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1 **Female reproductive senescence**  
2 **across mammals: a high diversity of**  
3 **patterns modulated by life history**  
4 **and mating traits**

5

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21 ABSTRACT

22

23 Senescence patterns are highly variable across the animal kingdom. However, while empirical  
24 evidence of actuarial senescence in vertebrates is accumulating in the wild and life history  
25 correlates of actuarial senescence are increasingly identified, both the extent and variation of  
26 reproductive senescence across species remain poorly studied. Here, we performed the first  
27 large-scale analysis of female reproductive senescence across 101 mammalian species that  
28 encompassed a wide range of Orders. We found evidence of reproductive senescence in  
29 68.31% of the species, which demonstrates that reproductive senescence is pervasive in  
30 mammals. As expected from allometric rules, the onset of reproductive senescence occurs  
31 later and the rate of reproductive senescence decreases with increasing body mass and  
32 delayed age at first reproduction. Moreover, for a given pace of life, females displaying a high  
33 level of multiple mating and/or with induced ovulation senesce earlier than females displaying  
34 a low level of multiple mating and/or with spontaneous ovulation. These results suggest that  
35 both female mating behavior and reproductive physiology shape the diversity of reproductive  
36 senescence patterns across mammals. We propose future avenues of research regarding the  
37 role played by environmental conditions or reproductive features (e.g. type of placentation) on  
38 the evolution of reproductive senescence.

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

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## 46 **1. Introduction**

47

48 From an evolutionary biology perspective, the process of senescence corresponds to a  
49 decrease in the age-specific contribution to fitness (Cohen et al., 2020; Gaillard and  
50 Lemaître, 2020; Monaghan et al., 2008). Therefore, senescence is mostly studied through a  
51 decline in demographic rates with increasing age (i.e. actuarial and reproductive senescence).  
52 Historically, senescence was thought to not show up in the wild because animals were  
53 expected to die from harsh environmental conditions or anthropogenic effects (e.g. hunting)  
54 before experiencing a decline in age-specific survival or reproductive rates (Nussey et al.,  
55 2013). Thanks to the increasing number of long-term field studies - where individuals are  
56 monitored from birth to death (Clutton-Brock & Sheldon 2010), and the subsequent  
57 demographic analyses of these populations, the view that demographic senescence does not  
58 occur in the wild has been totally revisited (Nussey et al. 2013). Yet, after pioneer descriptive  
59 studies suggesting that mortality increases in late life (e.g. Caughley, 1966), empirical  
60 evidence currently indicates that actuarial senescence is pervasive across vertebrates with  
61 determinate growth in the wild (Brunet-Rossinni and Austad, 2006; Nussey et al., 2013),  
62 whereas reproductive senescence was considered to be inexistent in the wild for a much  
63 longer period (e.g. Caughley, 1976). On the contrary, the negative effects of age on  
64 reproductive performance have been documented in laboratory rodents (e.g. Leslie and  
65 Ranson, 1940) and human populations (e.g. Tietze, 1957) for a while. The first reports of  
66 reproductive senescence in the wild only emerged in the late 70s (Coulson and Horobin,  
67 1976; Ollason and Dunnet, 1978; Perrins and Moss, 1974; Sinclair, 1977), following the  
68 insightful work by Emlen (1970), who stated that age-specific reproductive rates should  
69 increase to a peak, then stay relatively constant during a prime-age stage (i.e. the period of  
70 adulthood between the beginning of the reproductive peak and the onset of reproductive  
71 senescence) before declining in late life.

72 Empirical evidence of reproductive senescence from wild populations of vertebrates is  
73 now compelling (Nussey et al., 2013). So far, these case studies have been almost entirely  
74 performed on females (but see Lemaître and Gaillard, 2017 for a review of evidence in  
75 males), simply because accurate paternity assignments in the wild require the use of  
76 molecular tools. Age-specific declines in a wide array of traits reflecting female reproductive  
77 success have been documented, such as breeding proportions (e.g. Photopoulou et al., 2017),  
78 birth rates (e.g. Lee et al., 2016), number of offspring produced at birth (e.g. Sparkman et al.,  
79 2017) or at the end of parental care (i.e. at weaning or fledgling, e.g. Thorley et al., 2020), and

80 offspring survival (e.g. Karniski et al., 2018). Interestingly, it has been suggested that female  
81 reproductive senescence patterns can markedly differ across species (Baudisch and Stott,  
82 2019; Jones et al., 2014), even between closely related species. For instance, a population-  
83 level comparison of reproductive senescence in terms of breeding success across three  
84 albatross species has revealed that the age at the onset of reproductive senescence was much  
85 earlier in the wandering albatross (*Diomedea exulans*) than in both the black-browed albatross  
86 (*Thalassarche melanophris*) and the grey-headed albatross (*Thalassarche chrysostoma*) (Froy  
87 et al., 2017). Likewise, the southern fulmar (*Fulmarus glacialisoides*) showed clear evidence of  
88 senescence in breeding success, whereas the snow petrel (*Pagodroma nivea*) did not (Berman  
89 et al., 2009). Despite these reports of contrasted patterns of age-specific decline in  
90 reproductive performance with increasing age, there has been so far no attempt to quantify the  
91 occurrence and the variation in reproductive senescence across a wide range of species, or to  
92 identify the ecological and biological factors underlying the diversity of patterns. This  
93 contrasts with the increasing number of comparative analyses that focused on actuarial  
94 senescence (Bronikowski et al., 2011; Lemaître et al., 2020c; Péron et al., 2019b; Ricklefs,  
95 1998, 2006; Ricklefs and Scheuerlein, 2001), which have notably revealed that life-history  
96 strategies (e.g. Garratt et al., 2013; Ricklefs, 2010) and environmental conditions (Colchero et  
97 al., 2019; Lemaître et al., 2013; Tidière et al., 2016) modulate both the onset and the rate of  
98 actuarial senescence. So far, most comparative analyses of age-specific reproductive data in  
99 mammals have focused on the evolution of post-reproductive lifespan (e.g. Alberts et al.,  
100 2013; Cohen, 2004; Ellis et al., 2018) and did not investigate among-species differences in the  
101 onset or rate of reproductive senescence. Only Jones and colleagues (2008) analyzed  
102 interspecific differences in female reproductive senescence patterns (i.e. measured as the age-  
103 specific decline in the number of recruited offspring) across 19 species of birds and mammals.  
104 They found that the rate of reproductive senescence decreased with increasing generation  
105 time, a reliable measure of the species position along the slow-fast continuum (Gaillard et al.,  
106 2005). Thus, slow-living species had a lower rate of reproductive senescence than fast-living  
107 species (Jones et al., 2008; see also Gaillard et al., 2016).

