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3  
4 **Sex differences in adult lifespan and aging**  
5 **rates of mortality across wild mammals**  
6

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28  
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30 designed and conducted the analyses. All authors collected the data. JFL, VR and JMG wrote the  
31 first version of the paper, which then received input from all other authors.  
32

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34

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36  
37  
38

39 **Abstract**

40 In human populations, women consistently **display** longer lifespan than men, which  
41 suggests profound biological foundations for sex differences in survival. Quantifying  
42 whether such sex differences are also pervasive in wild mammals is a crucial challenge in  
43 both evolutionary biology and biogerontology. Here, we compile demographic data from  
44 **134 mammal populations, encompassing 101 species, to show that the female's median**  
45 **lifespan is** on average **18.6%** longer than conspecific males, whereas in humans the female  
46 advantage is on average **7.8%**. On the contrary, we do not find any consistent sex  
47 differences in aging rates. In addition, sex differences in adult lifespan and aging rates are  
48 both highly variable across species. **Our analyses suggest that local environmental**  
49 **conditions, rather than sexual selection, likely shape the magnitude of sex differences in**  
50 **mammalian mortality patterns.**

51  
52

53 **Significance**

54 In human populations, women live longer than men. While it is commonly assumed that this  
55 pattern of long-lived females versus short-lived males constitutes the rule in mammals, the  
56 magnitude of the sex differences in lifespan and increase of mortality rate with advancing age  
57 remain to be quantified. Here, we demonstrate that mammalian females live longer than males  
58 but do not display faster aging rates in the wild. Contrary to a widespread hypothesis in  
59 evolutionary biology, we reveal that sex differences in life history strategies do not detectably  
60 influence the magnitude of sex differences in either lifespan or aging rates. Instead, our findings  
61 suggest that these differences are predominantly shaped by local environmental conditions.

62  
63

64 In all countries worldwide, women **live** a longer life than men (1–3). This pattern of longer-lived  
65 women is consistent from the mid-18<sup>th</sup> century (when the first accurate birth records became  
66 available) till now (2, 4), and explains why about 90% of supercentenarians (i.e. people reaching  
67 110 years old or more) are women. While social factors reinforce the gender gap in longevity (1),  
68 the greater survival prospects of women over men are observed even when both sexes share the  
69 same social habits (5). The female advantage in lifespan has thus been labelled as one of the  
70 most robust features of human biology (2). How much sexes differ in mortality patterns is a  
71 question of paramount importance associated with severe economical and biomedical  
72 implications (6, 7). Indeed, men and women show differences in the dynamics of age-associated  
73 diseases, which are currently increasing in prevalence due to a growing aging population (8). It is  
74 usually assumed that female mammals generally live longer than males (9, 10). However, this  
75 belief is driven by studies performed across human populations and relies either on a few  
76 detailed case studies or from longevity records in captivity (11), where lifespan and aging  
77 patterns are often not representative of conspecifics in the wild (12). Identifying the evolutionary  
78 mechanisms underlying sex-specific mortality requires a thorough overview of the  
79 sex differences in lifespan across mammals in the wild, which has been lacking to date.

80 **Dissimilarities in sex-chromosome content (i.e. heterogametic sex hypothesis) and**  
81 **asymmetric inheritance of mitochondrial DNA (i.e. mother's curse hypothesis) have been**  
82 **proposed to explain sex differences in mortality patterns (13–16). The first hypothesis suggests**  
83 **that within species, the heterogametic sex (i.e. XY males in mammals) should suffer from**  
84 **impaired survival compared to the homogametic sex (13, 14) while the second proposes that the**  
85 **maternal inheritance of mitochondrial DNA should lead to the accumulation of mutations**  
86 **specifically deleterious for male's fitness, e.g. notably in terms of increased mortality (15, 16).**

87 Until now, these hypotheses have been mostly investigated under laboratory conditions (16, 17,  
88 but see 18), as the level of genetic data required to tackle them has prevented any large-scale  
89 comparative analysis across mammalian species living in free-ranging conditions (16, 20).

90 These genetic mechanisms proposed to explain the evolution of sex differences in  
91 mortality patterns do not make any explicit distinction between the evolution of sex-differences  
92 in lifespan and aging rate of mortality (i.e. defined as the exponential rate of increase of mortality  
93 risk with increasing age, hereafter 'aging rate', see also Table 1). Yet, these two demographic  
94 traits can be largely uncoupled, as recently evidenced by a comparative analysis that revealed  
95 that the age-specific increase in mortality accounts for less than 50% of the observed variation in  
96 mammalian lifespan, a contribution that increases with body mass (21). Therefore, while the  
97 above-mentioned evolutionary mechanisms could influence the evolution of sex-differences in  
98 lifespan, they are not necessarily associated with the evolution of sex differences in the rate of  
99 aging. Overall, this emphasizes that studies investigating the direction and magnitude of sex  
100 differences in aging, as well as the underlying mechanisms need to consider independently adult  
101 lifespan and rate of aging.

102 In his pioneering contribution to the evolutionary biology of aging, George C. Williams  
103 was the first to launch a theory including nine predictions to explain the evolution of aging.  
104 Among them, he proposed that the sex exposed to the highest level of environmentally-driven  
105 mortality should undergo a faster aging rate (22). Since then, the association between high adult  
106 mortality and faster aging rate has been discussed and refined (see 23 for a recent review), and  
107 factors such as condition-dependent mortality, being able to act in a sex-specific way, can  
108 mitigate this prediction (24). This can explain why sex differences in adult mortality do not

109 automatically translate into sex differences in the rate of aging (e.g. (25) in wild boar, *Sus*  
110 *scrofa*).

