BRIEF COMMUNICATION

doi:10.1111/evo.12519

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

Marlène Gamelon,[1,2] Stefano Focardi,[3] Jean-Michel Gaillard,[4] Olivier Gimenez,[5] Christophe Bonenfant,[4] Barbara Franzetti,[6] Rémi Choquet,[5] Francesca Ronchi,[6] Eric Baubet,[7] and Jean-François Lemaître[4]

[1] *Department of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, N-7491 Trondheim, Norway*

[2] *E-mail: marlene.gamelon@ntnu.no*

[3] *Istituto per i Sistemi Complessi, CNR, via Madonna del Piano 10, 50019 Sesto Fiorentino, Italy*

[4] *Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, F-69622, Villeurbanne, France*

[5] *Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, Campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France*

[6] *Istituto Superiore per la Protezione e la Ricerca Ambientale, Via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia, Bologna, Italy*

[7] *Office National de la Chasse et de la Faune Sauvage, 2 Bis Rue des Religieuses, BP 19, 52120 Châteauvillain, France*

Received February 27, 2014
Accepted August 12, 2014

Actuarial senescence is widespread 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 overcompensated 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*) females have an unusual life-history strategy among large mammals by associating both early and high reproductive effort with potentially long lifespan. Therefore, wild boar females 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. Using a long-term monitoring (18 years) of a wild boar population, 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. Both sexes displayed similar senescence rates. Our study indicates that the timing of senescence, not the rate, 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.

KEY WORDS: Aging, capture–mark–recapture, fertility, life history, mortality, *Sus scrofa*.

To understand aging in the light of the evolutionary theory, Medawar (1952) proposed more than 60 years ago that actuarial senescence (hereafter senescence), defined as the decline of survival with increasing age, originated from the decline of the forces of natural selection with age in growing age-structured populations. This idea was later expanded by Williams (1957), who suggested that genes with deleterious effects in late life could be selected if they increase fitness at an earlier stage. Finally, Hamilton (1966) predicted that high fertility rates should be associated with high rates of senescence: "The model shows

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

that higher fertility will be a primary factor leading to the evolution of higher rates of senescence" (see Hamilton 1966, p. 12). Hamilton mathematically demonstrated that senescence is "an inevitable outcome of evolution in age-structured populations." The relative input of these three theories has rapidly been merged into a unique theoretical framework to explain why organisms show senescence, which is commonly entitled the Medawar–Williams–Hamilton theory of aging. Although the generality of an inevitable senescence is questionable outside age-structured populations (Vaupel et al. 2004; Caswell and Salguero-Gomez 2013; see also Jones et al. 2014 for empirical studies of species exhibiting negligible or even negative senescence), senescence has been repeatedly documented in wild species of vertebrates (see Nussey et al. 2013 for a review). However, empirical evidence has become available only recently, thanks to the development of long-term individual monitoring of known-aged animals (Clutton-Brock and Sheldon 2010).

Until now, intraspecific studies have provided good evidence for a relationship between early allocation to reproduction and fitness-related traits, such as survival (e.g., Boonekamp et al. 2014) and components of reproductive success (e.g., Nussey et al. 2006) in late life, in line with the disposable soma theory of aging (Kirkwood 1977; Kirkwood and Austad 2000). 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). However, no study has tested yet the prediction issued from our current evolutionary theory of senescence that actuarial senescence is more intense in species for which females exhibit high reproductive effort. In their major contribution, Medawar (1952), Williams (1957), and Hamilton (1966) limited their theoretical predictions to the rate of senescence, assuming that the age at the onset of senescence was immutably set at the first reproduction. This probably explains why most empirical studies performed to date have exclusively focused on changes in senescence rates. In contrast, putative changes in the age of onset of senescence and the factors underlying this variability have remained poorly investigated (but see Jones et al. 2008; Péron et al. 2010). However, recent evidence suggests that the age at the onset of senescence in free-ranging populations can be delayed according to the breeding effort during early life (Hammers et al. 2013). We thus explicitly tested the hypothesis that high female fertility was associated with an earlier onset of senescence, in addition to considering the senescence rate.

Moreover, empirical evidence that females live much longer than males in most mammals studied so far is compelling (Carey and Judge 2000). However, whether and how age-specific trajectories differ between sexes remains an open question (Maklakov and Lummaa 2013; Nussey et al. 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. Indeed, starvation and antagonistic 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 2012) and should therefore have higher senescence rate than females.

