Original Article

Male survival patterns do not depend on male allocation to sexual competition in large herbivores

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Understanding causes of between-sex differences in survival patterns is a long-standing challenge in evolutionary biology. Interspecific differences in male allocation to sexual competition have been suggested to shape species-specific patterns of male adult survival and actuarial senescence, and thereby the extent of between-sex differences in these parameters. Sexual competition is complex and involves both competition for gaining mating (i.e., precopulatory competition) and competition for fertilization opportunities (i.e., postcopulatory competition). However, to date, studies seeking for a relationship between allocation to precopulatory competition and male absolute adult survival have led to contrasting results and the influence of postcopulatory competition on these parameters has never been yet investigated. To fill the gap, we performed a comparative study in large herbivores using median lifespan (i.e., age at which only half of the initial cohort is still alive) and actuarial intensity of senescence (i.e., number of years elapsed between the median lifespan and the age where only one-tenth of the initial cohort is still alive). As expected, we found a lower adult survival and a stronger actuarial intensity of senescence in males than in females. Conversely, we did not find any evidence that variation in male allocation to pre- and/or postcopulatory traits explain between-species differences of both absolute and relative adult survival and intensity of actuarial senescence. These results challenge the idea that allocation to specific traits associated with sexual competition is responsible for between-sex differences in survival and senescence patterns generally reported in mammals. *Key words:* actuarial senescence, aging, sexual selection, sexual size dimorphism, testes mass, ungulates, weapon size. *[Behav Ecol]*

INTRODUCTION

Senescence is the progressive deterioration of an organism with age, which leads to the loss of biological functions and eventually death (Monaghan et al. 2008). Recent evidence from long-term studies of natural populations has shown that senescence is pervasive in vertebrates (Reznick et al. 2002; Gaillard and Bonenfant 2008; Nussey et al. 2008, 2012; Bouwhuis et al. 2012) and that within species males and females often differ in their senescence patterns (Smith 1989; Loison et al. 1999; Clutton-Brock and Isvaran 2007). Understanding the origin and the magnitude of these between-sex differences (also called sex bias) in senescence has now become a key challenge in evolutionary biology (Promislow 2003; Monaghan et al. 2008). In many species, senescence in survival (called actuarial senescence) is stronger in males compared with females, independently of the age class considered (Trivers 1972; Loison et al. 1999; Clutton-Brock and Isvaran 2007; Sherratt et al. 2011). Indeed, higher adult mortality of males compared with females has been reported in primates (e.g., rhesus monkey, *Macaca mulatta*; Meikle and Vessey 1988), pinnipeds (e.g., Southern elephant seals, *Mirounga leonina*; Pistorius et al. 1999), and rodents (e.g., common dormouse, *Muscardinus avellanarius*; Juškaitis 1999). Sexual selection has been suggested to be the main

driver of sex-biased mortality because sexual competition has driven the evolution of costly sexual traits and/or behavior that could account for higher mortality rates found in males compared with females (Owens and Bennett 1994; Promislow 2003; Bonduriansky et al. 2008). This hypothesis is rooted in the disposable soma theory proposed by Kirkwood (1977), according to which senescence corresponds to a trade-off of metabolic resources between allocation to reproduction and somatic maintenance (Kirkwood and Austad 2000). In other words, if an individual invests substantially in sexual competition during its life, it should suffer from a relatively early death.

Hence, the intensity of sexual competition should correlate with the intensity of actuarial senescence in males (Bonduriansky et al. 2008). To date, the few studies that have tried to relate absolute male or sex-biased mortality or actuarial senescence with sexual competition have led to contrasting results (e.g., Moore and Wilson 2002; Toïgo and Gaillard 2003; Clutton-Brock and Isvaran 2007). For example, using the duration of effective breeding as a measure of the intensity of sexual competition, Clutton-Brock and Isvaran (2007) found that between-sex differences of life expectancy among species of birds and mammals are strongly correlated with between-sex differences in the duration of effective breeding, whereas the sexual size dimorphism (SSD), another measure of male sexual competition, was not related to between-sex differences in adult survival of ungulates (Toïgo and Gaillard 2003). These discrepancies between studies suggest that relationships between sexual selection and both male and sex difference in senescence rates are yet to be

fully understood (see also Bonduriansky et al. 2008) and that using several measures of the intensity of sexual competition simultaneously may help to understand the relationship more accurately (Klug et al. 2010). Moreover, most studies have to date used different measures of survival that do not represent actuarial senescence per se. For instance, Toïgo and Gaillard (2003) used prime-age survival and Promislow (1992) computed sex bias in mortality rates from male and female life expectancy, whereas a metric of decrease in survival from the start of adulthood would be more appropriate to test evolutionary hypotheses of the evolution of senescence (Ricklefs 2010).