111 Sex-specific life history strategies are further invoked to explain the inconsistency in the  
112 direction and magnitude of sex differences in aging rates of mortality observed in empirical  
113 studies (26, 27). In particular, the role played by sexual selection in shaping sex differences in  
114 mortality patterns has been intensively debated (9, 10, 26, 28). Males have been hypothesized to  
115 pay survival costs of substantial allocation to sexual competition through the growth and  
116 maintenance of conspicuous sexual traits or through the expression of risky behavior (9, 29),  
117 which should ultimately translate into a shorter adult lifespan and/or a faster rate of aging  
118 compared to females (22, 26, 27). A few comparative analyses have focused on the possible role  
119 of sexual selection to explain sex-differences in lifespan and in the rate of aging. However, these  
120 studies have made limited use of metrics that accurately assess the rate of aging (see (28) for a  
121 review). Overall, evidence reported so far is equivocal at best (13, 28) and relies on small  
122 datasets (9, 10, 29) or on captive populations (28).

123 In the present study, we compile or reconstruct (e.g. in the case of Capture-Recapture  
124 studies, see Methods) age-specific mortality estimates for 134 populations of 101 species  
125 spanning the wide diversity of orders existing in mammals to quantify for the first time both the  
126 consistency and magnitude of sex differences in adult lifespan and aging rate. Taking advantage  
127 of this unique compilation of sex- and age-specific mortality estimates, we then perform a  
128 thorough evaluation of the role played by sexual selection in shaping the diversity of sex  
129 differences in adult lifespan and aging rates observed across mammals.

130

## 131 **Results and Discussion**

132 We found that females have on average an adult lifespan 15.1 % (mean value of four  
133 longevity metrics, see Table 1) longer than males in wild mammals, after synthesizing the most  
134 complete compilation of mammalian age- and sex-specific mortality estimates ever done (Fig. 1,  
135 see Materials and Methods). The magnitude of sex differences in adult lifespan was robust with  
136 respect to four metrics of longevity commonly used (coefficient of variation: 26 %, Table 1) and  
137 the bias towards a longer lifespan for females was consistent across 60% populations included in  
138 our dataset whatever the lifespan metric analyzed (see supplement data 3). We thus report results  
139 obtained with the median adult lifespan (see Methods, Table 1). Mammalian females have an  
140 adult median lifespan 18.6% longer than males and we find that sex differences in adult median  
141 lifespan are also larger in longitudinal than in transversal studies (*SI Appendix*, Fig. S1). As  
142 individuals are closely monitored throughout their adult lifetime in longitudinal studies, these  
143 provide the most accurate demographic estimates (30), revealing that females live on average  
144 20.3% longer than males (64 populations encompassing 50 species) in the best studied  
145 populations. Although sex differences in adult lifespan from culturally and geographically  
146 distinct human populations (Americans: 6.2%, Japanese: 5.1%, Swedish: 2.0%, Aché: 17.5%)  
147 are consistent with our estimates from non-human mammals, non-human females display a  
148 survival advantage greater than women in 66.4% of the sampled populations (Fig. 1).

149 To investigate whether sex differences in the rate of aging matched sex differences in  
150 adult lifespan, we estimated the rate of aging in populations where information on the  
151 distribution of ages at death was available (83 populations representing 66 species). Empirical  
152 evidence accumulated to date indicates that the onset of actuarial senescence markedly varies  
153 across mammals and does not consistently start at the age of first reproduction (31). We thus  
154 estimated the rate of aging by fitting a Siler model (32), which does not require any assumption

155 on when the onset of senescence occurs contrary to the commonly used Gompertz model (33).  
156 We did not find any consistent difference in aging rates between males and females (Table 2,  
157 Fig. 2), even when our investigation was limited to longitudinal data (Table 2). The overall sex  
158 bias in adult lifespan we report across mammalian populations is therefore shaped by a multitude  
159 of sex-specific demographic features that characterize a species or a population, but does not  
160 systematically involve a higher rate of aging in males. Thus, longer adult lifespan in females  
161 does not systematically involve a lower rate of aging but can simply result from lower mortality  
162 at all adult ages (21). Such a decoupling between adult lifespan and rate of aging matches the  
163 human mortality pattern because age-specific mortality in studied human populations increases  
164 at the same rate in both sexes even though women live longer than men (2, 6, 34). The absence  
165 of consistent sex differences in rates of aging we document here across wild populations of  
166 mammals does not preclude any potential sex differences in the rate of aging displayed by other  
167 phenotypic traits (e.g. body mass, components of the immune system), as illustrated by recent  
168 evidence that physiological and demographic aging patterns can be uncoupled in the wild (31,  
169 35). However, age- and sex-specific data on physiological traits remain scarce, which currently  
170 prevents any large-scale investigation of sex differences in aging at the physiological level.

171         Sex differences in both adult lifespan and rate of aging are highly variable across species  
172 (coefficient of variation of 182% and 291% for adult lifespan and rate of aging, respectively, Fig.  
173 1, Fig. 2). Dissimilarities in sex-chromosome content is an influential explanation for sex  
174 differences in mortality (13, 14, 17), which suggests that within species, the heterogametic sex  
175 (i.e. XY males in mammals) should suffer from impaired survival compared to the homogametic  
176 sex. While the exact biological mechanisms linking sex chromosomes and lifespan remain  
177 unclear (13), this hypothesis successfully explains the direction of sex ratio bias (potentially



178 caused by sex differences in mortality) across tetrapods (19). However, our findings demonstrate  
179 that even within mammalian species that all share the same sex determination system, variation  
180 in the magnitude of sex differences in adult lifespan and rate of aging is particularly large. These  
181 between-species differences were not explained by phylogenetic closeness, which accounts only  
182 weakly for variation in sex differences in both adult lifespan ( $H^2 = 15\%$ ) and rate of aging ( $H^2 =$   
183  $29\%$ ) occurring across species, even though phylogenetic closeness is the key driver of the  
184 variation in sex-specific adult lifespan and rate of aging across species ( $H^2 = 86\%$  and  $H^2 = 85\%$   
185 for female and male adult lifespan, respectively;  $H^2 = 87\%$  and  $H^2 = 88\%$  for female and male  
186 rate of aging, respectively). These findings indicate that allometry (through the species-specific  
187 body size (36)) and pace of life (through the species-specific position along the slow-fast  
188 continuum (37)), which both closely track phylogenetic closeness (38), mostly determine the  
189 mortality pattern observed in a given mammalian species (39) but have little influence on the  
190 difference between sexes in either adult lifespan or rate of aging. Overall the extant sexual  
191 dimorphism in survival metrics is likely fine-tuned by variation in environmental conditions  
192 among and within populations, which vary strongly within a given species.

