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

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

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

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

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

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

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 SENESENCE 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

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

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

SURVIVAL PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED UNGULATES

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

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

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

Results

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: $\chi^2(61) = 102.743$, $P < 0.0001$; for female juveniles: $\chi^2(72) = 128.411$, $P < 0.0001$). 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: $\chi^2(27) = 31.273$, $P = 0.260$; for females: $\chi^2(33) = 27.575$, $P = 0.734$). 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 ($\Phi_{age1} = 0.68 [0.64; 0.72]$), 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 -

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

SURVIVAL PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED UNGULATES

As expected, across ungulate species, the senescence rate tended to decrease (slope: -
0.11, SE: 0.18) and the onset of senescence to be delayed (slope: 0.17, SE: 0.12) when body
mass increased (Fig. 3). From the relationship between senescence rate and body mass (on a
log-log scale) performed using 9 populations belonging to 7 different species, the expected
rate of senescence for wild boar females was similar to the expectation (expected value of
0.16 vs. observed value of 0.14, Fig. 3a). On the other hand, the onset of senescence was
much earlier than expected. From the relationship between the onset of senescence and body
mass (on a log-log scale), the expected value was 8.56 years, whereas it was estimated to only
3 years in our analysis (Fig. 3b). Wild boar females had thus markedly earlier, but not stronger
senescence (Fig. 3) for their body size compared to other ungulates.

Discussion

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

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

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

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

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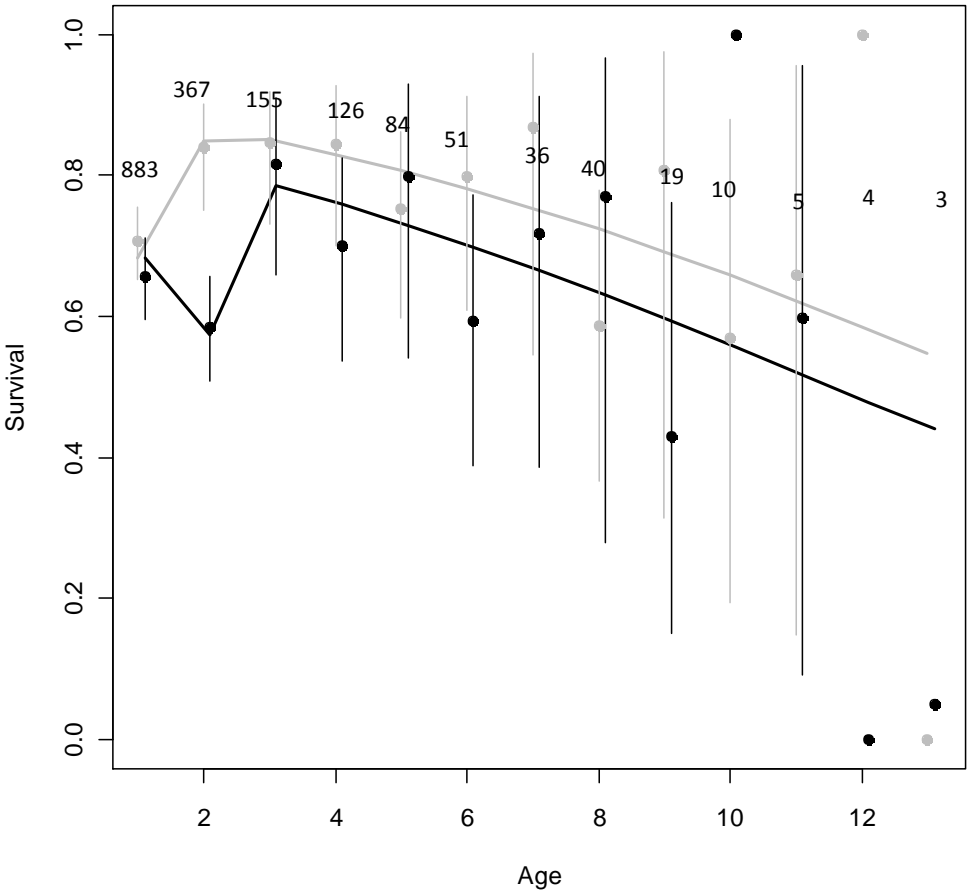
Figure legends

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).