Another pitfall in studies seeking to relate sexual selection to survival is that they are only focused on precopulatory sexual selection (Promislow 1992; Toïgo and Gaillard 2003; Clutton-Brock and Isvaran 2007) although male allocation to sexual competition is generally more complex. Indeed, male intrasexual competition involves both competition for gaining mating opportunities (precopulatory competition) and competition for fertilization opportunities (postcopulatory competition) (Parker 1998; Andersson and Simmons 2006). To date, the consequences of male allocation to postcopulatory competition on male and sex-difference in rate of senescence of males are still untested (but see Liker and Székely 2005 for a relationship between testes mass and sex-specific annual mortality rates in birds) although there is compelling evidence that allocation to postcopulatory competition through a high level of sperm production can be energetically costly (Parapanov et al. 2008). For instance, castrated Soay sheep (*Ovis aries*) males outlived noncastrated males (Jewell 1997) maybe because allocation to testes mass and testosterone production is closely linked in mammals (Preston et al. 2012) and can lead to a decrease in survival through a decrease in the immune system efficiency (see Kruczek and Styrna 2009 and Mills et al. 2010 for an example in bank voles *Myodes glareolus*).

In the present study, we investigated how male overall allocation to sexual competition can account for both male and sex differences in survival and for actuarial intensity of senescence among species of large herbivores by measuring survival as the ages, where only 50% of individuals of a given cohort are still alive (i.e., median lifespan) and actuarial intensity of senescence as the number of years between ages, where only 50% and 10% of individuals of a given cohort are still alive. Large herbivores are particularly well suited for such investigations because information on sex- and age-specific survival is available for a high number of free-ranging populations from detailed individual long-term monitoring (Nussey et al. 2008). Moreover, males of large herbivores face both a strong level of sexual competition (Bro-Jørgensen 2011) and have developed costly adaptations in response to such sexual selection for gaining mating and fertilization events (Ginsberg and Rubenstein 1990; Bro-Jørgensen 2007). First, there is evidence that in this group SSD has evolved because larger males often monopolize mating opportunities (Pérez-Barbería et al. 2002; Preston et al. 2003) and ultimately obtain a higher lifetime reproductive success (Pemberton et al. 1992; McElligott et al. 2001). Second, males from most species of large herbivores bear weapons that have also evolved in response to the degree of competition to secure mating (Bro-Jørgensen 2007). Similar to SSD, male weapon size is a strong determinant of male mating success in natural conditions (Coltman et al. 2002). Finally, in mammals such as rodents, carnivores, or primates, males that face a high level of sperm competition have developed larger testes relative to their body mass and higher sperm concentration (Lemaître et al. 2009; Soulsbury and Iossa 2010) as predicted by models of sperm competition (Parker 1998). In large herbivores, female promiscuity is

common (e.g., *Cervus nippon*: Endo and Doi 2002, *Odocoileus virginianus*: DeYoung et al. 2002, and *O. aries*: Preston et al. 2003) and males from these species have also developed heavy testes relative to their body mass (Ginsberg and Rubenstein 1990). For instance, Soay sheep males that allocate substantially to testes size increase their siring success (Preston et al. 2003). Although the influence of SSD on male survival has been previously studied (e.g., prime-age survival, Toïgo and Gaillard 2003), no study to our knowledge has yet looked for possible additional influence of male weapon size and testes mass in mammals. Moreover, senescence per se has never been studied in this context, at least in mammals. In the present study, we expected that a substantial male allocation to both pre- and postcopulatory competition should be related to a small median lifespan and a high intensity of senescence in males but also to an important sex bias in median lifespan and intensity of senescence. Additionally, males from different ungulate species can exhibit various mating tactics that might influence the intensity of intra-male competition (Clutton-Brock 1989; Toïgo and Gaillard 2003; Bro-Jørgensen 2011). For instance, Bro-Jørgensen (2007) recently proposed that territoriality reduces the opportunity for sexual selection because in bovids, SSD and male horn length are smaller in territorial than in nonterritorial species. Therefore, we also tested the influence of mating tactics on male adult survival and actuarial intensity of senescence and on the sex bias in survival and senescence intensity. Following Bro-Jørgensen (2007), we predict a lower median lifespan and a stronger intensity of actuarial senescence in species exhibiting female defense tactic (i.e., nonterritorial) than in territorial species.