193 We then conducted additional analyses focused on sexual selection, which is commonly  
194 assumed to shape sexual dimorphism in mortality patterns (26, 28). These broad scale analyses  
195 on mammals in the wild reveal that sexual size dimorphism (but not mating system) is only  
196 weakly associated with the direction and magnitude of sex differences in adult lifespan (slope of  
197  $-0.23$  [95% CI:  $-0.49;0.04$ ], Table S1, Fig. 3) and is not associated with the rate of aging (*SI*  
198 *Appendix*, Tables S2), which challenges the current thinking in evolutionary biology of aging (9,  
199 16, 27, 40). Moreover, these findings contrast with a previous comparative analysis performed  
200 on captive populations where sex differences in lifespan were unambiguously higher in

201 polygynous than in monogamous ruminants (28). In zoological gardens, animals live in sheltered  
202 environments where environmentally-driven mortality risks are buffered (e.g. through food  
203 provisioning or preventive veterinary medicine, see 41). Male physiological costs caused by the  
204 growth and maintenance of a large body size and secondary sexual traits might therefore be more  
205 likely to translate into a greater overall reduction in male survival relative to females in captivity,  
206 where individuals are protected from environmental severity. In such captive conditions  
207 adaptations to sexual competition might be the main driver of sex differences in lifespan, since  
208 both sexes are sheltered from additional mortality sources that can influence lifespan in sex-  
209 dependent and independent ways (28). By contrast, in the wild, we hypothesize that local  
210 environmental conditions and the myriad of associated mortality risks (e.g. climate harshness,  
211 pathogen richness) predominantly shape sex differences in adult lifespan and rate of aging, over-  
212 riding and/or interacting with costs of sexual selection. For instance, adult females from hunted  
213 populations ( $N = 21$ ) tend to live longer relative to males than adult females from non-hunted  
214 populations (34.5% vs. 16.7%, respectively, Fig. 3). Trophy hunting constitutes one extreme  
215 example of environmental conditions (i.e. anthropogenic activities) that shape the magnitude of  
216 sex differences in mortality patterns across mammalian populations in the wild.

217 From an evolutionary perspective, sex-specific gene expression and physiological  
218 systems are the direct consequences of both natural and sexual selection pressures that have been  
219 exerted independently on males and females (27, 40, 42). For instance, sexual selection has led  
220 to the evolution of species with high sexual dimorphism for many phenotypic traits (e.g. body  
221 size) that differentially sensitize either sex to specific environmental conditions. This is  
222 particularly well illustrated by the three longitudinally-monitored populations of bighorn sheep  
223 (*Ovis canadensis*) included in our dataset. In this polygynous ungulate, males and females show

224 almost no difference in lifespan in the National Bison Range population where resources are  
225 consistently available. However, males live much shorter life in Ram Mountain where winter  
226 severity is particularly pronounced leading to marked sex differences in lifespan (43).

227 In humans and laboratory rodents sex differences in mortality patterns extend to sex  
228 differences in frailty, neurological decline and comorbidity (6). In laboratory mice and rats, the  
229 survival benefits associated with anti-aging interventions (genetic or pharmacological) are also  
230 frequently sex-specific (6, 44). These sex-specific responses can be attributed to sex differences  
231 in physiological systems (e.g. hormonal profiles), which are also expected to modulate adult  
232 lifespan and aging (45). Therefore, we propose that variation in the magnitude of sex differences  
233 in both adult lifespan and rate of aging **in wild populations** is likely a response to interactions  
234 between sex-specific physiological pathways and the diversity of environmental conditions met  
235 by mammals across the world. **For instance, sexual dimorphism is partly physiologically driven**  
236 **by a higher production of androgens in males, particularly during early adulthood (46), which**  
237 **directly controls the growth of many secondary sexual traits (e.g. ornaments and armaments) (13,**  
238 **27). Circulating androgens also modulate immune performance and when present at high levels**  
239 **can impair some aspects of the immune defense (47), making males more sensitive to pathogens.**  
240 **Therefore, whether highly sexually dimorphic species living in the wild show marked sex**  
241 **differences in lifespan and aging rate of mortality is likely to depend on local conditions (e.g.**  
242 **pathogens richness), which can either exacerbate or buffer the magnitude of these sex differences**  
243 **(48).** Albeit challenging, research programs that solve this complex network will undoubtedly  
244 provide innovative insights into the evolutionary roots and physiology underlying aging in both  
245 sexes.

