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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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In most mammals, both sexes display different survival patterns, often involving faster senescence in males. Being under intense sexual competition to secure mating opportunities, males of polygynous species allocate resources to costly behaviors and conspicuous sexual traits, which might explain these observed differences in longevity and senescence patterns. However, comparative studies performed to date have led to conflicting results. We aimed to resolve this problem by first reviewing case studies of the relationship between the strength of sexual selection and age-specific survival metrics. Then, we performed a comprehensive comparative analysis to test whether such relationships exist among species of captive ruminants. We found that the strength of sexual selection negatively influenced the onset of actuarial senescence in males, with males senescing earlier in polygynous than in monogamous species, which led to reduced male longevity in polygynous species. Moreover, males of territorial species senesced earlier but slower, and have a shorter longevity than males of species displaying other mating tactics. We detected little 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 a side effect of physiological mechanisms linked to sexual selection, and potentially accounts for observed differences in longevity.

KEY WORDS: Ageing, intrinsic physiological costs, mating system, ungulates.

Over the last two decades, demographic analyses based on long-term studies have demonstrated that actuarial senescence, a progressive decrease in survival with age (Monaghan et al. 2008), is almost a 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 (measured as the combination between the timing (onset) and strength (rate) of senescence) across the tree of life (Nussey et al. 2013; Jones et al. 2014), with species differences in survival patterns being generally driven by the pace of life (Jones et al. 2008), strongly associated with body mass (Calder 1984), phylogeny (Gaillard et al. 1989), habitat (Wiersma et al. 2007), and mode of reproduction (Müller et al. 2012).

Within species, the intensity of actuarial senescence also varies, especially according to sex (Clutton-Brock and Isvaran 2007; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014). For example, mammalian males generally live shorter and senesce faster than females in a given species (Ramp et al. 2010; Lemaître and Gaillard 2013a; but see Gamelon et al. 2014). The magnitude of such between-sex differences is assumed to be associated with the strength of sexual selection (Clutton-Brock and Isvaran 2007; Lemaître and Gaillard 2013a), which causes the evolution of traits and/or behaviors associated with mating success (Darwin 1859). Individuals from species subjected to strong sexual selection will generally experience high costs of production and maintenance of these sexually selected traits. These costs are paid in terms of reduced survival or reproduction (e.g., increased reproductive senescence for males controlling the largest harems in the polygynous red deer, *Cervus elaphus*; Lemaître et al. 2014a) in line with the evolutionary theories of ageing that predict a trade-off between reproduction in early life and somatic maintenance, and thereby survival or reproduction late in life (e.g., antagonistic pleiotropy or disposable soma theory; see Lemaître et al. 2015 for a review). In most mammalian species, the intensity of sexual selection is stronger in males than in females, whereas fathers generally allocate much less than mothers to the production (in terms of body mass gain) and rearing of offspring (Bateman 1948; Trivers 1972; Andersson 1994). Therefore, males can allocate much more than females to intraspecific sexual competition to obtain additional mating opportunities, thereby increasing their individual reproductive success. Males of species with low sexual competition will experience lower sexual selection pressure, might allocate less energy to reproduction and more to somatic maintenance, and thereby enjoy higher survival and lesser senescence than males of species heavily allocating in intrasexual competition (Bonduriansky et al. 2008). Sexual selection leads to the production and maintenance of costly sexual traits in males, which are likely to cause accelerated senescence and higher mortality, and thus increased between-sex differences in actuarial senescence (Williams 1957; Owens and Bennett 1994; Bonduriansky et al. 2008). We therefore expect a greater sex bias in the intensity of senescence, with an earlier timing (i.e., onset) and a stronger strength (i.e., rate) of actuarial senescence in males of species subjected to a high intensity of sexual competition.

The influence of the strength of sexual selection on survival patterns is a key topic of evolutionary biology that is currently highly debated. From a literature survey, we identified 11 studies on the link between sexual selection and survival patterns across species (Table 1), but only six of these provided support for a cost of sexual selection in terms of survival. Only four studies involved actuarial senescence sensu stricto. The others focused on age-independent metrics such as maximum longevity, life expectancy, or average adult mortality, which do not provide reliable information about actuarial senescence and are highly dependent on sample size (Krementz et al. 1989; Moorad et al. 2012). Moreover, for a given metric, the measure actually used differed between studies. For example, sexual size dimorphism (SSD), a commonly used metric of the strength of sexual selection, was measured either as the ratio between male and female body masses (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 masses as additive covariates in the model (Lemaître and Gaillard 2013a), or as the Lovich and Gibbons's (1992) ratio of the mean size between males and females when males are larger (Bro-Jørgensen 2012). Such a diversity of SSD measures often makes comparing results across studies difficult.

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 detect any 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 strength of actuarial senescence, but did not include any influence of the onset of senescence.

The onset of senescence provides another potentially powerful metric of the intensity of senescence sensu stricto that is 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, two recent studies have shown long-term reproductive costs in terms of onset rather than rate of senescence (Hammers et al. 2013; Gamelon et al. 2014). These recent findings 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 for a 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 ruminants living in captivity. In large herbivores, males are often subjected to intense sexual competition (Clutton-Brock 1989; Bro-Jørgensen 2011) and there is large variation in the intensity of sexual selection among species. To gain mating opportunities, males subjected to strong sexual selection often display phenotypic responses

Table 1. Survey of comparative analyses investigating the relationship between the strength of sexual selection and mortality or actuarial senescence metrics across species.

Reference	Taxa	Population status	Number of Species	Statistical Analysis	Sex	Sexual Selection Intensity	Metric	Survival or Senescence Variables	Metric	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	● Positive correlation between SSD and male bias adult mortality ● Female bias in adult mortality in monogamous taxa
Promislow et al. (1992)	Birds (only North American Passerine)	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	● 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 (only Western Palearctic species)	Wild	37	PICs	Male Female	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	● No mortality cost associated with SSD or SPD

(*Continued*)

Table 1. Continued.

Reference	Taxa	Population status	Number of Species	Statistical Analysis	Sex	Sexual Selection Intensity	Metric	Survival or Senescence Variables	Metric	Conclusion
Toïgo and Gaillard (2003)	Mammals (only ruminants)	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 two and seven years of age Sex bias: male survival	● 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	● 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	Ratio of male lifespan to female lifespan	● Bigger sex difference of lifespan in polygynous species than monogamous species
								Rate of actuarial senescence	**Difference in slope obtained from linear regression fitted on age-specific data**	● **Bigger sex differences in senescence rates for polygynous species than for monogamous species**

(*Continued*)

Table 1. Continued.

