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1 **Do age-specific survival patterns of wild boar fit current evolutionary**
2 **theories of senescence?**

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18

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20

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25 Actuarial senescence is an inevitable outcome of evolution in age-structured populations. In
26 growing populations, the progressive decline of Hamiltonian forces of selection with age
27 leads to decreasing survival. As actuarial senescence is over-compensated by a high fertility,
28 actuarial senescence should be more intense in species with high reproductive effort, a
29 theoretical prediction that has not been yet explicitly tested across species. Wild boar (*Sus*
30 *scrofa*) has an unusual life-history strategy among large mammals by associating both early
31 and high reproductive effort with potentially long lifespan. Therefore, wild boar should show
32 stronger actuarial senescence than similar-sized related mammals. Moreover, being
33 polygynous and much larger than females, males should display higher senescence rates than
34 females. From a long-term monitoring of 1,783 individuals, we tested these predictions. We
35 provided clear evidence of actuarial senescence in both sexes. Wild boar females had earlier
36 but not stronger actuarial senescence than similar-sized ungulates and both sexes displayed
37 similar senescence rates. Our study indicates that the timing of senescence, not the tempo, is
38 associated with the magnitude of fertility in ungulates. This demonstrates the importance of
39 including the timing of senescence in addition to its rate to understand variation in senescence
40 patterns in wild populations.

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49 Actuarial senescence (hereafter senescence) defined as the decline of survival with
50 increasing age, has been repeatedly documented in wild species of vertebrates (see Nussey et
51 al. 2013 for a review). However, empirical evidence has increased only recently,
52 thanks to the development of long-term individual monitoring of known-aged animals
53 (Clutton-Brock and Sheldon 2010). William D. Hamilton already demonstrated nearly fifty-
54 years ago (Hamilton 1966) that senescence was an inevitable outcome of evolution in age-
55 structured populations. More specifically, based on the decline of the forces of natural
56 selection with age in growing age-structured populations (Medawar 1952), Hamilton
57 predicted that an increase in fertility should be selected at the costs of a survival decrease at
58 old ages. In other words, high fertility should be associated with high rates of senescence
59 (Hamilton 1966). Until now, intraspecific studies have provided good evidence for a
60 relationship between early allocation to reproduction and fitness-related traits, such as
61 survival (Hammers et al. 2013) and components of reproductive success (Nussey et al. 2006)
62 in late life, in line with the disposable soma theory of ageing (Kirkwood 1977; Kirkwood and
63 Austad 2000). On the other hand, while some recent comparative studies have revealed an
64 association between intensity of actuarial senescence and pace of life across species within
65 and among classes of vertebrates (Jones et al. 2008, Péron et al. 2010, Lemaître and Gaillard
66 2013), no study has tested yet the exact Hamilton's prediction of a direct link between
67 fecundity and intensity of actuarial senescence across species.

68

69 Moreover, while empirical evidence that females live much longer than males in most
70 mammals studied so far is compelling (Carey and Judge 2000), whether and how age-specific
71 trajectories differ between sexes remains an open question (Nussey et al. 2013, Maklakov and
72 Lummaa 2013), although the theoretical basis for such sex differences has been established
73 for a long time (Williams 1957). Hamiltonian forces of selection again provide the

74 explanation for more intense senescence in males when these latter suffer from higher
75 mortality during the prime-age stage. Starvation and antagonist contests during the mating
76 season are likely to cause increased mortality rates in males compared to females in
77 polygynous species (Bonduriansky et al. 2008), especially when environmental conditions are
78 harsh (Toïgo and Gaillard 2003). Thus, under current life history theory, males from highly
79 polygynous and dimorphic species should exhibit a 'live fast, die young' life history strategy
80 (Vinogradov 1998, Bonduriansky et al. 2008, Festa-Bianchet 2013) and should therefore have
81 higher senescence rate than females.