246

## 247 **Materials and Methods**

248 **Data collection.** Age- and sex-specific mortality data were extracted from published life tables  
249 or graphs using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). We limited our  
250 literature search to mortality or survival estimates published for both sexes for wild populations  
251 of mammals, for a total of 184 populations encompassing 128 species. Based on the methods  
252 used to estimate age-specific mortality in the initial source, we distinguished three main  
253 categories of **study**. The first type of **study** corresponds to age-specific mortality estimates  
254 obtained from the long-term monitoring of individuals marked during early life when age can be  
255 accurately assessed (i.e. longitudinal data). The second type of **study** corresponds to age-specific  
256 mortality estimates obtained from dead animals collected in the field (i.e. transversal data using  
257 the standard  $dx$  series (49)). Finally, the third type of **study** corresponds to age-specific mortality  
258 estimates computed from the sampling of individuals alive in the population (i.e. transversal data  
259 using the standard  $lx$  series (49)). For transversal data, population size has to be considered as  
260 constant or with a known growth rate and the distribution of ages of dead or alive individuals in  
261 the population as stable (49). Mortality estimates extracted from transversal data also depend on  
262 the precision of the methods used to assess the age of the individuals. Longitudinal data based on  
263 known-aged individuals regularly **monitored by Capture-Recapture methods** provide much more  
264 accurate estimates of age-specific mortality than transversal data (50). Sampled populations were  
265 also classified as hunted vs. non-hunted according to the information reported in the original  
266 publication. All data and associated references are provided in Supplementary Tables.

267 To compare results obtained from wild populations to humans, we recovered age- and sex-  
268 specific mortality data from four human populations (all longitudinal). These data were extracted  
269 for three contemporary countries (Japan, Sweden and USA (51)) and for one **traditional**

270 population (Aché (52)). We used a similar procedure (see section ‘Estimation of adult lifespan  
271 and rate of mortality aging’ below) to compute adult lifespan and rate of aging in wild mammals  
272 and humans using 13 years of age as **the onset of adulthood** following reported data for the  
273 populations of Sweden, Japan and USA (53) and previous comparative analyses of mortality  
274 patterns (54). However, human estimates were only used in comparison with wild populations of  
275 mammals and were not included in the analysis.

276 For each species, we collected data on life history traits that could explain sex differences in  
277 adult lifespan and aging rates. As both sexual selection and sociality have been suggested to  
278 influence sex-specific mortality (9, 55), we collected data on mating system, social system and  
279 sex-specific body mass (to measure sexual size dimorphism). Following previous comparative  
280 studies in mammals (e.g. (28)), we classified the species in terms of mating (i.e. monogamous,  
281 polygynous, or promiscuous) and social (i.e. cooperative breeders vs. non-cooperative breeders)  
282 systems. The intensity of sexual selection is expected to be smaller in monogamous species  
283 compared to polygynous and promiscuous species, which might reduce sex differences in  
284 mortality patterns (9). In cooperative breeders, costs of reproduction are generally shared among  
285 females (56), which might also increase sex differences in mortality patterns through a reduced  
286 female mortality. For each life-history trait, we prioritized data recovered from the same  
287 population (see Supplementary Data and associated references for each life-history trait used in  
288 the analysis).

289

### 290 **Estimation of adult lifespan and rate of mortality aging.**

291 We excluded juvenile mortality because it is generally higher than adult mortality in mammals  
292 and can vary considerably among species and populations and even among years within a same

293 population (57). In the wild, juveniles are not easily detected or recovered, which can lead to  
294 inaccurate juvenile mortality estimates in life tables built from transversal data. Moreover, in the  
295 longitudinal studies compiled in our work, the age where individuals are marked for the first time  
296 differs among studies compiled even if all individuals were first marked within the first year of  
297 life when it is possible to assign age without error. We thus excluded the juvenile stage from our  
298 analyses and focused on adult data only. To define the adulthood period, we used the species-  
299 specific female age at first reproduction as the onset of adulthood.

300 *Rate of mortality aging.* For the ‘longitudinal’ and ‘transversal-dx’ data, the exact age at death of  
301 each individual was reported. The mortality rate at each age was estimated while accounting for  
302 differences in the number of individuals at risk. For instance, at old ages, mortality rates are  
303 typically computed from the few individuals that are still alive, which makes those rates less  
304 reliable than those at earlier ages. While aging is commonly assumed to start at the age of first  
305 reproduction (22, 58), empirical evidence suggests that the onset of aging is often delayed and  
306 show considerable variation among mammals (31). Therefore, models that allow flexibility in the  
307 age at the onset of aging provide better fit than the Gompertz model fitted from the age of first  
308 reproduction. We thus fit a Siler model on age-specific mortality data (32) for each population to  
309 obtain comparable metrics. The five-parameter Siler model is given by

$$310 \quad \mu(x) = a_0 \exp(-a_1 x) + c + b_0 \exp(b_1 x) \quad (1)$$

311 where  $a_1, a_1, b_0, b_1, c \geq 0$  are the parameters of the mortality function and  $x$  the age in years. The  
312 first exponential function on the right-hand side of Eq. (1) corresponds to the decline in mortality  
313 in the early adult stage (e.g. subadult mortality), the  $c$  parameter provides the lower limit of  
314 mortality during the adult stage, and the second exponential function corresponds to the mortality  
315 increase during the senescent stage. As a metric of rate of aging we used the  $b_1$  parameter of the

316 Siler model (see Eq. (1)) that measures the exponential increase in mortality rate with age during  
317 the senescence stage. We restricted the analyses to populations that included at least 30 males  
318 and 30 females at the female age at first reproduction. To account for different sample size  
319 among ages we used the R package BaSTA (59). For transversal-lx data, we only had access to  
320 the age distribution for individuals alive. As the range of ages covered was quite low for some  
321 species (e.g. (60) for an example in weasels, *Mustela nivalis*), it was not possible to fit the Siler  
322 model using transversal-lx data and these populations were excluded from the rate of aging  
323 analysis.

