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

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30 designed and conducted the analyses. All authors collected the data. JFL, VR and JMG wrote the
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34
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38

39 **Abstract**

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

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 remains to be quantified. Here, we demonstrate that, in the wild, mammalian females live longer
58 than males but we did not detect any sex differences in aging rates. Contrary to a widespread
59 hypothesis, we reveal that sex differences in life history strategies do not detectably influence the
60 magnitude of sex differences in either lifespan or aging rates. Instead, our findings suggest that
61 these differences are predominantly shaped by complex interactions between local environmental
62 conditions and sex-specific reproductive costs.

63
64

65 In all countries worldwide, women live on average a longer life than men (1–3). This pattern of
66 longer-lived women is consistent from the mid-18th century (when the first accurate birth records
67 became available) until now (2, 4), and explains why about 90% of supercentenarians (i.e. people
68 reaching 110 years old or more) are women. While social factors reinforce the gender gap in
69 longevity (1), the greater survival prospects of women over men are observed even when both
70 sexes share the same social habits (5). The female advantage in lifespan has thus been labelled as
71 one of the most robust features of human biology (2). How much sexes differ in mortality
72 patterns is a question of paramount importance associated with striking economical and
73 biomedical implications (6, 7). Indeed, men and women show differences in the dynamics of
74 age-associated diseases, which are currently increasing in prevalence due to a growing aging
75 population (8).

76 It is usually assumed that female mammals generally live longer than males (9, 10).
77 However, this belief is driven by studies performed across human populations, a small number of
78 case studies on wild mammals, or records of mammals housed in captivity (11), where lifespan
79 and aging patterns are often not representative of conspecifics in the wild (12). Identifying the
80 evolutionary mechanisms underlying sex-specific mortality requires a thorough overview of the
81 sex differences in lifespan across mammals in the wild, which has been lacking to date.

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

88 specifically deleterious for male's fitness, e.g. notably in terms of increased mortality (15, 16).
89 Until now, these hypotheses have been mostly investigated under laboratory conditions (17, 18),
90 as the type of data required to tackle them (e.g. mitochondrial DNA mutation rate, transposable
91 element content of the sex chromosomes, see (13)) has so far prevented any large-scale
92 comparative analysis across mammalian species living in free-ranging conditions (16, 19).

93 These genetic mechanisms proposed to explain the evolution of sex differences in
94 mortality patterns do not make any explicit distinction between the evolution of sex-differences
95 in lifespan and aging rate of mortality (i.e. defined as the exponential rate of increase of mortality
96 risk with increasing age, hereafter 'aging rate', see also Table 1). Yet, these two demographic
97 traits can be largely uncoupled, as recently shown by a comparative analysis revealing that
98 although the observed variation in mammalian lifespan explained by the rate of aging increases
99 with the species body mass, the aging rate never accounts for more than 50% of this variation
100 (20). Therefore, while the above-mentioned evolutionary hypotheses (i.e. heterogametic sex and
101 mother's curse) could influence the evolution of sex differences in lifespan, they are not
102 necessarily associated with the evolution of sex differences in the rate of aging. Overall, this
103 emphasizes that studies investigating the direction and magnitude of sex differences in mortality
104 patterns, as well as the underlying mechanisms need to consider independently adult lifespan and
105 rate of aging.

106 In his pioneering contribution to the evolutionary biology of aging, George C. Williams
107 was the first to launch a theory including nine predictions to explain the evolution of aging.
108 Among them, he proposed that the sex exposed to the highest level of environmentally-driven
109 adult mortality (i.e. mortality due to the interactive effects of both environment and genetic
110 background, see (21)) should undergo a faster aging rate (22). Since then, the association

111 between high adult mortality and faster aging rate has been discussed and refined (23), and
112 factors such as condition-dependent mortality have been highlighted as moderators that can
113 shape the relationship between adult mortality and aging rate in a sex-specific way (24). For
114 instance, in wild boar (*Sus scrofa*), aging rates are similar between sexes despite a consistently
115 higher mortality in males than in females throughout adulthood (25). It has been postulated that
116 stronger condition-dependent mortality in males might cause a higher viability selection in this
117 sex, ultimately buffering the expected occurrence of sex-differences in aging rate (25).

118 From gamete production to parental care, males and females show striking differences in
119 reproductive physiology and life history strategies. These differences are commonly proposed as
120 determinants of the direction and magnitude of sex differences in aging rates of mortality
121 observed in empirical studies (26, 27). In particular, the role played by sexual selection in
122 shaping sex differences in mortality patterns has been intensively debated (9, 10, 26, 28). Males
123 have been hypothesized to pay survival costs due to greater allocation to sexual competition in
124 the form of the growth and maintenance of conspicuous sexual traits or through the expression of
125 more risky behavior (9, 29), which should ultimately translate into a shorter adult lifespan and/or
126 a faster rate of aging compared to females (22, 26, 27). A few comparative analyses have
127 focused on the possible role of sexual selection in explaining sex-differences in lifespan and in
128 the rate of aging. However, these studies have made limited use of metrics that accurately assess
129 the rate of aging (see (28) for a review). Overall, evidence reported so far is equivocal at best
130 (13, 28) and relies on small datasets (9, 10, 29) or on captive populations (28).