Using an 18-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 an unusual association between strong sexual-size dimorphism and high female fertility (Carranza 1996). Indeed, compared to similar-sized ungulates, wild boar females give birth for the first time earlier (less than one when intensively hunted vs. two to three years of age, Gethöffer et al. 2007), 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 our current evolutionary theory of senescence, wild boar females should show faster senescence than 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 wild boar population in the 6000 ha fenced preserve of Castelporziano (41°44′N, 12°24′E) in Italy (Focardi et al. 2008). From 1995 to 2012, a total of 1783 juvenile (less than one year of age) and yearling (one to two years old) wild boars were marked (930 males and 853 females) 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 to 88 feeding sites (Franzetti et al. 2012) to allow counts and identification of marked animals from year to year. In addition to weak hunting efforts to control population size, some individuals were randomly removed from the forest and released outside the study area.

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. Of the 1783 animals monitored throughout the studied period, 280 (133 males and 147 females) were removed under population control plans (i.e., killed by hunting or removed from the forest) and right-censored to allow estimating natural survival. As the preserve was fenced, no dispersal occurred so that true survival was estimated.

We started by testing the goodness-of-fit (GOF, Pradel et al. 2005) of the survival models using U-CARE (Choquet et al. 2009a). Because ignoring heterogeneity of detection could lead to biased estimates of the rate of senescence (see Gimenez et al. 2008 for a case study on roe deer, *Capreolus capreolus*), we accounted for heterogeneity in the detection process of juveniles (see Results) by modeling two different recapture probabilities according to whether an individual was previously detected (trap dependence: 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 allowing estimating a survival rate p per age x. From the latter, age-specific mortality rates were calculated as $q(x) = 1 - p(x)$. Although the Gompertz law of mortality refers to age-specific force of mortality ($\mu(x)$) rather than to age-specific mortality rates $q(x)$, we measured the rate of senescence as the slope of the regression of log-transformed age-specific mortality rates on age. Using $q(x)$ allowed us a direct comparison with the exponential rate of increasing mortality with age previously published in ungulates (Gaillard et al. 2003). Indeed, senescence rates in that study were estimated as the slope of the linear regression between mortality rates (on a log-scale) and age. According to the current evolutionary theory of senescence, the age at the onset of senescence should correspond to the age at first reproduction (Williams 1957; Hamilton 1966). To avoid confounding effects of growth or reproduction on age-specific survival, we analyzed wild boar female survival from two years of age onward, when growth has been completed and sexual maturity has been reached (Servanty et al. 2011). Considering the pronounced growth between two and three years of age in male wild boar (>30 kg, Konjevic et al. 2008) and that males in similar-sized polygynous and dimorphic ungulates do not usually reproduce before three years of age (Festa-Bianchet 2012), we used three years as the first age at reproduction in male wild boar.

We tested the validity of such assessment by estimating the age at the onset of senescence from the survival data. To do that, 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 then 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 in rates 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).

Table 1. **Model selection for age-specific survival patterns in the wild boar population of Castelporziano, Italy.**

Model notation	Np	AIC	ΔAIC
$\Phi_1[\Phi_2]$.Sex $[\Phi_{(3–13)}]$+Sex	25	6422.88	0.00
$[\Phi_1\Phi_2]$.Sex $[\Phi_{(3–13)}]$+Sex	26	6423.06	0.18
$\Phi_1[\Phi_2\ \Phi_{(3–13)}]$.Sex	26	6424.74	1.86
$[\Phi_1\Phi_2\Phi_{(3–13)}]$.Sex	27	6424.94	2.06
$\Phi_1[\Phi_2]$.Sex $\Phi_3[\Phi_{(4–13)}]$+Sex	26	6425.24	2.36
$[\Phi_1\Phi_2]$.Sex $\Phi_3[\Phi_{(4–13)}]$+Sex	27	6425.35	2.47
$\Phi_1[\Phi_2]$.Sex $\Phi_3[\Phi_{(4–13)}]$.Sex	27	6426.61	3.73
$\Phi_1[\Phi_2\Phi_3]$.Sex $[\Phi_{(4–13)}]$+Sex	27	6426.81	3.93
$[\Phi_1\Phi_2\Phi_3]$.Sex $[\Phi_{(4–13)}]$+Sex	28	6426.98	4.10
$\Phi_1[\Phi_2\Phi_3\Phi_{(4–13)}]$.Sex	28	6428.38	5.50

$\Phi_{(x\text{-}13)}$ corresponds to a linear relationship (on a logit-scale) between age and survival from *x* years of age. The brackets "[]" correspond to the ages when the sex effect has been applied. Displayed are the number of parameters (Np), the AIC of the 10 best models, and the difference between each tested model and the best one (ΔAIC).