324

325 *Adult lifespan.* We estimated sex-specific median adult lifespan (in years) for populations from  
326 our dataset. We first defined adult survivorship as the cumulative survival conditioned on  
327 reaching adulthood, and thus, at the age of the onset of adulthood, adult survivorship is equal to  
328 1. The median adult lifespan corresponds to the age when 50% of the individuals alive at the  
329 onset of adulthood were dead (i.e. when cumulative survivorship reaches 0.5). For the  
330 ‘longitudinal’ and ‘transversal-dx’ data, median lifespan was estimated from the Siler model by  
331 solving numerically the following equation:

332

$$333 \quad e^{\left(\frac{a_0}{a_1}(e^{-a_1x}-1)-cx+\frac{b_0}{b_1}(1-e^{b_1x})\right)} = 0.5 \quad (2)$$

334

335 For transversal-lx, we fitted a Gompertz model given by:

$$336 \quad \mu(x) = a \exp(b x) \quad (3)$$

337 on the observed distribution of ages among individuals alive where  $a > 0$  and  $b \geq 0$  are the  
338 Gompertz parameters (33), with  $a$  representing the baseline mortality at the starting age and  $b$  the

339 exponential rate of increase in mortality with age. As individuals for transversal-lx data are all  
340 sampled only once and are thus not monitored through their entire life, we took a larger sample  
341 size threshold for our selection procedure. Therefore, for transversal-lx data, we excluded  
342 populations when the sample size was below 50 individuals for at least one of the two sexes. For  
343 the ‘transversal-lx’ data, median lifespan was estimated from the Gompertz model by solving  
344 numerically the following the equation:

$$346 \quad e^{\frac{a}{b}(1-e^{bx})} = 0.5 \quad (4)$$

347  
348 To assess the accuracy of the adult lifespan estimate based on a Gompertz model fitted to the age  
349 distribution of animals alive, we also used this method to estimate adult lifespan from  
350 longitudinal and transversal-dx data. The correlation between estimates of adult lifespan obtained  
351 with the two methods (Siler vs. Gompertz models fitted to longitudinal and transversal-dx data  
352 only) was extremely high ( $R^2 = 0.99$ , Fig. S1), which indicates that these two approaches did not  
353 influence the outcome of our analyses of adult lifespan. Moreover, to verify the robustness of our  
354 results, we analysed sex differences in adult lifespan using three other metrics of longevity. For  
355 each population we computed the age when 80% of the individuals alive at the onset of  
356 adulthood were dead (i.e. when cumulative survivorship reaches 0.2, a metric also called adult  
357 lifespan 80%) and life expectancy at the onset of adulthood, which correspond to the mean adult  
358 lifespan from the distribution of ages at death (using longitudinal and transversal-dx data with no  
359 censoring at old age). Finally, although it is highly sensitive to sample size (61), we also reported  
360 maximum adult lifespan for each sex because it is still the most often studied survival metric in



361 comparative studies of aging. Results obtained with the four longevity metrics are displayed in  
362 Table 1.

363

#### 364 **Statistical analyses.**

365 **Adult lifespan.** For each population, we quantified sex differences in adult lifespan as the ratio  
366 between male and female adult lifespan on a log scale (*difference adult lifespan* =  
367  $\log\left(\frac{\text{adult lifespan male}}{\text{adult lifespan female}}\right)$ ). For the analysis of sex differences in adult lifespan, we ran a  
368 Bayesian hierarchical model using the package MCMCglmm (62) with the magnitude of sex  
369 differences in adult lifespan as the response variable. As species from our dataset were not  
370 independent because they share phylogenetic relatedness, we corrected all our analyses for  
371 phylogeny using the phylogenetic variance-covariance matrix extracted from a mammalian  
372 phylogenetic tree (63). Moreover, in some species ( $N = 21$ ), estimates from several populations  
373 were available and the data from these populations were thus not independent. Therefore, we  
374 fitted the species independently of the phylogeny as a random effect because individuals from  
375 the same species can share different ecological characteristics, which are not necessarily linked  
376 to the phylogenetic relatedness. To test the sensitivity of the results to the priors, we used two  
377 sets of priors for the random effects in the model (uninformative inverse Wishart prior with  
378  $\nu=0.02$  and  $V=1$  and expanded prior with  $\nu=1$   $V=1$   $\alpha.\nu=0$   $\alpha.V=1000$ ). Models with  
379 different priors did not show any detectable difference (Gelman and Rubin's convergence  
380 diagnostic very close to 1 for each MCMC chain (64)). From this model we were able to extract  
381 the percentage of the total variance explained by the phylogenetic effect (named phylogenetic  
382 heritability  $H^2$ ) (65). The value of  $H^2$  can be interpreted as a direct equivalent to the phylogenetic  
383 signal ( $\lambda$ ) of Pagel, with a value close to 1 meaning that there is a strong phylogenetic signal and

384 a value close to 0 that there is no phylogenetic signal. For each parameter, we reported the mean  
385 of highest posterior density distribution, the lower and upper limits of the 95 % credibility  
386 interval and **sample size**.

387 The first aim of our analyses was to estimate the average sex difference in adult lifespan  
388 across the whole set of mammals. We thus ran the model of sex difference in adult lifespan  
389 without any independent covariate or factor and found a longer adult lifespan for females in the  
390 dataset with an overall negative effect (see *SI Appendix*, Table S3 for all coefficients). In a  
391 second step, we tested whether some species-specific traits **associated with sex-specific life**  
392 **history strategies and sexual competition** (sexual size dimorphism, mating system, social system,  
393 sex-bias in **dispersal**) explained sex differences in adult lifespan observed across mammals. We  
394 included sexual size dimorphism (**SSD, computed as the log-scaled ratio between male and**  
395 **female body mass**) and the occurrence of sex-biased **dispersal assessed through** sex-biased  
396 individual detection (likely bias vs. unlikely bias). Indeed, in some mammalian populations,  
397 males are more difficult to detect than females because they wander at a much larger extent, by  
398 doing breeding dispersal and/or not defending a territory. Such lower male detection can lead to  
399 **underestimates of** male survival when not corrected for and thereby to bias estimates of sex  
400 differences in adult lifespan and rate of aging. To overcome this problem, we considered that  
401 populations that are spatially constrained (e.g. living on island or in mountain ranges), monitored  
402 longitudinally, or of species where males defend a territory, are unlikely to display biased  
403 estimates of sex differences in adult lifespan. On the other hand, populations of non-territorial  
404 species (with an expected high breeding dispersal propensity) or without clear information on the  
405 mating tactic available in the literature are likely to display more biased estimates of sex  
406 differences in adult lifespan. For all the models, **we controlled for the potential confounding**

407 effect of the hunting status of the population (i.e. hunted vs. non-hunted) and of data quality  
408 (longitudinal vs. transversal data). All the two-way interactions among these factors were  
409 included in candidate models.

