasiveness and interdigitation (Wildman, 2011), which ultimately modulates the degree and the surface for nutrient transfer during gestation (Capellini et al., 2011). Therefore, the placenta constitutes a critical organ for parent-offspring conflicts (Haig, 1993). It has already been observed that the embryo growth rate is approximately twice as fast in more interdigitated placentas (Capellini et al., 2011) and that placenta types covary with the pace of life. Slow-living species are generally characterized by an invasive placenta (i.e. hemochorial placenta) while fast species are most often characterized by less invasive placenta types (i.e. endotheliochorial or epitheliochorial placenta) (Garratt et al., 2013). The evolution of a less invasive placenta has allowed mothers to limit fetal manipulation (i.e. when food transfer during gestation is largely under the fetus(es) control) and to control better food provisioning among offspring and across reproductive events (Garratt et al., 2013). Therefore - everything else being equal - such placenta types might confer to females a way to buffer reproductive senescence.

As mentioned earlier, our work focused on female reproductive rate, as females concentrate the huge majority of the data published so far. However, recent studies have highlighted the evolutionary relevance of studying male reproductive senescence (Lemaître and Gaillard, 2017; Monaghan and Metcalfe, 2019), as well as its potential medical implications (Levine et al., 2018). As a consequence, evidence that male reproductive senescence is pervasive in the wild (reviewed in Lemaître and Gaillard, 2017) is accumulating. Similar to what we have discussed above for females, male reproductive senescence can be assessed through a large variety of traits, notably an age-specific decline in

secondary sexual traits, ejaculate quality, mating rate or reproductive success. However, to be directly comparable, male and female reproductive senescence need to be investigated on the same trait and the potential confounding effects of the partner's age need to be accounted for (Thorley et al., 2020). Surprisingly, we still lack a comprehensive theoretical framework for the evolution of sex differences in reproductive senescence. However, following our current life history framework, we can expect polygynous mammals where males disproportionately allocate to sexual competition to display most strongly male-biased reproductive senescence. Data available so far suggest that this scenario might be true. In the monogamous meerkat (*Suricata suricatta*), no sex difference in reproductive senescence has been detected (Thorley et al., 2020) while in polygynous red deer (*Cervus elaphus*), the rate of reproductive senescence (measured through annual fecundity) is much steeper in males than in females (Nussey et al., 2009; see also Muller et al., 2020 in chimpanzee, *Pan troglodytes schweinfurthii* but see Festa-Bianchet, 2012 for some counter-examples, e.g. Bighorn sheep, *Ovis canadensis*, in Ram mountain). Studies investigating these questions in a wider range of species are now required.

Acknowledgements:

We are thankful to Prof. Alan Cohen and Prof. Tamàs Fülöp for organizing the symposium “*Understanding the biology of aging to better intervene*” that stimulated the writing of this article. We are grateful to Alan Cohen, Marco Festa-Bianchet and one anonymous reviewer for their insightful comments that markedly improved our manuscript.

Author contributions

JFL and JMG designed the study. JFL, JMG and VR collected, analyzed and wrote the manuscript.

Funding sources

J. -F. L. and J. -M. G. were supported by a grant from the Agence Nationale de la Recherche (ANR-15-CE32-0002-01). This work was performed within the framework of the LABEX ECOFECT (ANR-11-LABX-0048) of Université de Lyon, within the program “Investissements d’Avenir” (ANR-11-IDEX-0007) operated by the French National Research Agency (ANR).

Declaration of Competing Interest

The authors declare no conflict of interest

Journal Pre-proof

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Captions for figures

Figure 1: Phylogenetic tree of the species analyzed. The inner band displays the occurrence of reproductive senescence (i.e. presence vs. absence), the middle band displays the *absolute* onset of reproductive senescence (in years) and the outer band displays the *relative* onset of reproductive senescence (absolute onset of reproductive senescence divided by the age of the oldest individual sampled in the population, in proportion).