SENESCENCE PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED UNGULATES

To test whether wild boar females show faster senescence than reported for similar-sized ungulates, we accounted for the confounding allometric effects of body mass. Allometric effects shape most observed variation in life-history traits (notably senescence, Ricklefs 2010) among species (Peters 1983; Calder 1984), including vertebrates (Gaillard et al. 1989) and mammals (Stearns 1983). We thus assessed the relationship (on a log-scale) between senescence rate and female body mass. We also assessed the relationship (on a log-scale) between onset of senescence and female body mass of similar-sized ungulates. Wild boar females are outliers compared to other ungulates in terms of reproductive effort (Focardi et al. 2008; Servanty et al. 2009; Gamelon et al. 2013). Based on this assessment, we tested whether wild boar females have, or not, faster senescence than similar-sized ungulates.

Females of nine intensively monitored populations belonging to seven ungulate species were included in the analysis, namely pronghorn (*Antilocapra americana*), Alpine ibex (*Capra ibex*), roe deer, mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), red deer (*Cervus elaphus*), and Pyrenean chamois (*Rupicapra pyrenaica*). Patterns of senescence across species should not be independent as a result of shared ancestry (Harvey and Pagel 1991). We thus controlled for this non-independence by using Phylogenetic Generalized Least-Squares (PGLS) models that provide an index of the phylogenetic signal called "λ" (varying in most cases between 0 in the complete absence of a phylogenetic signal and 1 when a strong phylogenetic signal occurs; see Freckleton et al. 2002). This parameter λ was then introduced in the model to account for the phylogenetic effect (Freckleton et al. 2002). We used the phylogeny derived from the phylogenetic super-tree 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 to body mass (all 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.

We conducted interspecific analyses linking senescence rate and onset of senescence to female body mass using standard linear models to avoid biased estimates (Revell 2010). To account for uncertainty in the response variable, we weighted the regression linking senescence rate and female body mass by the inverse of the estimated variance of senescence rate. Likewise, we weighted the regression linking onset of senescence and female body mass by the inverse of the estimated variance of onset of senescence. Senescence rates and their associated variances were extracted from Gaillard et al.'s (2003) study and onsets of senescence and their associated variances from Péron et al.'s (2010) study. From these linear models, expected rate and onset of senescence of wild boar females were estimated and compared with rates and onsets estimated in populations of other ungulates.

By correcting for reproductive effort, we expect senescence patterns of wild boar to be in line with those of other ungulates. We thus replicated the analyses detailed above by including fecundity in addition to female body mass as factors of variation in senescence metrics. As fecundity corresponds to the product of the number of litters per year with litter size (Allainé et al. 1987), and as all ungulate species considered here produced only one litter per year, we used litter size (on a log-scale) as a continuous measure of fecundity. 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

The GOF test indicated trap dependence for individuals of both sexes first captured as juveniles (global test: for male juveniles: χ^2 (61) = 102.743, $P < 0.0001$; for female juveniles: χ^2 (72) = 128.411, $P < 0.0001$). Thus, we accounted for trap dependence in the models. In contrast, 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, $P = 0.734$).

