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## Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants

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1 **Does sexual selection shape sex differences in longevity and**  
2 **senescence patterns across vertebrates? A review and new**  
3 **insights from captive ruminants**

4  
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25

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27

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32

33 **ABSTRACT** (200 words)

34 In vertebrates, both sexes mostly exhibit a different pattern of senescence and lifespan, often  
35 male-biased in mammals and female-biased in birds. Since polygynous males are under  
36 intense sexual competition to secure mating opportunities, they allocate into costly  
37 conspicuous sexual traits that might explain sex-differences in longevity and senescence  
38 patterns. However, comparative studies performed to date have led to conflicting results. We  
39 aimed to solve this problem by first reviewing and discussing published case studies of the  
40 relationship between the strength of sexual selection and age-specific survival metrics. Then,  
41 we performed a comparative analysis to test whether such relationships occur among species  
42 of captive large herbivores. We found that the strength of sexual selection negatively  
43 influenced the onset of actuarial senescence in males, with males both senescing earlier in  
44 polygynous than in monogamous species and showing greater between-sex differences in  
45 onset of senescence in favor of females. Moreover, males of territorial species had earlier  
46 onset of senescence than males of species displaying harem or tending mating tactics. We did  
47 not detect any influence of the strength of sexual selection on the rate of actuarial senescence.  
48 Our findings demonstrate that the onset of actuarial senescence, rather than its rate, is the  
49 target of sexual selection.

50

51

52           During the last two decades, demographic analyzes based on long-term studies have  
53 demonstrated that actuarial senescence, a progressive decrease of survival with age  
54 (Monaghan et *al.*, 2008), is almost an ubiquitous process in vertebrates (Brunet-Rossini and  
55 Austad, 2006; Gaillard and Bonenfant 2008; Nussey et *al.*, 2008, 2013). Nevertheless,  
56 actuarial senescence is not expressed with the same intensity across the tree of life (Nussey et  
57 *al.*, 2013; Jones et *al.*, 2014). These differences in the intensity of senescence among species  
58 are generally driven by the pace of life (Jones et *al.*, 2008) that is strongly associated with  
59 body mass (Calder, 1984), phylogeny (Gaillard et *al.*, 1989), and habitat (Wiersma et *al.*,  
60 2007).

61           Within species, the intensity of actuarial senescence also varies, especially according  
62 to sex (Clutton-Brock and Isvaran, 2007; Maklakov and Lummaa, 2013; Regan and Partridge,  
63 2013; Adler and Bonduriansky, 2014). For example, mammalian males generally live shorter  
64 and senesce faster than females in a given species or population (Lemaître and Gaillard,  
65 2013a; Ramp et *al.*, 2010; but see Gamelon et *al.*, 2014). The magnitude of such between-sex  
66 differences in actuarial senescence is generally assumed to be associated with the strength of  
67 sexual selection (Clutton-Brock and Isvaran, 2007; Lemaître and Gaillard, 2013a). Sexual  
68 selection causes the evolution of traits and/or behaviors that are associated with mating  
69 success (Darwin, 1859) and individuals from species subjected to a strong sexual selection  
70 will generally suffer from high cost of production and maintenance of these sexually selected  
71 traits (e.g. an increased reproductive senescence for males controlling the largest harems in  
72 the polygynous red deer, *Cervus elaphus*, Lemaître et *al.*, 2014a). In most species, the  
73 intensity of sexual selection is stronger in males than in females because fathers generally  
74 allocate much less than mothers to the production and rearing of offspring (Bateman, 1948;  
75 Trivers, 1972 Andersson, 1994). Then, males can allocate much more than females to intra-  
76 specific sexual competition to obtain additional mating and thereby to increase their

77 individual fitness. Males of species subjected to a low intra-sexual competition will both  
78 undergo a lower sexual selection pressure and allocate less energy to mate. They can then  
79 allocate more to somatic maintenance and thereby enjoy higher survival and weaker  
80 senescence than males of species deeply involved in intra-sexual competition (Bonduriansky  
81 et *al.*, 2008). Therefore, sexual selection leads to the production and maintenance of costly  
82 sexual traits in males and associated risky behaviors, which are likely to cause higher  
83 mortality and accelerated senescence, and thus increased between-sex differences in actuarial  
84 senescence (Williams, 1957; Owens and Bennett, 1994; Bonduriansky et *al.*, 2008). We thus  
85 expect a greater sex-bias in senescence pattern in favor of females to occur in species in  
86 which males are subjected to high levels of sexual competition.

87         The influence of the strength of sexual selection on senescence or survival patterns is a  
88 key topic of evolutionary biology that is currently highly debated. From a literature survey,  
89 we have identified 10 studies of the link between the strength of sexual selection and survival  
90 patterns at the inter-specific level (Table 1) and only six of these studies provided support for  
91 a cost of sexual selection in terms of survival. However, only three studies involved actuarial  
92 senescence *sensu stricto*. The other studies focused on age-independent metrics such as  
93 maximum longevity, lifespan, or average adult mortality, which do not provide any reliable  
94 information about actuarial senescence and are highly dependent of sample size (Krementz et  
95 *al.*, 1989; Moorad et *al.*, 2012). Moreover, for a given metric, the measure retained strongly  
96 differed from one study to another. For example, sexual size dimorphism (SSD), a commonly  
97 used proxy of the strength of sexual selection, was measured either as the ratio between male  
98 and female body mass (Promislow, 1992; Owens and Bennett, 1994), as the residuals from the  
99 linear regression of male body mass against female body mass (Toïgo and Gaillard, 2003), by  
100 including both male and female body mass as additive covariates in the model (Lemaître and  
101 Gaillard, 2013a), or as the Lovich and Gibbons (1992)'s ratio of the mean size between males

102 and females when males are larger (Bro-Jørgensen, 2012). Such a diversity of SSD measures  
103 often makes difficult to compare results among studies.

104 Conclusions from studies based on actuarial senescence metrics are also largely  
105 inconsistent. So far, only one provided evidence of a stronger male-biased senescence in  
106 species with strong inter-male competition for mating (Clutton-Brock and Isvaran, 2007). The  
107 other two studies did not report statistically significant relationship between different rates of  
108 actuarial senescence and the strength of sexual selection in either males (Lemaître and  
109 Gaillard, 2013a) or females (Lemaître and Gaillard, 2013b). Moreover, all these studies were  
110 based on the rate of senescence, which only depicts the intensity of actuarial senescence. The  
111 onset of senescence provides another potentially powerful metric that is most often  
112 overlooked in senescence studies. However, the few studies available for this trait have  
113 demonstrated its biological relevance by showing that observed variation in the onset of  
114 senescence across species is mostly shaped by variation in the pace of life (e.g. Jones et al.,  
115 2008; Péron et al., 2010). Moreover, a recent study has shown that the highly fecund wild  
116 boar (*Sus scrofa*) females suffered from earlier, not stronger, actuarial senescence than  
117 similar-sized female mammals with much lower fecundity (Gamelon et al., 2014). These  
118 recent findings thus emphasize that the onset of senescence could potentially better assess the  
119 potential costs of sexual selection in terms of actuarial senescence.