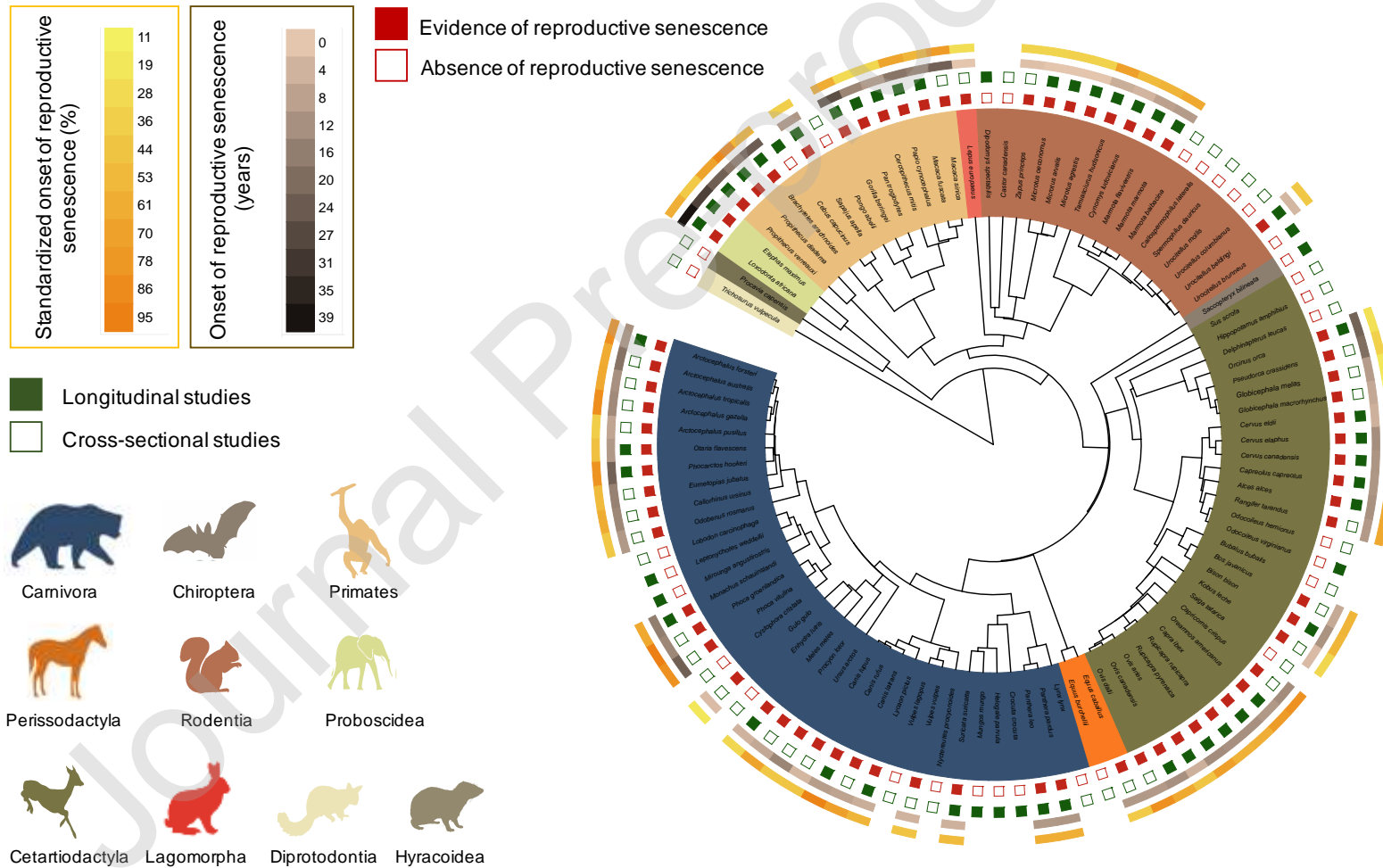
Figure 2: Age-specific m_x in Bighorn sheep, *Ovis canadensis* at Ram mountain. The fit of the selected two-threshold segmented model is presented. There are three distinct phases in the age-specific reproductive trajectory. The section (A) corresponds to the increasing phase of the reproductive output for young adult females. The section (B) corresponds to a phase for prime-age females during which m_x slightly increases and the section (C) corresponds to a senescent phase characterized by both an onset and a rate of reproductive senescence.