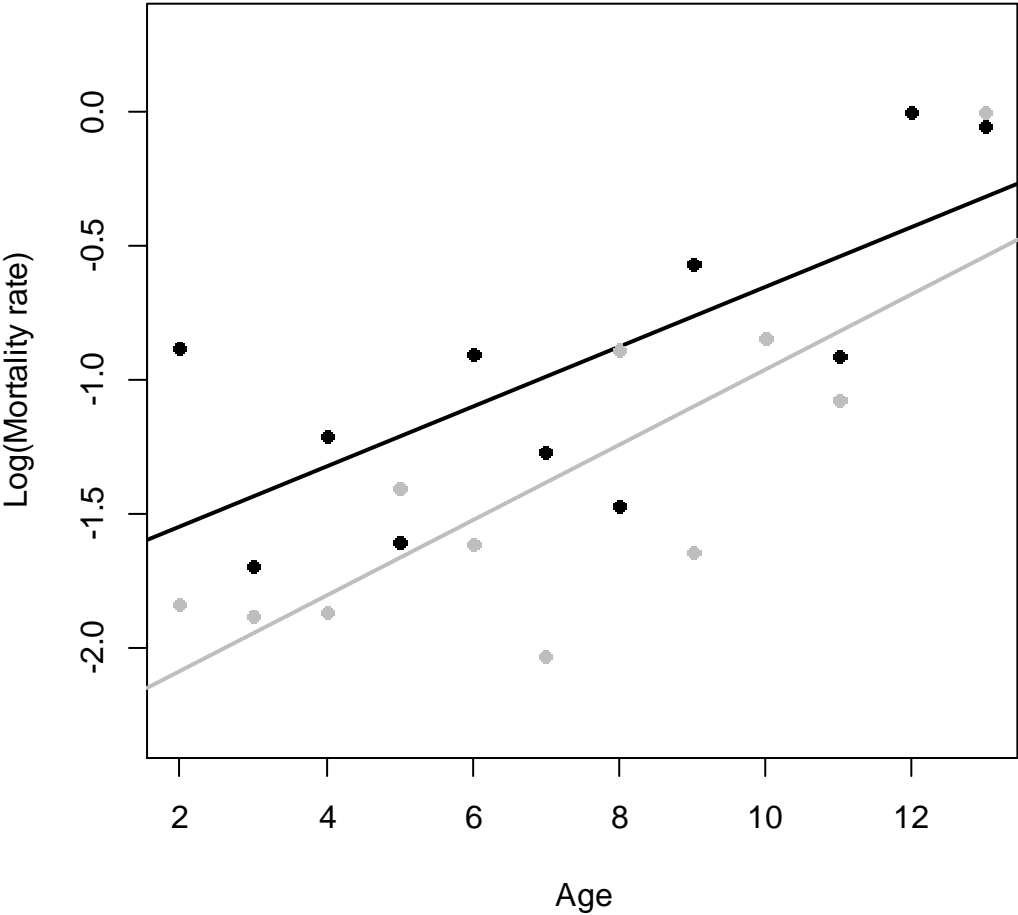
Figure 3. Relationships **(a)** between senescence rates and body mass (in g) (on a log-log scale) and **(b)** between onsets of senescence (in years) and body mass (in g) (on a log-log scale) for females in populations belonging to 7 different ungulate species (values obtained from Gaillard et al. 2003 and Péron et al. 2010) for 1- *Antilocapra americana* at Montana (USA), 2- *Capra ibex*, at Belledune (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 Orly (France). The observed values for wild boar females (from this study, red circle, not included in the allometric 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.**