120 In the present study, we strive to make a fairly comprehensive investigation of the  
121 relationship between various metrics of actuarial senescence and survival and the strength of  
122 sexual selection both across species and between sexes. For this purpose, we analyzed a high  
123 quality dataset on age-specific survival of large herbivores living in captivity. In large  
124 herbivores, males are often subjected to intensive sexual competition (Clutton-Brock, 1989;  
125 Bro-Jørgensen, 2011) and there is a large variation in the intensity of sexual selection among  
126 species. To gain mating opportunities males subjected to strong sexual selection often display

127 phenotypic responses (Preston et *al.*, 2003), which can be costly and lead to increased  
128 mortality. In particular, these males allocate a lot in body mass, which confers advantages in  
129 contest with competing males (Jarman, 1983; Andersson, 1994). Thus, a positive correlation  
130 between the magnitude of SSD and male-biased mortality is expected because of the high  
131 energy requirements associated with large body size (Jarman, 1983; Weckerly, 1998).  
132 Moreover, large herbivores exhibit different mating systems (Clutton-Brock, 1989; Bro-  
133 Jørgensen, 2012) that are likely to mediate the intensity of male-male competition, and thus  
134 traits such as SSD (Loison et *al.*, 1999a). In large herbivores, three types of mating systems  
135 are predominant: monogamy when males mate with the same female in several reproductive  
136 attempts, promiscuity when males and females mate with several partners and there is no  
137 continuing bond between individual males and females after mating, and polygyny when  
138 males mate with the same group of females in successive mating attempts (Clutton-Brock,  
139 1989). Inter-male competition for mating is expected to be higher in polygynous species, a  
140 little less in promiscuous species, and much lower in monogamous species. This explains why  
141 monogamous species are generally less dimorphic in size than promiscuous and polygynous  
142 species (Jarman, 1983). Furthermore, in both promiscuous and polygynous species, the  
143 mating tactic can differ markedly (Clutton-Brock, 1989), encompassing territoriality (when  
144 female groups are stable and home-range defensible, or when females are constrained to use a  
145 given area, males defend part or all the home range of a female group), harem (a male defends  
146 access to a group of females rather than to a territory), and tending (when female groups are  
147 stable with a home range too large to be defensible or when females are solitary or live in  
148 small groups and are unpredictably distributed, males range widely searching for oestrus  
149 females, pairing with them and defending them against other males during oestrus).  
150 Defending a territory should be more energetically costly than defending a harem, and even  
151 more than doing tending because the time and energy devoted to harem or territory defense is



152 no longer available to repair injuries, DNA damages or to fight against diseases. In the same  
153 way, allocating in sexually selected traits like horns or antlers should increase the intensity of  
154 senescence because of inherent trade-offs in energy allocation between reproduction and  
155 maintenance (Williams, 1966). In support, the relationship between antler or horn size and  
156 strength of sexual selection in large herbivores is now well established (Plard *et al.*, 2011;  
157 Bro-Jørgensen, 2007; Lemaître *et al.*, 2014b).

158 We used data from 64 species of large herbivores living in captivity, which were  
159 obtained from the International Species Information System (ISIS) database that combines  
160 individual data for each animal living in captivity in 850 member institutions from more than  
161 80 countries. Such protected conditions allow eliminating mortality due to environmental  
162 causes such as predation, climatic harshness or disease transmission, and thereby better  
163 identifying the underlying causes of senescence. To assess the relationship between the  
164 magnitude of the male-bias of actuarial senescence and the strength of sexual selection, we  
165 used different measures of the intensity of sexual competition simultaneously: SSD, mating  
166 system, mating tactic (in polygynous and promiscuous species only) and horn size  
167 dimorphism (HSD) (in bovids only). We had too few cervids ( $N = 14$ ) in our dataset to  
168 include male antler size in a specific analysis. In addition, we measured the intensity of male  
169 survival costs and of sex differences in actuarial senescence and survival using different  
170 measures previously selected in other comparative studies: maximum longevity (Bro-  
171 Jørgensen, 2012), Gompertz rate of senescence (Ricklefs, 2010), age at the onset of  
172 senescence (Péron *et al.*, 2010) and a linear rate of senescence between well-defined cut-off  
173 ages (Jones *et al.*, 2008; Lemaître and Gaillard, 2013a), for each sex. We investigated whether  
174 increasing allocation by males in sexual selection leads to increasing mortality and actuarial  
175 senescence in males on both an absolute scale and relative to females. More specifically, we  
176 tested the following predictions. First, we expected that (i) males of polygynous species

177 and/or with large SSD and HSD should have earlier and stronger actuarial senescence and  
178 should live shorter than males of monogamous species and/or with a weak SSD and HSD.  
179 Within polygynous and promiscuous species, we expected males of territorial species to have  
180 earlier and stronger actuarial senescence than males of non-territorial species. (ii) between-sex  
181 differences in actuarial senescence and longevity should be greater in species in which males  
182 face strong sexual selection.

183

## 184 **Materials and methods**

### 185 **METRICS OF SURVIVAL AND ACTUARIAL SENESCENCE**

186 We first estimated survival at each age for each sex of each species of large herbivores  
187 present in the International Species Information System (ISIS) (Müller *et al.*, 2011; Lemaître  
188 *et al.*, 2013), which combines individual data for a given species since 1973, from 850  
189 member institutions (Zoos, national parks) in over 80 countries. Thus, for each individual,  
190 information such as sex and dates of birth and death are available. Considering each species  
191 of captive population of each zoo as a "meta-population", it is possible to compute the  
192 parameters that characterize the average population living in captivity. In sum, this "meta-  
193 population" describes the average performance for each species in captivity and not a specific  
194 population. We only used cohorts of animals for which both dates of birth and death were  
195 known, which implies that animals were born in captivity. The complete dataset included data  
196 for 95 species of large herbivores. However, we kept only species for which 25 individuals at  
197 least were alive at 1 year-old (N = 64 species) to get accurate estimates of age-specific  
198 survival.

199 To measure species- and sex-specific pattern of survival and senescence, we used four  
200 different and complementary metrics: the maximum longevity, the Gompertz rate of  
201 senescence, the onset of senescence, and the linear rate of senescence between two well-

202 defined cut-off ages (between 6 and 12 years of age) (See Table S1). Such a diversity of  
203 metrics is important for two reasons. First it allows comparing our finding with previous  
204 results published in the literature and second it helps to disentangle possible confounding  
205 effects between the rate (i.e. intensity) and the onset (i.e. timing) of senescence.

206 We extracted the maximum longevity recorded for each sex from species-specific life  
207 tables. This trait (called ‘longevity’ hereafter) is not a direct measure of senescence because it  
208 does not include any information about age-dependent survival. However, longevity allows  
209 measuring the overall difference in survival between the sexes and can therefore be linked  
210 with the energy allocation in maintenance during the lifespan.

211 The second metric we used was the Gompertz rate of senescence (after called  
212 ‘Gompertz rate’) that measures the sex- and species-specific average exponential rate of  
213 mortality with age. To measure actuarial senescence, many mathematical functions have been  
214 proposed (Ricklefs and Scheuerlein, 2002). The Gompertz function is the most commonly  
215 used to study human survival, survival in laboratory or in captivity (Ricklefs and Scheuerlein,  
216 2002) and has been shown to provide a reliable description of age-specific survival in large  
217 herbivores (Gaillard *et al.*, 2004). We first built the capture history of each individual of each  
218 sex and each of the 64 species of large herbivores included in our dataset (coded as "1" when  
219 the individual was observed alive and as "0" when it was dead at a given age from birth).  
220 These capture histories were then loaded into a CMR (capture-mark-recapture) software (E-  
221 SURGE, Choquet *et al.*, 2009) to get reliable age-specific estimates (Lebreton *et al.*, 1992),  
222 knowing that detection probabilities were equal to 1 in captivity. We then fitted different age-  
223 dependent models including a model with a constant survival (i.e. no age-dependence), a  
224 model with two age-classes (first year of life vs. older ages) to account for the lower survival  
225 in juveniles than in older individuals that characterizes large herbivores (Gaillard *et al.*, 2000),  
226 a model with full age-dependence (i.e. one survival rate per age), and a series of Gompertz

227 models with onsets of senescence varying between 1 year of age and the age corresponding to  
228 the first two thirds of lifespan for each sex in each species. In Gompertz models, age variation  
229 in survival was constrained from the age at the onset of senescence to be linear on a log(-log)  
230 scale (Gaillard et al., 2004). We selected a final model using AIC (Akaike's Information  
231 Criterion, Burnham and Anderson, 2002). Then, we retained the estimate of the Gompertz rate  
232 in species for which a Gompertz model provided a better fit than either the constant or the  
233 two-age class model (N = 54 species, see Table S2).