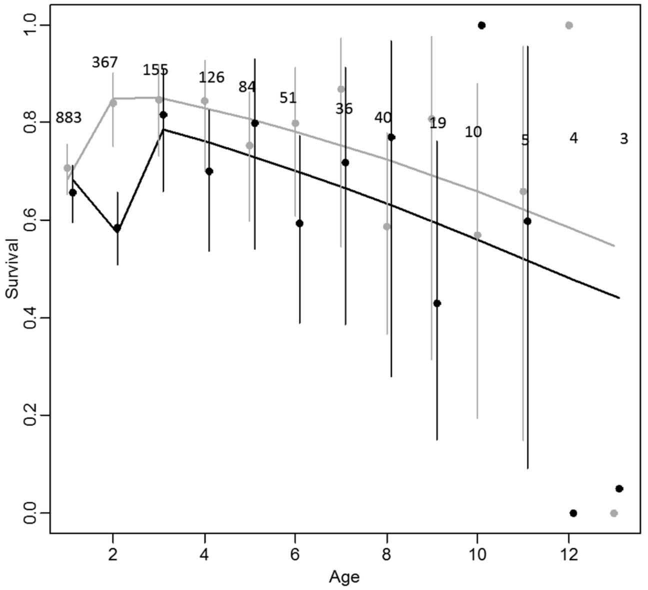

Figure 1. Sex- and age-specific survival of wild boar at Castelporziano, Italy (gray for females, black for males). Filled circles display the estimates from the full age-dependent model (with standard errors). The line corresponds to the selected model involving a linear decrease (on a logit-scale) of survival from three years old onward. To improve plot readability, data for males and females were shifted. Numbers denote wild boars captured for the last time in each age class.

The best model included marked between-sex differences at age 2 (Fig. 1), a linear relationship between survival and age from three years old onward, and year-dependent probabilities of capture (Table 1). Males and females had the same survival at age 1 (0.68 [0.64; 0.72]), but males survived substantially less than females at two years of age ($\Phi_{\text{male}} = 0.57$ [0.50; 0.64], $\Phi_{\text{female}} = 0.85$ [0.77; 0.91]). From three years old onwards, males consistently had lower survival than females (Fig. 1) but both sexes had similar senescence rates. Survival estimates from the selected model were remarkably similar to those obtained from model averaging performed using the top nine models (Table 1). The three oldest individuals were 13 years of age and only 22 of the 1783 individuals reached the age 10 (Fig. 1). The model that only included between-sex differences (i.e., no age effect) on survival (Φ.Sex) received no support (ΔAIC of 24.01).

To compare wild boar with similar-sized ungulates, senescence rates were reestimated using the linear regression between

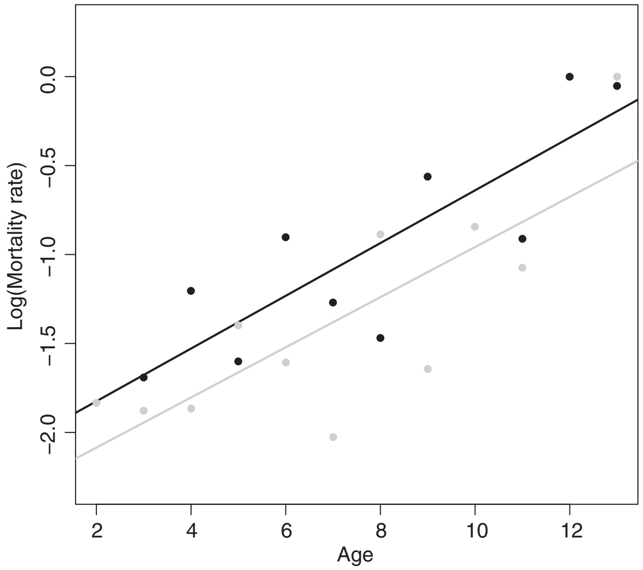

Figure 2. Relationship between log-transformed mortality rates and age in the wild boar population at Castelporziano, Italy (gray for females, black for males).

mortality rates (on a log-scale) and age from two years of age onward for females and from three years of age onward for males. After removing survival rates at 10 and 12 years old for males and females, respectively, which were estimated on the bounds of the interval [0, 1] (see Fig. 1), we found clear evidence of actuarial senescence in both sexes (rates of 0.15 [SE: 0.03] for males [Wald test: 19.6, $P < 0.0001$] and 0.14 [SE: 0.04] for females [Wald test: 16.0, $P < 0.0001$], Fig. 2), with no detectable between-sex difference (Wald test: 0.15, $P = 0.88$). It is noteworthy that using an onset of actuarial senescence ranging between three and six years of age in males and/or females (instead of two in females and three in males) led to similar estimates of senescence rates and to an absence of between-sex differences (results not shown here).