131 In the present study, we compile or reconstruct (e.g. in the case of Capture-Recapture
132 studies, see Material and Methods) age-specific mortality estimates for 134 populations of 101
133 species spanning the wide diversity of orders existing in mammals to quantify for the first time

134 both the consistency and magnitude of sex differences in adult lifespan and aging rate. Taking
135 advantage of this unique compilation of sex- and age-specific mortality estimates, we then
136 perform a thorough evaluation of associations between proxies of sexual selection and sex
137 differences in adult lifespan and aging rates observed across mammals.

138

139 **Results and Discussion**

140 We found that females have on average an adult median lifespan 18.6% longer than
141 males in wild mammals, after synthesizing the most complete compilation of mammalian age-
142 and sex-specific mortality estimates to date (Fig. 1, see Materials and Methods). The magnitude
143 of sex differences in adult lifespan was robust with respect to four metrics of longevity
144 commonly used (coefficient of variation: 26 %, Table 1) although statistical significance was
145 only reached for one metric (i.e. Adult lifespan 80%; Table 1). The bias towards a longer
146 lifespan for females was consistent across 60% populations included in our dataset whatever the
147 lifespan metric analyzed (see supplement data 3). We found that sex differences in adult median
148 lifespan are also larger in longitudinal than in transversal studies (*SI Appendix*, Fig. S1). As
149 individuals are closely monitored throughout their adult lifetime in longitudinal studies, these
150 provide the most accurate demographic estimates (30), revealing that females live on average
151 20.3% longer than males (64 populations encompassing 50 species) in the best studied
152 populations. Although sex differences in adult median lifespan from culturally and
153 geographically distinct human populations (Americans: 6.2%, Japanese: 5.1%, Swedish: 2.0%,
154 Aché: 17.5%) are consistent with our estimates from non-human mammals, non-human females
155 display a survival advantage greater than women in 66.4% of the sampled populations (Fig. 1).

156 To investigate whether the direction and the magnitude of sex differences in the rate of
157 aging were similar to those observed for the sex differences in adult lifespan, we estimated the
158 rate of aging in populations where information on the distribution of ages at death was available
159 (83 populations representing 66 species). Empirical evidence accumulated to date indicates that
160 the onset of aging markedly varies across mammals and does not consistently start at the age of
161 first reproduction (31). We thus estimated the rate of aging by fitting a Siler model (32), which
162 does not require any assumption on when the onset of aging occurs, contrary to the commonly
163 used Gompertz model (33). We did not find any consistent difference in aging rates between
164 males and females (Table 2, Fig. 2), even when our investigation was limited to longitudinal data
165 (Table 2). The overall sex bias in adult lifespan we report across mammalian populations is
166 therefore shaped by a multitude of sex-specific demographic features that characterize a species
167 or a population, but does not systematically involve a higher rate of aging in males. Thus, longer
168 adult lifespan in females does not systematically involve a lower rate of aging but can simply
169 result from lower mortality at all adult ages (20).

170 Such a decoupling between adult lifespan and rate of aging matches the human mortality
171 pattern, because age-specific mortality in studied human populations increases at the same rate in
172 both sexes even though women live on average longer than men (2, 6, 34). The absence of
173 consistent sex differences in rates of aging we document here across wild populations of
174 mammals does not preclude any potential sex differences in the rate of aging displayed by other
175 phenotypic traits (e.g. fertility, reproductive performance, body mass, components of the immune
176 system), as illustrated by recent evidence that physiological and demographic aging patterns can
177 be uncoupled in the wild (31, 35). However, age- and sex-specific data on physiological traits

178 remain scarce, which currently prevents any large-scale investigation of sex differences in aging
179 at the physiological level.

180 Sex differences in both adult lifespan and rate of aging are highly variable across species
181 (coefficient of variation of 182% and 291% for adult lifespan and rate of aging, respectively, Fig.
182 1, Fig. 2). Dissimilarities in sex-chromosome content is an influential explanation for sex
183 differences in mortality (13, 14, 17), which suggests that within species, the heterogametic sex
184 (i.e. XY males in mammals) should suffer from impaired survival compared to the homogametic
185 sex. While the exact biological mechanisms linking sex chromosomes and lifespan remain
186 unclear (13), this hypothesis successfully explains the direction of sex ratio bias (potentially
187 caused by sex differences in mortality) across tetrapods (36). However, our findings demonstrate
188 that even within mammalian species that all share the same sex determination system, variation
189 in the magnitude of sex differences in adult lifespan and rate of aging is particularly large. These
190 between-species differences in mortality patterns were not explained by phylogenetic
191 relatedness, which only weakly accounts for the variation observed in sex differences in adult
192 lifespan ($H^2 = 15\%$) or rate of aging ($H^2 = 29\%$) across species. This contrasts with the
193 estimations of analyses focused on males and females separately, which highlight that
194 phylogenetic relatedness explains most of the variation in adult lifespan and rate of aging for a
195 given sex ($H^2 = 86\%$ and $H^2 = 85\%$ for female and male adult lifespan, respectively; $H^2 = 87\%$
196 and $H^2 = 88\%$ for female and male rate of aging, respectively). These findings indicate that
197 allometry (through the species-specific body size (37)) and pace of life (through the species-
198 specific position along the slow-fast continuum (38)) that both closely track phylogenetic
199 relatedness likely determine the mortality pattern observed within a given mammalian species
200 (39) but have little influence on the difference between sexes in either adult lifespan or rate of

201 aging. Overall the extant sexual dimorphism in survival metrics is mostly independent of
202 phylogenetic relatedness and is thus shaped by other sources of variation (e.g. variation in
203 environmental conditions among and within populations).

