1 **Do age-specific survival patterns of wild boar fit current evolutionary**

2 **theories of senescence?**

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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.

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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.

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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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Materials and methods

STUDY SITE AND DATA COLLECTION

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

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

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

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

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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**
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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 ($\lambda_{rate} < 0.0001$ and $\lambda_{onset} < 0.0001$), 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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ESTIMATING AGE-SPECIFIC SURVIVAL, RATE AND ONSET OF SENESCENCE IN MALE AND FEMALE WILD BOAR

By only including individuals first captured as juveniles, the GOF test indicated some lack of fit for both sexes (global test: for male juveniles: χ^2 (61) = 102.743, P < 0.0001; for female juveniles: χ^2 (72) = 128.411, P < 0.0001). More precisely, trap-dependence was detected for both sexes and accounted for in the model. On the contrary, the GOF test indicated no lack of fit for individuals first captured as yearlings (global test: for males: χ^2 (27) = 31.273, P = 0.260; for females: χ^2 (33) = 27.575, P = 0.734). Tested models thus satisfactorily fitted data when trap-dependence was included in capture probabilities of juveniles.

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

To compare senescence rates between wild boar and similar-sized ungulates, senescence rates were re-estimated using the linear regression between mortality rates (on a log scale) and age. These rates exactly correspond to the Gompertz rates (i.e. the exponential rate of increasing mortality with age) and slightly differ from the rates estimated directly from analyses provided above (which do not exactly correspond to Gompertz rates, Loison et al. 1999). After removing survival rates at 10 and 12 years old for males and females, respectively, estimated on the bounds of the interval [0, 1] (see Fig. 1), we found evidence of 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.

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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 (Toïgo 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.

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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.

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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 (ΔAIC).