234         The Gompertz rates we estimated were thus dependent on the onset of senescence. An  
235 early onset of senescence is indeed associated with a low actuarial senescence rate ( $0.27 \pm$   
236  $0.13$ ;  $t = 2.07$ ;  $P = 0.04$ ;  $\lambda < 0.001$ ). In other words, delaying the onset of senescence should  
237 lead to increase the rate of senescence. To correct for that constraint, we estimated the onset  
238 of senescence and the rate of senescence independently from the Gompertz models. The age  
239 at the onset of senescence was then estimated as the age at which the mortality rate was the  
240 lowest (Jones et al., 2008). However, to avoid extreme mortality values caused by a small  
241 number of old individuals, we restricted the range of ages to the first two thirds of the  
242 maximum lifespan recorded for a given sex in a given species (See Figure S1 for an example).

243         We also measured the rate of senescence as the proportional decrease of survival  
244 between 6 and 12 years of age. We fixed these age thresholds because most of large  
245 herbivores species initiated their senescence between these age threshold as demonstrated on  
246 detailed analyzes of age-specific variation in intensively monitored populations of large  
247 herbivores (e.g. Loison et al., 1999b; Festa-Bianchet et al., 2003; Gaillard et al., 2004; Toïgo  
248 et al., 2007), which allowed us to make estimates directly comparable among species. Saïga  
249 (*Saïga tartarica*), Speke's gazelle (*Gazella spekii*), Goitered gazelle (*Gazella subgutturosa*)  
250 and Greater kudu (*Tragelaphus strepsiceros*) were excluded for this analysis because all  
251 males died before 12 years of age in these species. Therefore, the rate of senescence of males

252 between 6 and 12 years of age was analyzed using data from 60 species. In addition, the  
253 longest-lived female of Water deer (*Hydropotes inermis*) died before reaching 12 years of  
254 age. We therefore restricted the analysis of between-sex differences in senescence rate of  
255 females between 6 and 12 years of age to 59 species.

256 Dependent variables (longevity, Gompertz rate, onset of senescence and rate of  
257 senescence between 6 and 12 years of age) were all log-transformed to account for the  
258 allometric nature of the relationships (see Houle et al., 2011). For longevity and onset of  
259 senescence, the between-sex difference was calculated as the female value minus the male  
260 value. For both rates of senescence, the between-sex difference was calculated as the male  
261 rate minus the female rate. All data are provided in Table S1.

262

## 263 METRICS OF SEXUAL SELECTION

264 To assess thoroughly the strength of sexual selection in a given species, we used 4  
265 metrics: sexual size dimorphism (SSD), mating system, mating tactic (only for polygynous  
266 and promiscuous species) and horn size dimorphism (HSD) for bovids only (See Table S2).  
267 The first and most commonly used metric in such analyzes is the SSD (Toïgo and Gaillard,  
268 2003; Table 1), which allows taking into account the difference in mass between sexes,  
269 assuming that males will invest more strongly than females to increase their probability of  
270 success in male-male competition (Bateman, 1948; Bonduriansky et al., 2008). Sex-specific  
271 body masses (in kg) were collected for both sexes in the same free-ranging populations as  
272 used by Bro-Jørgensen (2012) for bovids and Plard et al. (2011) for cervids, and completed  
273 using more specific sources when required. As several measures of SSD have been previously  
274 used (see Table 1), we replicated the analyzes using other SSD measures but results remained  
275 qualitatively unchanged. We thus report results from analyzes including both male and female  
276 body masses as covariates in the model (both log-transformed) as advocated by Freckleton

277 (2009) to avoid potentially biased estimates in phylogenetically controlled analyzes.  
278 Moreover, doing that allows to correct analyzes for among-species variation in the pace of  
279 life, because of the strong allometric relationship linking body mass and generation time, a  
280 reliable metric for assessing the pace of life (Gaillard et al., 2005).

281 We assessed the mating system (monogamous, promiscuous or polygynous) of  
282 each species according to Zerbe et al. (2012)'s classification. This metric was entered as a  
283 discrete factor in models, using monogamous species as a reference. In the same way, we  
284 identified the mating tactic (territoriality, harem or tending) of each species thanks to further  
285 studies (listed in Table S3) using the tending tactic as a reference.

286 Finally, we used the horn size dimorphism (HSD) of bovids as a last metric of the  
287 strength of sexual selection. Female bovids bear horns like males, but generally of smaller  
288 size (Bro-Jørgensen, 2007). We thus assumed that increasing sexual selection leads to  
289 increase horn size in males relatively to females. For this study, we included only 37 species  
290 because we were not able to find horn size data for at least one sex in 11 species (American  
291 bison *Bison bison*, European bison *Bison bonasus*, Gaur *Bos gaurus*, Wild goat *Capra*  
292 *aegargus*, Blesbok *Damaliscus pygargus*, Mountain gazelle *Gazella gazella*, Dama gazelle  
293 *Nanger dama*, Scimitar oryx *Oryx dammah*, Bighorn sheep *Ovis Canadensis*, Mouflon *Ovis*  
294 *orientalis* and Common eland *Tragelaphus oryx*). Data of horn size were also obtained from  
295 free-ranging populations.

296

## 297 **ACCOUNTING FOR POSSIBLE CONFOUNDING VARIABLES**

298 We controlled for possible confounding factors previously reported to influence  
299 survival and actuarial senescence in captive large herbivores. First, body mass was included to  
300 control for the strong allometric relationship linking body mass and adult survival or actuarial  
301 senescence rates in large herbivores (Sacher, 1959; Gaillard et al., 2003; Lemaître and

302 Gaillard, 2013b). Moreover, accounting for body mass allows taking into account most  
303 variation generated by the pace of life because of the strong allometric component of the pace  
304 of life in large herbivores (Gaillard *et al.*, 2008). The average species-specific body mass for  
305 each sex was recovered from the literature (see above and Table S3).

306         Additionally, in captivity, food supplied to large herbivores is sometimes not optimal  
307 (Müller *et al.*, 2011) and grazers (whose diet consists mainly of grass) generally meet their  
308 food needs in captivity better than browsers (whose diet consists mainly of leaves or twigs).  
309 This leads grazers to have a longer longevity and a reduced actuarial senescence in captivity  
310 compared to their wild counterparts while the opposite is observed for browsers (Müller *et al.*,  
311 2011; Lemaître *et al.*, 2013). Therefore, diet is a structuring factor for survival and senescence  
312 in large herbivores and in the present study, the effect of diet on different metrics for males  
313 has been included to avoid confounding effects of a poorly adapted diet for browsers in  
314 captivity. To do that, the percentage of grass in a species' natural diet has been obtained from  
315 Zerbe *et al.* (2012)'s supplement data (see Table S3) and included as a covariate in our  
316 models.

317

## 318 **STATISTICAL ANALYZES**

319         To avoid biased assessment of the relationships between sexual selection and survival  
320 patterns due to phylogenetic inertia, we controlled all the analyzes for the non-independence  
321 between species due to sharing ancestry using "Phylogenetic Generalized Least-Squares"  
322 (PGLS) models (Freckleton *et al.*, 2002). The PGLS method provides an estimate of the  
323 phylogenetic signal  $\lambda$ , which allows controlling for the phylogenetic dependence (between 0  
324 and 1). If  $\lambda$  is not statistically different from 0, phylogeny does not have a detectable effect  
325 and a linear regression without correcting for phylogeny can be safely used. A phylogeny of  
326 the 64 species of large herbivores used in this study (see Figure 1) was built using the

327 phylogenetic super-tree of mammals published by Bininda-Emonds et al. (2007, 2008). This  
328 near completed, at the species-level, super-tree is building using a 66-gene alignment in  
329 conjunction with 30 cladistically robust fossil calibration points. Branch lengths are  
330 proportional to time. To confirm our results, analyzes were repeated with Agnarsson and  
331 May-Collado (2008)'s near species-completed phylogeny of 266 species of Cetartiodactyla  
332 based on cytochrome b sequence data and using recent Figuet et al. (2014)'s phylogenetic tree  
333 reconstructed from complete mitochondrial genome of 201 species of Cetartiodactyla. In all  
334 cases, results were qualitatively similar and we only present in this paper those obtained with  
335 the phylogenetic super-tree of mammalian species (Bininda-Emonds et al., 2007, 2008).  
336 Phylogenetically controlled analyzes were performed using the package *caper* (Orme, 2012).