SENESCENCE PATTERNS OF WILD BOAR COMPARED TO SIMILAR-SIZED UNGULATES

As expected, across ungulate species, the senescence rate tended to decrease (slope: −0.10, SE: 0.25) and the onset of senescence was delayed (slope: 0.42, SE: 0.03) when body mass increased. From the relationship between senescence rate and body mass (on a log–log scale) performed using nine populations belonging to seven species, the rate of senescence observed for wild boar females was similar to the expectation (an observed value of 0.14 vs. an expected value of 0.18), whereas the onset of senescence occurred much earlier than expected (three vs. 9.08 years).

As expected, once litter size had been accounted for, the senescence rate increased with the litter size (slope: 0.78, SE: 0.26) and there was no variation in senescence rate across ungulates when body mass increased (slope: 0.02, SE: 0.18; Fig. 3A). The senescence rate observed for wild boar females was similar to the expectation (an observed value of 0.14 vs. an expected value of 0.17; Fig. 3A). Given its litter size, wild boar should even exhibit higher senescence rate than actually had (star, Fig. 3A), meaning that the senescence rate did not increase in response to the high reproductive output. Once litter size had been accounted for, the onset of senescence was delayed when body mass increased (slope: 0.46, SE: 0.06; Fig. 3B). Onset of senescence tended to be also delayed when litter size increased (slope: 0.13, SE: 0.17), highlighting no support for an earlier onset of senescence with increasing litter size. This absence of effect of litter size on the onset of senescence could be due to the small range of observed litter sizes (from 1 for *Ovis canadensis* to 2 for *Antilocapra americana*). These results highlight that a threshold litter size has likely to be reached before an effect on the onset of reproduction (i.e., an earlier onset of senescence) could be detected. The onset of senescence observed for wild boar females occurred much earlier than expected, once confounding effects of litter size have been accounted for (an observed value of three years vs. an expected value of 9.23 years; Fig. 3B). Wild boar females had thus markedly earlier, but not stronger, actuarial senescence 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 interspecific test of the Medawar–Williams–Hamilton's prediction, our findings show that wild boar females have earlier, but not stronger, senescence than females from related species once the confounding effects of body size have been accounted for. Indeed, our findings emphasize that the high reproductive output of wild boar females (with litter size up to 14, Servanty et al. 2007) is associated with earlier, but not stronger, decline in survival with age. As the Medawar–Williams–Hamilton's evolutionary theory of senescence was strictly focused on variation in 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 age from which the decline of the forces of natural selection occurs, which indicates that the timing of senescence, in addition to the rate, constitutes a key component of the theory of senescence. We thus propose to expand the classical theory to include potential responses of the timing of senescence to increased fertility,