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

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

117         Following comparative analyses of many life history traits (e.g. Kamilar and Cooper,  
118 2013; Wootton, 1987), notably the rate of actuarial senescence (e.g. Lemaître et al., 2020b),  
119 we expected closely related species to share more similar reproductive senescence patterns  
120 than distant species across the phylogeny. We also expected the onset and the rate of  
121 senescence to occur earlier and to increase, respectively, with increasingly fast-living life  
122 history as a direct consequence of the covariation among all biological times (i.e. life history  
123 traits expressed in time units that positively covary across species, see Gaillard et al., 2016;  
124 Ronget and Gaillard, 2020). Moreover, we investigated whether the number of mating  
125 partners and the ovulation mode influenced the timing and intensity of reproductive  
126 senescence. In most mammals, females generally copulate with more than one male during a  
127 given reproductive event (Gomendio et al., 1998; Hayssen and Orr, 2017; Soulsbury, 2010).  
128 The propensity of females to mate repeatedly within a reproductive event increases from  
129 monogamous species to polyandrous or polygynandrous species, which is considered as a  
130 way to increase fitness through genetic benefits (e.g. increased genetic diversity among  
131 offspring, Jennions and Petrie, 2000; Stockley, 2003). However, multiple mating promotes  
132 sperm competition ( i.e. when sperm from two or more males compete to fertilize a given set  
133 of ova, Parker, 1970), which in turn can lead to intense sexual conflicts between sexes  
134 (Stockley, 1997). Physiological and subsequent fertility costs associated to these sexual  
135 conflicts have been widely documented (see Arnqvist and Rowe, 2005; Stockley, 1997 for  
136 reviews) and might increase with female age. Thus, the risk of contracting infectious diseases  
137 increases steadily with age in species displaying high levels of multiple mating (Nunn et al.,  
138 2014) and the negative consequences of such infections in terms of female fertility are likely  
139 to be amplified at old ages due to the progressive (and taxonomically widespread) decline un  
140 immune performance throughout the lifetime (Peters et al., 2019). We thus tested whether the  
141 degree of multiple mating by females leads to an earlier and/or steeper reproductive  
142 senescence. We also investigated whether the ovulation mode influences mammalian  
143 reproductive senescence. Ovulation is a physiological process governed by complex  
144 interactions between hormonal levels and external cues (e.g. photoperiod, mating) (Hayssen  
145 and Orr, 2017). Mammalian females are typically divided between spontaneous and induced  
146 ovulators (Soulsbury and Iossa, 2010). When spontaneous, ovulation is mostly triggered by  
147 endogenous hormonal changes, whereas with induced ovulation, the mating event triggers a

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

155

## 156 **2. Material and methods**

157

### 158 **2.1. Data collection**

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

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

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

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

214

## 215 **2.2. Measures of reproductive senescence**

216 In living organisms, age-specific fertility is predicted to “rise with age to a peak, which may  
217 occur at almost any age depending on the sort of organism considered, and then fall” (Emlen  
218 1970). When looking at age-specific variation in reproductive rates across mammals, this  
219 prediction is most likely verified but also associated with substantial variation across species  
220 in the strength of the initial increase, the form of the reproductive pattern near the peak of  
221 reproduction and the strength of the decrease. For instance, in the bighorn sheep (*Ovis*  
222 *canadensis*), three distinct phases are observed (Figure 2). First, the reproduction rate steadily  
223 increases with age from 2 to 4 years of age and then slightly increases during the prime-age  
224 stage between 4 and 12 years of age when the reproduction rate peaks and then reproductive  
225 senescence begins to occur (i.e. fertility is decreasing with increasing age from 12 years of  
226 age onwards). Although many mammalian species display this three-phase pattern, there is  
227 still a lot of variation. For instance, the prime-age stage associated with high and constant  
228 reproductive rates is not consistently observed. Reproductive rates can slightly but  
229 consistently increase (such as in Bighorn sheep, Figure 2) or decrease during this prime-age  
230 stage or this plateau phase can simply not exist when reproductive senescence occurs for  
231 instance right after the age at first reproduction (e.g. in Short-finned pilot whale,  
232 *Globicephala macrorhynchus*, Kasuya and Marsh, 1984). Lastly, reproductive senescence has  
233 not been detected in all mammal species studied so far (e.g. Northern elephant seal, *Mirounga*  
234 *angustirostris*, Le Boeuf and Laws, 1994).

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

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

273

### 274 **2.3. Statistical analyses of the factors influencing reproductive senescence**

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

283 varies between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the  
284 phylogeny; similarity among species scales proportionally to their shared evolutionary time  
285 following a Brownian motion model; Pagel, 1999). As it is not possible to estimate  $\lambda$  for  
286 binary data, we used the  $D$  statistic for this specific analysis (Fritz and Purvis, 2010), which  
287 we estimated with the R-package *caper* (Orme et al., 2013). The  $D$  statistic is equal to 1 if the  
288 trait of interest has a phylogenetically random distribution across the species included in the  
289 phylogeny and to 0 if its evolution follows a Brownian motion model (Fritz and Purvis,  
290 2010). For all the phylogenetically-controlled analyses, data were linked to a super-tree of  
291 extant mammals that provides information on both topology and branch length (Bininda-  
292 Emonds et al., 2008, 2007). To identify factors shaping the interspecific variation in both the  
293 onset and the rate of reproductive senescence, our statistical analyses were run in the  
294 following four steps.