204 We then conducted additional analyses focused on sexual selection, which is commonly
205 assumed to shape sexual dimorphism in mortality patterns (26, 28), using both sexual size
206 dimorphism and mating system as proxies of the strength of sexual selection (see (40) and
207 Material and Methods). These broad scale analyses on mammals in the wild reveal that sexual
208 size dimorphism (but not mating system) is only weakly associated with the direction and
209 magnitude of sex differences in adult lifespan (slope of -0.23 [95% CI: -0.49;0.04], Table S1,
210 Fig. 3) and is not associated with the rate of aging (*SI Appendix*, Tables S2), which challenges
211 the classic view that sexual selection is the major driver of sex differences in mortality patterns
212 (9, 16, 27, 41). Moreover, these findings contrast with a previous comparative analysis
213 performed on captive populations where sex differences in lifespan were unambiguously higher
214 in polygynous than in monogamous ruminants (28). In zoological gardens, animals live in
215 sheltered environments where environmentally-driven mortality risks are buffered (e.g. through
216 food provisioning or preventive veterinary medicine, see 42). Therefore, the physiological costs
217 associated with the evolution of a large body size and conspicuous sexual traits under natural
218 conditions and over evolutionary times might be more likely to translate into a greater overall
219 reduction in male survival, relative to females, since individuals living in zoos are protected from
220 environmentally-driven causes of death. In such captive conditions adaptations to sexual
221 competition might be the main driver of sex differences in lifespan, since both sexes are
222 sheltered from additional mortality sources linked to environmental severity that can influence
223 lifespan in sex-dependent and independent ways (28). By contrast, in the wild, we hypothesize

224 that local environmental conditions and the myriad of associated mortality risks (e.g. climate
225 harshness, pathogen richness) predominantly shape sex differences in adult lifespan and rate of
226 aging by interacting with costs of sexual selection. More specifically, the substantial allocation
227 of resources in males towards the growth and maintenance of secondary sexual traits might,
228 everything else being equal, make males more vulnerable than females to harsh environmental
229 conditions. For instance, sexual dimorphism is partly physiologically driven by a higher
230 production of androgens in males, particularly during early adulthood (43), which directly
231 controls the growth of many secondary sexual traits (e.g. ornaments and armaments) (13, 27).
232 Circulating androgens also modulate immune performance and when present at high levels can
233 impair some aspects of the immune defense (44), making males more susceptible to pathogens.
234 Trophy hunting also constitutes one extreme example of environmental conditions (i.e.
235 anthropogenic activities) that shape the magnitude of sex differences in mortality patterns across
236 mammalian populations in the wild. Indeed, adult females from hunted populations ($N = 21$) tend
237 to live longer relative to males than adult females from non-hunted populations (34.5% vs.
238 16.7%, respectively, Fig. 3). Finally, we cannot dismiss that sex differences in mortality patterns
239 might also be influenced by interactions between local environmental conditions and the species-
240 specific female reproductive tactics. For instance, females from promiscuous species, displaying
241 multiple mating events during a single reproductive season, will be more likely to contract
242 infectious diseases when the local environment is particularly rich in pathogens (45), which
243 might be ultimately responsible for a shorter female lifespan or a stronger rate of aging. Overall,
244 investigating how local environmental conditions and sex-specific life-history strategies interact
245 to shape sex-specific mortality patterns across species and populations remains a challenging
246 initiative as it requires fine-scale data on various environmental traits.

247 In humans and laboratory rodents sex differences in mortality patterns extend to sex
248 differences in frailty, neurological decline and comorbidity (6). In laboratory mice and rats, the
249 survival benefits associated with anti-aging interventions (genetic or pharmacological) are also
250 frequently sex-specific (6, 46). These sex-specific responses can be attributed to sex differences
251 in physiological systems (e.g. hormonal profiles), which are also expected to modulate adult
252 lifespan and aging (47). We propose that variation in the magnitude of sex differences in both
253 adult lifespan and rate of aging in wild populations is likely a response to interactions between
254 sex-specific physiological pathways and the diversity of environmental conditions met by
255 mammals across the world. From an evolutionary perspective, sex-specific gene expression and
256 physiological systems are the direct consequences of both natural and sexual selection pressures
257 that have been exerted independently on males and females (27, 41, 48). For instance, sexual
258 selection has led to the evolution of species with high sexual dimorphism for many phenotypic
259 traits (e.g. body size) that differentially sensitize either sex to specific environmental conditions.
260 This is particularly well illustrated by the three longitudinally-monitored populations of bighorn
261 sheep (*Ovis canadensis*) included in our dataset. In this polygynous ungulate, males and females
262 show almost no difference in lifespan in the National Bison Range population where resources
263 are consistently available. However, males live much shorter lives in Ram Mountain where
264 winter severity is particularly pronounced leading to marked sex differences in lifespan (49).
265 Therefore, whether highly sexually dimorphic species living in the wild show marked sex
266 differences in lifespan and aging rate of mortality is likely to depend on interactions between
267 sex-specific genetic variation arising from a selection towards specific alleles that are associated
268 in males with more extreme phenotypes (for physiological, morphological and behavioral traits)
269 and local conditions (e.g. pathogens richness), which can either exacerbate or buffer the

270 magnitude of these sex differences (50). Albeit challenging, research programs that solve this
271 complex network will undoubtedly provide innovative insights into the evolutionary roots and
272 physiology underlying aging in both sexes.