410 To identify the model of sex differences in adult lifespan with highest support, we fitted  
411 different models with all the possible combinations of variables from the full model ( $N = 19$   
412 models). These models were then ranked by the Deviance Information Criterion (66) (*SI*  
413 *Appendix*). The selected model included additive effects of hunting (i.e. sex differences in adult  
414 lifespan were highest in hunted populations) and data quality (i.e. higher sex differences  
415 occurred in adult lifespan with high quality data, *SI Appendix*, Table S3 and Fig. 3).

416 The effect of both mating and social systems were tested on a population subset ( $N = 132$   
417 populations) because this information was lacking for some species. In addition, the social  
418 system was highly correlated to the mating system. Indeed, except for the four-striped grass  
419 mouse (*Rhabdomys pumilio*) (67) all cooperative breeders ( $N = 6$ ) in our dataset were  
420 monogamous. We thus tested separately the influence of the mating and social systems, to avoid  
421 multicollinearities issues (68). The independent model including only mating system as a  
422 covariate did not reveal any effect on sex differences in adult lifespan (mean difference<sub>monogamous</sub>  
423 vs. polygynous = 0.001 [-0.325; 0.318], mean difference<sub>monogamous vs. promiscuous</sub> = 0.047 [-0.265; 0.392]).  
424 Similarly, the model including only social system did not reveal any detectable effect (mean  
425 difference<sub>cooperative vs. non-cooperative breeder</sub> = -0.015 [-0.366; 0.317]).

426  
427 *Rate of aging*. For each population, we computed sex differences in aging rates of mortality as  
428 the ratio between male and female rates of aging on a log scale (*difference aging rate* =  
429  $\log\left(\frac{\text{aging rate male}}{\text{aging rate female}}\right)$ ). We then followed the same procedure as used for sex differences in

430 adult lifespan. We found no statistical support for consistent sex differences in aging rates across  
431 species (*SI Appendix*, Table S1). We performed a second set of analyses to test whether our set  
432 of life history traits can explain possible sex differences observed in aging rates across mammals.  
433 Similar to the analyses performed for sex differences in adult lifespan, we included SSD and  
434 potential sex-biased individual detection (*SI Appendix*, Table S3) and we controlled for possible  
435 confounding effects of hunting status and data quality. All the two-way interactions between  
436 these variables were included in candidate models. We ranked all the models based on their DIC  
437 score to identify the variables influencing sex differences in aging rates. The Null model was  
438 ranked first, revealing that none of these variables influenced the magnitude and the direction of  
439 sex differences in aging rates (*SI Appendix*, Table S4). Moreover, additional analyses did not  
440 reveal any effect of either mating or social system (mean difference<sub>monogamous vs. polygynous</sub> = -0.04  
441 [-0.48; 0.41], mean difference<sub>monogamous vs. promiscuous</sub> = 0.01 [-0.45; 0.46], mean difference<sub>cooperative</sub>  
442 vs. non-cooperative breeder = -0.17 [-0.57; 0.23]).

443

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606 **Table 1.** Mean percentage differences and mean log-transformed lifespan differences (with 95%  
607 credibility intervals (CI)) between males and females of mammalian populations for four  
608 longevity metrics. *N* corresponds to the number of populations included in the analyses. We  
609 focused on the adult stage to avoid any confounding effect of variation in juvenile mortality. We  
610 defined the adult life stage from the age of female age at first reproduction onwards. The average  
611 difference across the four longevity metrics is 15.1 %.

612

Metrics	Mean percentage differences	Mean log-transformed differences	Lower CI	Upper CI	<i>N</i>
Median adult lifespan <sup>1</sup>	18.6	-0.171	-0.376	0.036	134
Adult life expectancy <sup>2</sup>	11.0	-0.104	-0.332	0.130	57
Adult lifespan 80% <sup>3</sup>	18.6	-0.171	-0.333	-0.016	134
Maximum adult lifespan <sup>4</sup>	12.2	-0.115	-0.256	0.017	107

613

614 <sup>1</sup> Age at which 50% of the individuals alive at the onset of adulthood were dead (i.e. when  
615 cumulative survivorship reaches 0.5).

616 <sup>2</sup> Mean age at death of the individuals alive at the onset of adulthood.

617 <sup>3</sup> When 80% of the individuals alive at the onset of adulthood were dead (i.e. when cumulative  
618 survivorship reaches 0.2).

619 <sup>4</sup> Oldest age reached by individuals alive at the onset of adulthood.

620

621 **Table 2.** Mean of the posterior distribution of the difference between sexes in rate of mortality  
622 aging for (a) longitudinal and transversal dx data together (see Methods) and (b) longitudinal  
623 data only. *N* corresponds to the number of populations included in the analyses. The mean sex  
624 difference is associated with the 95% credibility interval and *N* corresponds to the number of  
625 populations included in the analyses.