337 In our analyzes dependent variables included longevity, Gompertz rate, onset of  
338 senescence and rate of senescence between 6 and 12 years of age. For each dependent  
339 variable entered in the full model we included the percentage of grass in a species' natural  
340 diet (only when studying male traits but not between-sex differences because diet is the same  
341 for both sexes, which leads their survival patterns to be biased in the same way), the SSD (by  
342 entering both male and female body mass, as repeatedly advocated, Freckleton, 2002, 2009),  
343 mating system, and the two-way interaction between mating system and male body mass. We  
344 added this interaction because the largest herbivores tend to be polygynous and the lightest  
345 ones tend to be monogamous, leading a cost of SSD to be possibly detected only in  
346 polygynous species. Moreover, as the estimate of the Gompertz rate depends on the age at the  
347 onset of senescence used to model senescence, the onset of senescence included in the  
348 selected model was entered as a covariate in the analysis of Gompertz rates.

349 To analyze the effects of mating tactics on survival patterns, the full model included  
350 diet, SSD, mating tactic and the two-way interaction between mating tactic and male body  
351 mass (because males of harem and territorial species tend to be larger than males of tending



352 species and senescence could potentially be only detected in harem and territorial species)  
353 (See Table S3).

354 When we analyzed bovids separately, the full model included diet, SSD, HSD (with  
355 male and female horn size added as covariate) and the two-way interaction between body  
356 mass and horn size (See Table S3). Dependent variables were the same as for the analysis of  
357 the entire dataset.

358 Finally, to select the best model of variation in longevity or senescence metrics, we  
359 used a model selection procedure based on the Akaike Information Criterion (AIC, Burnham  
360 and Anderson, 2002). For each senescence or survival metric, we retained the model with the  
361 lowest AIC. When the difference of AIC between competing models was less than 2, we  
362 retained the simplest model to satisfy parsimony rules (Burnham and Anderson, 2002). In  
363 addition, the AIC weight ( $w_i$ ) was calculated to measure the relative likelihood of each model  
364 to be the best among the set of fitted models. When lambda was not statistically different from  
365 0 we performed linear models without correcting for phylogeny to avoid any possible bias  
366 induced by the inclusion of a non-required phylogenetic index and provided estimates from  
367 linear models without correcting for phylogeny (Revell, 2010). However, results were  
368 qualitatively the same with and without this correction. When lambda was statistically  
369 different from 0, parameter estimates were obtained using the PGLS method (Tables 2 and 3).

370 Analyses were performed with R version 2.14.0 (R Development Core Team, 2011)  
371 and parameter estimates are given  $\pm$  SE.

372

## 373 **Results**

### 374 **INFLUENCE OF SEXUAL SELECTION ON MALE LONGEVITY AND** 375 **SENESCENCE PATTERNS**

376

377           Following parsimony rules, the model selected for male longevity included diet and  
378 male body mass ( $w_i = 0.22$ ;  $\lambda < 0.001$ ; Table S4). Longevity of males increased with the  
379 percentage of grass in the species natural diet (Table 2, Figure S2A) and longevity increased  
380 with body mass in males (Table 2, Figure S3A). Although the model with the lowest AIC  
381 included an additional effect of mating system ( $w_i = 0.30$ ;  $\lambda < 0.001$ ; Table S4), the effect size  
382 was very small, with males tending to live slightly longer in monogamous and in promiscuous  
383 than in polygynous species (difference of longevity compared to monogamous species: -1.02  
384 year for promiscuous species, 95%CI [-1.27 – 1.22]; -1.15 year for polygynous species,  
385 95%CI [-1.43 – 1.09]).

386           The selected model for Gompertz rates included the onset of senescence ( $w_i = 0.27$ ;  $\lambda$   
387  $< 0.001$ ; Table S4). As expected, males with earlier onset of senescence had lower Gompertz  
388 rates (Table 2). The models including additive effects of diet ( $\Delta AIC = 0.56$ ;  $w_i = 0.21$ ;  $\lambda <$   
389  $0.001$ ; Table S4), or of body mass ( $\Delta AIC = 1.00$ ;  $w_i = 0.16$ ;  $\lambda < 0.001$ ; Table S4) also  
390 provided good fits, although the effect sizes were very small in both cases. As expected, male  
391 senescence rate tended to decrease with both the proportion of grass in species natural diet ( $\beta$   
392  $= -0.0030 \pm 0.0026$ ; Figure S2B) and with males body mass ( $\beta = -0.057 \pm 0.058$ ; Figure S3B).

393           The selected model of onset of senescence in males ( $w_i = 0.51$ ;  $\lambda < 0.001$ ; Table S4)  
394 included diet, body mass and mating system. Males of grazer species senesced later than  
395 males of browser species (Table 2, Figure S2C), males of large species senesced later than  
396 males of small species (Table 2, Figure S3C), and compared to males of monogamous  
397 species, males of promiscuous and polygynous species tended to senesce 1.3 (95%CI [-1.8 –  
398 1.1]) and 1.6 (95%CI [-2.3 – -1.1]) years earlier (Table 2, Figure 2).

399           Lastly, the model selected for the rate of senescence between 6 and 12 years of age  
400 only included body mass ( $w_i = 0.28$ ;  $\lambda < 0.001$ ; Table S4). Males of small species senesced  
401 faster than males of large species (Table 2, Figure S2D). Just as for male longevity, the model

402 with the lowest AIC included additional effects of diet ( $w_i = 0.30$ ;  $\lambda < 0.001$ ; Table S4), and  
403 as predicted males of grazers senesced at a slower rate than males of browsers ( $\beta = -0.002 \pm$   
404  $0.001$ ; Figure S3D).

405 Analyzes restricted to polygynous and promiscuous species failed to detect any effect  
406 of mating tactic on either longevity or Gompertz rate (Table S5). However, the onset of  
407 senescence was influenced by the mating tactic with males of territorial species doing harem  
408 or tending senescing 1.4 (95%CI [-1.9 – -1.1]) years earlier than males of species doing harem  
409 or tending (Tables S5 and S6, Figure 3). In addition, the model selected for the senescence  
410 rate between 6 and 12 years of age included diet, body mass, mating tactic and the two-way  
411 interaction between mating tactic and male body mass ( $w_i = 0.88$ ;  $\lambda = 0.984$ ; Table S5).  
412 Territorial males senesced slower between 6 and 12 years of age than males of species with  
413 harem or tending mating tactics (difference of rate compared to males of tending species: -  
414  $0.49 \pm 1.20$  for species with harem;  $-2.61 \pm 0.84$  for territorial species; Table S6).

415 Complementary analyzes performed in bovids have revealed no effect of horn size  
416 dimorphism on longevity, onset of senescence, Gompertz rate and senescence rate between 6  
417 and 12 years of age (Appendix S1, Tables S7 and S8).

418  
419 **INFLUENCE OF SEXUAL SELECTION ON THE SEX-DIFFERENCES IN**  
420 **LONGEVITY AND SENESCENCE PATTERNS**

421  
422 Males had, on average, a shorter longevity than females (male: 16.3 years, 95%CI  
423 [15.5 – 17.2]; female: 19.1 years, 95% CI [18.3 – 20.0]), with a difference of 2.81 years (95%  
424 CI [2.1 – 3.5]). Male senesced earlier than females (male: 8.7 years, 95% CI [78.0 – 9.5];  
425 female: 10.3 years, 95%CI [9.6 – 11.0]), with a difference of 1.6 years (95%CI [0.9 – 2.3]),  
426 and their rate of senescence between 6 and 12 years of age was stronger than that of females  
427 (male: 0.69, 95%CI [0.65 – 0.74]; female: 0.56, 95%CI [0.09 – 0.17]) with a difference of  
428 0.13 (95%CI [2.1 – 3.5]). However, both sexes had similar Gompertz rates (male: 0.17,

429 95%CI [0.14 – 0.19]; female: 0.16, 95%CI [0.14 – 0.18]) with a non-significant difference of  
430 0.008 (95%CI [-0.013 – 0.028]).