273

274 **Materials and Methods**

275 **Data collection.** Age- and sex-specific mortality data were extracted from published life tables
276 or graphs using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). We limited our
277 literature search to mortality or survival estimates published for both sexes for wild populations
278 of mammals, for a total of 184 populations encompassing 128 species. Based on the methods
279 used to estimate age-specific mortality in the initial source, we distinguished three main
280 categories of study. The first type of study corresponds to age-specific mortality estimates
281 obtained from the long-term monitoring of individuals marked during early life when age can be
282 accurately assessed (i.e. longitudinal data). The second type of study corresponds to age-specific
283 mortality estimates obtained from dead animals collected in the field (i.e. transversal data using
284 the standard dx series (51)). Finally, the third type of study corresponds to age-specific mortality
285 estimates computed from the sampling of individuals alive in the population (i.e. transversal data
286 using the standard lx series (51)). For transversal data, population size has to be considered as
287 constant or with a known growth rate and the distribution of ages of dead or alive individuals in
288 the population as stable (51). Mortality estimates extracted from transversal data also depend on
289 the precision of the methods used to assess the age of the individuals. Longitudinal data based on
290 known-aged individuals regularly monitored by Capture-Recapture methods provide much more
291 accurate estimates of age-specific mortality than transversal data (52). Sampled populations were

292 also classified as hunted vs. non-hunted according to the information reported in the original
293 publication. All data and associated references are provided in Supplementary Tables.

294 To compare results obtained from wild populations to humans, we recovered age- and sex-
295 specific mortality data from four human populations (all longitudinal). These data were extracted
296 for three contemporary countries (Japan, Sweden and USA (53)) and for one hunter gatherer
297 population (Aché (54)). We used a similar procedure (see section ‘Estimation of adult lifespan
298 and rate of mortality aging’ below) to compute adult lifespan and rate of aging in wild mammals
299 and humans using 13 years of age as the onset of adulthood following reported data for the
300 populations of Sweden, Japan and USA (55) and previous comparative analyses of mortality
301 patterns (56). However, human estimates were only used in comparison with wild populations of
302 mammals and were not included in the analysis.

303 For each species, we collected data on life history traits that could explain sex differences in
304 adult lifespan and aging rates. As both sexual selection and sociality have been suggested to
305 influence sex-specific mortality (9, 57), we collected data on mating system, social system and
306 sex-specific body mass (to measure sexual size dimorphism). Following previous comparative
307 studies in mammals (e.g. (28)), we classified the species in terms of mating (i.e. monogamous,
308 polygynous, or promiscuous) and social (i.e. cooperative breeders vs. non-cooperative breeders)
309 systems. The intensity of sexual selection is expected to be smaller in monogamous species
310 compared to polygynous and promiscuous species, which might reduce sex differences in
311 mortality patterns (9). The intensity of sexual size dimorphism (i.e. increasingly larger males) is
312 also increasing with the intensity of sexual selection (40) and is thus logically higher in
313 polygynous than in monogamous mammals (58). In cooperative breeders, costs of reproduction
314 are generally shared among females (59), which might also increase sex differences in mortality

315 patterns through a reduced female mortality. For each life-history trait, we prioritized data
316 recovered from the same population (see Supplementary Data and associated references for each
317 life-history trait used in the analysis). All data are provided in SI appendix.

318

319 **Estimation of adult lifespan and rate of mortality aging.**

320 We excluded juvenile mortality because it is generally higher than adult mortality in mammals
321 and can vary considerably among species and populations and even among years within a same
322 population (60). To define the adulthood life stage, we used the species-specific female age at
323 first reproduction as the onset of adulthood.

324 *Rate of mortality aging.* For the ‘longitudinal’ and ‘transversal-dx’ data, the exact age at death of
325 each individual was reported. The mortality rate at each age was estimated while accounting for
326 differences in the number of individuals at risk. For instance, at old ages, mortality rates are
327 typically computed from the few individuals that are still alive, which makes those rates less
328 reliable than those at earlier ages. In a Gompertz model, aging is assumed to start at the species-
329 specific age at first reproduction (22, 61), leading this model to represent a biological model of
330 aging. However, empirical evidence suggests that the onset of aging is often delayed and show
331 considerable variation among mammals (31). Therefore, models that allow flexibility in the age
332 at the onset of aging provide better fit than the Gompertz model fitted from the age of first
333 reproduction. We thus fitted a Siler model on age-specific mortality data (32) for each population
334 to obtain comparable metrics. The five-parameter Siler model is given by

$$335 \quad \mu(x) = a_0 \exp(-a_1 x) + c + b_0 \exp(b_1 x) \quad (1)$$

336 where $a_0, a_1, c, b_0, b_1, c \geq 0$ are the parameters of the mortality function and x the age in years.