82

83 Using a 17 year-long monitoring of an Italian population of wild boar (*Sus scrofa*), we
84 filled these gaps by investigating the pattern of actuarial senescence for this large mammal
85 characterized by a unusual association between high fertility and high sexual size dimorphism
86 (Carranza 1996). Indeed, compared to similar-sized related species, wild boar females give
87 birth for the first time earlier (1 vs. 2-3 years of age, Servanty et al. 2009), at a lower body
88 mass (40% vs. 80% of adult body mass, Servanty et al. 2009), and produce larger litters (>3
89 vs. 1 or 2, Gamelon et al. 2013). By allocating early and heavily to reproduction, wild boar
90 females have an unusual life-history strategy among large mammals (Focardi et al. 2008).
91 Therefore, in accordance with Hamilton's theory, wild boar females should show faster
92 senescence than reported for similar-sized ungulates. Moreover, as wild boar males are
93 markedly heavier than females (90 vs. 70 kg for males and females, respectively, Gaillard et
94 al. 1992) and are highly polygynous (Delgado et al. 2008), they should suffer from more
95 intense senescence than females.

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99 **Materials and methods**

100 **STUDY SITE AND DATA COLLECTION**

101

102 We studied a weakly hunted and growing wild boar population in the fenced 6,000 ha
103 preserve of Castelporziano (41°44'N, 12°24'E) in Italy (Focardi et al. 2008). From 1995 to
104 2012, a total of 1,783 juvenile (< 1 year of age) and yearling (1 to 2 years old) wild boars
105 were marked with numbered and colored ear tags and released after handling. Between July
106 and September, wild boars were artificially fed three to six times per week on 80-88 feeding
107 sites (Franzetti et al. 2012) to allow counts and identification of marked animals from year to
108 year.

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110 **ESTIMATING AGE-SPECIFIC SURVIVAL, RATE AND ONSET OF SENESCENCE** 111 **IN MALE AND FEMALE WILD BOAR**

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113 We estimated natural survival rates of marked individuals using Capture-Mark-
114 Recapture analyses (Lebreton et al. 1992) of both recaptures and resightings. Animals
115 removed under population control plans were right-censored to allow estimating natural
116 survival. As the preserve was fenced, no dispersal occurred so that true survival was
117 estimated.

118 We first tested the goodness-of-fit (GOF) (Pradel et al. 2005) of the survival models
119 using U-CARE (Choquet et al. 2009a). We accounted for heterogeneity in the detection
120 process of juveniles (see Results) by modelling two different recapture probabilities according
121 to whether an individual was previously detected (trap-dependence: Gimenez et al. 2003;
122 Pradel and Sanz-Aguilar 2012). As capture effort varied among years (Focardi et al. 2008), we
123 included time-dependence in recapture probabilities. For survival probabilities, we fitted both
124 a model without any effect of age and the full age-dependent model. From the latter, the rate
125 of senescence was measured as the slope of the regression of log-transformed age-specific

126 mortality rates on age to compare with senescence rates previously reported in ungulates
127 (Gaillard et al. 2003). To avoid confounding effects of growth or reproduction, we analyzed
128 mortality rates from 2 years of age onward, when growth has been completed.

129 To estimate the age at the onset of senescence, we constrained survival to vary linearly
130 on the logit scale over different ranges of ages (ages 1, 2, 3, 4, 5, or 6; see Nichols et al. 1997
131 for a similar approach and table 1). The age at onset of senescence was defined as the age
132 when survival started to decline as assessed from the selected model. We thus fitted age-
133 specific survival models while testing for between-sex differences in age-specific survival and
134 rate of senescence. We used the Akaike's Information Criterion for model selection (Burnham
135 and Anderson 2002), selecting the model with the lowest AIC. All analyses were implemented
136 in E-SURGE (Choquet et al. 2009b).