431 When testing the effect of sexual selection on the sex-differences in longevity and  
432 senescence patterns, the model selected for longevity ( $w_i = 0.24$ ;  $\lambda < 0.001$ ; Table S9),  
433 Gompertz rate ( $w_i = 0.53$ ;  $\lambda < 0.001$ ; Table S9) and senescence rate between 6 and 12 years of  
434 age ( $w_i = 0.45$ ;  $\lambda < 0.001$ ; Table S9) was the constant model.

435 The model selected for the onset of senescence only included the mating system ( $w_i =$   
436  $0.45$ ;  $\lambda < 0.001$ ; Table S9) and the between-sex difference in the onset of senescence was  
437 greater in polygynous than in monogamous species (monogamy: -1.0 year, 95%CI [-1.4 –  
438 1.3]; promiscuity: 1.1 years, 95%CI [-1.2 – 1.6]; polygyny: 1.4 years, 95%CI [1.0 – 2.0];  
439 Table 3).

440 When focusing on the effects of mating tactic, in polygynous and promiscuous species  
441 only the selected model was the constant model, for longevity ( $w_i = 0.47$ ;  $\lambda < 0.001$ ; Table  
442 S10), Gompertz rate of senescence ( $w_i = 0.44$ ;  $\lambda < 0.001$ ; Table S10) and onset of senescence  
443 ( $w_i = 0.28$ ;  $\lambda < 0.001$ ; Table S10). However, the model with the lowest AIC for between-sex  
444 difference in the onset of senescence included mating tactic ( $w_i = 0.37$ ;  $\lambda < 0.001$ ; Table S10)  
445 with territorial species that tended to display a larger between-sex difference in the onset of  
446 senescence than harem-holding species and tending species (tending: 1.0 year, 95%CI [-1.3 –  
447 1.3]; harem: 1.3 years, 95%CI [-1.2 – 1.9]; territorial: 1.4 years, 95%CI [1.0 – 1.9]; Table  
448 S11). The model selected for between-sex differences in senescence rate between 6 and 12  
449 years of age included mating tactic, body mass and the two-way interaction between male  
450 body mass and mating tactic ( $w_i = 1.00$ ;  $\lambda < 0.001$ ; Table S10). The sex-bias in rate of  
451 senescence between 6 and 12 years of age increased with male body mass in territorial  
452 species, whereas it decreased with body mass in harem species and even more in tending  
453 species (Table S11).

454 In bovids, the sex-bias in longevity and senescence patterns was not affected by the  
455 HSD because no selected model included both male and female horn size (Tables S12 and  
456 S13).

457

## 458 **Discussion**

459 Our results suggest that in large herbivores the intensity of sexual competition affects  
460 male senescence patterns and consequently the sex-differences in senescence patterns. This  
461 finding principally relies on an effect of mating on the age of onset of senescence with males  
462 from polygynous species starting to senesce earlier (but not faster) than males from  
463 promiscuous and monogamous species, both on an absolute scale and relative to females.

464

465 Findings presented here, thus support the hypothesis that, at least in the range of  
466 species considered in our study, high level of sexual competition leads to severe survival  
467 costs. However, the impact was limited to the age at the onset of senescence (i.e. the timing of  
468 senescence) and did not affect the rate of senescence (i.e. the intensity of senescence). The  
469 absence of any relationship between our proxies of sexual competition level and actuarial  
470 senescence rates is in line with a previous report from Lemaître and Gaillard (2013a) based on  
471 a much smaller dataset of wild herbivores. In fact, the only reported effect of sexual selection  
472 on senescence rates comes from the finding that in birds and mammals, the sex-differences in  
473 senescence rates is bigger in polygynous than in monogamous species (Clutton-Brock and  
474 Isvaran, 2007, Table 1). Therefore, until now no inter-specific study have clearly  
475 demonstrated that high level of sexual competition fasten actuarial senescence rates in males.

476

477 Males of polygynous herbivores start to senesce earlier than males of promiscuous  
478 and monogamous species. For instance, if we compare two similar size ungulate species, we

479 observe than monogamous Bay duiker males (*Cephalophus dorsalis*) begin to senesce at 7  
480 years of age whereas polygynous Speke's gazelle males (*Gazella spekei*) start at 3 year-olds,  
481 which shows that costs associated with polygynous mating system lead to an earlier onset of  
482 senescence. Survival costs linked to species-specific mating systems have already been  
483 reported in a few studies (Table 1). For example, Promislow (1992) found that the mean adult  
484 mortality rate is female-biased in monogamous mammals and Müller et al., (2011) found a  
485 longer relative life expectancy in males of monogamous species compared to males of  
486 polygynous species. However, to our knowledge, we provide a first evidence of a cost in  
487 terms of earlier senescence. This notably comes from the fact that comparative studies  
488 interested in such questions have focused mostly on longevity and in a few instances on  
489 actuarial senescence rates, without considering a possible impact in terms of timing of  
490 senescence (Table 1). Recently, a wide diversity of senescence patterns have been described  
491 in the living world (Nussey et al., 2013; Jones et al., 2014) and the age at the onset of  
492 senescence is now increasingly recognized as a key factor characterizing senescence patterns  
493 (Jones et al., 2008; Péron et al., 2010; Jones et al., 2014; Gamelon et al., 2014). While it has  
494 already been shown that the onset of senescence co-varies with other time variable to shape  
495 the pace of life in mammals and birds (Jones et al., 2008), our study demonstrates that other  
496 factors such as the intensity of sexual selection contributes to the diversity of age at the onset  
497 of senescence observed in the wild.

498

499 In addition, we found that among polygynous and promiscuous species, males from  
500 territorial species also senesce earlier than males from species with harem-holding or tending  
501 mating tactic. Again, if we look at two similar size species, we can see that males Bighorn  
502 sheep males (*Ovis canadensis*) which display a tending mating tactic, start to senesce at 9  
503 years of age, whereas territorial Lechwe males (*Kobus leche*) senesce from 3 years of age.

504 Inter-specific differences in senescence patterns between territorial and non-territorial males  
505 are likely to arise from the important energetically and physical demands to maintain  
506 territories. For instance, in impala (*Aepyceros melampus*), Van Rooyen (1993) found that  
507 territorial males lose more body condition during the rut than males not involved in the  
508 defense of a territory, a decline that seems to result from a decrease in food intake in parallel  
509 to an increased activity both linked to territorial tenure (Murray, 1982). Moreover, such costs  
510 might be associated with an increased probability to face aggressive contests and injuries, as  
511 observed in males of territorial pudu (*Pudu puda*), where fights between males during rutting  
512 season includes cause injuries (MacNamara and Elridge, 1987) but also in other vertebrates  
513 such as lizards species, where male-male interactions in territorial species are more likely to  
514 lead to fighting than in non-territorial species (Vanhooydonck et al., 2005; Lailvaux and  
515 Irschick, 2007).