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

317 estimates of the rate of reproductive senescence independently of the onset of reproductive  
318 senescence (slope between rate and onset of reproductive senescence of  $-0.81 \pm 0.22$ ,  $R^2 =$   
319  $0.17$ ,  $\lambda = 0.87$ , Figure 3), we included the age at the onset of reproductive senescence among  
320 our set of covariates in the pool of models seeking to explain interspecific variation in the rate  
321 of reproductive senescence. To identify the best models of the onset and of the rate of  
322 reproductive senescence, we performed a model selection procedure using the AIC (see  
323 above). Fourth, we tested on a subset of species ( $N = 54$ ) for an effect of relative testes mass  
324 on both the onset and the rate of reproductive senescence. For these analyses, we added as  
325 covariates both testes mass and male body mass (Freckleton et al., 2002; Gage and  
326 Freckleton, 2003) to the factors found to influence reproductive senescence traits in the  
327 previous analyses, and we then updated the model selection. Fifth, we analyzed the influence  
328 of the ovulation mode (i.e. spontaneous vs. induced ovulation) using another subset of species  
329 ( $N = 40$ ). We followed the exact same procedure by adding the ovulation mode (as a  
330 categorical variable) to the previously identified set of factors influencing reproductive  
331 senescence and by running model selection, for the onset and the rate of reproductive  
332 senescence, respectively. For all the statistical analyses, the onset of reproductive senescence,  
333 the rate of reproductive senescence, the age at first reproduction, testes mass and both female  
334 and male body mass were log-transformed. All PGLS models were performed with R 4.0.0 (R  
335 Core Development Team) using the packages *ape* (Paradis et al., 2004) and *caper* (Orme et  
336 al., 2013). Unless otherwise stated, parameter estimates are given as  $\pm$  one standard error.

337

### 338 **3. Results**

339

#### 340 **3.1. Occurrence of female reproductive senescence across mammalian species**

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

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

353

### 354 **3.2. Factors modulating female reproductive senescence**

355 The age at the onset of senescence was strongly influenced by the phylogeny ( $\lambda=0.96$ , 95% CI  
356 [0.88, 0.99]). Species that displayed a late age at the onset of reproductive senescence were  
357 typically long-lived mammals (e.g. Proboscidae), which could confound the effect of the  
358 phylogeny (Figure 1). To disentangle these effects, we scaled the age at the onset of  
359 reproductive senescence by the age of the oldest individual sampled in the population. The  
360 influence of the phylogeny on the standardized age at the onset of reproductive senescence  
361 was still statistically significant but lower than the one previously observed for the *absolute*  
362 age at the onset of reproductive senescence ( $\lambda=0.66$ , 95% CI [0.22, 0.88]; Figure 1). Three  
363 cetaceans known to display extended periods of post-reproductive lifespan (see Péron et al.,  
364 2019a) showed very early *relative* ages at the onset of reproductive senescence (i.e. onset  
365 located at 11.5%, 24.5% and 35.4% of the lifespan for *G. macrorhynchus*, *O. orca* and *P.*  
366 *crassidens*, respectively). Interestingly, when applying our statistical procedure to study  
367 reproductive senescence in human populations (see *Appendix D* for an illustration), which  
368 display the longest post-reproductive life ever reported in mammals, we noted a possible  
369 association between an early onset of reproductive senescence and the existence of an  
370 extended period of post-reproductive lifespan.

371 The selected model of among-species variation in the age at the onset of reproductive  
372 senescence included both age at first reproduction (slope of  $0.45 \pm 0.12$ ) and body mass  
373 (slope of  $0.10 \pm 0.04$ ) (Table 1b, *Appendix C* - Table S2A). As expected from the existence of  
374 both time and allometric constraints on overall life histories, the onset of reproductive  
375 senescence increased with both age at first reproduction and female body mass (Figure 4a,  
376 4b). Once scaled, the effect of the age at first reproduction was stronger than the effect of  
377 body mass (slope of  $0.40 \pm 0.11$  vs.  $0.26 \pm 0.12$ ), with an effect 1.54 times stronger. Although  
378 not retained in the selected model, data quality and hunting status were also included in the  
379 model with the lowest AIC value (*Appendix C* - Table S2A) suggesting that, for a given age at  
380 first reproduction and a given body mass, the age at the onset of reproductive senescence  
381 tends to be later in populations monitored longitudinally and hunted (Table 1c, *Appendix C* -  
382 Figure S3).

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

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

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

414

#### 415 **4. Discussion**

##### 416 *The widespread occurrence of reproductive senescence in mammalian females*

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

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

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

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

440 Third, we might have failed to detect reproductive senescence in some of the species  
441 due to discrepancies between our approach and the approaches used in the original studies. To  
442 compare reproductive senescence across mammalian species, we had to apply a standardized  
443 approach to estimate parameters of reproductive senescence across all species, which has led  
444 to some differences in the data themselves (aggregated data per age in our study vs. individual  
445 data in the original study) and also in the way data were analyzed. For instance, in Columbian  
446 ground squirrels (*Spermophilus columbianus*), Broussard and colleagues (Broussard et al.,  
447 2003) detected reproductive senescence by comparing two groups of females (2-5 years old  
448 vs. 6-9 years old), whereas we did not detect reproductive senescence by analyzing the full  
449 age-dependent reproductive trajectory. Despite these constraints the species-specific estimates  
450 we reported for the onset of reproductive senescence closely matched the information  
451 provided in the original source (*Appendix A*, Table S2).