Reference	Taxa	Population status	Number of Species	Statistical Analysis	Sex	Sexual Selection Intensity	Metric	Survival or Senescence Variables	Metric	Conclusion
Müller et al. (2011)	Mammals (only ruminants)	Captive	78	PGLS	Male Female	Mating system	Monogamous/ tending/ polygynous	Relative life expectancy (rLE)	Life expectancy as proportion of longevity	● Higher rLE in males of monogamous than polygynous species. ● Higher rLE in females than males.
Bro-Jørgensen (2012)	Mammals (only bovids)	Captive	100	PICs(and PGLS)	Male Female	SSD	Lovich and Gibbons ratio^1	Longevity	Maximum longevity	● Longevity decrease with SSD only in males.
Lemaître and Gaillard (2013a)	**Mammals (only ruminants)**	**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	Age at which 50% of an initial cohort are still alive Sex bias: female–male	● Lower adult survival in males than in females. ● No relationship between male allocation to SSD, WSD, and/or RTM and interspecies difference of both absolute and relative adult lifespans
								Rate of actuarial senescence	**Slope obtained from linear regression fitted on age-specific data, from median lifespan to age at which 10% of an initial cohort are still alive** **Sex bias**: **female–male**	● **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 intensities of senescence.**

(*Continued*)

Table 1. Continued.

Reference	Taxa	Population status	Number of Species	Statistical Analysis	Sex	Sexual Selection Intensity	Metric	Survival or Senescence Variables	Metric	Conclusion
Lemaître and Gaillard (2013b)	**Mammals**	**Wild**	**24**	**PGLS**	**Female**	**Level of female polyandry**	**Relative testes mass or percentage of multiple paternity**	Median lifespan	Age at which 50% of an initial cohort are still alive	● Polyandry level does not affect female lifespan
								Rate of actuarial senescence	**Slope obtained from linear regression fitted on age-specific data, from the age at the onset of senescence to death**	● **Polyandry level does not affect female rate of senescence**
Tidière et al. (2014)	**Mammals (only ruminants)**	**Captive**	**56**	**PGLS**		**Length of mating season**	**Time during which 80% of birth occurs**	**Onset of senescence** **Rate of actuarial senescence**	**Age at which mortality rate was the lowest** **Proportional decrease of survival between six and nine years of age**	● **No relationship between the length of mating season and onset of senescence** ● **No relationship between the length of mating season and rate of actuarial senescence**

Gray-shaded results correspond to studies reporting support for a statistically significant association between the strength of sexual selection and level of mortality or actuarial senescence. Studies 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).

PICs, phylogenetically independent contrasts; PGLS, phylogenetically least square models; SSD, sexual size dimorphism.

[1] Ratio calculated as M/F if M > F and 2-F/M if F > M; M and F denote male and female body masses, respectively.

(Preston et al. 2003) that can be costly and lead to increased mortality. In particular, these males allocate resources in body mass, which confers advantages in contests with competing males (Jarman 1983; Andersson 1994). Thus, a positive correlation between the magnitude of SSD and male-biased mortality is expected due to the high energy requirements associated with large body size (Jarman 1983; Weckerly 1998). Moreover, ruminants exhibit different mating strategies (Clutton-Brock 1989; Bro-Jørgensen 2011) likely to mediate the intensity of male–male competition, and thus traits such as SSD (Loison et al. 1999b). In ruminants, three types of mating systems predominate: monogamy (males mate with the same female in successive reproductive attempts), promiscuity (males and females mate with several partners with no continuing bond between individuals), and polygyny (males mate with the same group of females in successive reproductive attempts, Clutton-Brock 1989). Intermale competition for mating is expected to be higher in polygynous species, a little less in promiscuous species, and much lower in monogamous species. Furthermore, within both promiscuous and polygynous species, mating tactic can vary 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 defending part or all of 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 females in estrus, pairing with them and defending them against other males during estrus). Defending a territory is expected be more energetically costly than defending a harem, and both to be more costly than tending (Owen-Smith 1977). Large males in harem species display large and complex weapons that generally lead to dissuade the small males to engage in a fight, whereas males in territorial species have short and sharp weapons often used in risky fights (Caro et al. 2003). Moreover, territorial males have to patrol and mark the territory they defend using glandular secretions, which is likely to be costly. Males of territorial species have been reported to be more often subject to injuries and exhaustion than males of harem species that only fight exceptionally (Geist 1966). In the same way, allocating to sexually selected traits such as horns or antlers (Bro-Jørgensen 2007; Plard et al. 2011; Lemaître et al. 2014c) should influence the onset or rate of senescence because of inherent trade-offs in energy allocation between reproduction and maintenance (Williams 1966).

We used data for 60 species of herbivores (all ruminants) from the International Species Information System (ISIS) database that combines individual data such as sex and dates of birth and death for animals born, raised, and maintained in captivity in 850 member institutions from more than 80 countries. Such protected conditions allow eliminating mortality due to environmental causes such as predation or climatic harshness, and thereby better identifying the underlying causes of senescence. Studying captive populations, in which intra-male agonistic interactions are avoided by husbandry practices, does not allow assessing direct costs of intraspecific male–male competition. Indeed, zoos avoid keeping multiple male rivals together. On the other hand, captive populations offer a unique opportunity to measure evolutionary physiological costs linked to sexually selected traits and behaviors. Moreover, by focusing mostly on individuals older than one year, effects of population management via culling were largely excluded because most husbandry practices involved juveniles. To assess the relationship between the magnitude of the male bias of actuarial senescence and strength of sexual selection, we used different measures of the intensity of sexual competition simultaneously: SSD, mating system, mating tactic (only in polygynous and promiscuous species), and horn size dimorphism (HSD, only in bovids). In addition, we measured the intensity of male and female survival costs and of sex differences in actuarial senescence and survival using different measures previously selected in other comparative studies: median longevity (Lemaître and Gaillard 2013a), 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 (Tidière et al. 2014), for each sex. We investigated whether increasing species-specific resource allocation in sexually selected traits leads to increasing mortality and actuarial senescence in males on both an absolute scale and a scale relative to females. More specifically, we tested the following predictions: (1) 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 nonterritorial species. Concerning females, we expected (2) an absence of relationships between sexual selection and senescence patterns. Contrary to males, female ruminants have not developed potentially costly morphological or physiological traits in response to sexual selection. Therefore, we expected that (3) 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 SENESCENCE

We first estimated survival at each age for each sex of each species of ruminants (Müller et al. 2011; Lemaître et al. 2013). Considering each individual of the captive population of all zoos as belonging to one "meta-population" makes it possible to compute the parameters characterizing 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, implying that animals were born in captivity. The complete dataset included 95 species of ruminants. However, we retained only species for which at least 25 individuals of each sex were alive at one year of age ($N = 60$ species) to get accurate estimates of age-specific mortality. These age-specific mortality rates are presented for each species in Figure S1 using *BaSTA* package (Colchero et al. 2012).