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138 **SURVIVAL PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED** 139 **UNGULATES** 140

141 To test whether wild boar females show faster and/or earlier senescence than reported
142 for similar-sized ungulates, we accounted for the confounding effect of body mass (Calder
143 1984). Indeed, it is well-established that the pace of life decreases with increasing mass
144 (Gaillard et al. 2005), leading large species to exhibit later onset and smaller rate of
145 senescence than small ones (Jones et al. 2008, Péron et al. 2010, Ricklefs 2010). We thus
146 assessed the relationship between senescence rate (on a log-scale) and female body mass (on a
147 log-scale) as well as the relationship between onset of senescence (on a log-scale) and female
148 body mass (on a log-scale) of similar-sized ungulates. Females of 9 intensively monitored
149 populations belonging to 7 different ungulate species were included in the analysis, namely
150 pronghorn (*Antilocapra americana*), Alpine ibex (*Capra ibex*), roe deer (*Capreolus*
151 *capreolus*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), red deer

152 (*Cervus elaphus*) and Pyrenean chamois (*Rupicapra pyrenaica*). Senescence rates were
153 extracted from Gaillard et al. (2003)'s study and onsets of senescence from Péron et al.
154 (2010)'s study.

155 Patterns of senescence across species might be not independent as a result of common
156 ancestry (Harvey and Pagel 1991). We thus controlled for this non-independence by using
157 Phylogenetic Generalized Least-Squares models (PGLS) that provide an index of the
158 phylogenetic signal called λ , varying in most of the cases between 0 (corresponding to the
159 complete absence of phylogenetic structure) and 1 (observed pattern predicted by the
160 phylogeny; see Freckleton et al. 2002). This parameter λ was then introduced in the model to
161 control for the phylogenetic effect (Freckleton et al. 2002). We used the phylogeny derived
162 from the phylogenetic supertree of mammals, which provides information on both topology
163 and branch length (Bininda-Emonds et al. 2007). However, in the models linking rate and
164 onset of senescence (on a log-scale) to body mass (on a log-scale) in similar-sized ungulates,
165 the phylogenetic signal (λ) did not differ from 0 ($\lambda_{\text{rate}} < 0.0001$ and $\lambda_{\text{onset}} < 0.0001$), meaning
166 that there was no detectable phylogenetic signal in both rate and onset of senescence.
167 Therefore, we conducted inter-specific analyses linking senescence rate and onset of
168 senescence to female body mass, using standard linear models (i.e. without any correction for
169 phylogeny) to avoid biased estimates (Revell 2010). From these linear models, expected rate
170 and onset of senescence of wild boar females were estimated and compared with rates and
171 onsets found in populations of similar-sized ungulates. All analyses were performed with the
172 R software (R Development Core Team 2012).

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176 **Results**

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178 **ESTIMATING AGE-SPECIFIC SURVIVAL, RATE AND ONSET OF SENESCENCE**
179 **IN MALE AND FEMALE WILD BOAR**
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181 By only including individuals first captured as juveniles, the GOF test indicated some
182 lack of fit for both sexes (global test: for male juveniles: $\chi^2(61) = 102.743$, $P < 0.0001$; for
183 female juveniles: $\chi^2(72) = 128.411$, $P < 0.0001$). More precisely, trap-dependence was
184 detected for both sexes and accounted for in the model. On the contrary, the GOF test
185 indicated no lack of fit for individuals first captured as yearlings (global test: for males: χ^2
186 $(27) = 31.273$, $P = 0.260$; for females: $\chi^2(33) = 27.575$, $P = 0.734$). Tested models thus
187 satisfactorily fitted data when trap-dependence was included in capture probabilities of
188 juveniles.

189 The best model included marked between-sex differences at age 2 (Fig. 1), a linear
190 relationship between survival and age from 3 years old onwards, and year-dependent capture
191 probabilities (table 1, appendix S1). Males and females had same survival at age 1 ($\Phi_{age1} =$
192 $0.68 [0.64; 0.72]$), but males survived a bit less than females at 2 years old ($\Phi_{age2\ male} = 0.57$
193 $[0.50; 0.64]$, $\Phi_{age2\ female} = 0.85 [0.77; 0.91]$). From 3 years old onwards, males consistently
194 had lower survival than females (Fig. 1) but both sexes had similar senescence rates (slope on
195 the logit scale = $-0.15 [-0.23; -0.08]$).