626

Parameters	Mean	Lower CI	Upper CI	<i>N</i>
Rate of aging <sup>1</sup>	0.194	-0.144	0.529	83
Rate of aging <sup>1</sup> (longitudinal only)	0.215	-0.103	0.577	64

627

628 <sup>1</sup> Exponential rate of mortality increase estimated from a Siler model fitted from the onset of  
629 adulthood (see Methods).

630 **Fig. 1.** Sex differences in adult lifespan across mammals. For a given population, the sex  
631 difference is measured as the ratio  $\log[(\text{Male adult lifespan})/(\text{Female adult lifespan})]$ . Multiple  
632 bars for a given species represent estimates gathered from different populations. Orange bars  
633 correspond to longitudinal data, grey bars correspond to transversal data, and dark grey bars  
634 correspond to the human populations. The black dot corresponds to the overall effect for non-  
635 human mammals and is associated with its 95 % credibility interval.

636 **Fig. 2.** Frequency distribution of the magnitude of sex differences in rate of aging across  
637 mammals in the wild (a). The black dot corresponds to the overall effect for non-human  
638 mammals and is associated with its 95 % credibility interval. Patterns of age-specific changes in  
639 mortality rate for three mammalian populations are displayed. For each population the mortality  
640 curve with the vertical line representing the median adult lifespan and the posterior distribution  
641 of the aging rate  $b_j$  are given in red for females and in blue for males. The mortality hazard  
642 corresponds to the instantaneous rate of mortality. In the three populations, adult females live  
643 longer than adult males. However, in (b) Asian elephant, *Elephas maximus* (Myanmar  
644 population), females have a higher aging rate, in (c) Yellow baboon, *Papio cynocephalus*  
645 (Amboseli National Park population) no difference in aging rates is observed while in (d) red  
646 deer, *Cervus elaphus*, (Isle of Rum population) males show a higher rate of aging than females.

647 **Fig. 3.** Effect of sexual size dimorphism (a), hunting (hunted vs. non-hunted populations) (b),  
648 and data quality (longitudinal-high quality vs. transversal-low quality) (c) on sex differences in  
649 median adult lifespan across mammals. The horizontal grey and dash line corresponds to the  
650 absence of sex differences in median adult lifespan.  
651

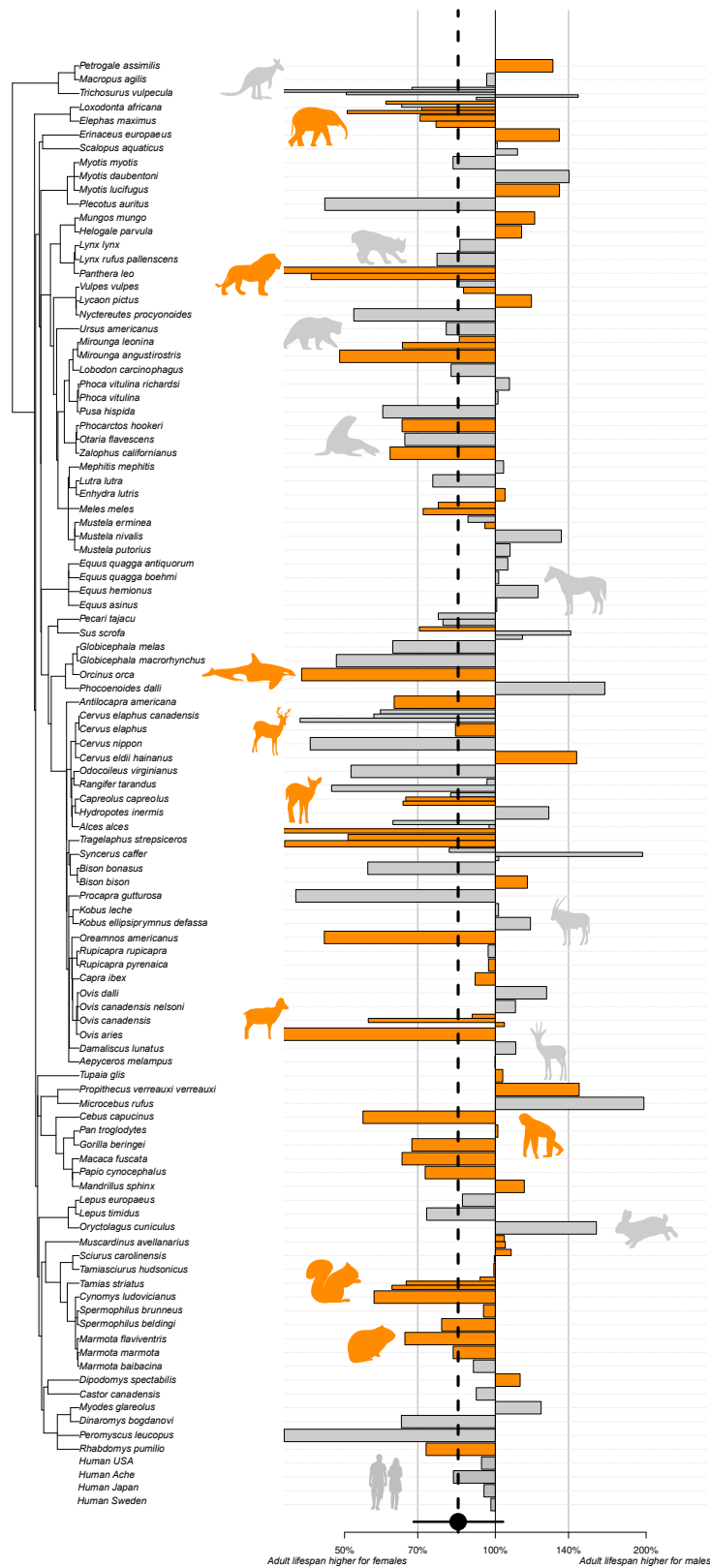
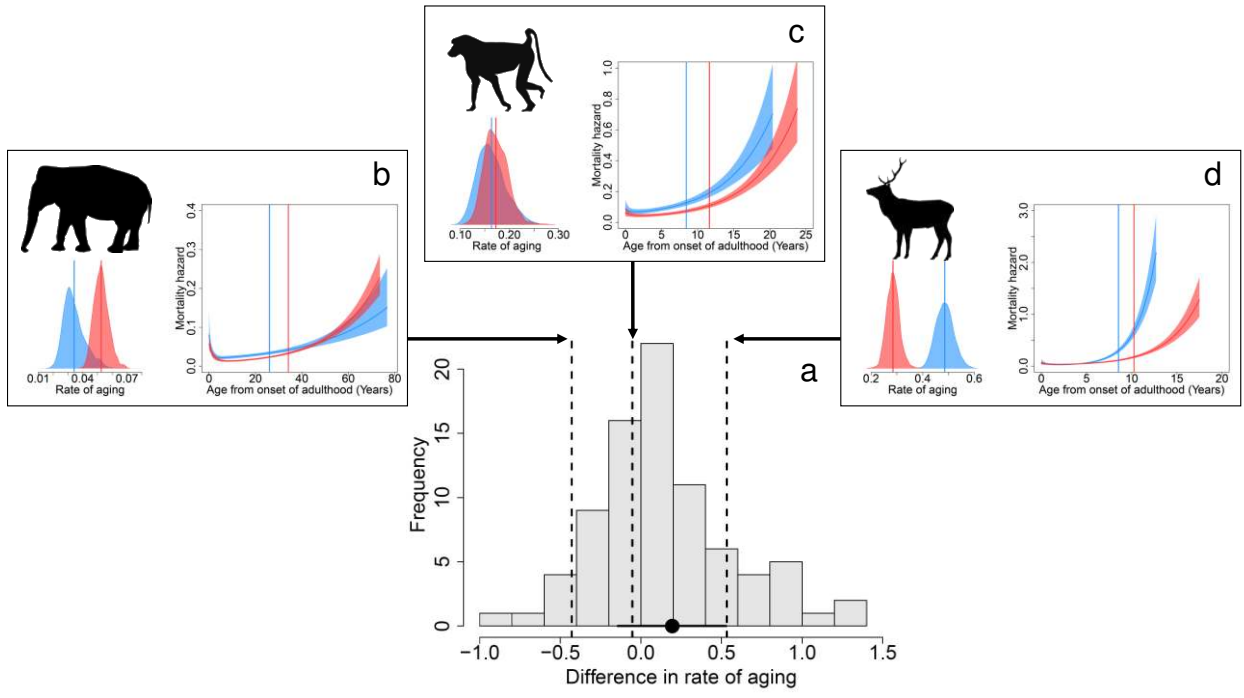