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

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

471

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

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

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

491         Once controlled for the species-specific pace of life, we found that traits associated  
492 with female mating behavior and physiology influenced the timing of reproductive  
493 senescence. Interestingly, the rate of reproductive senescence was not detectably influenced  
494 by mating patterns, which adds to the growing evidence that both the onset and the rate of  
495 senescence have to be investigated simultaneously when it comes to identify factors  
496 influencing senescence patterns. Contrary, to our expectations, the onset of reproductive  
497 senescence was earlier in species with induced ovulation than in those with spontaneous  
498 ovulation. This might seem surprising at first glance because the intensity of sperm  
499 competition (and its possible deleterious consequences for females) are known to be higher in  
500 presence of spontaneous ovulation (Iossa et al., 2008; Soulsbury and Iossa, 2010). Yet, two  
501 hypotheses can be proposed to explain this unexpected result. First, in many species with  
502 induced ovulation, males bear keratinized spines on the surface of the penis (e.g. Dixson,  
503 1991 common marmoset *Callithrix jacchus*; Lemaître et al., 2012 in bank voles, *Myodes*  
504 *glareolus*), which could be involved in the induction of ovulation during the mating (Parag et  
505 al., 2006; Stoddart and Milligan, 1979). The density of spines on the male genitalia can in  
506 some species be high, with spines being particularly sharp (Orr and Brennan, 2016; Parag et  
507 al., 2006; Stockley, 2002). On the long run, repeated injuries caused by spines to the female  
508 reproductive tract likely impair female's reproductive condition and might be responsible for  
509 the earlier age at the onset of reproductive senescence we reported for these species. While  
510 this hypothesis clearly deserves further consideration from studies performed both within and  
511 across species, it might not be the whole story, as some species with spontaneous ovulation  
512 can also bear spines (e.g. in some primates, see Stockley, 2002). Another (non-mutually  
513 exclusive) explanation is that the efficiency of the neuro-endocrinological pathway regulating  
514 the relationship between mating and ovulation (reviewed in Bakker and Baum, 2000)  
515 decreases with increasing age. So far, the ageing of many physiological functions governing  
516 female reproduction has been described in human and laboratory rodents (vom Saal et al.,  
517 1994). However, whether neuronal mechanisms controlling the cascade of physiological  
518 responses (e.g. release of reproductive hormones by the hypothalamic–pituitary–gonadal axis)

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

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

541

#### 542 *Future directions*

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

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

553 reproductive senescence. Empirical studies have revealed that the amount of resources  
554 available in the environment positively influences the female reproductive output (e.g.  
555 Persson, 2005). However, as females age, their ability to maintain large home range (e.g. Froy  
556 et al., 2018 in Soay sheep, *Ovis aries* and red deer, *Cervus elaphus*), to acquire resources (e.g.  
557 MacNulty et al., 2009 in wolves) or to eat and digest food (e.g. Gaillard et al. 2015 for a study  
558 on tooth wear in ruminants) are impaired, which ultimately decreases the efficiency of food  
559 provisioning to their progeny during the energy-demanding period of maternal care  
560 (Gittleman and Thompson, 1988; Clutton-Brock et al. 1989; see also below) and thereby  
561 jeopardizes their reproductive success. However, whether the quality and quantity of  
562 resources available in the environment mitigate the reproductive ageing cost of these  
563 functional declines remains to be investigated. Moreover, following a resource-based  
564 allocation trade-off, a high reproductive effort during early life can be paid in terms of  
565 increased reproductive senescence (Douhard et al., 2020; Lemaître et al., 2015; Nussey et al.,  
566 2006). For instance, it has been suggested that the early onset of reproductive senescence  
567 reported in domestic mammals might be due to the strong artificial selection for a high  
568 reproductive effort during early life in domestic animals (Myserud et al., 2002 for sheep,  
569 Grange et al. 2009 for horses, *Equus caballus*). Alternatively, whether these costs are rather  
570 induced by a mismatch with environmental conditions remains unknown. In that context,  
571 comparing mammalian populations facing contrasted environmental conditions would allow  
572 assessing whether some species simply escape reproductive senescence or whether  
573 particularly good environmental conditions prevent reproductive senescence to occur.

574         While we found that female mating behavior, ovulation mode, allometry and pace of  
575 life all shape reproductive senescence, many other biological factors are likely to influence  
576 either its onset or its rate. It is beyond the scope to list all of them but we can emphasize two  
577 aspects we consider as being particularly promising: the cost of lactation and the type of  
578 placentation. In mammals, the lactation period constitutes the most energy-demanding part of  
579 the reproductive cycle (Clutton-Brock et al., 1989) and to produce high quality milk in  
580 sufficient quantity, females need to increase their food intake. Interestingly, the magnitude of  
581 this extra food intake varies substantially across species (see Douhard et al., 2016; Hayssen  
582 and Orr, 2017 for reviews), and the energy intake required by lactating females can  
583 sometimes be two- or threefold that required during the non-breeding period (see Speakman,  
584 2008 for some striking examples in rodents and insectivores). The physiological costs  
585 associated to lactation are diverse and well-documented, ranging from organ remodeling (e.g.  
586 increased size of liver, pancreas and mammary glands) to a risk of hyperthermia or bone loss

587 (due to the need to transfer calcium to the offspring) (Dufour and Sautner, 2002; Jasienska,  
588 2013; Speakman, 2008). On the contrary, much less is known on the long-term fitness costs of  
589 lactation, notably in terms of ageing. We hypothesize that the repeated physiologically costly  
590 periods of lactation should translate into an earlier/and or stronger reproductive senescence.  
591 Moreover, such costs are likely to be buffered or exacerbated by the quality of the  
592 environment, which in turn might constitute selective pressures towards specific reproductive  
593 tactics. For instance, the harsh environmental conditions faced by female white-tailed deer  
594 (*Odocoileus virginianus*) in Minnesota (i.e. severe winters and wolf predation) might explain  
595 their relatively low allocation to reproduction throughout their lives, a tactic that might  
596 ultimately minimize reproductive senescence as reported by DelGuidice and colleagues  
597 (DelGiudice et al., 2007) in this population. Another interesting feature of the mammalian  
598 reproductive machinery is the structure of the placenta that can influence the amount of  
599 nutrients transferred by the mother to the fetus(es). Indeed, the morphology of the placenta is  
600 highly variable across species, notably in its degree of invasiveness and interdigitation  
601 (Wildman, 2011), which ultimately modulates the degree and the surface for nutrient transfer  
602 during gestation (Capellini et al., 2011). Therefore, the placenta constitutes a critical organ for  
603 parent-offspring conflicts (Haig, 1993). It has already been observed that the embryo growth  
604 rate is approximately twice as fast in more interdigitated placentas (Capellini et al., 2011) and  
605 that placenta types covary with the pace of life. Slow-living species are generally  
606 characterized by an invasive placenta (i.e. hemochorial placenta) while fast species are most  
607 often characterized by less invasive placenta types (i.e. endotheliochorial or epitheliochorial  
608 placenta) (Garratt et al., 2013). The evolution of a less invasive placenta has allowed mothers  
609 to limit fetal manipulation (i.e. when food transfer during gestation is largely under the  
610 fetus(es) control) and to control better food provisioning among offspring and across  
611 reproductive events (Garratt et al., 2013). Therefore - everything else being equal - such  
612 placenta types might confer to females a way to buffer reproductive senescence.