To measure species- and sex-specific patterns of survival and senescence, we used four different and complementary metrics: the median longevity, Gompertz rate of senescence, onset of senescence, and linear rate of senescence between two well-defined cut-off ages (between six and twelve years of age, see below and Table S1). Such a diversity of metrics is crucial for two reasons. First, it allows comparison of our finding with previous results published in the literature, and second, it helps to disentangle possible confounding effects between the rate and onset of actuarial senescence.

We extracted the age at death for each individual and we calculated the median and mean longevity for each sex of each species. We only reported analyses using median longevity because analyses based on mean longevity provided similar results (see Table S2). Median longevity (called "longevity" hereafter) is not a direct measure of senescence because it does not include any information about age-dependent survival. However, median longevity allows measuring the overall difference in survival between sexes and can therefore be linked with the energy allocation to maintenance during lifespan.

The second metric we used was the Gompertz rate of senescence (called "Gompertz rate" hereafter) that measures the sex- and species-specific average exponential rate of mortality with age. Many mathematical functions have been proposed to measure actuarial senescence (Ricklefs and Scheuerlein 2002). The Gompertz function is the most commonly used to study human survival or survival in captive conditions (Ricklefs and Scheuerlein 2002) and has been shown to provide a reliable description of age-specific survival in ruminants (Gaillard et al. 2004). We first built the capture history of each individual of each sex for the 60 species of ruminants included in our dataset (coded as "1" when the individual was observed alive and as "0" when it was dead at a given age). These capture histories were then loaded into 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 from birth onward, 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 ruminants (Gaillard et al. 2004), 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 one year of age and the age corresponding to the first two-thirds of maximum recorded 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). In species for which a Gompertz model provided a better fit than either the constant or the two-age-class model (selection was made by AIC, Akaïke Information Criterion; Burnham and Anderson 2002; see below for further details), we retained the estimates of the Gompertz rate and onset ($N = 47$ species, see Table S3).

The Gompertz rates we estimated were thus dependent on the corresponding onset of senescence. An early onset of senescence was indeed associated with a low actuarial senescence rate (Pearson correlation coefficient of 0.33 ± 0.13, $t = 2.49$, $P = 0.016$). To correct for that constraint, we first included the Gompertz onset of senescence as a covariate in the analysis of Gompertz rates. Moreover, we also estimated the onset of senescence and rate of senescence independently of the Gompertz models.

Estimating a reliable age at the onset of actuarial senescence is difficult and several metrics or proxies have been used (Jones et al. 2008; Lemaître et al. 2013). To avoid inaccurate estimates, we determined the age at the onset of senescence using seven distinct metrics in a restricted range of ages between one year and the first two-thirds of the maximum lifespan recorded for a given sex in a given species, to avoid extreme mortality values caused by a small number of old individuals (see Appendix S1 and Table S4 for a definition of these metrics). Indeed, detailed CMR analyses performed so far on ruminants provide evidence that the onset of actuarial senescence consistently occurs within the first half of maximal observed longevity (see, e.g., Gaillard et al. 1993 on roe deer *Capreolus capreolus*, Benton et al. 1995 on red deer, Toïgo et al. 2007 on ibex *Capra ibex*). Results obtained with these seven metrics were qualitatively similar (see Tables S5, S6) and we report below results from analyses performed with the median value of these different estimates (see Fig. S2 for the onsets of males and females in each species).

We also measured the rate of senescence as the proportional decrease of survival between six and twelve years of age. We fixed these age thresholds because in most ruminant species, senescence begins between these age thresholds as demonstrated by detailed analyses of age-specific variation in intensively monitored populations (e.g., Loison et al. 1999a; Festa-Bianchet et al. 2003; Gaillard et al. 2004; Toïgo et al. 2007), which allowed us to make estimates directly comparable among species. Saiga (*Saiga tatarica*), Speke's gazelle (*Gazella spekei*), Goitered gazelle (*Gazella* *subgutturosa*), and Greater kudu (*Tragelaphus strepsiceros*) were excluded from this analysis because all males died before twelve years of age. Therefore, the rate of senescence of males between six and twelve years of age was analyzed using data from 56 species. In addition, the longest-lived female of Chinese water deer (*Hydropotes inermis)* died before reaching twelve years of age. We therefore restricted the analysis of between-sex differences in senescence rate between six and twelve years of age to 55 species. Restricting the analyses on the range between six and nine years of age as performed in a previous study using ISIS data (Tidière et al. 2014), and adding median longevity as a covariate in the analysis to correct for variation among species, allowed considering more species (59 vs. 56 species when using the rate between six and twelve years of age) but did not change the results (Table S7).

No between-sex correlation was detected for longevity, Gompertz rate, or onset of senescence. However, a positive between-sex correlation occurred for the rate of senescence between six and 12 years of age (Table S8).

METRICS OF SEXUAL SELECTION

To assess the strength of sexual selection in a given species, we used four metrics: SSD, mating system, mating tactic (only for polygynous and promiscuous species) and HSD only for bovids (see Table S9). The first and most commonly used metric in such analyses is the SSD (Toïgo and Gaillard 2003, Table 1), which allows taking into account the difference in masses 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 (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 analyses using other SSD measures but results remained qualitatively unchanged (see Table S10). We thus report results from analyses 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 analyses.

We assessed the mating system (monogamous, promiscuous, or polygynous) of each species according to the classification of the mating type in Zerbe et al. (2012). 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 S9) using the tending tactic as a reference.

Finally, we used the HSD of bovids as the last metric of the strength of sexual selection. Female bovids can have horns, but generally of smaller size than males (Bro-Jørgensen 2007). We thus assumed that increasing sexual selection leads to increased horn size in males relative to females. For this study, we included only 37 species because we were not able to find reliable horn size data for at least one sex in seven species (American bison *Bison bison*, European bison *Bison bonasus*, Gaur *Bos gaurus*, Wild goat *Capra aegagrus*, Blesbok *Damaliscus pygargus*, Bighorn sheep and Mouflon *Ovis orientalis*). Data for horn size were also obtained from free-ranging populations. As for the SSD, we report results from analyses including both male and female horn sizes as covariates in the model (both log-transformed). Moreover, as females of some species have no horns, we used the log-transformation of (horn size + 1) for males and females of all species. Having too few cervids ($N = 13$ species) in our dataset, we did not perform a specific analysis including male antler size. However, when analyses were performed for longevity as well as actuarial senescence metrics in cervid males, the best model selected was always the model without any predictor (Table S11).