MATERIALS AND METHODS

Database

To compute median lifespan and actuarial intensity of senescence in both sexes, information on sex- and age-specific mortality from long-term studies of free-ranging population is needed (Nussey et al. 2008; Clutton-Brock and Sheldon 2010). However, such studies are still scarce and we thus started our search protocol by looking for the published studies including age-specific mortality for both sexes within the same natural population. We first collected information on age-specific mortality using the keyword "life table" in the topic window of *Web of Knowledge*. Then, we focused our protocol search on papers citing the 2 following "classics": Deevey (1947) and Caughley (1966). These 2 papers indeed report the first comprehensive analysis of age-specific mortality data in mammals and have been highly cited (752 and 332 citations, respectively, on 1 March 2012). Therefore, they are likely to have been quoted by most mammalian studies containing age-specific survival data. We thus checked all articles quoting at least 1 of these 2 references. We restricted our analysis to spontaneous ovulator species because these species show the highest allocation to testes mass (Soulsbury and Iossa 2010) and to species bearing weapons (horns or antlers). Therefore, we excluded Proboscidea and Perissodactylae from our database. At the end of our literature survey, we ended up with age-specific survival data for both sexes in 24 species of large herbivores (17 Bovidae and 7 Cervidae). The only species for which we had age-specific mortality for males only was the fallow deer (*Dama dama*) (McElligott et al. 2002) and was kept in the subsequent analysis involving male median lifespan and senescence. Moreover, because we aimed to test the effect of sexual competition on both male and sex bias in median lifespan and actuarial intensity of senescence, we did not consider studies providing mortality data for females only.

To compute male and sex bias in median lifespan, we used age-specific mortality to obtain ages when 50% of an initial cohort is still alive for both sexes. Sex differences in median lifespan were then computed as between-sex difference (female–male) of age when 50% of a cohort was still alive. We computed male actuarial intensity of senescence as the difference of years between ages when 50% and 10% of an initial cohort are still alive for both sexes. As for survival, we computed sex bias in actuarial intensity of senescence as between-sex difference (female–male) of differences in ages when 50% and 10% of an initial cohort are still alive. In ungulates, this time difference between ages when 50% and 10% of a given cohort are still alive provides a good proxy of actuarial intensity of senescence while avoiding an underestimation of senescence intensity due to high-quality individuals (last 10%) that may have an exceptionally long life. To avoid strong variation due to differences in survival between birth and 1 year of age (the most variable life stage in large mammals, Gaillard et al. 2000), we fixed 100% of the cohort alive at 1 year old (i.e., cohort initialized at 1 year of age). For 4 species (African buffalo, *Syncerus caffer*; bighorn sheep, *Ovis canadensis*; reindeer, *Rangifer tarandus*; and roe deer, *Capreolus capreolus*) estimates were available for more than 1 population and we thus computed survival and intensity of senescence metrics as the median value across populations. We assessed the reliability of our metric by comparing our measure of intensity of senescence with rates of senescence estimated from the Gompertz model extracted from Gaillard et al. (2003) on a subset of 8 species present in both data sets (bighorn sheep; reindeer; roe deer; mountain goat, *Oreamnos americanus*; moose, *Alces alces*; alpine ibex, *Capra ibex*; isard, *Rupicapra pyrenaica*; and red deer, *Cervus elaphus*) and with rate of senescence of the Weibull model extracted from Ricklefs (2010) on a subset of 10 species present in both data sets (topi, *Damaliscus lunatus*; Dall's sheep, *Ovis dalli*; chamois, *Rupicapra rupicapra*; impala, *Aepyceros melampus*; African buffalo; bighorn sheep; isard; roe deer; reindeer; and red deer). In both cases, correlations between our measures of intensity of senescence and rate of senescence from the literature were in the expected direction (Pearson coefficient of correlation: $r = 0.37$ with Gaillard et al. 2003 and $r = 0.36$ with Ricklefs 2010) although relationships were not statistically significant, which is probably due to the inevitably reduced sample size. Finally, methods used to assess age-specific mortality differed markedly between studies, which can potentially influence interspecific patterns of senescence (Péron et al. 2010). Therefore, we categorized as "0" studies that used longitudinal data and as "1" studies that used cross-sectional studies of wild populations. Sample sizes for each category were 12 and 13, respectively (Table S1, see supplementary data).