196 To compare senescence rates between wild boar and similar-sized ungulates,
197 senescence rates were re-estimated using the linear regression between mortality rates (on a
198 log scale) and age. These rates exactly correspond to the Gompertz rates (i.e. the exponential
199 rate of increasing mortality with age) and slightly differ from the rates estimated directly from
200 analyses provided above (which do not exactly correspond to Gompertz rates, Loison et al.
201 1999). After removing survival rates at 10 and 12 years old for males and females,
202 respectively, estimated on the bounds of the interval $[0, 1]$ (see Fig. 1), we found evidence of
203 actuarial senescence in both sexes (rates of 0.11 (SE: 0.04) for males (Wald test: 9.7, $df = 1$, p-

204 value = 0.002) and 0.14 (SE: 0.04) for females (Wald test: 16.0, df = 1, p-value < 0.0001),
205 Fig. 2).

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207 **SURVIVAL PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED**
208 **UNGULATES**
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210 As expected, across ungulate species, the senescence rate tended to decrease (slope: -
211 0.11, SE: 0.18) and the onset of senescence to be delayed (slope: 0.17, SE: 0.12) when body
212 mass increased (Fig. 3). From the relationship between senescence rate and body mass (on a
213 log-log scale) performed using 9 populations belonging to 7 different species, the expected
214 rate of senescence for wild boar females was similar to the expectation (expected value of
215 0.16 vs. observed value of 0.14, Fig. 3a). On the other hand, the onset of senescence was
216 much earlier than expected. From the relationship between the onset of senescence and body
217 mass (on a log-log scale), the expected value was 8.56 years, whereas it was estimated to only
218 3 years in our analysis (Fig. 3b). Wild boar females had thus markedly earlier, but not stronger
219 senescence (Fig. 3) for their body size compared to other ungulates.

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229 **Discussion**

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231 Our results provide clear evidence for actuarial senescence in male and female wild
232 boar and add to the spate of studies that have recently found senescence in free-living
233 vertebrates (Nussey et al. 2013). More importantly, using a pioneering inter-specific test of the
234 Hamilton's prediction of a link between fecundity and intensity of actuarial senescence, our
235 findings show that wild boar females have earlier, but not stronger senescence than related
236 species once the confounding effects of body size has been accounted for. Indeed, our
237 findings emphasize that the high reproductive output of wild boars (with litter size up to 14,
238 Servanty et al. 2007) is associated with earlier, but not stronger decline in survival with age.
239 As Hamilton's theory was strictly focused on senescence rates, our study did not provide a
240 direct support for it. However, we show that actuarial senescence occurred much earlier in
241 wild boar females than in other ungulates. High and early fertility in wild boar females during
242 the prime-age stage might advance the decline of the forces of natural selection, which
243 indicates that the timing of senescence, in addition to the rate, constitutes a key component of
244 Hamilton's theory of senescence. We thus propose to expand Hamilton's theory to include
245 potential responses of the timing of senescence to increased fertility, by considering both the
246 timing and the intensity of senescence patterns to test reliably evolutionary theories of ageing.
247

248 When looking at sex-differences in senescence patterns, we did not detect any
249 difference in the rate of senescence between male and female wild boar. This finding contrasts
250 with a few studies that reported greater actuarial senescence in males compared to females in
251 large herbivores (Gaillard et al. 2003; Lemaître and Gaillard 2013), a pattern that is generally
252 attributed to the polygynous mating system of these species (Clutton-Brock and Isvaran 2007,
253 Bonduriansky et al. 2008). The red deer (*Cervus elaphus*) case study provides a striking
254 example of higher senescence rates (but not earlier onset) in males than in females (Catchpole
255 et al. 2004). Our results are thus particularly surprising from both empirical (Loison et al.