ACCOUNTING FOR POSSIBLE CONFOUNDING VARIABLES

We controlled for possible confounding factors previously reported to influence survival and actuarial senescence in captive ruminants. First, body mass was included to control for the strong allometric relationship linking body mass and adult survival or actuarial senescence in ruminants (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 ruminants (Gaillard et al. 2005). The average species-specific body mass for each sex was recovered from the literature (see above and Table S9).

Additionally, in captivity, food supplied to ruminants is sometimes not optimal (Müller et al. 2011) and the dietary requirements of grazers (whose natural diet consists mainly of grass) are generally met better than those of browsers (whose natural diet consists mainly of leaves or twigs). This leads to a longer longevity and a reduced actuarial senescence in captive grazers as compared with their wild counterparts, whereas the opposite is observed for browsers (Müller et al. 2011; Lemaître et al. 2013). Therefore, because diet is a structuring factor for survival and senescence in ruminants in captivity, the effect of the natural diet on different metrics for males has been included to avoid confounding effects of a less-adapted diet for browsers in captivity. To do that, the percentage of grass in a species' natural diet was obtained from Zerbe et al.'s (2012) supplement data (see Table S9) and included as a covariate in our models.

STATISTICAL ANALYSES

To avoid biased assessment of the relationships between sexual selection and survival patterns, we controlled all the analyses for the non-independence between species due to shared 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 60 species of ruminants used in this study (see Fig. S1) was built using the phylogenetic supertree of mammals published by Bininda-Emonds et al. (2007, 2008). This supertree was built using a 66-gene alignment in conjunction with 30 cladistically robust fossil calibration points. Branch lengths are proportional to time. To confirm our results, analyses were repeated with Agnarsson and May-Collado's (2008) phylogeny of 266 species of Cetartiodactyla based on cytochrome b sequence data and using the recent Figuet et al.'s (2014) 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 study those obtained with the phylogenetic supertree of mammalian species (Bininda-Emonds et al. 2007, 2008). Phylogenetically controlled analyses were performed in R version 2.14.0 (R Development Core Team 2011) using the function "pgls" of the package *caper* (Orme 2012).

Dependent variables (longevity, Gompertz rate, onset of senescence, and rate of senescence between six and 12 years of age) were all log-transformed to account for the allometric nature of the relationships (see Houle et al. 2011). For each dependent variable entered in the full model for analyses of males or females, we included the percentage of grass in a species' natural diet, the SSD (by entering both male and female body masses; Freckleton 2002, 2009), mating system, and the two-way interaction between mating system and male (or female) body mass. We added this interaction because the largest ruminants are mostly polygynous and the lightest ones monogamous. As the estimate of the Gompertz rate depends on the age at the onset of senescence used to model senescence, the Gompertz 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, the full model included diet, SSD, mating tactic, and the two-way interaction between mating tactic and male body mass (because harem and territorial species are generally larger than tending species and senescence could potentially be only detected in harem and territorial species). Finally, to analyze the influence of HSD, only in bovids, the full model included diet, SSD, HSD (with male and female horn sizes added as covariate), and the two-way interaction between body mass and horn size. Dependent variables were the same as for the analysis of the entire dataset. To analyze the between-sex difference of survival and actuarial senescence patterns, we used the male/female ratio (log-transformed values).

Finally, to select the best model of variation in longevity or senescence metrics, we used a model selection procedure based on the AIC (Burnham and Anderson 2002). For each senescence or survival metric, we retained the model with the lowest AIC. When the difference of AICs between competing models was less than 2, we retained the simplest to satisfy parsimony rules (Burnham and Anderson 2002). The model with the lowest AIC was also identified and discussed. 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 fitted linear models without correcting for phylogeny to avoid any possible bias induced by the inclusion of a non-required phylogenetic correction and provided estimates from simple linear models (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 2–4). Analyses were performed with R version 2.14.0 (R Development Core Team 2011) and parameter estimates are given ± SE.

Results

LONGEVITY AND SENESCENCE PATTERNS OF MALES IN RELATION TO THE STRENGTH OF SEXUAL SELECTION

The model selected for male longevity included additive effects of male body mass and mating system ($w_i = 0.47$; $\lambda < 0.001$, λ 95% CI [0.000;0.463], Table S12). Longevity increased with body mass (Table 2, Fig. S3A). Males of monogamous species lived longer than males of polygynous species (difference of –0.512, 95% CI [–0.923;–0.101], corresponding to –1.6 years, Fig. 1), and to a lesser extent than promiscuous species (difference of –0.247, 95% CI [–0.677;0.182], corresponding to –0.9 year).

The selected model for Gompertz rates included the Gompertz onset of senescence ($w_i = 0.35$; $\lambda < 0.001$, λ 95% CI [0.000; 0.208], Table S12). As expected, males with earlier onset of senescence had lower Gompertz rates (Table 2). The models including an additional effect of diet (ΔAIC = 1.09, $w_i = 0.20$, Table S12), or effects of body mass (ΔAIC = 1.74, $w_i = 0.15$, Table S12) also provided satisfactory fits, although the effect sizes were very small in both cases (not presented). As expected, the Gompertz rate tended to decrease with both increasing body mass ($\beta = -0.030 \pm 0.061$, Fig. S3B) and increasing proportion of grass in species natural diet ($\beta = -0.0024 \pm 0.0026$, Fig. S4B). However, the Gompertz rate was not affected by the mating system (Fig. 1).

The selected model of onset of senescence included additive effects of diet and mating system ($w_i = 0.51$; $\lambda < 0.001$, λ 95% CI [0.000;0.374], Table S12). Males of grazer species senesced later than males of browser species (Table 2, Fig. S4C), and compared with males of monogamous species, males of promiscuous species tended to senesce 1.8 years earlier ($\beta = -0.085 \pm 0.207$), and

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 ruminant species living in captivity.