337 The first exponential function on the right-hand side of Eq. (1) corresponds to the decline in

338 mortality in the early adult stage (e.g. subadult mortality), the c parameter provides the lower
339 limit of mortality during the adult stage, and the second exponential function corresponds to the
340 mortality increase during the senescent stage. As a metric of rate of aging we used the b_1
341 parameter of the Siler model (see Eq. (1)) that measures the exponential increase in mortality rate
342 with age during the aging stage. This stage is defined from an onset of aging estimated from the
343 analysis of the age-dependent mortality curve. The Siler model thus corresponds to a
344 demographic model of aging. We restricted the analyses to populations that included at least 30
345 males and 30 females at the female age at first reproduction. To account for different sample size
346 among ages we used the R package BaSTA (62). For transversal-lx data, we only had access to
347 the age distribution for individuals alive. As the range of ages covered was quite low for some
348 species (e.g. (63) for an example in weasels, *Mustela nivalis*), it was not possible to fit the Siler
349 model using transversal-lx data and these populations were excluded from the rate of aging
350 analysis.

351

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

359

$$360 \quad e^{\left(\frac{a_0}{a_1}(e^{-a_1x}-1)-cx+\frac{b_0}{b_1}(1-e^{b_1x})\right)} = 0.5 \quad (2)$$

361

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

363
$$\mu(x) = a \exp(b x) \tag{3}$$

364 on the observed distribution of ages among individuals alive where $a > 0$ and $b \geq 0$ are the
365 Gompertz parameters (33), with a representing the baseline mortality at the starting age and b the
366 exponential rate of increase in mortality with age. As individuals for transversal-lx data are all
367 sampled only once and are thus not monitored through their entire life, we took a larger sample
368 size threshold for our selection procedure. Therefore, for transversal-lx data, we excluded
369 populations when the sample size was below 50 individuals for at least one of the two sexes. For
370 the ‘transversal-lx’ data, median lifespan was estimated from the Gompertz model by solving
371 numerically the following the equation:

372

373
$$e^{\frac{a}{b}(1-e^{bx})} = 0.5 \tag{4}$$

374

375 To assess the accuracy of the adult lifespan estimate based on a Gompertz model fitted to the age
376 distribution of animals alive, we also used this method to estimate adult lifespan from
377 longitudinal and transversal-dx data. The correlation between estimates of adult lifespan obtained
378 with the two methods (Siler vs. Gompertz models fitted to longitudinal and transversal-dx data
379 only) was extremely high ($R^2 = 0.99$, Fig. S1), which indicates that these two approaches did not
380 influence the outcome of our analyses of adult lifespan. Moreover, to verify the robustness of our
381 results, we analysed sex differences in adult lifespan using three other metrics of longevity. For
382 each population we computed the age when 80% of the individuals alive at the onset of
383 adulthood were dead (i.e. when cumulative survivorship reaches 0.2, a metric also called adult

384 lifespan 80%) and life expectancy at the onset of adulthood, which corresponds to the mean adult
385 lifespan from the distribution of ages at death (using longitudinal and transversal-dx data with no
386 censoring at old age). Finally, although it is highly sensitive to sample size (64), we also reported
387 maximum adult lifespan for each sex because it is still the most often studied survival metric in
388 comparative analyses of aging. Results obtained with the four longevity metrics are displayed in
389 Table 1.

390

391 **Statistical analyses.**

392 *Adult lifespan.* For each population, we quantified sex differences in adult lifespan as the ratio
393 between male and female adult lifespan on a log scale (*difference adult lifespan* =
394 $\log\left(\frac{\text{adult lifespan male}}{\text{adult lifespan female}}\right)$). For the analysis of sex differences in adult lifespan, we ran a
395 Bayesian hierarchical model using the package MCMCglmm (65) with the magnitude of sex
396 differences in adult lifespan as the response variable. As species from our dataset were not
397 independent because they share phylogenetic relatedness, we corrected all our analyses for
398 phylogeny using the phylogenetic variance-covariance matrix extracted from a mammalian
399 phylogenetic tree (66). Moreover, in some species ($N = 21$), estimates from several populations
400 were available and the data from these populations were thus not independent. Therefore, we
401 fitted the species independently of the phylogeny as a random effect because individuals from
402 the same species can share different ecological characteristics, which are not necessarily linked
403 to the phylogenetic relatedness. To test the sensitivity of the results to the priors, we used two
404 sets of priors for the random effects in the model (uninformative inverse Wishart prior with
405 $\nu=0.02$ and $V=1$ and expanded prior with $\nu=1$ $V=1$ $\alpha.\nu=0$ $\alpha.V=1000$). Models with
406 different priors did not show any detectable difference (Gelman and Rubin's convergence

407 diagnostic very close to 1 for each MCMC chain (67)). From this model we were able to extract
408 the percentage of the total variance explained by the phylogenetic effect (named phylogenetic
409 heritability H^2) (68). The value of H^2 can be interpreted as a direct equivalent to the phylogenetic
410 signal (λ) of Pagel, with a value close to 1 meaning that there is a strong phylogenetic signal and
411 a value close to 0 that there is no phylogenetic signal. For each parameter, we reported the mean
412 of highest posterior density distribution, the lower and upper limits of the 95 % credibility
413 interval and sample size.