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

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

636

637

638

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644

### 645 **Author contributions**

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

648

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655

656 **Declaration of Competing Interest**

657 The authors declare no conflict of interest

658

659

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- 1000

1001 **Table 1:** Phylogenetically controlled comparative analyses of the probability to detect  
 1002 reproductive senescence and on factors influencing both the onset and the rate of reproductive  
 1003 senescence. This table provides parameter estimates from the models discussed in the text  
 1004 (statistically significant effects occur in bold). For each model displayed below, the estimates  
 1005 are not scaled.

	<b>Dependent variables</b>	<b>Independent variables</b>	<b>Slope ± SE</b>	<b>t</b>	<b>λ [95% CI]</b>	<b>N</b>	<b>R<sup>2</sup></b>
<b>a</b>	Probability to detect reproductive senescence	Intercept	1.29 ± 0.40	3.22	NA	101	NA
		<b>Sample size</b>	<b>0.36 ± 0.15</b>	<b>2.32</b>			
		Hunting status	<b>-1.24 ± 0.55</b>	<b>-1.72</b>			
		Data quality	-0.71 ± 0.41	-1.72			
<b>b</b>	Onset of reproductive senescence	Intercept	0.78 ± 0.59	1.31	0.75 [NA; 0.93]	69	0.4
		<b>Age at first reproduction</b>	<b>0.45 ± 0.12</b>	<b>3.68</b>			
		<b>Female body mass</b>	<b>0.10 ± 0.04</b>	<b>2.19</b>			
<b>c</b>	Onset of reproductive senescence	Intercept	0.95 ± 0.51	1.85	0.63 [NA; 0.91]	69	0.5
		<b>Age at first reproduction</b>	<b>0.52 ± 0.12</b>	<b>4.39</b>			
		Female body mass	0.08 ± 0.04	1.92			
		Hunting status	0.26 ± 0.16	1.6			
		<b>Data quality</b>	<b>-0.28 ± 0.13</b>	<b>-2.19</b>			
<b>d</b>	Onset of reproductive senescence	Intercept	0.42 ± 0.47	0.91	0 [NA; 0.80]	54	0.704
		<b>Age at first reproduction</b>	<b>0.62 ± 0.13</b>	<b>5.05</b>			
		Testes mass	-0.12 ± 0.07	-1.75			
		<b>Male body mass</b>	<b>0.16 ± 0.07</b>	<b>2.35</b>			
<b>e</b>	Onset of reproductive senescence	Intercept	1.70 ± 0.13	13.04	0 [NA; 0.367]	40	0.74
		<b>Age at first reproduction</b>	<b>0.71 ± 0.09</b>	<b>7.96</b>			
		<b>Ovulation mode</b>	<b>-0.50 ± 0.18</b>	<b>-2.71</b>			
<b>f</b>	Onset of reproductive senescence	Intercept	0.45 ± 0.55	0.81	0 [NA; 0.45]	34	0.78
		<b>Age at first reproduction</b>	<b>0.53 ± 0.13</b>	<b>4.11</b>			
		<b>Ovulation mode</b>	<b>-0.74 ± 0.22</b>	<b>-3.38</b>			
		<b>Testes mass</b>	<b>-0.25 ± 0.10</b>	<b>-2.44</b>			
		<b>Male body mass</b>	<b>0.23 ± 0.09</b>	<b>2.61</b>			
<b>g</b>	Rate of reproductive senescence	Intercept	0.81 ± 0.96	0.85	0.58 [0.18; 0.86]	69	0.49
		<b>Age at first reproduction</b>	<b>-0.64 ± 0.23</b>	<b>-2.78</b>			
		<b>Female body mass</b>	<b>-0.31 ± 0.08</b>	<b>-3.85</b>			

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1007

1008 **Captions for figures**

1009

1010 **Figure 1:** Phylogenetic tree of the species analyzed. The inner band displays the occurrence  
1011 of reproductive senescence (i.e. presence vs. absence), the middle band displays the *absolute*  
1012 onset of reproductive senescence (in years) and the outer band displays the *relative* onset of  
1013 reproductive senescence (absolute onset of reproductive senescence divided by the age of the  
1014 oldest individual sampled in the population, in proportion).

1015

1016 **Figure 2:** Age-specific  $m_x$  in Bighorn sheep, *Ovis canadensis* at Ram mountain. The fit of the  
1017 selected two-threshold segmented model is presented. There are three distinct phases in the  
1018 age-specific reproductive trajectory. The section (A) corresponds to the increasing phase of  
1019 the reproductive output for young adult females. The section (B) corresponds to a phase for  
1020 prime-age females during which  $m_x$  slightly increases and the section (C) corresponds to a  
1021 senescent phase characterized by both an onset and a rate of reproductive senescence.

1022

1023 **Figure 3:** Relationship between the rate of reproductive senescence and the onset of  
1024 reproductive senescence (on a log-log scale) (Slope of  $-0.81 \pm 0.22$ ;  $R^2 = 0.17$ ;  $N=69$  species).

1025

1026 **Figure 4:** Relationship between the age at the onset of reproductive senescence (a) or the rate  
1027 of reproductive senescence (c), and the age at first reproduction (on a log-log scale) ( $N=69$   
1028 species). In panels (a) and (c) data are represented independently of female body mass while  
1029 in panels (b) and (d) data are split according to the female body mass category (light,  $N= 34$   
1030 species, heavy,  $N = 35$  species in each body mass category).