256 1999, Lemaître and Gaillard 2013) and theoretical (Williams 1957) viewpoints. Indeed,
257 because males had higher mortality rates at all ages from 2 years old onwards than females,
258 they were expected to show greater actuarial senescence (Williams 1957, Hamilton 1966).
259 The higher mortality rates of male wild boar during the whole adult stage might be due to sex-
260 specific reproductive tactics and associated mortality risks (Bonduriansky et al. 2008, Festa-
261 Bianchet 2013) or to the occurrence of harsh environmental conditions in the study site.
262 Indeed, harsh environments are more likely to influence male than female survival (Toigo and
263 Gaillard 2003). In wild boar, the differential mortality suffered by males do not translate into
264 stronger senescence. Although the causes of similar senescence rates in both sexes despite
265 higher mortality rates in male wild boar remain unknown, it is interesting to notice that
266 similar patterns have been reported in humans (Austad 2011). In both wild boar and humans,
267 the between-sex differences in adult mortality was quite low (about 10%), which might be not
268 enough to trigger substantial between-sex differences in the decline of Hamilton's forces of
269 selection with age. Simulation studies will be required to test this hypothesis.

270

271 Alternatively, differential sources of mortality between sexes could account for the
272 absence of sex differences in actuarial senescence we reported in wild boar. Indeed, recent
273 laboratory experiments have demonstrated that the cause of mortality at early ages can
274 modulate senescence patterns (Chen and Maklakov 2012, Chen et al. 2013). Basically, when
275 the source of mortality is random, all animals in the population have the same probability of
276 dying, independently of their individual phenotype. On the contrary, when mortality is
277 condition-dependent, the probability of dying acts as a filter in the population by removing
278 weakest individuals, which ultimately decreases the intensity of senescence at the population
279 level (Vaupel et al. 1979). In support, an experiment on wild type derived nematodes
280 (*Caenorhabditis remanei*) has shown high rates of condition-dependent mortality promotes a

281 deceleration of ageing, independently of sex, within only 12 generations (Chen et al. 2013). In
282 wild boar, differential sources of mortality between sexes could explain our findings in wild
283 boar if condition-dependent mortality only occurs in males. The twofold higher mortality rate
284 of male wild boar at 2 years compared to females might provide the potential filter to keep the
285 best phenotypes at old ages. However, whether mortality at 2 years of age is condition-
286 dependent in males remains to be explored.

287

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447 **Table 1.** Model selection for age-specific survival patterns in the wild boar population of
448 Castelporziano, Italy. $\Phi_{a(x-13)}$ corresponds to a linear relationship (on a logit-scale) between
449 age and survival from x year of age. Displayed are the number of parameters (Np), the AIC of
450 the 10 best models and the difference between each tested model and the best one (Δ AIC).

Model notation	Np	AIC	ΔAIC
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$\Phi_1[\Phi_2].\text{Sex } [\Phi_{a(3-13)}]+\text{Sex}$	25	6422.88	0.00
$[\Phi_1\Phi_2].\text{Sex } [\Phi_{a(3-13)}]+\text{Sex}$	26	6423.06	0.18
$\Phi_1[\Phi_2 \Phi_{a(3-13)}].\text{Sex}$	26	6424.74	1.86
$[\Phi_1\Phi_2\Phi_{a(3-13)}].\text{Sex}$	27	6424.94	2.06
$\Phi_1[\Phi_2].\text{Sex } \Phi_3[\Phi_{a(4-13)}]+\text{Sex}$	26	6425.24	2.36
$[\Phi_1\Phi_2].\text{Sex } \Phi_3[\Phi_{a(4-13)}]+\text{Sex}$	27	6425.35	2.47
$\Phi_1[\Phi_2].\text{Sex } \Phi_3[\Phi_{a(4-13)}].\text{Sex}$	27	6426.61	3.73
$\Phi_1[\Phi_2\Phi_3].\text{Sex } [\Phi_{a(4-13)}]+\text{Sex}$	27	6426.81	3.93
$[\Phi_1\Phi_2\Phi_3].\text{Sex } [\Phi_{a(4-13)}]+\text{Sex}$	28	6427.46	4.58
$\Phi_1[\Phi_2\Phi_3\Phi_{a(4-13)}].\text{Sex}$	28	6428.38	5.50