414 The first aim of our analyses was to estimate the average sex difference in adult lifespan
415 across the whole set of mammals. We thus ran the model of sex differences in adult lifespan
416 without any independent covariate or factor and found a longer adult lifespan for females in the
417 dataset with an overall negative effect (see *SI Appendix*, Table S3 for all coefficients). In a
418 second step, we tested whether some species-specific traits associated with sex-specific life
419 history strategies and sexual competition (sexual size dimorphism, mating system, social system,
420 sex-bias in dispersal) explained sex differences in adult lifespan observed across mammals. We
421 included sexual size dimorphism (SSD, computed as the log-scaled ratio between male and
422 female body mass) and the occurrence of sex-biased dispersal assessed through sex-biased
423 individual detection (likely bias vs. unlikely bias). Indeed, in some mammalian populations,
424 males are more difficult to detect than females because they wander at a much larger extent, by
425 doing breeding dispersal and/or not defending a territory. Such lower male detection can lead to
426 underestimates of male survival when not corrected for and thereby to bias estimates of sex
427 differences in adult lifespan and rate of aging. To overcome this problem, we considered that
428 populations that are spatially constrained (e.g. living on island or in mountain ranges), monitored
429 longitudinally, or of species where males defend a territory, are unlikely to display biased

430 estimates of sex differences in adult lifespan. On the other hand, populations of non-territorial
431 species (with an expected high breeding dispersal propensity) or without clear information on the
432 mating tactic available in the literature are likely to display more biased estimates of sex
433 differences in adult lifespan. For all the models, we controlled for the potential confounding
434 effect of the hunting status of the population (i.e. hunted vs. non-hunted) and of data quality
435 (longitudinal vs. transversal data). All the two-way interactions among these factors were
436 included in candidate models.

437 To identify the model of sex differences in adult lifespan with highest support, we fitted
438 different models with all the possible combinations of variables from the full model ($N = 19$
439 models). These models were then ranked by the Deviance Information Criterion (69) (*SI*
440 *Appendix*). The selected model included additive effects of hunting (i.e. sex differences in adult
441 lifespan were highest in hunted populations) and data quality (i.e. higher sex differences
442 occurred in adult lifespan with high quality data, *SI Appendix*, Table S3 and Fig. 3).

443 The effect of both mating and social systems were tested on a population subset ($N = 132$
444 populations) because this information was lacking for some species. In addition, the social
445 system was highly correlated to the mating system. Indeed, except for the four-striped grass
446 mouse (*Rhabdomys pumilio*) (70) all cooperative breeders ($N = 6$) in our dataset were
447 monogamous. We thus tested separately the influence of the mating and social systems, to avoid
448 multicollinearities issues (71). The independent model including only mating system as a
449 covariate did not reveal any effect on sex differences in adult lifespan (mean difference_{monogamous}
450 vs. polygynous = 0.001 [-0.325; 0.318], mean difference_{monogamous vs. promiscuous} = 0.047 [-0.265; 0.392]).
451 Similarly, the model including only social system did not reveal any detectable effect (mean
452 difference_{cooperative vs. non-cooperative breeder} = -0.015 [-0.366; 0.317]).

453

454 *Rate of aging.* For each population, we computed sex differences in aging rates of mortality as
455 the ratio between male and female rates of aging on a log scale (*difference aging rate* =
456 $\log\left(\frac{\text{aging rate male}}{\text{aging rate female}}\right)$). We then followed the same procedure as used for sex differences in
457 adult lifespan. We found no statistical support for consistent sex differences in aging rates across
458 species (*SI Appendix*, Table S1). These results were qualitatively similar when using aging rates
459 estimated from Gompertz models instead of Siler models (Figure S4). We performed a second
460 set of analyses to test whether our set of life history traits can explain possible sex differences
461 observed in aging rates across mammals. Similar to the analyses performed for sex differences in
462 adult lifespan, we included SSD and potential sex-biased individual detection (*SI Appendix*,
463 Table S3) and we controlled for possible confounding effects of hunting status and data quality.
464 All the two-way interactions between these variables were included in candidate models. We
465 ranked all the models based on their DIC score to identify the variables influencing sex
466 differences in aging rates. The Null model was ranked first, revealing that none of these variables
467 influenced the magnitude and the direction of sex differences in aging rates (*SI Appendix*, Table
468 S4). Moreover, additional analyses did not reveal any effect of either mating or social system
469 (mean difference_{monogamous vs. polygynous} = -0.04 [-0.48; 0.41], mean difference_{monogamous vs. promiscuous}
470 = 0.01 [-0.45; 0.46], mean difference_{cooperative vs. non-cooperative breeder} = -0.17 [-0.57; 0.23]).

471

472 **Data availability.** All data and code are provided in supporting information.

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

654

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

655

656 ¹ Age at which 50% of the individuals alive at the onset of adulthood were dead (i.e. when
657 cumulative survivorship reaches 0.5).

658 ² Mean age at death of the individuals alive at the onset of adulthood.

659 ³ When 80% of the individuals alive at the onset of adulthood were dead (i.e. when cumulative
660 survivorship reaches 0.2).

661 ⁴ Oldest age reached by individuals alive at the onset of adulthood.