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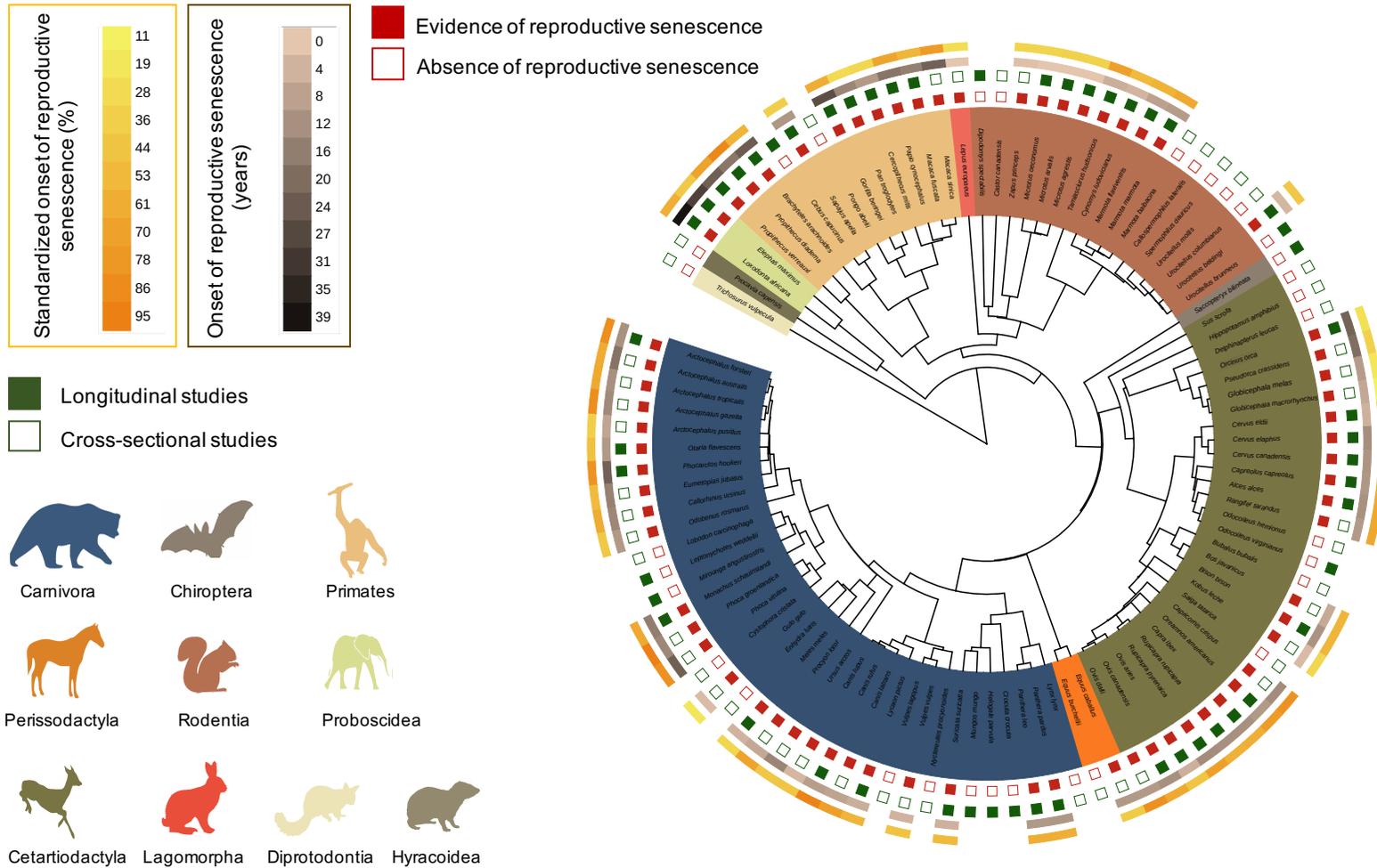
1032 **Figure 5:** Relationship between the onset of reproductive senescence and the relative testes  
1033 mass ( $N=54$  species). The onset of reproductive senescence corresponds to the residuals of the  
1034 regression of the onset of reproductive senescence against the age at first reproduction (on a  
1035 log-log scale). The relative testes mass corresponds to the residuals of the regression of the  
1036 testes mass against the male body mass (on a log-log scale). In this model, the influence of the  
1037 phylogeny is not statistically different from 0 ( $\lambda = 0$  [NA, 0.80]) and the residuals of the  
1038 models were thus computed with Ordinary Least Square regressions.

1039

1040 **Figure 6:** Box-plot displaying the differences in the onset of reproductive senescence between  
1041 species with spontaneous ( $N= 28$ ) and induced ( $N = 12$ ) ovulation. The onset of reproductive  
1042 senescence corresponds to the residuals of the regression of the onset of reproductive  
1043 senescence against the age at first reproduction (on a log-log scale,  $N=40$  species). In this  
1044 model, the influence of the phylogeny is not statistically different from 0 ( $\lambda = 0$  [NA, 0.37])  
1045 and the residuals of the models were thus computed with Ordinary Least Square regressions.