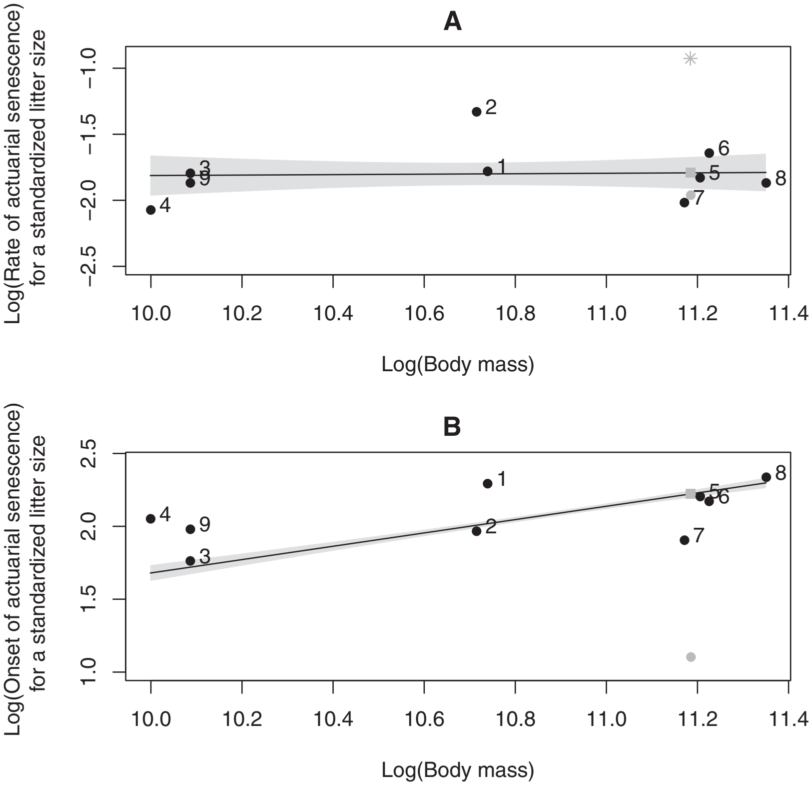

Figure 3. **Relationships between (A) senescence rates for a standardized litter size and body mass (in grams) (on a log–log scale) and (B) onsets of senescence (in years) for a standardized litter size and body mass (in grams, on a log–log scale) for females in populations belonging to seven ungulate 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 fitted lines are plotted for the average log-scaled litter size of the dataset. The observed values for wild boar females (from this study, gray circles, not included in the allometric relationship) and the expected values for wild boar from the allometric relationship (gray squares) are displayed. The expected value for wild boar accounting for the positive effect of litter size on senescence rate was symbolized by a gray star (using a litter size of 3.74, from Servanty et al. 2011). The comparison shows that wild boar females have a rate of senescence close to the expectation, but a much earlier onset of actuarial senescence.**

by considering both the timing and the intensity of senescence patterns to test reliably evolutionary theories of aging.

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 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 than females at all ages from two years onward, 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 2012) or to the occurrence of harsh environmental conditions in the study site. Indeed, harsh environments are more likely to influence male than female survival (Toïgo and Gaillard 2003). However, in wild boar, the differential mortality suffered by males does 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 noteworthy that similar patterns have been reported in humans (Austad 2011). In both wild boar and humans, between-sex differences in adult mortality were quite weak (about 10%), which might not be enough to trigger substantial between-sex differences in the decline of Hamilton's forces of selection with age.

Alternatively, it has been recently suggested that condition-dependent mortality can be sex-specific, notably in species in which males and females differ in their reproductive optima (Bonduriansky et al. 2008; Maklakov and Lummaa 2013). In a sexually dimorphic species such as wild boar (Delgado et al. 2008), that could account for the absence of sex differences in actuarial senescence we reported. Basically, when the source of mortality is random, all animals in the population have the same probability of dying, independently of their individual phenotype. In contrast, when mortality is condition dependent, the probability of dying acts as a filter in the population by removing the weakest individuals, which ultimately decreases the intensity of senescence at the population level (Vaupel et al. 1979). Whether mortality at two years of age is condition dependent in wild boar males remains to be carefully explored but we expect stronger condition-dependence in survival of males compared to females. Indeed, males are most costly to raise by mothers in highly polygynous and sexually dimorphic species such as wild boar (Trivers and Willard 1973). Therefore, the absence of sex differences in senescence rates we report in wild boar could be a demographic response to sex-specific condition-dependent mortality in early life.

The critical role of mortality sources in shaping various aging trajectories is now widely accepted (Williams and Day 2003; Abrams 2004; Williams et al. 2006). They include both a viability selection having consequences at the population level (demographic response) and microevolutionary processes spanning over several generations leading to select the most robust individuals (evolutionary response). For instance, an experimental evolutionary study on wild type derived nematodes (*Caenorhabditis remanei*) has shown that high rates of condition-dependent mortality promote a deceleration of aging and longer lifespan, independently of sex, within only 12 generations (Chen and Maklakov 2012; Chen et al. 2013). The twofold higher mortality rate of male wild boar at two years of age compared to females might provide the potential filter to keep the best phenotypes at old ages only in males. However, whether this demographic response also involves evolutionary changes through a selection for divergent aging trajectories between the sexes in wild boar remains currently unknown. Overall, our findings stress the importance of investigating the sex-specific sources of mortality that can affect individuals in the wild, which should in the near future greatly improve our understanding of the diversity of senescence patterns in the wild.

ACKNOWLEDGMENTS

We warmly thank A. Maklakov and two anonymous referees for their helpful and constructive comments that markedly improved our article. We thank the Segretariato per la Presidenza della Repubblica for allowing the study at Castelporziano, for its financial support and the data availability.

LITERATURE CITED

Abrams, P. A. 2004. Mortality and lifespan. Nature 431:1048–1049.

Allainé, D., D. Pontier, J. M. Gaillard, J. D. Lebreton, J. Trouvilliez, and J. Clobert. 1987. The relationship between fecundity and adult body weight in homeotherms. Oecologia 73:478–480.