662

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

668

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

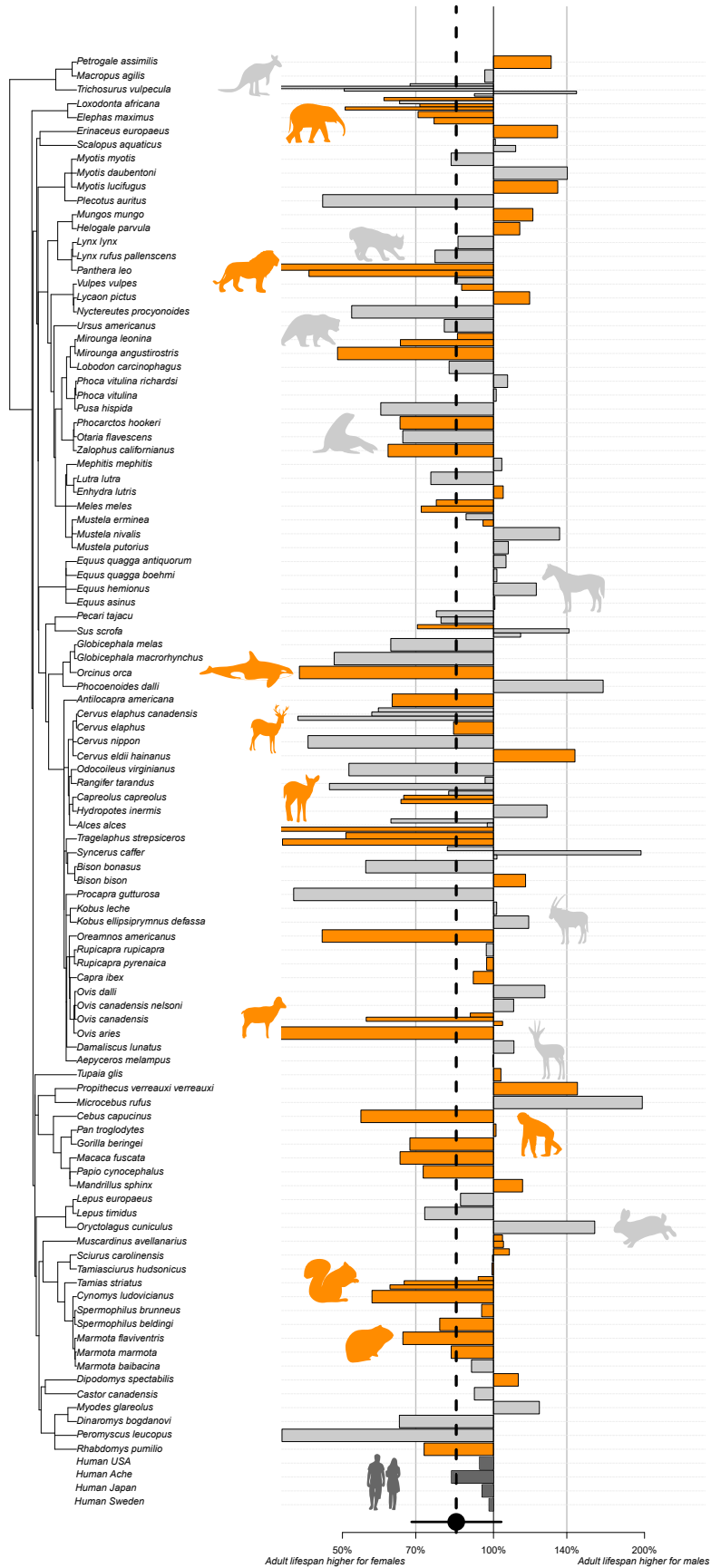
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670 ¹ Exponential rate of mortality increase estimated from a Siler model fitted from the onset of
671 adulthood (see Methods).