516

517         Although we provided clear evidence that both mating systems and tactics influence  
518 the age at the onset of senescence, we did not find any relationship between sexual size  
519 dimorphism and any of our metrics of survival and senescence. This is surprising because the  
520 large amount of energy required for male growth compared to female growth in highly  
521 sexually dimorphic species is expected to cause survival or ageing costs (e.g. Toïgo and  
522 Gaillard, 2003; Bro-Jørgensen, 2012). Interestingly, our review of the literature reveals that  
523 the relationship between sexual size dimorphism and senescence *per se* has almost never been  
524 investigated (but see Lemaître and Gaillard 2013a). Most studies so far have documented  
525 survival costs of sexual size dimorphism through a negative relationship between SSD and  
526 adult mortality (Promislow, 1992; Promislow et al., 1992; but see Owens and Bennett, 1994  
527 and Toïgo and Gaillard, 2003) or longevity (Bro-Jørgensen 2012). However, these studies  
528 have used different metrics to assess the level of sexual size dimorphism. For instance,

529 Promislow (1992) measured SSD as the ratio of male body mass on female body mass while  
530 Bro-Jørgensen (2012) used the Lovich and Gibbons (1992)'s ratio. In the present study, we  
531 measured SSD by adding both male and female body mass as covariates in our analyzes, a  
532 method that has been repeatedly advocated in comparative studies to avoid bias resulting  
533 when predictors are collinear in multi-factorial analyzes (Freckleton *et al.*, 2002; Freckleton  
534 2009). However, when we replicated our analyzes using other metrics previously used of  
535 sexual size dimorphism, all results remained qualitatively unchanged (Tables S14 and S15).  
536 Therefore, the observed discrepancy between the results we report here and previously  
537 published studies are likely to involve either the absence of corrections for confounding  
538 factors (e.g. pace of life, see below) or the type and quality of data analyzed. For instance, for  
539 a trait like longevity the use of different sources can rapidly lead to divergent outcomes (see  
540 Lemaître *et al.*, 2014c for an example). In the present study, we have used data from the ISIS  
541 database rather than published records of longevity. ISIS data allows working on long-term  
542 population with the huge advantage of not having to consider capture probabilities as  
543 individuals living in captivity are known without doubt to be alive or dead in a given year.  
544 This allows getting highly reliable estimates of survival and senescence. Furthermore, life in  
545 captivity eliminates environmentally-driven sources of mortality (e.g. predation or climate  
546 harshness) and allows to better assessing how costs associated with sexual selection and thus  
547 intrinsic changes in animals conditions influence survival.

548

549         Since sexual selection acts primarily on males, female longevity and senescence  
550 patterns are not expected to be directly influenced by the intensity of sexual competition.  
551 Therefore, if sexual selection generates sex-differences in survival and senescence patterns,  
552 the effect should be mainly driven by changes in males. Our results are in full agreement with  
553 this assumption. Indeed, similarly to our analyzes strictly focused in males, we found an effect



554 of mating system on the sex-differences in the age at the onset of senescence, with larger  
555 differences in onset of senescence in polygynous species than in promiscuous and  
556 monogamous species. Although not focused on the onset of senescence, results from  
557 comparative analyzes that have investigated this topic have revealed a link between the  
558 mating system and the sex-differences in longevity or senescence patterns. These studies  
559 looked at the between-sex differences of longevity in mammals (Clutton-Brock and Isvaran,  
560 2007; Müller et al., 2011) and birds (Clutton-Brock and Isvaran, 2007), or the between-sex  
561 differences in adult mortality in birds (Liker and Székely, 2005), have systematically been  
562 found to be higher in polygynous than in monogamous species. In the present study, we  
563 reported strong between-sex differences as strong as 1.5 years in the onset of senescence in  
564 polygynous species, whereas this difference was less than 1 year in monogamous species.  
565 These results show that the sex-bias in senescence patterns is driven by costs linked to mating.  
566

567 In addition, our study documents a strong allometric relationship between body mass  
568 and senescence metrics. In large herbivores, body mass is tightly linked to the pace of life  
569 (Gaillard et al., 2003), with small species having a relatively fast pace of life, characterized by  
570 an early and fast senescence compared to larger species. In addition, and in accordance with  
571 previous reports (Müller et al., 2011; Lemaître et al., 2013), we found that diet is associated  
572 with senescence in captive ungulates. Typically, grazer species (e.g. African buffalo, *Syncerus*  
573 *caffer*) have a delayed onset of senescence, a slower rate of senescence, and live longer  
574 compared to browser species such as roe deer (*Capreolus capreolus*). Overall, these analyzes  
575 emphasize the importance of correcting for the pace of life and for diet when working on  
576 captive populations to avoid biased results. However, most studies listed in Table 1 failed to  
577 control for such confounding variables, which might explain part of the discrepancy observed  
578 between these studies. Using the three different methods employed to assess SSD in the

579 context of sexual selection (see Table 1), we thus tested in complementary analyses how an  
580 absence of correction for body mass, diet or both variables influences our results.  
581 Interestingly, when body mass or both body mass and diet are removed from the models,  
582 mating system was found in best models for longevity, onset of senescence and rate of  
583 senescence between two ages, and SSD was associated with onset of senescence in large  
584 herbivore in the expected direction (i.e. a positive association between the intensity of sexual  
585 selection and the intensity of senescence, see Tables S16 and S17). This demonstrates the  
586 importance to control analyzes for confounding effects of diet and pace of life to assess  
587 reliably the relationship between sexual selection and senescence pattern at inter-specific level  
588 and stress the importance to consider sparingly results from analyzes non-corrected for these  
589 factors.

590

591 Finally, our analyzes and review of the literature show that the relationship between  
592 the intensity of sexual selection and the strength of male senescence is complex. Then, the  
593 lack of SSD effect along with the clear evidence of an effect of the mating system on the  
594 onset of senescence in males indicate that the costs associated with sexual selection via intra-  
595 sexual competition are generated by risky and energy-demanding behaviours rather than by  
596 large size in itself. These results demonstrate that only some traits like the timing of actuarial  
597 senescence and/or behaviors like territoriality involved in sexual selection are costly in terms  
598 of survival.

599

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603

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- 781

782 **Table 1:** Survey of comparative analyzes investigating the relationship between the strength of sexual selection and mortality or actuarial senescence metrics  
783 across species. Gray-shaded results correspond to studies reporting support for a statistically significant association between the strength of sexual selection and  
784 the level of mortality or actuarial senescence. Results in bold correspond to studies based on metrics of actuarial senescence *per se*. To identify these  
785 comparatives studies, we entered the keywords ‘*senescence*’, ‘*ag(e)ing*’, and ‘*sexual selection*’ into the search engine database of *Web of Science* (SCI-  
786 Expanded).

Study	Taxa	Population	N	Statistical analysis	Sex	Sexual selection intensity (measure)	Survival or senescence variables (measure)	Conclusion		
Promislow, 1992	Mammals	wild	35	PICs	Sex-difference	SSD Mating system	Ratio of male to female length Monogamy / Polygyny	Adult mortality rate Ratio of female to male life expectancy from the average age at maturity	<ul style="list-style-type: none"> <li>• Positive correlation between SSD and male bias adult mortality.</li> <li>• Female-bias in adult mortality in monogamous taxa.</li> </ul>	
Promislow et al., 1992	Birds (North American Passerine only)	wild	28	PICs	Male Female Sex-difference	SSD Brightness Plumage Difference	Male minus female values Scale from 1 (dull) to 5 (bright) male - females score	Adult mortality rate Sex-specific mortality rate extracted from literature Sex-bias : male – female values	<ul style="list-style-type: none"> <li>• Positive correlation between male adult mortality and SSD.</li> <li>• Positive correlation between sex-biased mortality and both SSD and male brightness.</li> </ul>	
Owens and Bennett, 1994	Birds (western Palearctic species only)	wild	37	PICs	Males Females	SSD Sexual Plumage Dimorphism (SPD)	Ratio of male to female body mass Difference expressed on a scale from 0 (monomorphic) to 10 (maximum dimorphism) for five body regions	Adult mortality rate Sex-specific annual mortality rate Sex-bias: male/female	<ul style="list-style-type: none"> <li>• No mortality cost associate to SSD neither SPD.</li> </ul>	
Toïgo and Gaillard, 2003	Mammals (Large herbivores only)	wild	18	PICs	Male Sex-difference	SSD Male mating tactic	Residuals male to female body mass territoriality / tending / harem-holding	Adult survival rate Prime-age survival between 2 and 7 years of age Sex-bias: male - survival	<ul style="list-style-type: none"> <li>• Male survival is lower than female survival.</li> <li>• SSD has no effect on male-biased mortality.</li> <li>• No relationship between mating tactic and male-biased mortality.</li> </ul>	
Liker and Székely, 2005	Birds	wild	194	PICs	Male Female	Mating system Relative testes size	Monogamy / Polygyny Testes size and male body mass in covariate	Adult mortality rate Sex-specific mortality rate Sex-bias : male – female values	<ul style="list-style-type: none"> <li>• Male-male competition and relative testis size are positively associated to male biased mortality.</li> <li>• Females have higher adult mortality than males.</li> </ul>	
<b>Clutton-Brock and Isvaran, 2007</b>	<b>Mammals and birds</b>	<b>wild</b>	<b>30</b>	<b>PGLS</b>	<b>Sex-difference</b>	<b>Mating system</b>	<b>Monogamy/polygyny: average number of adult females in breeding group</b>	<b>Lifespan</b>  <b>Rate of actuarial senescence</b>	<b>Ratio of male lifespan to female lifespan</b>  <b>Difference in slope obtained from linear regression fitted on age-specific data</b>	<ul style="list-style-type: none"> <li>• <b>Bigger sex difference of lifespan in polygynous species than monogamous species.</b></li> <li>• <b>Bigger sex differences in senescence rates for polygynous species than for monogamous species</b></li> </ul>