Austad, S. N. 2011. Sex differences in longevity and aging. Pp. 479–495 *in* E. J. Masoro and S. N. Austad, eds. Handbook of the biology of aging. Academic Press, San Diego, CA.

Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. Nature 446:507–512.

Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. Funct. Ecol. 22:443–453.

Boonekamp, J. J., M. Salomons, S. Bouwhuis, C. Dijkstra, and S. Verhulst. 2014. Reproductive effort accelerates actuarial senescence in wild birds: an experimental study. Ecol. Lett. 17:599–605.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Verlag, New York.

Calder, W. A. 1984. Size, function, and life history. Harvard Univ. Press, Cambridge, MA.

Carey, J. R., and D. S. Judge. 2000. Longevity records: life spans of mammals, birds, amphibians, reptiles and fish. Odense Univ. Press, Odense.

Carranza, J. 1996. Sexual selection for male body mass and the evolution of litter size in mammals. Am. Nat. 148:81–100.

Caswell, H., and R. Salguero-Gomez. 2013. Age, stage and senescence in plants. J. Ecol. 101:585–595.

Catchpole, Y. F., B. J. T. Morgan, T. H. Clutton-Brock, and T. Coulson. 2004. Dimorphism, survival and dispersal in red deer. JABES 9:1–26.

Chen, H., and A. A. Maklakov. 2012. Longer life span evolves under high rates of condition-dependent mortality. Curr. Biol. 22:2140–2143.

Chen, H., F. Zajitschek, and A. A. Maklakov. 2013. Why ageing stops: heterogeneity explains late-life mortality deceleration in nematodes. Biol. Lett. 9:20130217.

Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. Ecography 32:1071–1074.

Choquet, R., L. Rouan, and R. Pradel. 2009b. Program E-SURGE: a software application for fitting multievent models. Pp. 845–865 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, eds. Modeling demographic processes in marked populations. Vol. 3. Springer-Verlag, New York.

Clutton-Brock, T. H., and K. Isvaran. 2007. Sex differences in ageing in natural populations of vertebrates. Proc. R. Soc. B 274:3097–3104.

Clutton-Brock, T. H., and B.C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Tends Ecol. Evol. 25:562–573.

Delgado, R., P. Fernandez-Llario, M. Azevedo, A. Beja-Pereira, and P. Santos. 2008. Paternity assessment in free-ranging wild boar (*Sus scrofa*) – are littermates full-sibs? Mamm. Biol. 73:169–176.

Festa-Bianchet, M. 2012. The cost of trying: weak interspecific correlations among life-history components in male ungulates. Can. J. Zool. 90:1072–1085.

Focardi, S., J. M. Gaillard, F. Ronchi, and S. Rossi. 2008. Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. J. Mamm. 89:1113–1123.

Franzetti, B., F. Ronchi, F. Marini, M. Scacco, R. Calmanti, A. Calabrese, A. Paola, M. Paolo, and S. Focardi. 2012. Nocturnal line transect sampling of wild boar (*Sus scrofa*) in a Mediterranean forest: long-term comparison with capture-mark-resight population estimates. Eur. J. Wild. Res. 58:385–402.

Freckleton, R., P. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat. 160:712–726.

Gaillard, J. M., D. Pontier, D. Allainé, J. D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56:59–76.

Gaillard, J. M., D. Pontier, S. Brandt, J. M. Jullien, and D. Allaine. 1992. Sex differentiation in postnatal growth rate: a test in a wild boar population. Oecologia 90:167–171.

Gaillard, J. M., A. Loison, M. Festa-Bianchet, N. G. Yoccoz, and E. Solberg. 2003. Ecological correlates of life span in populations of large herbivorous mammals. Popul. Dev. Rev. 29:39–56.

Gamelon, M., J. M. Gaillard, E. Baubet, S. Devillard, L. Say, S. Brandt, and O. Gimenez. 2013. The relationship between phenotypic variation among offspring and mother body mass in wild boar: evidence of coin-flipping? J. Anim. Ecol. 82:937–945.

Gethöffer, F., G. Sodeikat, and K. Pohlmeyer. 2007. Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. Eur. J. Wildl. Res. 53:287–297.

Gimenez, O., A. Viallefont, A. Charmantier, R. Pradel, E. Cam, C. R. Brown, M. D. Anderson, M. B. Brown, R. Covas, and J. M. Gaillard. 2008. The risk of flawed inference in evolutionary studies when detectability is less than one. Am. Nat. 172:441–448.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. J. Theor. Biol. 12:12–45.