	Method	Variables	β	95% CI	Adjusted R^2	Λ
Longevity	LM	Promiscuity	–0.247	–0.677;0.182	0.23	<0.001[1]
($N = 60$ species)		**Polygyny**	**–0.512**	**–0.923;–0.101**		
		Male body mass	**0.142**	**0.055;0.228**		
Gompertz rate of senescence ($N = 47$)	LM	**Gompertz onset**	**0.334**	**0.071;0.596**	0.10	<0.001[1]
Onset of senescence	LM	Promiscuity	–0.085	–0.491;0.321	0.25	<0.001[1]
($N = 60$)		Polygyny	–0.370	–0.799;0.059		
		Diet	**0.009**	**0.005;0.012**		
Rate of senescence between six and 12 years of age ($N = 56$)	LM	**Male body mass**	**–0.142**	**–0.206;–0.077**	0.24	<0.001[1]

In all analyses performed, phylogeny had no statistically significant effects ($\lambda < 0.001$) and parameters were thus estimated from LM without any phylogenetic correction. Effect sizes statistically different from 0 are in bold.

[1] Lambda not statistically different from 0.

LM, linear models.

Table 3. Parameter estimates from the models selected to account for among-species variation observed in longevity and metrics of actuarial senescence in females of ruminant species living in captivity.

	Method	Variables	β	95% CI	Adjusted R^2	λ
Longevity	LM	**Female body mass**	**0.002**	**0.0002;0.0046**	0.52	<0.001[1]
($N = 60$ species)		**Diet**	**0.173**	**0.119;0.227**		
Gompertz rate of	LM	**Gompertz onset**	**0.257**	**0.120;0.394**	0.26	<0.001[1]
senescence ($N = 45$)		**Female body mass**	**–0.091**	**–0.173;–0.009**		
Onset of senescence	LM	**Promiscuity**	**0.877**	**0.309;1.445**	0.11	<0.001[1]
($N = 60$)		**Polygyny**	**0.852**	**0.286;1.418**		
Rate of senescence	LM	**Diet**	**–0.003**	**–0.005;–0.001**	0.43	<0.001[1]
between six and 12 years of age ($N = 58$)		**Female body mass**	**–0.150**	**–0.209;–0.091**		

In all analyses performed, phylogeny had no statistically significant effects ($\lambda < 0.001$) and parameters were thus estimated from LM without any phylogenetic correction. Effect sizes statistically different from 0 are in bold.

LM, linear models.

[1] Lambda not statistically different from 0.

males of polygynous species tended to senesce 2.7 years earlier ($\beta = -0.370 \pm 0.219$; Table 2, Fig. 1).

Lastly, the model selected for the rate of senescence between six and 12 years of age only included body mass ($w_i = 0.30$, $\lambda < 0.001$, λ 95% CI [0.000;0.372], Table S12). Males senesced faster in small than in large species (Table 2, Fig. S3D). Moreover, the second-best model included additional effects of diet (ΔAIC = 0.48, $w_i = 0.24$, Table S12) with, as predicted, males of grazer species senescing at a slower rate than males of browser species ($\beta = -0.0019 \pm 0.0016$, Fig. S4D). However, the rate of senescence was not influenced by any metric of sexual selection (Table S12, Fig. 1D).

When restricting the analyses to polygynous and promiscuous species, an effect of mating tactic occurred for longevity, onset of senescence, and rate of senescence between six and 12 years of age, but not for the Gompertz rate (Table S13). Males of territorial species lived three years less than males of species with a tending tactic (Table S14). Moreover, males of harem-holding and territorial species tended to senesce earlier than males of tending species (Tables S13, S14). In addition, the model selected for the senescence rate between six and 12 years of age included diet, body mass, mating tactic, and the two-way interaction between mating tactic and male body mass (Table S13) with males of territorial species senescing at a slower rate than males of tending species (Table S14). The difference in senescence rate between mating tactics increased with body mass (Table S14). Results obtained from males of harem-holding species were difficult to interpret due to the small number of

Table 4. Parameter estimates from the models selected to account for between-sex variation observed among species of ruminants living in captivity in longevity and metrics of actuarial senescence.

	Method	Variables	β	95% CI	Adjusted R^2	λ
Longevity ($N = 60$ species)	LM	Promiscuity **Polygyny**	–0.326 **–0.572**	–0.713;0.060 **–0.958;–0.187**	0.13	<0.001[1]
Gompertz rate of senescence ($N = 47$)	LM	No predictor				<0.001[1]
Onset of senescence ($N = 60$)	LM	Promiscuity Polygyny	–0.585 –0.729	–1.279;0.109 –1.420;–0.037	0.04	<0.001[1]
Rate of senescence between six and 12 years of age ($N = 56$)	LM	No predictor				<0.001[1]

In all analyses performed, phylogeny had no statistically significant effects ($\lambda < 0.001$) and parameters were thus estimated from LM without any phylogenetic correction. Effect sizes statistically different from 0 are in bold.

LM, linear models.

[1] Lambda not statistically different from 0.

species ($N = 6$). Complementary analyses performed in bovids revealed no effect of HSD on longevity, onset of senescence, Gompertz rate, or senescence rate between six and 12 years of age (Table S15).

LONGEVITY AND SENESCENCE PATTERNS OF FEMALES IN RELATION TO THE STRENGTH OF SEXUAL SELECTION

Neither the mating system nor SSD influenced female longevity or any of the rates of senescence (Table S16, Fig. 1). However, the onset of senescence was influenced by sexual selection. Indeed, the mating system was included in the selected model (Table S16): females of polygynous and promiscuous species started to senesce later than females of monogamous species (Table 3, Fig. 1). However, the rate of senescence between six and 12 year of age tended to be faster in females of polygynous species than in females of monogamous species (difference between monogamous and promiscuous species: $\beta = 0.006 \pm 0.167$; between monogamous and polygynous species: $\beta = 0.166 \pm 0.168$; $\lambda < 0.001$; λ 95% CI [0.000;0.357], Fig. 1D). We observed that the mating tactic did not influence senescence rates. However, females of territorial species lived shorter and had later onset of senescence than females of species displaying harem-holding or tending tactics (Table S17). Finally, neither HSD nor SSD influenced any survival or senescence metric in female bovids (Table S18).

BETWEEN-SEX DIFFERENCE IN LONGEVITY AND SENESCENCE PATTERNS IN RELATION TO THE STRENGTH OF SEXUAL SELECTION

The mating system was retained in selected models for the difference of longevity and onset of senescence between sexes, whereas the model with no predictor was selected for both senescence rates (Table S19). Males of ruminant species had shorter lifespan but senesced later than females (Fig. 1, C). Moreover, the between-sex difference of longevity was larger in polygynous and promiscuous than in monogamous species. On the other hand, the between-sex difference of onset of senescence tended to be larger in monogamous than in promiscuous and polygynous species (Table 4, Fig. 1).