Müller <i>et al.</i> , 2011	Mammals (Large herbivores only)	captive	78	PGLS	Male Female	Mating system	Monogamous / Tending / Polygynous	Relative life expectancy (rLE)	Life expectancy as proportion of longevity	<ul style="list-style-type: none"> <li>Higher rLE in males of monogamous than polygynous species.</li> <li>Higher rLE in females than males.</li> </ul>
Bro-Jørgensen, 2012	Mammals (Bovids only)	captive	100	PICs (and PGLS)	Male Female	SSD	Lovich & Gibbons ratio*	Longevity	Maximum longevity	<ul style="list-style-type: none"> <li>Longevity decrease with SSD in male only.</li> </ul>
Lemaître and Gaillard, 2013a	Mammals (Large herbivores only)	wild	24	PGLS	Male Sex-difference	SSD Weapon size dimorphism (WSD) Relative testes mass (RTM) Male mating tactic	Male and female body mass in covariate Male and female body mass in covariate Testes mass and male body mass in covariate Territoriality / tending, /harem following	Median lifespan  Rate of actuarial senescence	Age at which 50% of an initial cohort are still alive Sex-bias : female – male  Slope obtained from linear regression fitted on age-specific data, from median lifespan to age where 10% of an initial cohort is still alive Sex-bias : female - male	<ul style="list-style-type: none"> <li>Lower adult survival in males than in females.</li> <li>No relationship between male allocation to SSD, WSD and/or RTM and inter-species difference of both absolute and relative adult lifespan.</li> <li>Stronger rate of senescence in males than in females.</li> <li>No relationship between male allocation to SSD, WSD and/or RTM and between-species difference of both absolute and relative actuarial intensity of senescence.</li> </ul>
Lemaître and Gaillard, 2013b	Mammals	wild	24	PGLS	Female	Level of female polyandry	Relative testes mass or percentage of multiple paternity	Median lifespan  Rate of actuarial senescence	Age at which 50% of an initial cohort are still alive  Slope obtained from linear regression fitted on age-specific data, from the age at the onset of senescence to death	<ul style="list-style-type: none"> <li>Polyandry level does not affect female lifespan.</li> <li>Polyandry level does not affect female rate of senescence.</li> </ul>

N, number of species; PICs, Phylogenetically Independent contrasts; PGLS, PhyloGenetically Least Square models; SSD, Sexual Size Dimorphism; rLE, relative Life Expectancy.

\* ratio calculated as M/F if M>F and 2-F/M if F>M, M and F denote male and female body mass respectively.

788 **Table 2:** Parameter estimates from the models selected to account for among-species  
789 variation observed in longevity and metrics of actuarial senescence in males of large  
790 herbivore species living in captivity. In all analyzes performed, phylogeny had no statistically  
791 significant effects ( $\lambda < 0.001$ ) and parameters were thus estimated from linear models (LM)  
792 without any phylogenetic correction. Effect size statistically different from 0 occur in bold.

	Method	Variables	$\beta$	95%CI	Adjusted-R <sup>2</sup>	$\lambda$
Longevity (N=64)	LM	<b>Diet</b>	<b>0.002</b>	<b>0.000 ; 0.004</b>	0.18	< 0.001
		<b>Male body mass</b>	<b>0.054</b>	<b>0.011 ; 0.097</b>		
Gompertz rate of senescence (N=54)	LM	<b>Gompertz onset</b>	<b>0.273</b>	<b>0.015 ; 0.530</b>	0.06	< 0.001
Onset of senescence (N=64)	LM	Promiscuity	-0.244	-0.599 ; 0.112	0.23	< 0.001
		<b>Polygyny</b>	<b>-0.456</b>	<b>-0.817 ; -0.096</b>		
		<b>Diet</b>	<b>0.004</b>	<b>0.001 ; 0.008</b>		
		<b>Male body mass</b>	<b>0.099</b>	<b>0.025 ; 0.172</b>		
Rate of senescence between 6 and 12 years-old (N=60)	LM	<b>Male body mass</b>	<b>-0.137</b>	<b>-0.198 ; -0.076</b>	0.24	< 0.001

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795 **Table 3:** Parameter estimates from the models selected to account for between-sex variation  
796 observed among species of large herbivores living in captivity in longevity and metrics of  
797 actuarial senescence. In all analyzes performed, phylogeny had no statistically significant  
798 effects ( $\lambda < 0.001$ ) and parameters were thus estimated from linear models (LM) without any  
799 phylogenetic correction. Effect size statistically different from 0 occur in bold.

800

	Method	Variables	$\beta$	95%CI	Adjusted-R <sup>2</sup>	$\lambda$
Longevity (N=64)	LM	Constant				< 0.001
Gompertz rate of senescence (N=52)	LM	Constant				< 0.001
Onset of senescence (N=64)	LM	Promiscuity	0.132	-0.204 ; 0.468	0.07	< 0.001
		Polygyny	<b>0.346</b>	<b>0.014 ; 0.678</b>		
Rate of senescence between 6 and 12 years-old (N=59)	LM	Constant				< 0.001

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802

803 **FIGURE LEGENDS:**

804

805 **Figure 1:** Phylogenetic tree built on 64 species of large herbivores used in our analysis (based  
806 on Bininda-Emonds (2007, 2008)'s phylogenetic tree. Cervid species are specified in bold,  
807 *Tragulus javanicus* (Tragulidae), *Giraffa camelopardalis* (Giraffidae) and *Antilocapra*  
808 *americana* (Antilocapridae) are in grey, and other are bovid species. For graphical  
809 representation, the SSD was calculated as the ratio of male body mass on female body mass.

