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

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ABSTRACT (200 words)

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

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

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

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

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

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

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

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

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

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

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

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

Materials and methods

METRICS OF SURVIVAL AND ACTUARIAL SENESENCE

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

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

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

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

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

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

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

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

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

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

METRICS OF SEXUAL SELECTION

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

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

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

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

ACCOUNTING FOR POSSIBLE CONFOUNDING VARIABLES

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

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

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

STATISTICAL ANALYZES

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

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

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

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

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

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

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

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

Results

INFLUENCE OF SEXUAL SELECTION ON MALE LONGEVITY AND SENESCENCE PATTERNS

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

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

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

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

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

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

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

INFLUENCE OF SEXUAL SELECTION ON THE SEX-DIFFERENCES IN LONGEVITY AND SENESCENCE PATTERNS

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

N, number of species; PICs, Phylogenetically Independent contrasts; PGLS, PhyloGenetically Least Square models; SSD, Sexual Size Dimorphism; rLE, relative Life Expectancy.
* ratio calculated as M/F if M>F and 2-F/M if F>M, M and F denote male and female body mass respectively.

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

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

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

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

FIGURE LEGENDS:

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

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

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

Figure 1

Figure 2

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824 **Figure 3**