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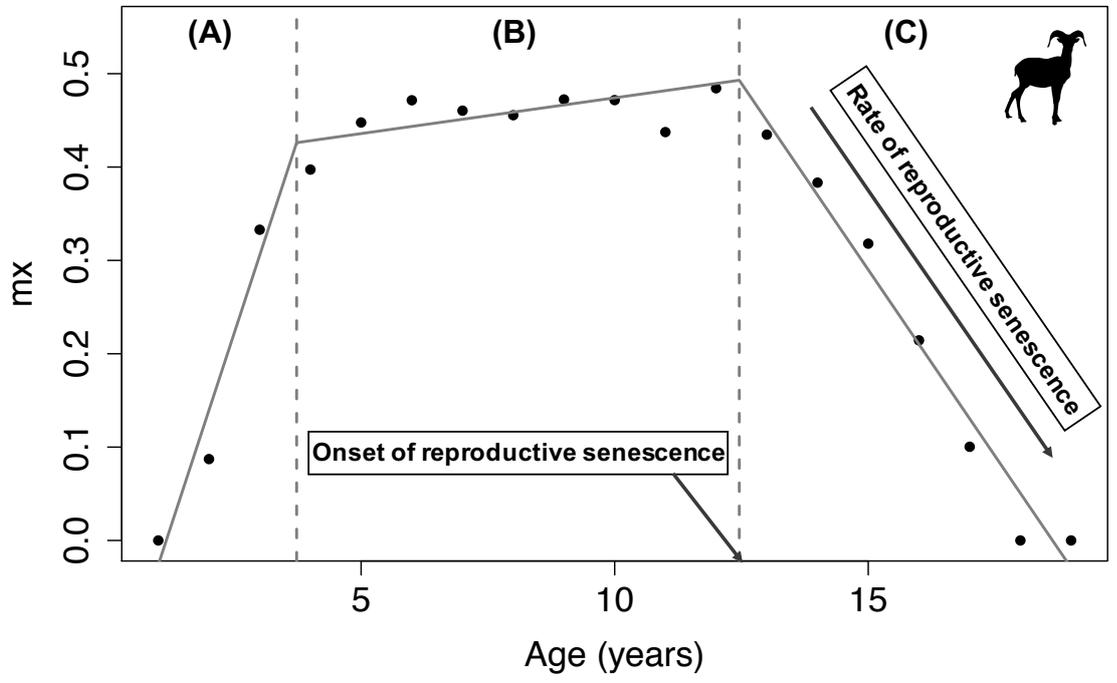


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FIGURE 1

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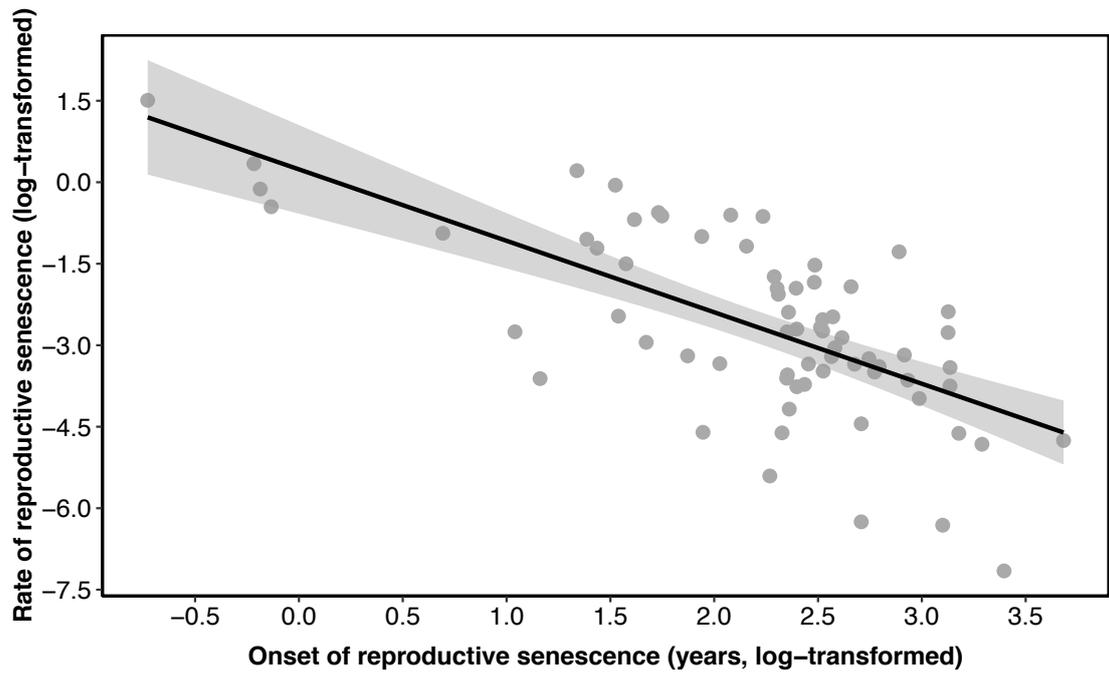
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FIGURE 2

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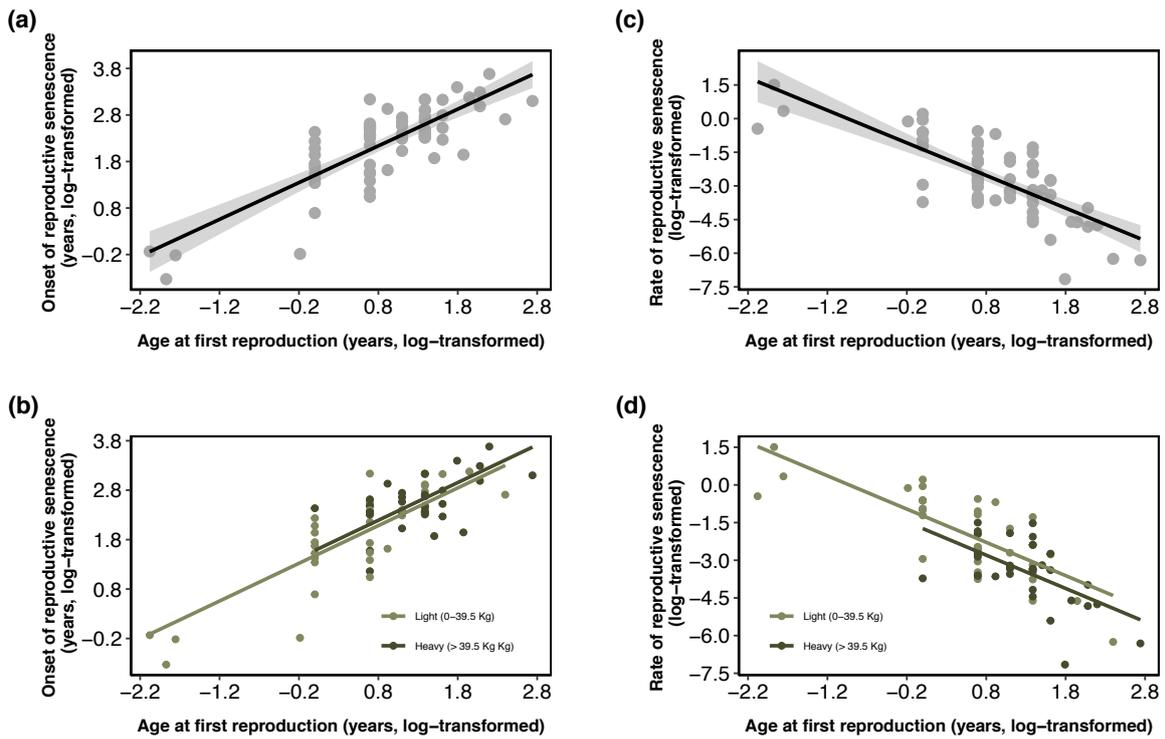