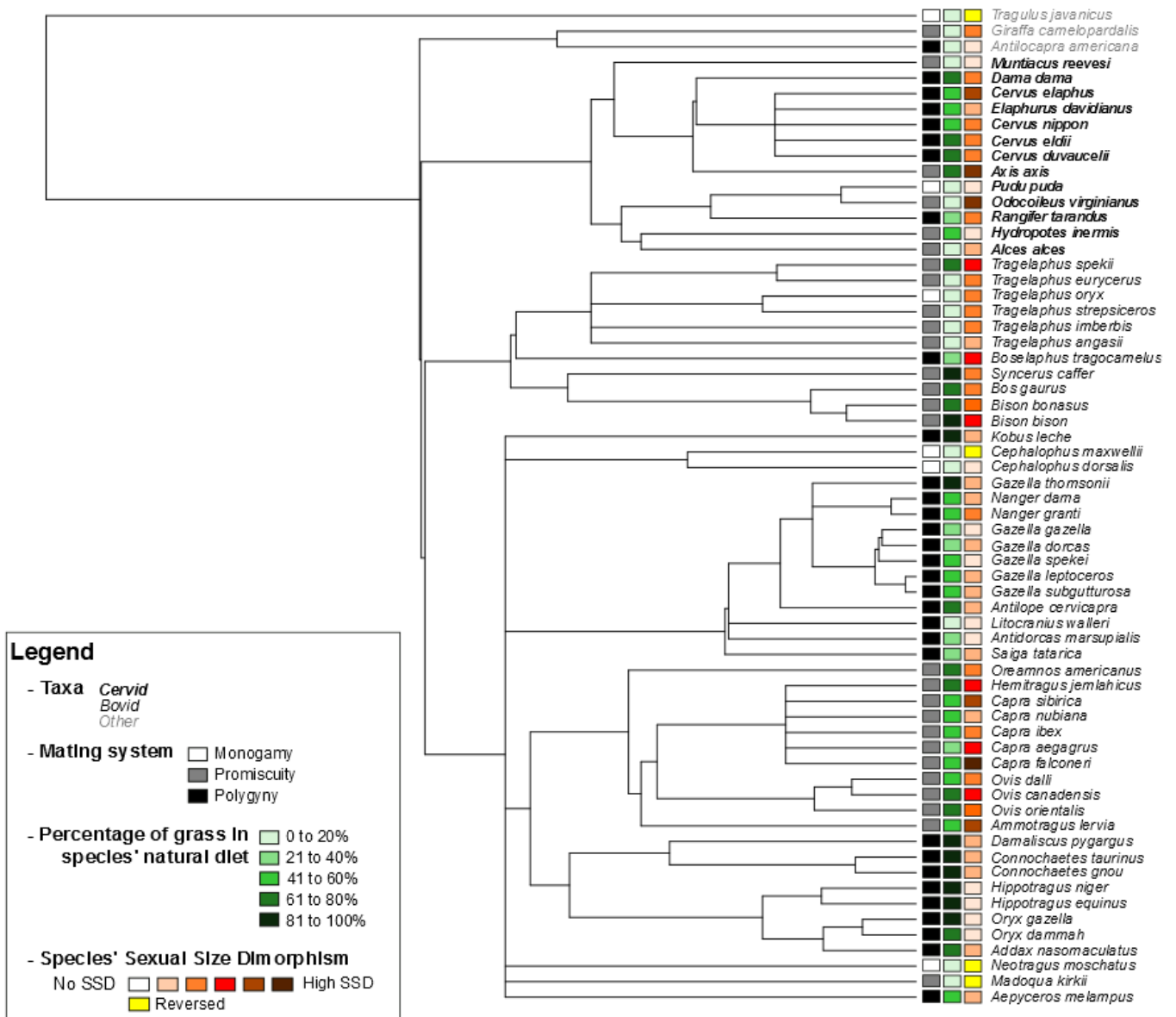
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811 **Figure 2:** Relationships between the age at the onset of actuarial senescence in males  
812 (corrected for both diet and body mass), and the mating system (N = 64 species).

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814 **Figure 3:** Relationships between the age at the onset of actuarial senescence in males  
815 (corrected for diet), and the mating tactic (N = 37 species).

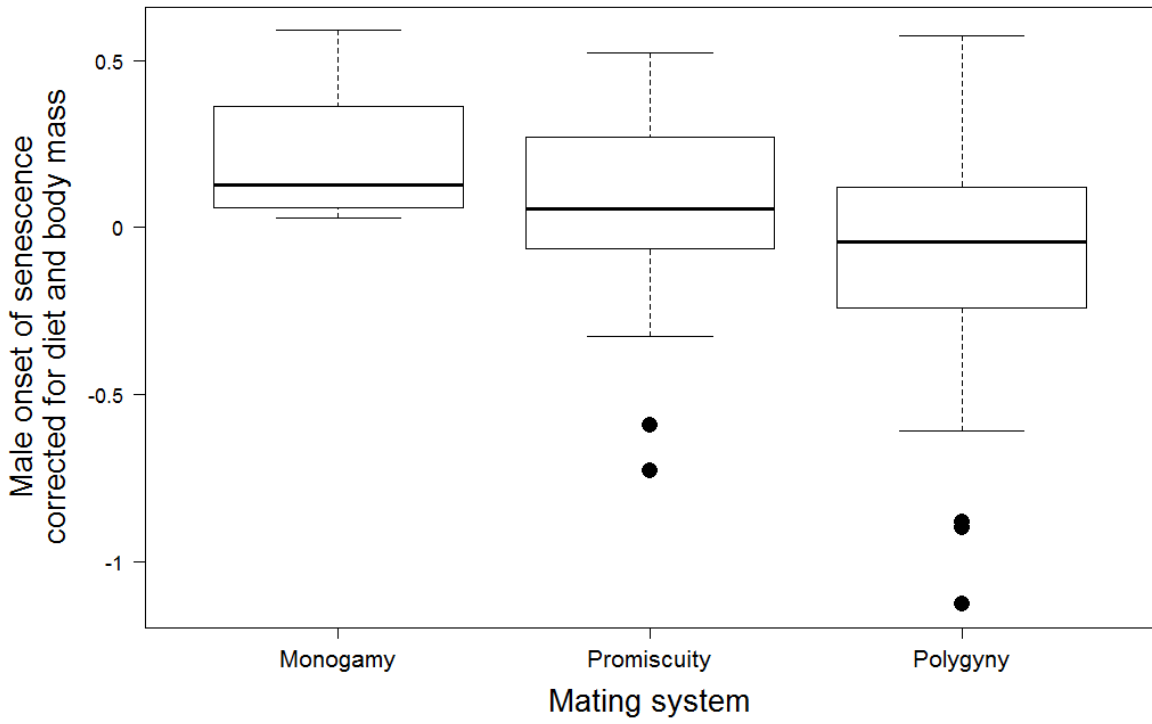
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818 **Figure 1**

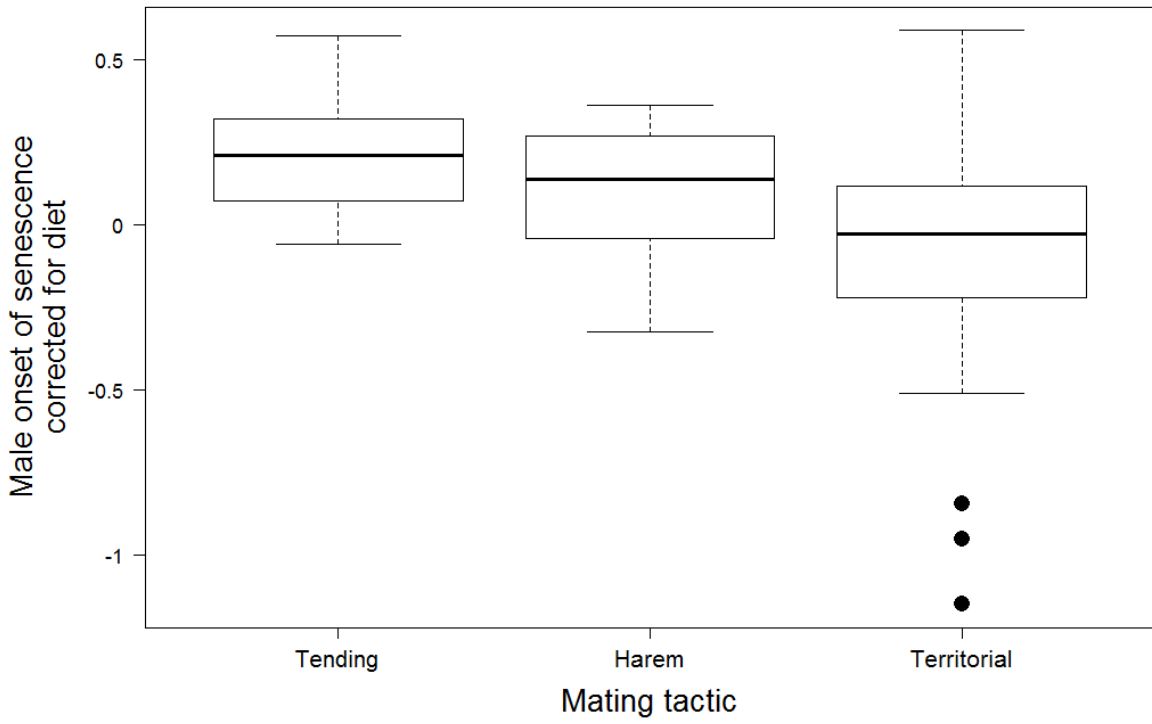
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821 **Figure 2**

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824 **Figure 3**