To measure SSD, we gathered data on male and female adult mass for each species from the literature. We looked for studies that reported separate body mass for both sexes from the same population. Information on male and female weapons came from recent comparative studies (e.g., Bro-Jørgensen 2007; Plard et al. 2011) that provided data collected on adult individuals only. Because ungulate species show variability in their weapon type (e.g., horns that grow continuously in Bovidae and antlers that are shed annually in Cervidae) and potentially in their function during sexual competition, we included a variable "weapon type" into our analysis (see below). Data on adult testes mass (measured without epididymis) came principally from published reviews (e.g., Ginsberg and Rubenstein 1990) and in our data set testes mass showed a linear allometric relationship with body mass ($N = 16$, $\beta = 0.39 \pm 0.20$, $P = 0.07$). Importantly, because we measured survival and senescence from ages at which sexual traits have already reached their asymptotic values, we avoided the possible confounding effect of age-specific relationships between our measures of sexual competition and survival. We identified the main male mating tactic of the species as territoriality, tending, or harem-holding following Clutton-Brock's (1989) classification. In territorial species, males defend territory for a variable duration (from the period of rut to all the year along) that includes part or totality of female home ranges. On the other hand, tending males range widely in search of estrous females. Harem-holders defend access to a group of females rather than to an area (Clutton-Brock 1989). It is noteworthy that data quality and phenotypic variation across environmental conditions (e.g., SSD: Leblanc et al. 2001) or geographical areas (e.g., testes mass: Firman and Simmons 2008) can influence sexual traits investigated in this study. However, data used in this study corresponded to average values of sexual traits measured on several males across several populations. They thus reflect the average value of the species phenotype for these traits. Similarly, although mating tactics of males can vary at the intraspecific level among populations, within populations, and even for a given male (see Lott 1991 for a review), it was possible to identify a dominant mating tactic for all species.

Finally, because there is now good evidence that measure of longevity and senescence are correlated with the pace of life in mammalian species (Jones et al. 2008), we computed generation time as a proxy of species position along the slow–fast continuum (Gaillard et al. 2005). Indeed, species can be ranked along a slow–fast continuum, where fast species have (compared with slow species) a substantial allocation to reproduction early in life, a short generation time, and a steep rate of senescence (Stearns 1992). To estimate generation time, we built Leslie matrix models with complete information about age-specific reproduction and survival for all species. We used a prebreeding census matrix type in which the first row includes age-specific recruitment (i.e., the product between the probability of a female of age x to give birth, the number of females produced at birth by a female of age x, and the survival probability of females produced at birth by a female of age x to survive to 1 year of age) and the subdiagonal includes age-specific survival starting with the survival of females between 1 and 2 years of age in the first column of the second row (see Caswell 2000 for further details). Finally, we calculated the elasticity of each matrix element and calculated generation times as the mean weighted age of females that give birth (sensu Leslie 1966) as the inverse of the sum of the elasticities of the recruitment parameters (i.e., the inverse of the sum of elasticities of the matrix elements in the first row) as advocated by Brooks and Lebreton (2001).

Overall, we collected information on male median lifespan and actuarial intensity of senescence for 25 species of large herbivores including 17 Bovidae and 8 Cervidae and on male relative adult survival and actuarial senescence for 24 species (17 Bovidae and 7 Cervidae). We obtained body masses and mating tactics for all species in our data set ($N = 25$). However, information on male weapons length and testes mass were more limited (21 and 16 species, respectively). All data and associated references are reported in Tables S1 and S2 (see supplementary information).

Data analysis

We used a comparative method to account for phylogenetic dependence among species that occurs in response to shared ancestry (Harvey and Pagel 1991). First, we constructed a phylogenic tree of all species included in our database from the phylogenetic super-tree of mammals published by

Bininda-Emonds et al. (2007), which provides information on both topology and branch length. We then performed the analysis by using phylogenetic generalized least-squares models (PGLS) following the procedure implemented in R by Gage and Freckleton (2003), using a variance–covariance matrix extracted with APE (Paradis et al. 2004). This statistical method provides an estimate of the phylogenetic signal (named "λ"), which is further introduced into the analysis to control for the phylogenetic dependence (Freckleton et al. 2002). When the λ value was not different from 0, we used multiple regression without correcting for phylogeny (Revell 2010).