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

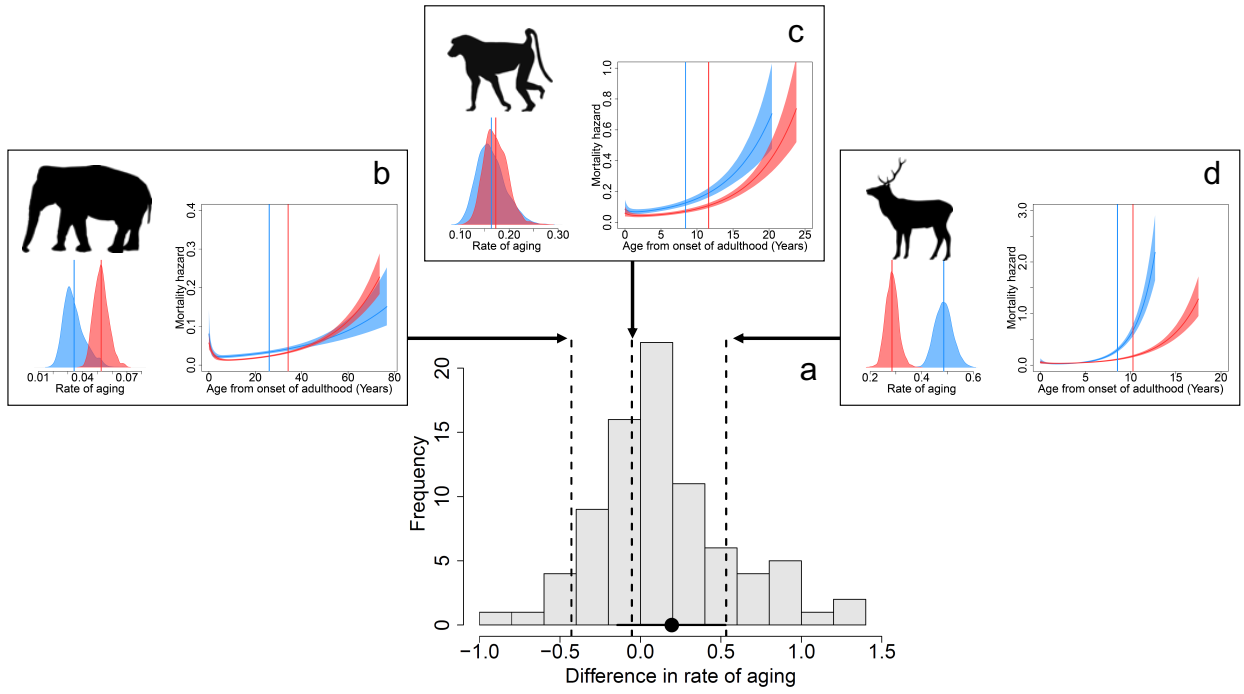
678 **Fig. 2.** Frequency distribution of the magnitude of sex differences in rate of aging across
679 mammals in the wild (a). The black dot corresponds to the overall effect for non-human
680 mammals and is associated with its 95 % credibility interval. Patterns of age-specific changes in
681 mortality rate for three mammalian populations are displayed. For each population the mortality
682 curve with the vertical line representing the median adult lifespan and the posterior distribution
683 of the aging rate b_I are given in red for females and in blue for males. The mortality hazard
684 corresponds to the instantaneous rate of mortality. In the three populations, adult females live on
685 average longer than adult males. However, in (b) Asian elephant, *Elephas maximus* (Myanmar
686 population), females have a higher aging rate, in (c) Yellow baboon, *Papio cynocephalus*
687 (Amboseli National Park population) no difference in aging rates is observed while in (d) red
688 deer, *Cervus elaphus*, (Isle of Rum population) males show a higher rate of aging than females.

689 **Fig. 3.** Effect of sexual size dimorphism (a), hunting (hunted vs. non-hunted populations) (b),
690 and data quality (longitudinal-high quality vs. transversal-low quality) (c) on sex differences in
691 median adult lifespan across mammals. The horizontal grey and dash line corresponds to the
692 absence of sex differences in median adult lifespan.
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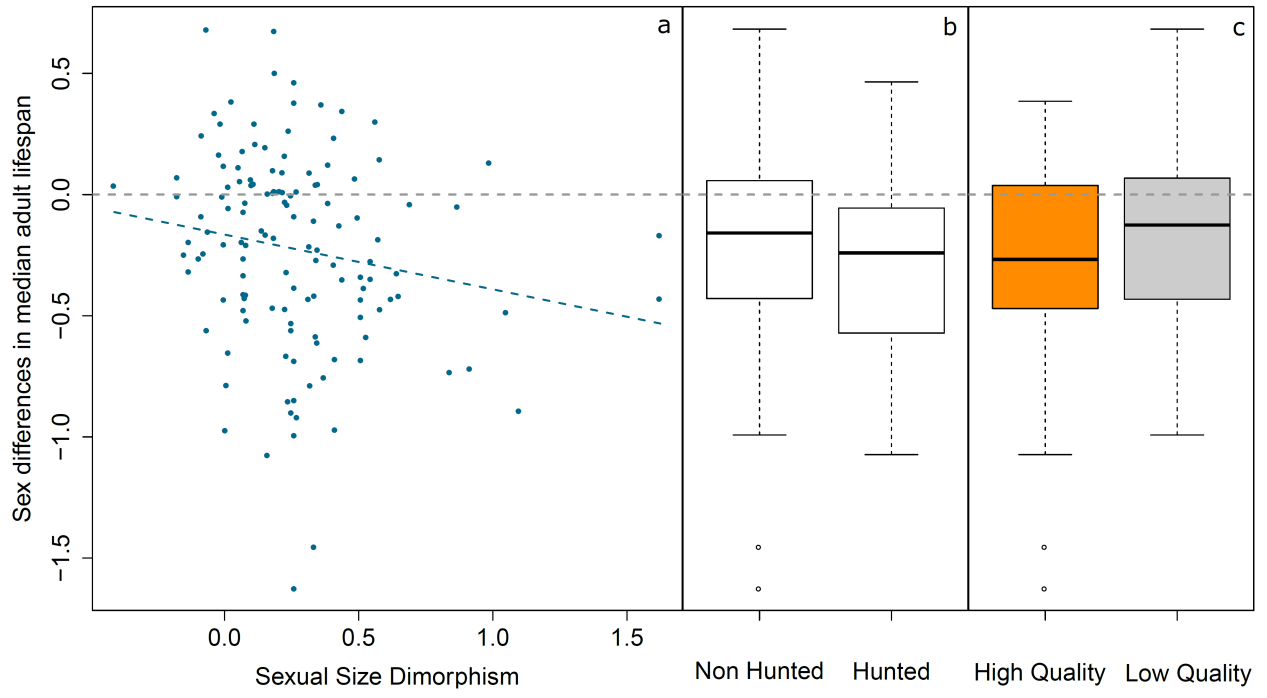
Fig. 1



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Fig. 2

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Fig. 3