Hammers, M., D. S. Richardson, T. Burke, and J. Komdeur. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. J. Evol. Biol. 26:1999–2007.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, U.K.

Jones, O. R., J.-M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, and M. Charpentier. et al. 2008. Senescence rates are determined by ranking on the fast–slow life-history continuum. Ecol. Lett. 11:664–673.

Jones, O. R., A. Scheuerlein, R. Salguero-Gomez, C. G. Camarda, R. Schaible, B. B. Casper, J. P. Dahlgren, J. Ehrlen, M. B. Garcia, and E. S. Menges. et al. 2014. Diversity of ageing across the tree of life. Nature 505:169–173.

Kirkwood, T. B. L. 1977. Evolution of ageing. Nature 270:301–304.

Kirkwood, T. B. L., and S. N. Austad. 2000. Why do we age? Nature 408:233–238.

Konjevic, D., M. Grubesic, K. Severin, M. Hadziosmanovic, K. Tomljanovic, L. Kozacinski, Z. Janicki, and A. Slavica. 2008. Contribution to knowledge of body growth of wild boars in their plan habitats in the Republic of Croatia. Meso 10:385–389.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62:67–118.

Lemaître, J. F., and J. M. Gaillard. 2013. Male survival patterns do not depend on male allocation to sexual competition in large herbivores. Behav. Ecol. 24:421–428.

Loison, A., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and J. M. Jullien. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. Ecology 80:2539–2554.

Maklakov, A. A., and V. Lummaa. 2013. Evolution of sex differences in lifespan and aging: causes and constraints. Bioessays 35:717–724.

Medawar, P. B. 1952. An unsolved problem of biology. Lewis, Lond.

Nichols, J. D., J. E. Hines, and P. Blums. 1997. Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina*. Ecology 78:1009–1018.

Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie, and T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecol. Lett. 9:1342–1350.

Nussey, D. H., H. Froy, J. F. Lemaître, J. M. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Res. Rev. 12:214–225.

Péron, G., O. Gimenez, A. Charmantier, J. M. Gaillard, and P. A. Crochet. 2010. Age at onset of senescence in birds and mammals is predicted by early-life performance. Proc. R. Soc. B. 277:2849–2856.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge.

Pradel, R., and A. Sanz-Aguilar. 2012. Modeling trap-awareness and related phenomena in capture-recapture studies. PLOS One 7:e32666.

Pradel, R., O. Gimenez, and J. D. Lebreton. 2005. Principles and interest of GOF tests for multistate capture-recapture models. Anim. Biodivers. Conserv. 28:189–204.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L. J. 2010. Phylogenetic signal and linear regression on species data. Methods Ecol. Evol. 1:319–329.

Ricklefs, R. E. 2010. Life-history connections to rates of aging in terrestrial vertebrates. Proc. Natl. Acad. Sci. USA 107:10314–10319.

Servanty, S., J. M. Gaillard, D. Allainé, S. Brandt, and E. Baubet. 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behav. Ecol. 18:427–432.

Servanty, S., J. M. Gaillard, C. Toïgo, S. Brandt, and E. Baubet. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. J. Anim. Ecol. 78:1278–1290.

Servanty, S., J. M. Gaillard, F. Ronchi, S. Focardi, E. Baubet, and O. Gimenez. 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. J. Appl. Ecol. 48:835–843.

Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. Oikos 41:173–187.

Toïgo, C., and J. M. Gaillard. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos 101:376–384.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Vaupel, J. W., K. G. Manton, and E. Stallard. 1979. Impact of heterogeneity in individual frailty on the dynamics of mortality. Demography 16:439–454.

Vaupel, J. W., A. Baudisch, M. Dolling, D. A. Roach, and J. Gampe. 2004. The case for negative senescence. Theor. Popul. Biol. 65:339–351.

Vinogradov, A. E. 1998. Male reproductive strategy and decrease longevity. Acta Biotheor. 46:157–160.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398–411.

Williams, P. D., and T. Day. 2003. Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. Evolution 57:1478–1488.

Williams, P. D., T. Day, Q. Fletcher, and L. Rowe. 2006. The shaping of senescence in the wild. Trends Ecol. Evol. 21:458–463.

Associate Editor: A. Maklakov