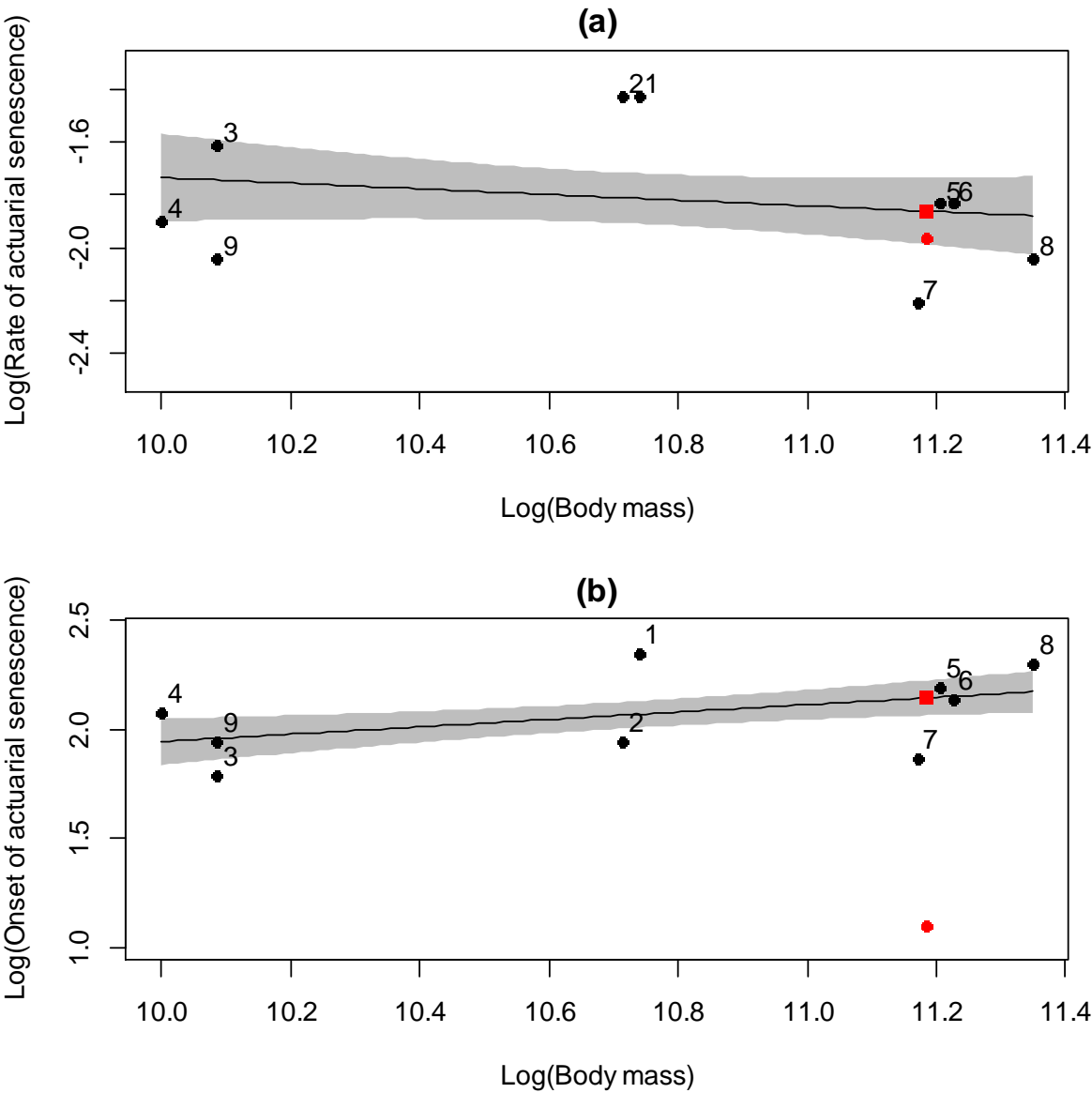
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476 **Figure 2.**



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478 **Figure 3.**



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