Model notation	Np	AIC	ΔAIC

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

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Figure legends

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

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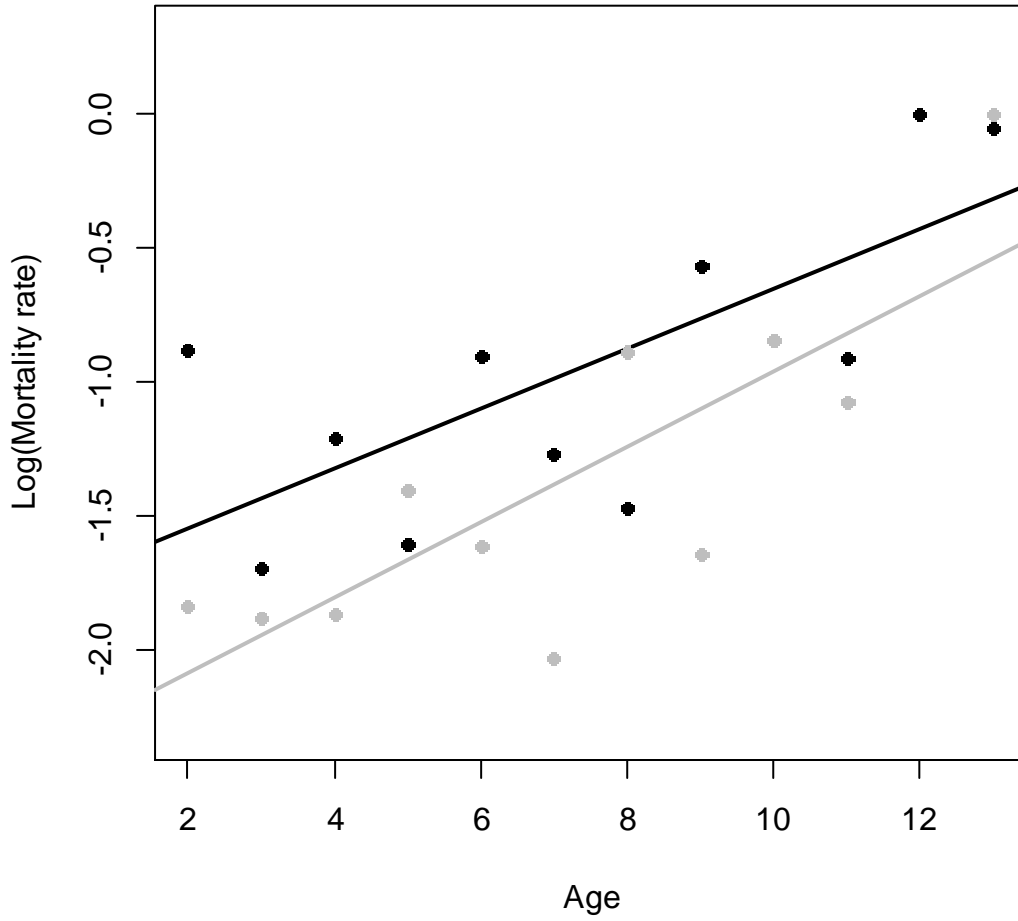
Figure 3. Relationships **(a)** between senescence rates and body mass (in g) (on a log-log scale) and **(b)** between onsets of senescence (in years) and body mass (in g) (on a