When investigating the effects of mating tactic on between-sex difference, the mating tactic was included in the selected model for longevity and the rate of senescence between two ages (Table S20). The between-sex difference of longevity was larger in territorial species than in tending species and no detectable difference occurred between tending and harem-holding species (Table S21). However, the between-sex difference of rate of senescence between six and 12 years of age was higher in tending than in territorial species and no detectable difference was found between tending and harem-holding species (Table S21). For the between-sex difference of Gompertz rate and onset of senescence, the model with no predictor was retained (Table S20). However, for the onset of senescence, the model including mating tactic had the lowest AIC (Table S20): the sex difference of onset of senescence was higher in tending species with females senescing earlier than males (male/female ratio for tending species: 4.963 ± 1.895), whereas harem-holding and territorial species had a lower between-sex difference of onset of senescence with males senescing earlier than females (difference between tending species and harem-holding species: –7.036 ± 3.655, difference between tending species and territorial species: –5.164 ± 2.013). In bovids, the sex bias in longevity and senescence patterns was not affected by the HSD because no selected model included any effect of the interaction between horn size and sex (Table S22).

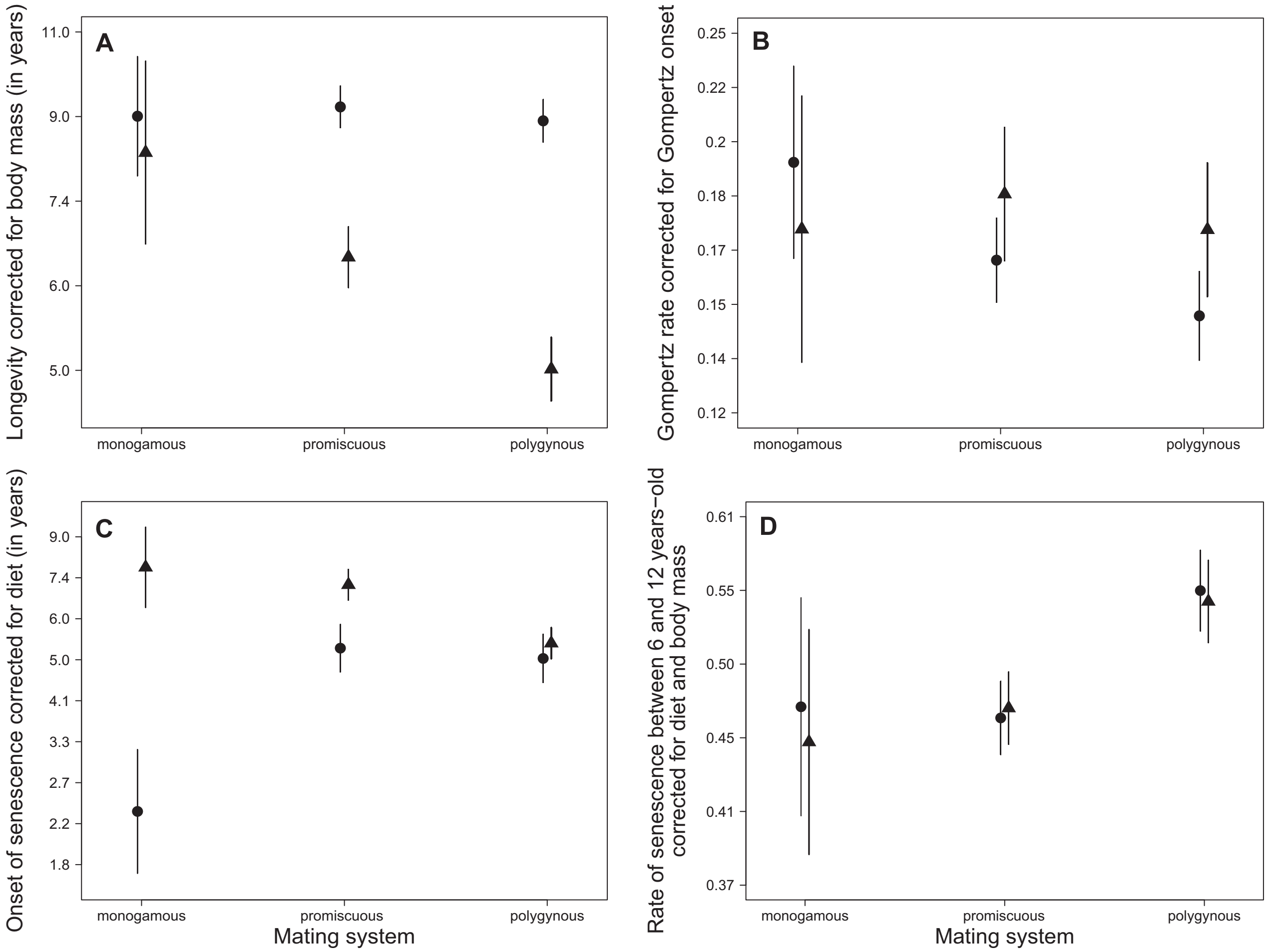

Figure 1. **Relationships among the longevity (A, $N = 60$ species), Gompertz rate of senescence (B, $N = 47$ species), age at the onset of actuarial senescence (C, $N = 60$ species), rate of senescence between six and 12 years of age (D, $N = 56$ species), and mating system in males (triangles) and females (circles).**

Discussion

Our results show that, in males of ruminant species, the intensity of actuarial senescence increases with the intensity of sexual selection. Males of monogamous species live longer and senesce later (but not faster) than males of promiscuous and polygynous species. Surprisingly, the pattern of actuarial senescence displayed by females is different, with females of monogamous species senescing earlier but at a slower rate than females of promiscuous and polygynous species. In males, a strong sexual selection pressure causes an earlier onset of senescence, which leads to a shorter longevity. On the other hand, for females, the later onset of senescence observed in species under strong sexual selection pressure is offset by a faster rate of senescence, resulting in no effect on longevity. Our results also showed that between-sex difference in longevity was stronger in polygynous and promiscuous species than in monogamous species whereas the between-sex difference of the onset of senescence was stronger in monogamous than in promiscuous and polygynous species.