Fig. 1

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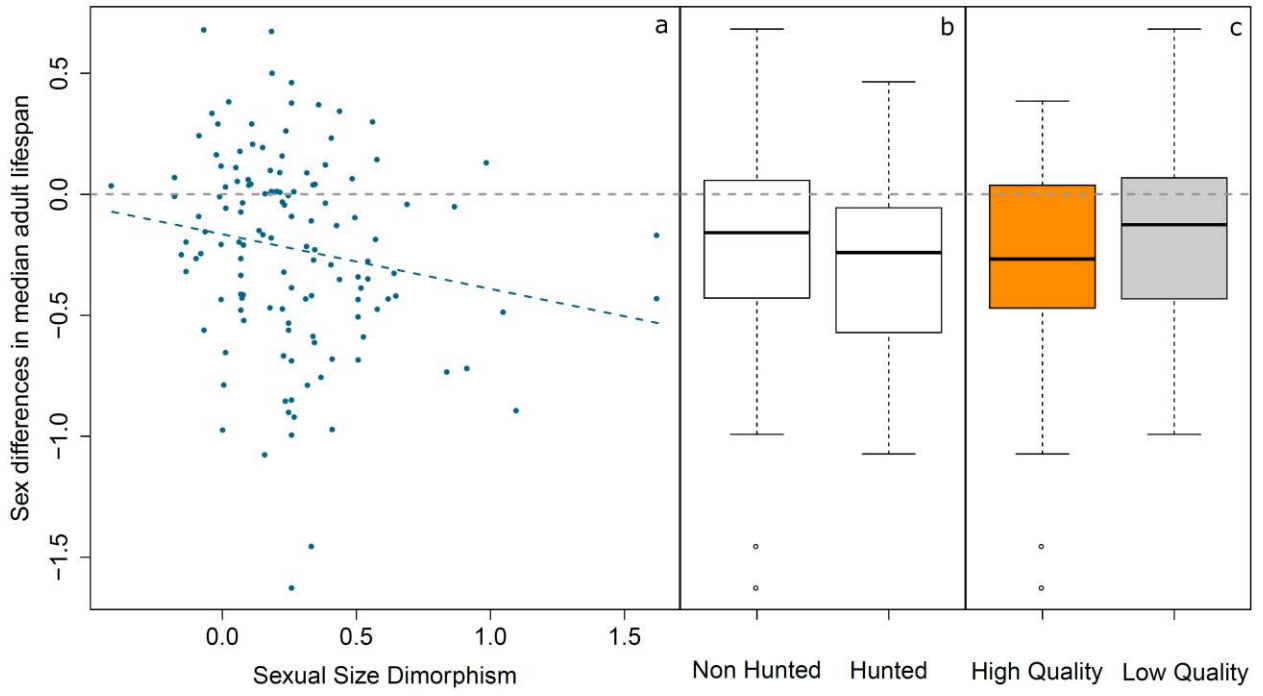
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Fig. 2

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Fig. 3