In the present study, we first used paired t-tests to compare differences between males and females in their median lifespan and actuarial intensity of senescence to test the expectation that males suffer from a lower adult survival and a stronger senescence than females. Then we ran a series of PGLS to assess how male and sex bias in median lifespan and actuarial intensity of senescence changed with variation in male allocation to sexual competition. Because the number of species with simultaneous information on body mass, weapon size, and testes mass was low ($N = 13$ species), we analyzed these sexual traits in a series of separate models to avoid the risk of model overparameterization. In all models fitted, male absolute or relative survival and senescence were included as dependent variables, and sexual traits associated with "mating type," "weapon type," or "quality" terms were included as independent variables. To avoid the use of residuals that can lead to bias estimates (Freckleton 2002, 2009), we analyzed SSD by adding both male and female body mass in the models, weapon size dimorphism by adding both male and female weapon size in the models, and relative testes mass by adding testes mass and male body mass in the models. All variables were log-transformed except male and female weapon size, where we used the transformation $\log(x + 1)$ to account for the possible absence of weapons in females (see Bro-Jørgensen 2007). Because the intensity of senescence is expected to be shaped by the species-specific pace of life (Gaillard et al. 2005; Jones et al. 2008), generation time was included as an independent variable in these models to correct for this confounding effect. However, we kept generation time in the models only when it improved the fit of the model compared with the constant model. Best models were selected based on the Akaike's information criterion corrected (AICc) for small sample size. We calculated AICc weights (w_i) to assess the relative likelihood of each model to be the best among all the fitted models (Burnham and Anderson 2002). We selected the model with the lowest AICc as the best model. When the difference of AICc (noted △AICc) of 2 competing models was within 2 units, we retained the simplest model to satisfy parsimony rules. Analyses were performed with R version 2.12.1 (R Development Core Team 2011), and parameter estimates are given ±SE.

RESULTS

Between-sex differences in median lifespan and intensity of senescence

We first compared male and female median lifespan using age when 50% of an initial cohort is still alive and we found that males have, on average, a lower adult survival than females (male: 6.21 ± 2.98 years, female: 8.02 ± 3.40 years; $t_{23} = -4.39$; $P < 0.001$) with a difference of 1.81 ± 2.54 years. Male intensity of senescence was also higher than female intensity of senescence (male: 4.17 ± 1.56 years, female: 5.27 ± 2.23 years; $t_{19} = -3.26$; $P = 0.004$).

Median lifespan and senescence intensity of males

As in all models, λ was rather low (<0.01; Table S3); we presented the results of linear regressions without correcting for phylogeny. However, it is noteworthy that all results were qualitatively the same with or without correcting for phylogeny (see Table S3).

The best model of variation in male median lifespan in relation to SSD was the model including generation time only ($w_i = 0.49$; Table 1), revealing a positive relationship between these 2 traits ($N = 25$, $\beta = 0.65 \pm 0.27$, $P = 0.02$; Figure 1). For the weapon size dimorphism and relative testes mass analysis, best models only included generation time, although according to parsimony rules, this model did not really improve the fit compared with the constant model (Table S4). Male median lifespan was not influenced by allocation to pre- or postcopulatory competition because any of the sexual traits investigated had a detectable effect on the male median lifespan (Table 1, Table S5). Similar to male median lifespan, male intensity of senescence was not related to any aspect of male allocation to pre- and postcopulatory competition considered in this study because models selected were in all cases constant models (Table 1, Table S4).

Sex bias in median lifespan and senescence intensity

In most of the models reported in these analyses, λ values were also quite low (Table S5). We, thus, also reported only

Table 1

Summary of the selected models explaining male median lifespan and male intensity of senescence

Models	Selected model variables	Male median lifespan			
		k	Deviance	AICc	w_i
SSD ($N = 25$)	Generation time	4	27.72	34.86	0.49
Weapon size dimorphism ($N = 21$)	Constant	5	23.64	28.31	0.30
Relative testes mass ($N = 16$)	Constant	3	17.5	22.42	0.42