Findings reported here thus support the hypothesis that, at least in the range of species considered, a high level of sexual competition leads to severe survival costs for males. The impact of the strength of sexual selection was limited to the age at the onset of senescence (i.e., the timing of senescence), with a repercussion on longevity, and did not affect the rate of senescence (i.e., the strength of senescence). The absence of any relationship between our proxies of sexual competition and the rate of actuarial senescence is in line with a previous work (Lemaître and Gaillard 2013a) based on a much smaller dataset of wild herbivores. In fact, the only reported effect of sexual selection on senescence rate comes from the finding that in birds and mammals, sex differences in senescence rates are larger in polygynous than in monogamous species (Clutton-Brock and Isvaran 2007, Table 1).

Males of polygynous herbivores start to senesce earlier than males of promiscuous and monogamous species. For instance, by comparing two similar-sized ruminant species, we observe that monogamous Pudu males (*Pudu puda*) begin to senesce at six years of age, whereas polygynous Speke's gazelle males start at three years of age, indicating that physiological costs associated with a polygynous mating system, such as putatively higher levels of metabolism associated with the readiness to defend a territory or harem, 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). Promislow (1992) found that the mean adult mortality rate is female biased in monogamous free-ranging mammals and Müller et al. (2011) found a longer relative life expectancy in captivity in males of monogamous species compared with males of polygynous species. However, to our knowledge, we provide the first evidence of a cost of sexual selection in terms of an earlier senescence in males. Comparative studies interested in such questions have notably focused mostly on longevity and, in a few instances, on actuarial senescence rate, without considering a possible impact in terms of timing of senescence (but see Tidière et al. 2014 [Table 1] for the absence of relationship between the onset of senescence and length of the mating season). Recently, a wide diversity of senescence patterns has been described in the living world (Nussey et al. 2013; Jones et al. 2014) and the onset of senescence is now increasingly recognized as a key factor characterizing senescence patterns (Jones et al. 2008; Péron et al. 2010; Hammers et al. 2013; Gamelon et al. 2014). Although it has already been shown that the onset of senescence covaries with other time variables 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 contribute to the diversity of ages at the onset of senescence.

We expected that males of territorial and harem-holding species should express stronger actuarial senescence and shorter longevity than males of tending species. However, although males of territorial species lived shorter and senesced earlier than males of tending species, they also senesced at a slower rate. Once again, at the level of the mating tactic this time, the strength of sexual selection caused the onset of senescence to occur earlier, resulting in a shorter longevity in males, and the deceleration of the senescence rate did not seem to be strong enough to compensate for the observed shift in the timing. If we look at two similar-sized species, we can see that Bighorn sheep males, which display a tending mating tactic, start to senesce at nine years of age, whereas territorial Lechwe males (*Kobus leche*) senesce from three years of age. Interspecific differences in senescence patterns between males' mating tactics must reflect species-specific costly physiological and behavioral attributes of territory or harem tenure, which have an effect on senescence even in the absence of actual competitors (as observed in the studied captive populations). Territorial and harem-holding males have thus probably evolved physiological and behavioral mechanisms that are costly in terms of timing of senescence, and then in terms of longevity, and have also evolved an (imperfect) compensatory lower senescence rate. Indeed, territorial males have to patrol and mark the territory they defend using glandular secretions or hormone production, which could be costly. In the same way, harem-holding males have to defend their harem from predators and other males (Owen-Smith 1977). Another possibility might be that typical rutting behavior such as chasing of females or scent marking may be also displayed in absence of competing males even in captivity. Such mechanisms could explain why we found an earlier senescence in captive males of territorial and harem-holding species than in males of species displaying tending tactics, even in the absence of direct male–male interactions, as these behaviors might also be demonstrated under captive conditions.

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 SSD and any of our metrics of survival and actuarial senescence. This is surprising, because the large amount of energy required for male growth compared with female growth in highly sexually dimorphic species is expected to cause survival or ageing costs (e.g., Toïgo and Gaillard 2003; Bro-Jørgensen 2012). However, the unrestrained food availability under conditions in captivity might eliminate the costs of growing faster or longer. Interestingly, our review of the literature reveals that the relationship between SSD and senescence per se has almost never been investigated (but see Lemaître and Gaillard 2013a). Most studies so far have documented survival costs of SSD 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 SSD (see Introduction). In the present study, we measured SSD by adding both male and female body masses as covariates in our analyses, to avoid bias resulting when predictors are collinear in multifactorial analyses (Freckleton 2002, 2009). However, when we replicated our analyses using other metrics of SSD, all results remained qualitatively unchanged (Table S10). Therefore, the observed discrepancy between the results we report here and those previously published are likely to involve either the absence of corrections for confounding factors (e.g., pace of life; see below), the type and quality of data analyzed, or a lack of such effects under captive conditions. For instance, for a trait such as longevity, the use of different reference sources can rapidly lead to divergent outcomes (e.g., Lemaître et al. 2014b). In the present study, we have used data from the ISIS database rather than published records of longevity. ISIS data allow working on long-term populations with the 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 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 better assessment of how costs associated with physiological adaptations to sexual selection influence survival.

Within the range of species analyzed here, males live shorter and senesce later (but not faster) than females. Sexual selection acts primarily on males, so 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 sexual selection modifying male survival and senescence patterns. However, this modification might be responsible for the modification of female longevity and senescence patterns as well, as a result of a genetic correlation between sexes. Studies looking 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 pointed out that these sex differences are higher in polygynous than in monogamous species. However, although males of polygynous species senesce earlier than promiscuous and monogamous species, we observed a surprising, unpredicted tendency for a stronger between-sex difference of onset of senescence in monogamous species compared with promiscuous and polygynous species. In our view, the ad hoc explanation that females of monogamous species are almost always territorial and subject to high social competition for resources is plausible. Females in territorial species might exhibit similar costs as territorial males (Owen-Smith 1977). In contrast, females from polygynous species often live in social groups, which might decrease costs associated to predator avoidance or male harassment commonly observed in promiscuous species. There is then an advantage to live in group and share costs with other individuals, suggesting that sociality might decrease survival costs (e.g., Bro-Jørgensen 2012 for longevity).

In addition, our study documents a strong allometric relationship between body mass and senescence metrics. In non-volant mammals, body mass is tightly linked to the pace of life (Gaillard et al. 2005), with small species having a relatively fast pace of life, characterized by an early and fast senescence compared with 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 ruminants. Typically, grazer species (e.g., African buffalo, *Syncerus caffer*) have a delayed onset of senescence, a slower rate of senescence, and live longer compared with browser species such as roe deer. Overall, these analyses emphasize the importance of correcting for body mass and other potentially limiting factors, such as diet in the case of ruminants, when working on captive populations to avoid biased results. Interestingly, diet had no effect on the life expectancy of males in the study by Müller et al. (2011), but mating tactic was also detected as a factor affecting male life expectancy. However, most studies listed in Table 1 failed to control for such confounding variables, which might explain part of the discrepancy observed among these studies. We have tested how the absence of correcting for body mass, diet, or both factors might influence the results. None of our metrics were influenced by the SSD when body mass and diet were accounted for, whereas longevity of males was affected by SSD when body mas and diet were removed from models (see Table S23). This demonstrates the importance to control analyses for confounding effects of diet and pace of life to assess reliably the relationship between sexual selection and senescence pattern at interspecific level, and cautions against analyses not correcting for these factors.