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452 **Figure legends**

453 **Figure 1.** Age-specific survival for the wild boar population of Castelporziano, Italy (grey for
454 females, black for males). Filled circles display the estimates from the full age-dependent
455 model (with standard errors). The line corresponds to the selected model involving a linear
456 decrease (on a logit-scale) of survival from 3 years old onwards. Numbers denote wild boars
457 captured for last time in each age class.

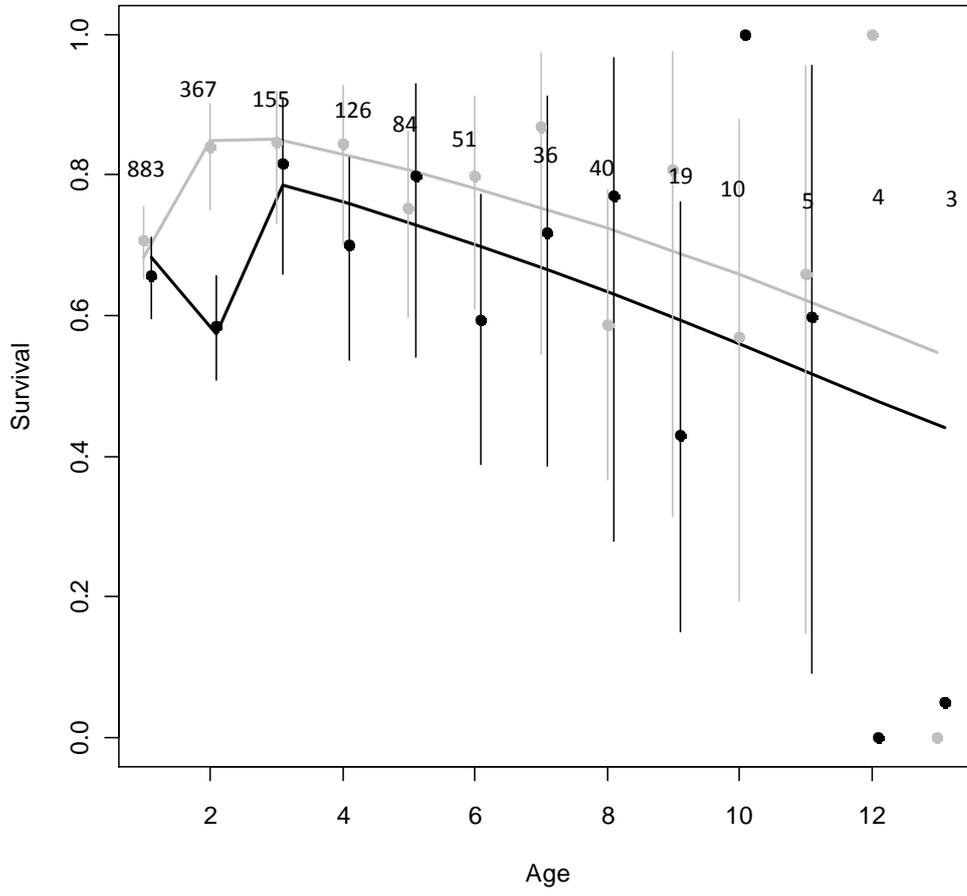
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459 **Figure 2.** Relationship between log-transformed mortality rates and age in the wild boar
460 population of Castelporziano, Italy (grey for females, black for males).