Figure 3: Relationship between the rate of reproductive senescence and the onset of reproductive senescence (on a log-log scale) (Slope of -0.81 ± 0.22 ; $R^2 = 0.17$; $N=69$ species).

Figure 4: Relationship between the age at the onset of reproductive senescence (a) or the rate of reproductive senescence (c), and the age at first reproduction (on a log-log scale) ($N=69$ species). In panels (a) and (c) data are represented independently of female body mass while in panels (b) and (d) data are split according to the female body mass category (light, $N= 34$ species, heavy, $N = 35$ species in each body mass category).

Figure 5: Relationship between the onset of reproductive senescence and the relative testes mass ($N=54$ species). The onset of reproductive senescence corresponds to the residuals of the regression of the onset of reproductive senescence against the age at first reproduction (on a log-log scale). The relative testes mass corresponds to the residuals of the regression of the testes mass against the male body mass (on a log-log scale). In this model, the influence of the phylogeny is not statistically different from 0 ($\lambda = 0$ [NA, 0.80]) and the residuals of the models were thus computed with Ordinary Least Square regressions.

Figure 6: Box-plot displaying the differences in the onset of reproductive senescence between species with spontaneous ($N= 28$) and induced ($N = 12$) ovulation. The onset of reproductive senescence corresponds to the residuals of the regression of the onset of reproductive senescence against the age at first reproduction (on a log-log scale, $N=40$ species). In this model, the influence of the phylogeny is not statistically different from 0 ($\lambda = 0$ [NA, 0.37]) and the residuals of the models were thus computed with Ordinary Least Square regressions.