Models	Selected model variables	Male intensity of senescence			
		k	Deviance	AICc	w_i
SSD ($N = 25$)	Constant	3	26.80	31.35	0.33
Weapon size dimorphism ($N = 21$)	Constant	3	19.54	24.21	0.43
Relative testes mass ($N = 16$)	Constant	3	15.46	20.38	0.41

k represents the number of parameters in the model and N the number of species. A summary of all models fitted can be found in supplementary data (Table S4).
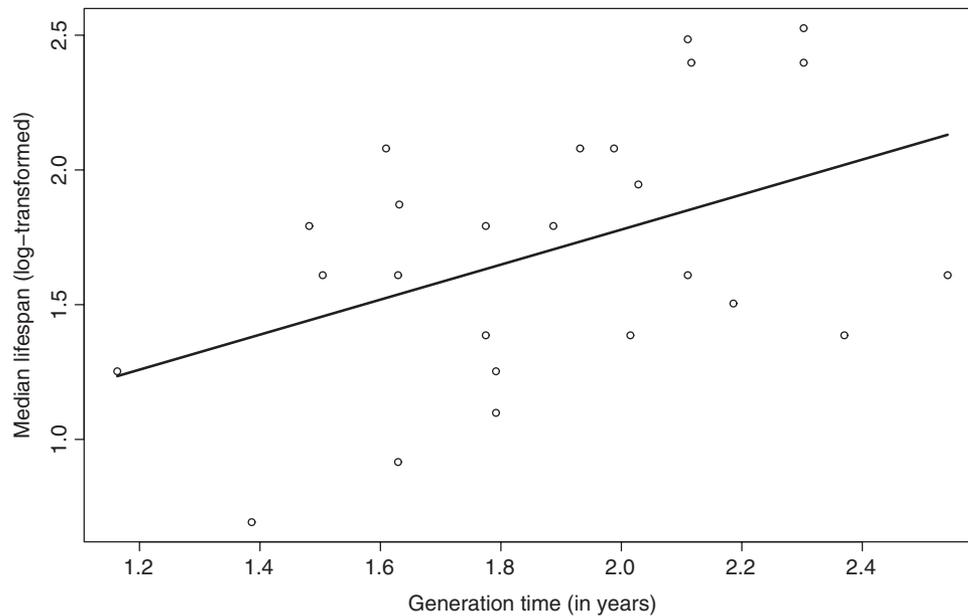
Figure 1
Relationship between male median lifespan (log-transformed) and generation time (log-transformed) in 25 species of large herbivores.

results from the analyses without correcting for phylogeny. Again, analysis including correction for phylogeny led to similar results (see Table S5). As for male median lifespan, none of the measure of male allocation to precopulatory sexual competition had any effect on sex bias in median lifespan (Table 2, Table S6) and the best model of observed variation in sex bias in median lifespan was the model including "weapon type" only (Table 2, Table S6). Indeed, between-sex differences in median lifespan were, on average, higher in species bearing antlers (Cervidae) than in species bearing horns (Bovidae) ($N = 24$; Cervidae: 3.82 ± 2.79, Bovidae: 0.98 ± 1.97, $P = 0.02$). Similar to sex bias in median lifespan, the sex bias in relative senescence intensity was not related to male allocation to pre- and postcopulatory competition because in the 3 cases, constant models were retained (Table 2, Table S6).

DISCUSSION

In mammals, there is now compelling evidence that males suffer from a stronger intensity of senescence than females (see example in Introduction). These between-sex differences have been assessed using a wide range of metrics and statistical approaches (e.g., Toïgo and Gaillard 2003; Clutton-Brock and Isvaran 2007), and the innovative method applied in this study on an extended data set provides similar results than previous methods, with a higher intensity of actuarial senescence found in males compared with females. Moreover, from our sample of 24 species, we found that the male median lifespan is reached 1.81 years earlier than females. In other words, males have a lower adult survival than females. As for other metrics of senescence (e.g., Jones et al. 2008; Péron et al. 2010), we found that median lifespan decreases with faster pace of life of the species. Generation time is a good proxy of mammalian pace of life (Gaillard et al. 2005) and our results emphasize the importance of correcting for the species position along the slow–fast continuum when looking for relationships among life-history traits in mammals. Conversely, our results do not suggest that data quality influenced the results because none of the metrics of lifespan and intensity of senescence we used differs between longitudinal and cross-sectional studies.