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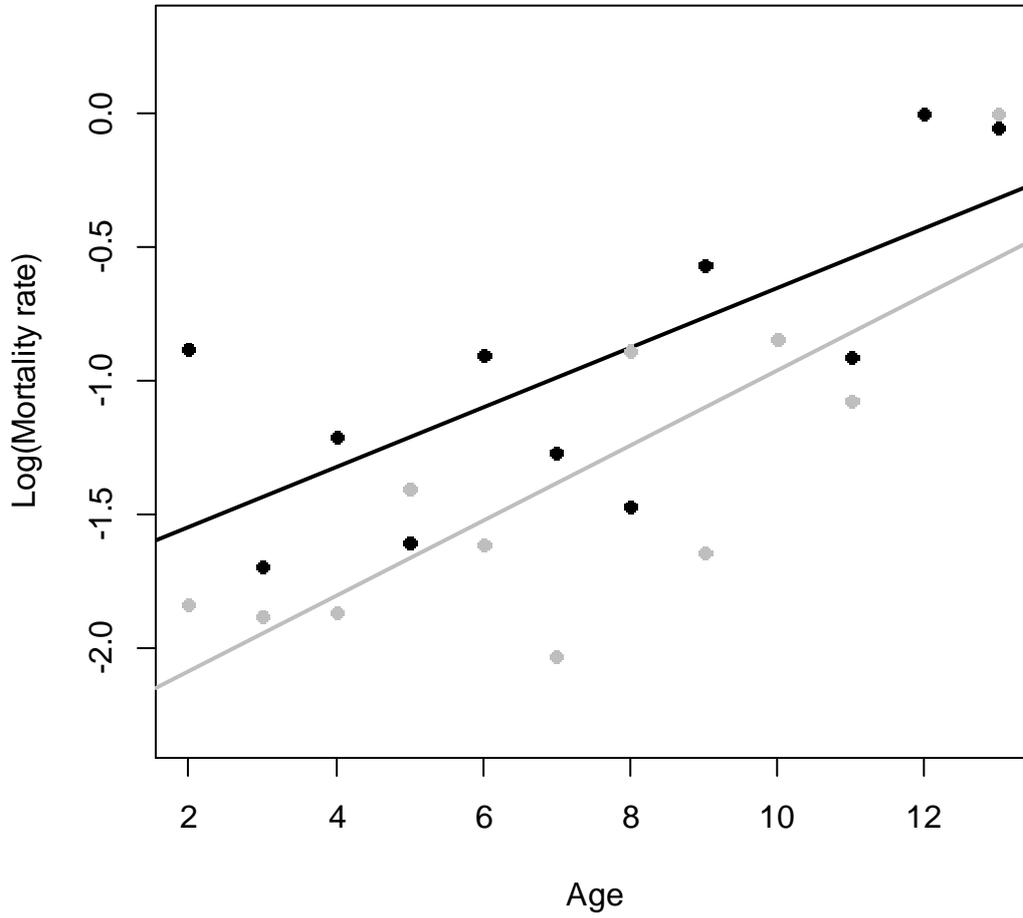
462 **Figure 3.** Relationships **(a)** between senescence rates and body mass (in g) (on a log-log
463 scale) and **(b)** between onsets of senescence (in years) and body mass (in g) (on a log-log
464 scale) for females in populations belonging to 7 different ungulate species (values obtained
465 from Gaillard et al. 2003 and Péron et al. 2010) for 1- *Antilocapra americana* at Montana
466 (USA), 2- *Capra ibex*, at Belledone (France), 3- *Capreolus capreolus* at Trois-Fontaines
467 (France), 4- *Capreolus capreolus* at Chizé (France), 5- *Oreamnos americanus* at Caw Ridge
468 (Canada), 6- *Ovis canadensis* at Sheep River (Canada), 7- *Ovis canadensis* at Ram Mountain
469 (Canada), 8- *Cervus elaphus* at Rum (Scotland), 9- *Rupicapra pyrenaica* at Orly (France). The
470 observed values for wild boar females (from this study, red circle, not included in the
471 allometric relationship) and the expected values for wild boar from the allometric relationship
472 (red square) are displayed. The comparison shows that wild boar females have a rate of
473 senescence close to the expectation, but a much earlier onset of senescence.