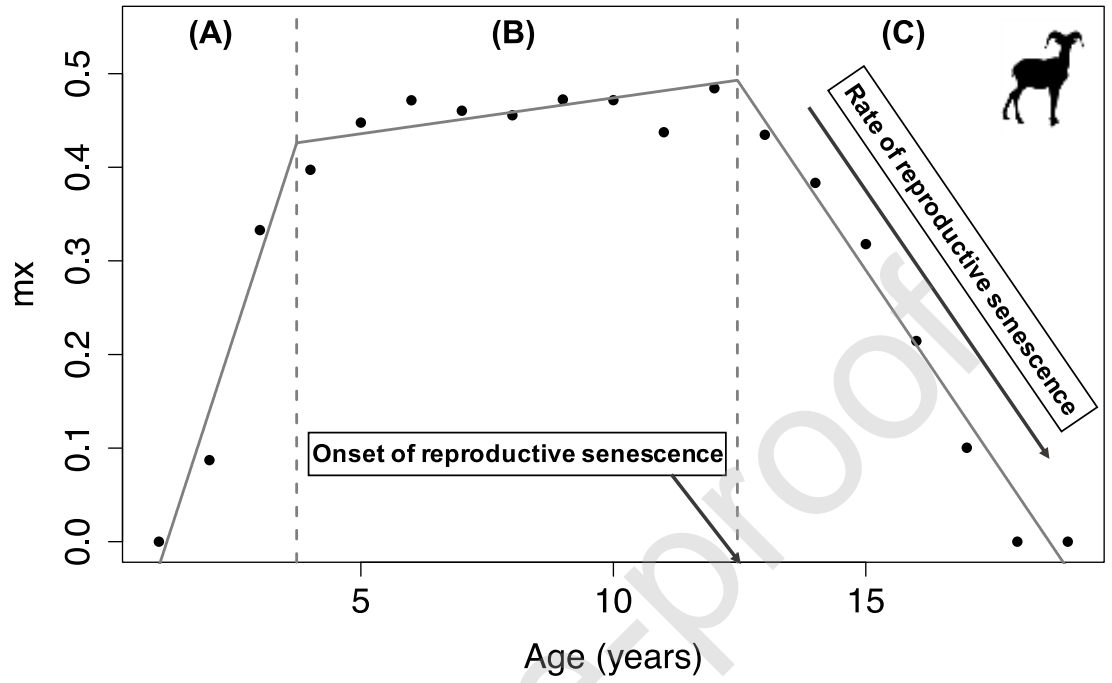


FIGURE 2



FIGURE 3

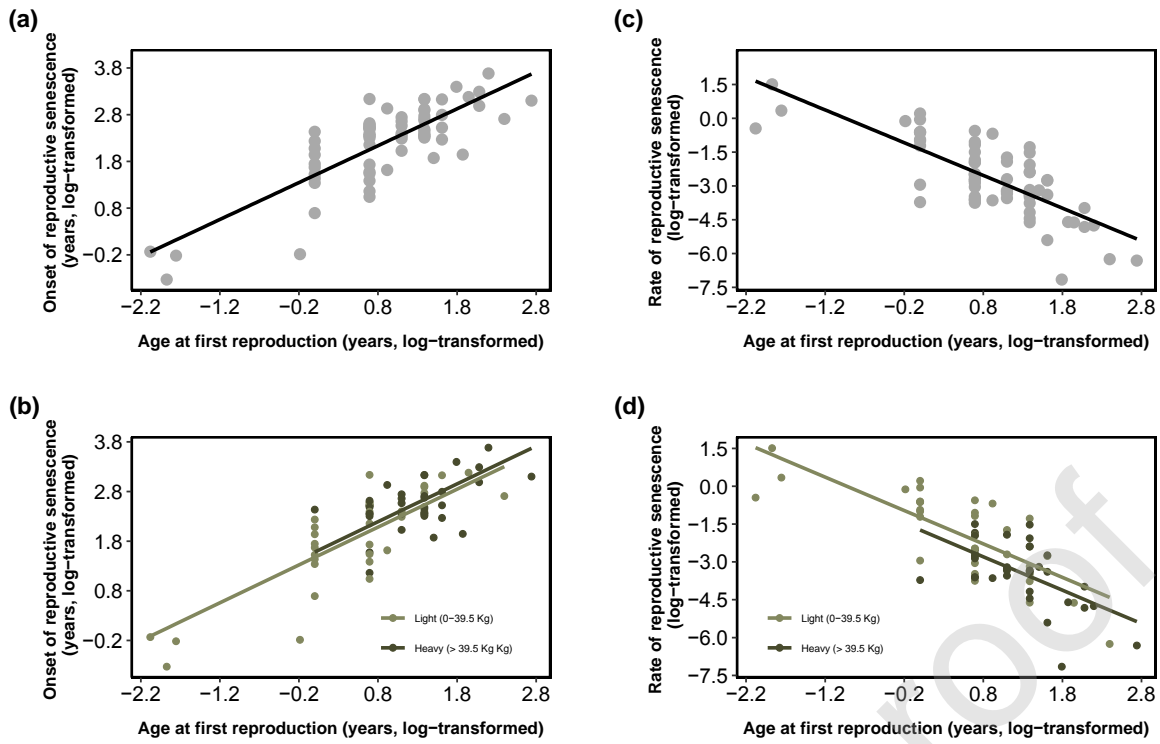


FIGURE 4

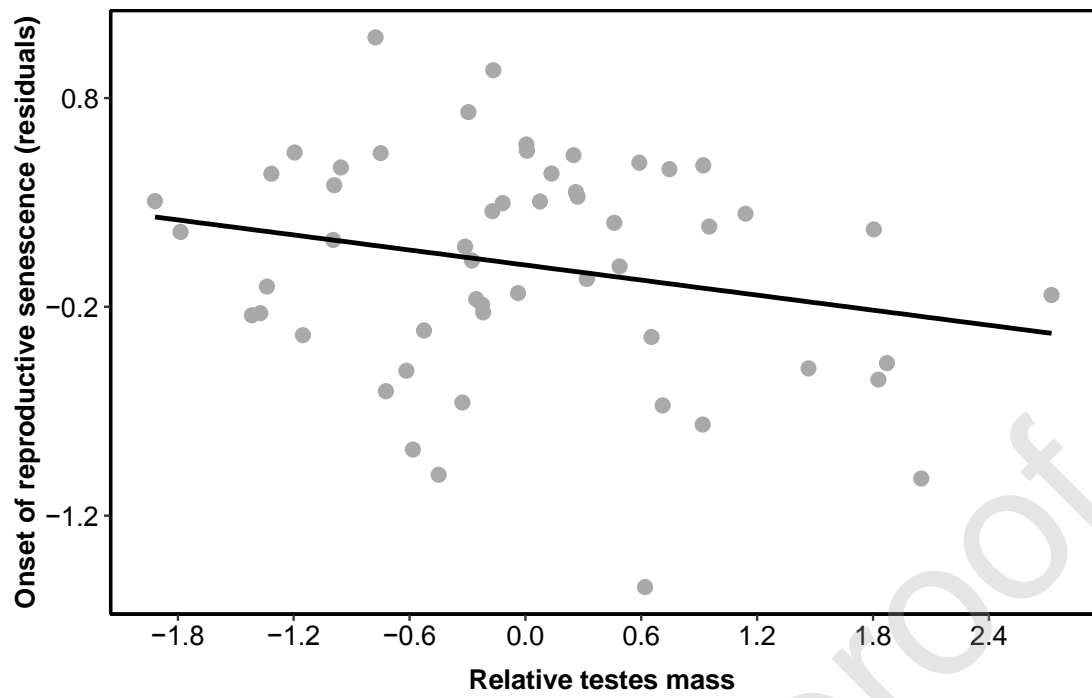


FIGURE 5

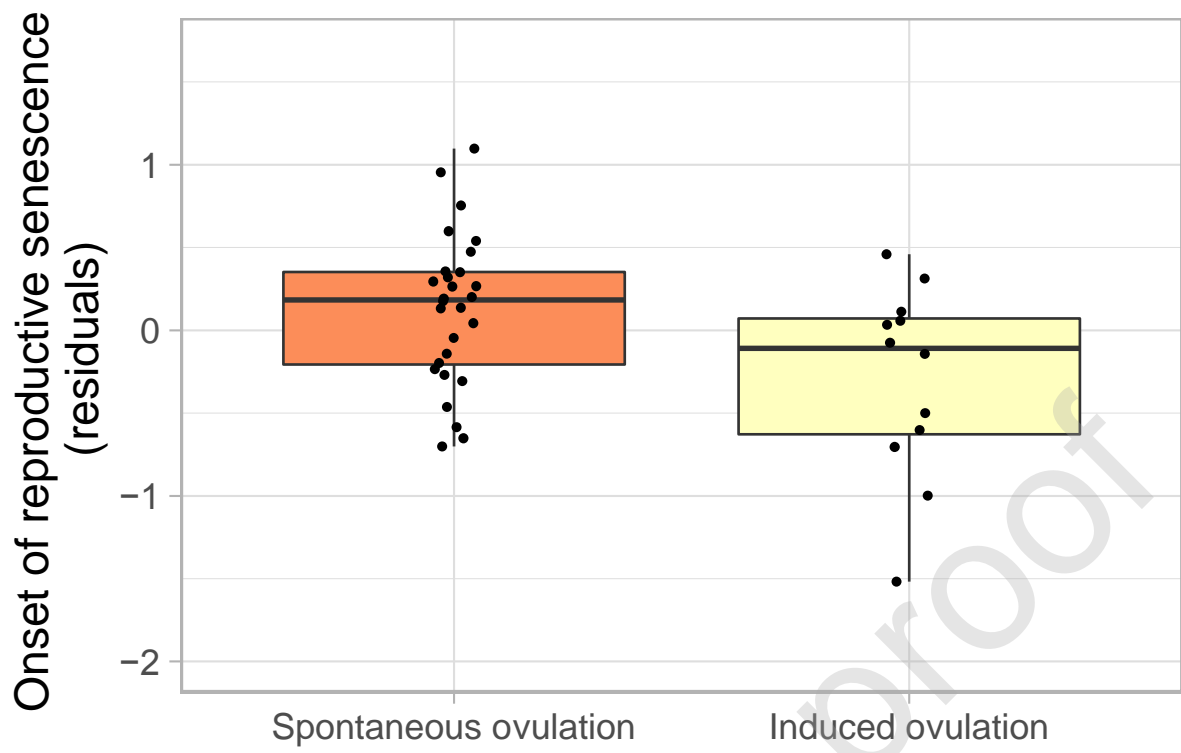


FIGURE 6

Table 1: Phylogenetically controlled comparative analyses of the probability to detect reproductive senescence and on factors influencing both the onset and the rate of reproductive senescence. This table provides parameter estimates from the models discussed in the text (statistically significant effects occur in bold). For each model displayed below, the estimates are not scaled.

	Dependent variables	Independent variables	Slope ± SE	t	λ [95% CI]	N	R²