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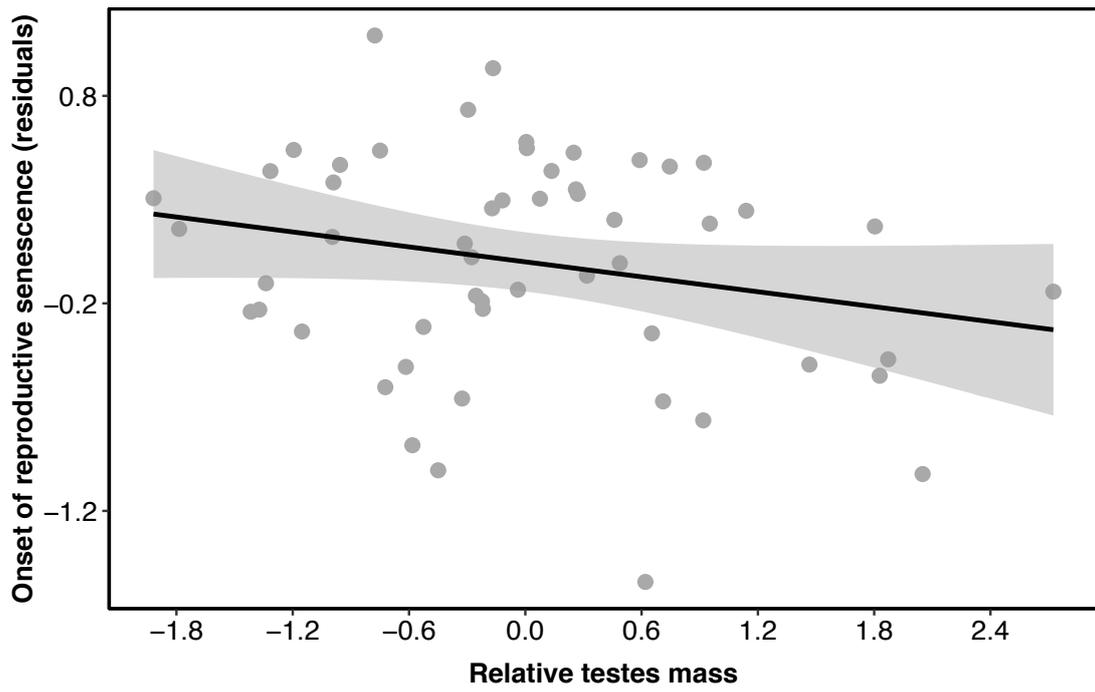
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**FIGURE 3**



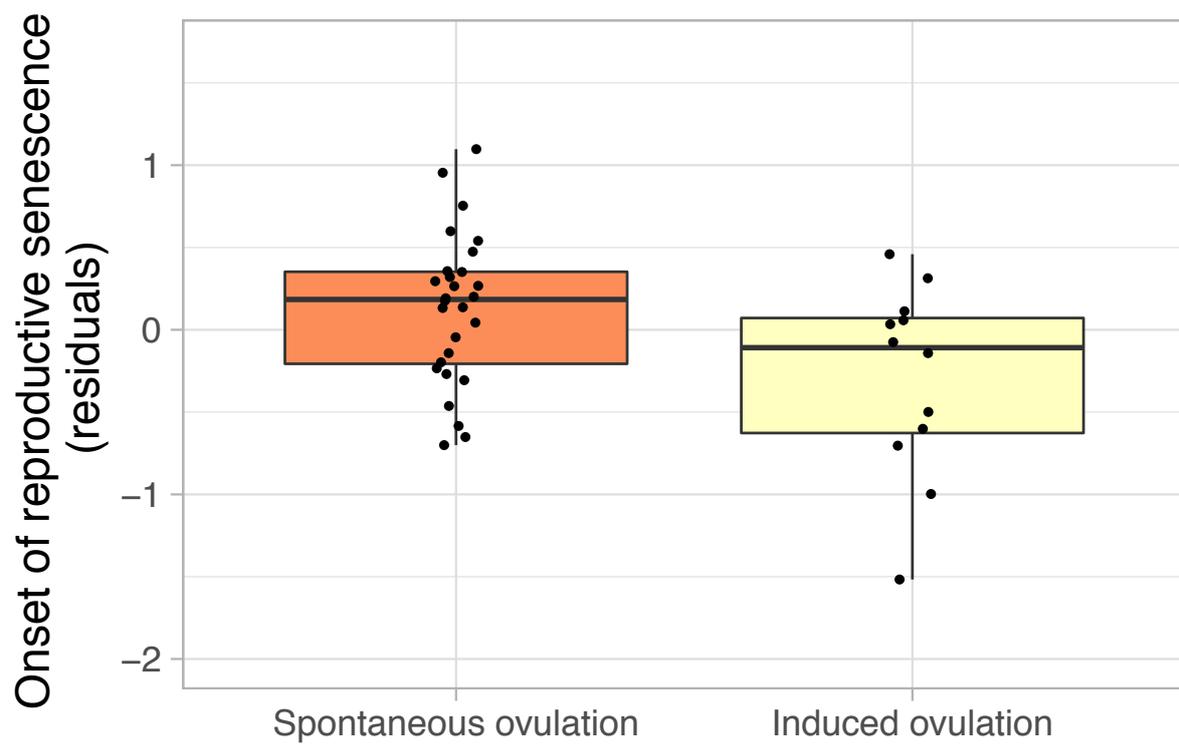
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FIGURE 4



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**FIGURE 5**



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**FIGURE 6**