474 **Figure 1.**



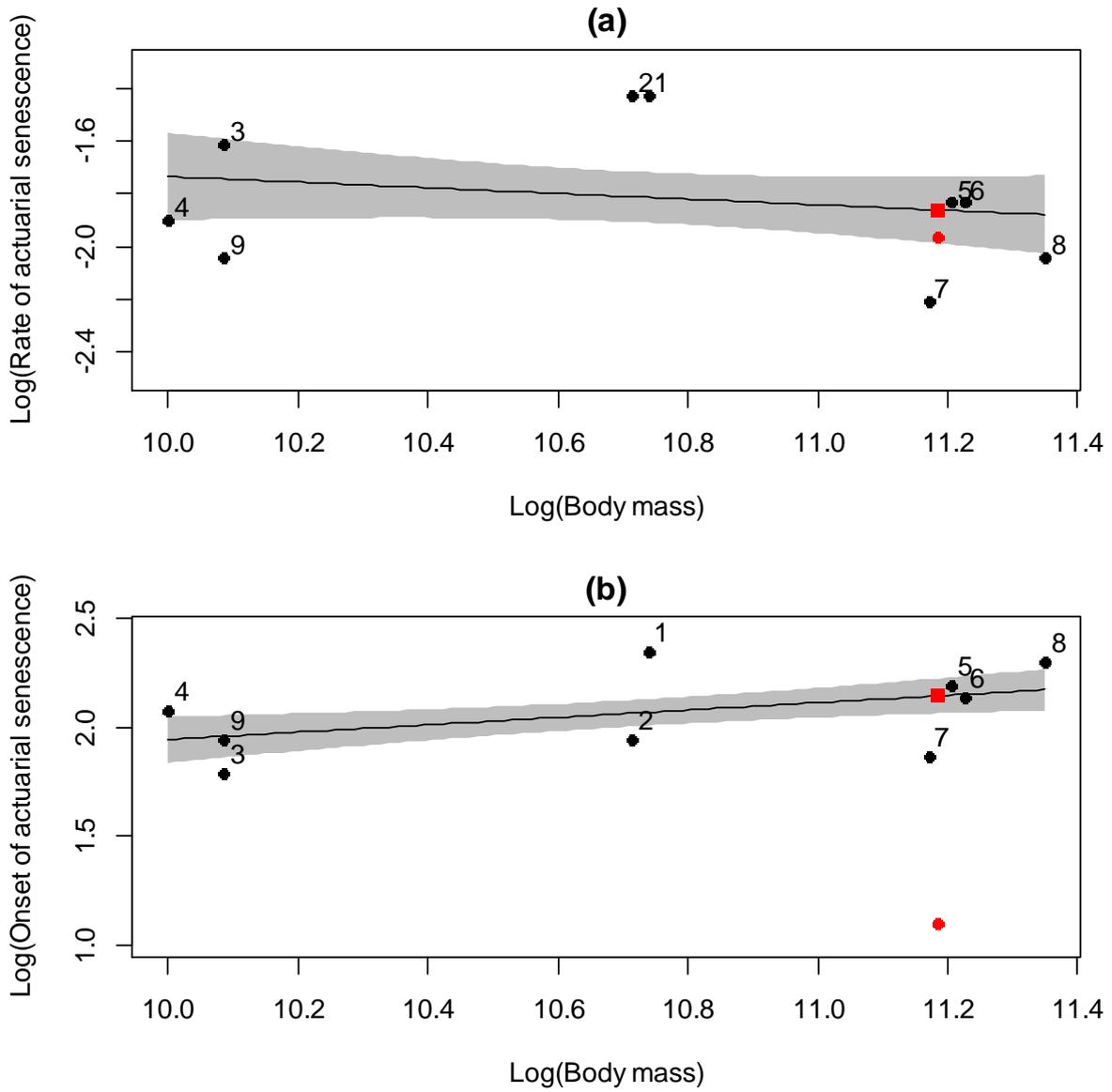
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476 **Figure 2.**



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478 **Figure 3.**



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