Finally, our analyses and review of the literature show that the relationship between the intensity of sexual selection and strength of male senescence is complex. The lack of an SSD effect, along with the clear evidence of an effect of the mating system on the onset of senescence and longevity in males, indicates that the costs associated with sexual selection via intrasexual competition are generated by physiological and behavioral mechanisms linked to the mating system, rather than by large size in itself. These results demonstrate that only some physiological traits linked to mating systems (and mating tactics) involved in sexual selection are costly in terms of survival, and the side effect of sexual selection pressure is an advanced timing of senescence in males leading to a reduction of longevity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Longevity and actuarial senescence data in males (M) and females (F) of 60 ruminant species living in captivity.
Table S2. Set of models fitted to explain variation in mean longevity and median longevity in ruminant males according to variation in diet, body mass (male BM), mating system (MS), and sexual size dimorphism (male BM + female BM).
Table S3. Akaïke Information Criterion of model tested to describe sex-specific survival per age for each species of ruminant.
Table S4. Metrics used to assess the onset of actuarial senescence.
Table S5. Set of models fitted to explain variation in onsets of actuarial senescence of ruminant males, which were measured using 10 different metrics (seven original metrics + three synthetic metrics, cf. Table S4), according to variation in diet, body mass (male BM), mating system (MS), and sexual size dimorphism (male BM + female BM).
Table S6. Set of models fitted to explain variation in onsets of actuarial senescence of ruminant females, which were measured using 10 different metrics (seven original metrics + three synthetics metrics, cf. Table S4), according to variation in diet, body mass (female BM), mating system (MS), and sexual size dimorphism (male BM + female BM).
Table S7. Set of models fitted to explain variation in rates of senescence between six and 12 years of age and between six and nine years of age with or without including median longevity (MLm, male median longevity; MLf, female median longevity) as a covariate in analysis according to variation in diet, body mass (BMm, male body mass; BMf, female body mass), mating system (MS), and sexual size dimorphism (BMm + BMf).
Table S8. Between-sex correlation of senescence and survival metrics.
Table S9. Data on diet, mating system, mating tactic, body mass, and horn size (only for ruminant bovids) used in this study.
Table S10. Models selected for each metric of survival and senescence of males depending on the SSD metric considered.
Table S11. Set of models fitted to explain variation in survival and actuarial senescence metrics in males of ruminant cervid species in relation to variation in diet, body mass (male BM), sexual size dimorphism (male BM + female BM), and antler length (AL).
Table S12. Set of models fitted to explain observed variation in longevity and metrics of actuarial senescence in ruminant males in relation to variation in diet, body mass (male BM), mating system (MS), and sexual size dimorphism (male BM + female BM).
Table S13. Set of models fitted to test for a mating tactic effect on variation in longevity and actuarial senescence metrics in ruminant males (only polygynous and promiscuous species) in relation to variation in mating tactic (MT), body mass (male BM), and diet.
Table S14. Parameter estimates from the models selected to assess the effects of mating tactic on longevity and senescence metrics in ruminant males (only polygynous and promiscuous species).
Table S15. Set of models fitted to explain observed variation in longevity and metrics of actuarial senescence in males of ruminant bovid species in relation to variation in diet, body mass (male BM), horn size (male HS), sexual size dimorphism (male BM + female BM), and horn size dimorphism (male HS + female HS).
Table S16. Set of models fitted to explain observed variation in longevity and metrics of actuarial senescence in ruminant females in relation to variation in diet, body mass (female BM), mating system (MS), and sexual size dimorphism (male BM + female BM) in ruminants.
Table S17. Set of models fitted to test for a mating tactic effect on variation in longevity and actuarial senescence metrics in ruminant females (only polygynous and promiscuous species) in relation to variation in mating tactic (MT), body mass (female BM), and diet.
Table S18. Set of models fitted to explain observed variation in longevity and metrics of actuarial senescence in females of ruminant bovid species in relation to variation in diet, body mass (female BM), horn size (female HS), sexual size dimorphism (male BM + female BM), and horn size dimorphism (male HS + female HS).
Table S19. Set of models fitted to explain observed sex differences variation in longevity and metrics of actuarial senescence in relation to variation in body mass (BM), mating system (MS), and interaction between body mass and mating system (BM:MS) in ruminants.
Table S20. Set of models fitted to explain observed sex-differences variation in longevity and metrics of actuarial senescence (only polygynous and promiscuous species) in relation to variation in mating tactic (MT), body mass (BM), and interaction between body mass and mating tactic (BM:MT) in ruminants.
Table S21. Parameter estimates from the models selected to account for the effects of mating tactics on between-sex differences in four senescence and survival metrics of ruminants (only polygynous and promiscuous species).
Table S22. Set of models fitted to explain observed sex-differences variation in longevity and metrics of actuarial senescence in ruminant bovid species in relation to variation in body mass dimorphism (male BM + female BM), horn size dimorphism (male HS + female HS), and interaction between body mass and horn size (male BM:male HS).
Table S23. Models selected for each metric of survival and senescence of males depending on the SSD metric considered and in relation with or without correction for body mass and/or diet.
Appendix S1. Method used to obtain the synthetic metric "median onset."
Figure S1. Phylogenetic trees built on the 60 species of ruminants analyzed (based on Bininda-Emonds et al. 's [2007, 2008] phylogenetic tree) according to the percentage of grasses (A), mating system (B), and sexual size dimorphism (C).
Figure S2. Log of age-specific mortality rate for males (in red) and females (in gray) of each ruminant species.
Figure S3. Relationship among longevity DA0, Gompertz rate DB0, age at the onset of senescence DC0 or rate of senescence between six and 12 years of age DD0, and body mass in males of 60 ruminant species.
Figure S4. Relationship among longevity DA', Gompertz rate DB', age at the onset of senescence DC' or rate of senescence between six and 12 years of age DD', and percentage of grass in species' natural diet in males of 60 ruminant species.