a	Probability to detect reproductive senescence	Intercept	1.29 ± 0.40	3.22	NA	101	NA
		Sample size	0.36 ± 0.15	2.32			
		Hunting status	-1.24 ± 0.55	-1.72			
		Data quality	-0.71 ± 0.41	-1.72			
b	Onset of reproductive senescence	Intercept	0.78 ± 0.59	1.31	0.75 [NA; 0.93]	69	0.4
		Age at first reproduction	0.45 ± 0.12	3.68			
		Female body mass	0.10 ± 0.04	2.19			
c	Onset of reproductive senescence	Intercept	0.95 ± 0.51	1.85	0.63 [NA; 0.91]	69	0.5
		Age at first reproduction	0.52 ± 0.12	4.39			
		Female body mass	0.08 ± 0.04	1.92			
		Hunting status	0.26 ± 0.16	1.6			
		Data quality	-0.28 ± 0.13	-2.19			
d	Onset of reproductive senescence	Intercept	0.42 ± 0.47	0.91	0 [NA; 0.80]	54	0.704
		Age at first reproduction	0.62 ± 0.13	5.05			
		Testes mass	-0.12 ± 0.07	-1.75			
		Male body mass	0.16 ± 0.07	2.35			
e	Onset of reproductive senescence	Intercept	1.70 ± 0.13	13.04	0 [NA; 0.367]	40	0.74
		Age at first reproduction	0.71 ± 0.09	7.96			
		Ovulation mode	-0.50 ± 0.18	-2.71			
f	Onset of reproductive senescence	Intercept	0.45 ± 0.55	0.81	0 [NA; 0.45]	34	0.78
		Age at first reproduction	0.53 ± 0.13	4.11			
		Ovulation mode	-0.74 ± 0.22	-3.38			
		Testes mass	-0.25 ± 0.10	-2.44			
		Male body mass	0.23 ± 0.09	2.61			
g	Rate of reproductive senescence	Intercept	0.81 ± 0.96	0.85	0.58 [0.18; 0.86]	69	0.49
		Age at first reproduction	-0.64 ± 0.23	-2.78			
		Female body mass	-0.31 ± 0.08	-3.85			