log-log scale) for females in populations belonging to 7 different ungulate species (values obtained from Gaillard et al. 2003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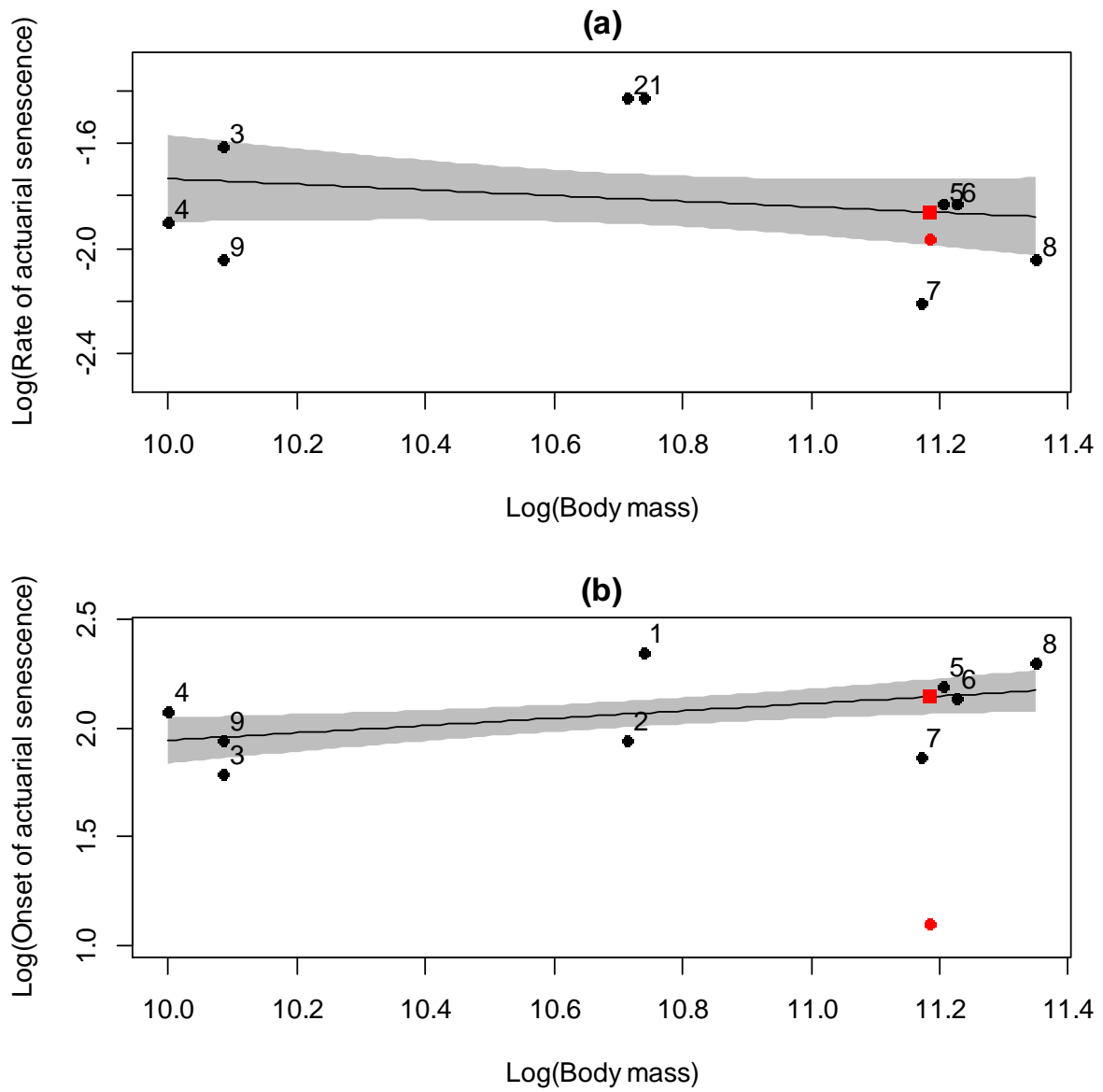
474   **Figure 1.**
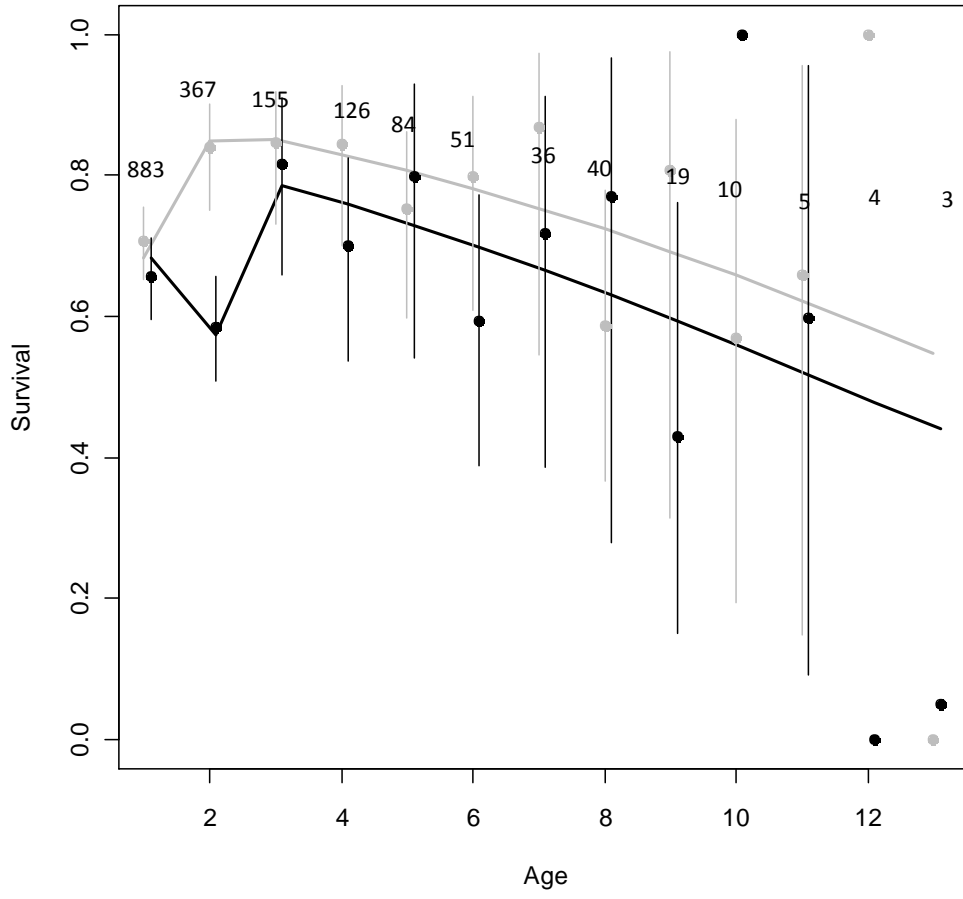
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476 **Figure 2.**

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478 **Figure 3.**

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