Table 2

Summary of the selected models explaining sex bias in median lifespan and sex bias in intensity of senescence

Models	Selected model variables	Sex differences in median lifespan			
		k	Deviance	AICc	w_i
SSD ($N = 24$)	Weapon type	4	2.34	10.14	0.62
Weapon size dimorphism ($N = 20$)	Weapon type	4	1.62	9.12	0.51
Relative testes mass ($N = 15$)	Weapon type	4	−4.44	3.74	0.87
Models	Selected model variables	Sex differences in intensity of senescence			
		k	Deviance	AICc	w_i
SSD ($N = 20$)	Constant	3	−7.18	−2.48	0.43
Weapon size dimorphism ($N = 16$)	Constant	3	−20.3	−15.38	0.41
Relative testes mass ($N = 12$)	Constant	3	−2.24	3.08	0.63

k represents the number of parameters in the model and N the number of species. A summary of all models fitted can be found in supplementary data (Table S6).

Male allocation to precopulatory sexual competition is often evoked to explain male bias in survival or intensity of senescence of mammals (e.g., Promislow 1992; Clutton-Brock and Isvaran 2007). Surprisingly, our results suggest that allocation to precopulatory competition does not explain either male or between-sex differences in adult median lifespan and actuarial senescence intensity (with and without correction for the pace of life). Therefore, we found no evidence that high allocation to body mass or weapon size is costly for males in terms of lifespan or intensity of senescence. These results are in accordance with Toïgo and Gaillard (2003) who found no relationship between SSD and adult survival in ungulates. One possible explanation for the absence of relationships is that although well correlated with the individual reproductive success (Pemberton et al. 1992; McElligott et al. 2001; Coltman et al. 2002), SSD and weapon size dimorphism might not be the best descriptors of intensity of precopulatory sexual competition in any species of large herbivores. Using 10 vertebrate species, Clutton-Brock and Isvaran (2007) recently found a positive relationship between the magnitude of sex differences in life expectancy and the magnitude of sex differences in the duration of effective breeding. In other words, males that face a strong competition for breeding opportunities experience a short duration of effective breeding (compared with conspecific females) and have a low life expectancy (also compared with conspecific females) (Clutton-Brock and Isvaran 2007). Therefore, the duration of effective breeding that represents the life period over which individuals are likely to breed successfully (Clutton-Brock and Isvaran 2007) might be a better indicator of the intensity of precopulatory sexual competition than body mass or weapon size dimorphism. However, to some extent, we could predict that duration of effective breeding should correlate well with the level of sexual dimorphism because there is good evidence that male body mass and weapon size evolved with the level of sexual competition (Pérez-Barbería et al. 2002; Bro-Jørgensen 2007). Unfortunately, information on male duration of effective breeding is scarce (as it requires age-specific reproductive success data) and was therefore unavailable for the vast majority of the species included here. However, using the available information (see Clutton-Brock and Isvaran 2007), we observed only little difference in the duration of effective breeding between *C. elaphus* (6.67 years) and *O. aries* (6.82 years), whereas *C. elaphus* is much more dimorphic in body mass than *O. aries* (Table S2), which might suggest why the use of these variables lead to contrasted results.

Until now, the effect of postcopulatory competition on lifespan and intensity of senescence in mammals has remained untested. Contrary to the expectation, we did not provide any evidence that allocation by males to testes mass was associated with a lower median lifespan or a more intense senescence in males and cannot therefore explain the variability of sex bias in median lifespan and actuarial intensity of senescence we observed among species of large herbivores. These results differ from the results for birds for which a positive association between sex-biased mortality and relative testis size was reported (Liker and Székely 2005). This difference between the 2 groups is surprising because the relative testis size of both mammals and birds has evolved in response to the level of sperm competition (see Pitcher et al. 2005 for birds and Soulsbury 2010 for mammals). However, there is now evidence that birds and mammals differ in some aspects of testes physiology such as daily sperm production rate, which is higher for birds (see Lüpold et al. 2011). If sperm production rate correlates with oxidative damage in the soma, this could potentially explain why relative testis size is associated with sex-biased mortality rates in birds but not in mammals.

Moreover, birds face specific physiological costs due to flying constraints and are more limited than mammals in their allocation to body mass. These physiological constraints might reinforce the cost of sperm production through heavy testes and lead to a stronger impact on male median lifespan and actuarial intensity of senescence in birds than in mammals. Finally, it is important to note that the comparative study in birds (Liker and Székely 2005) encompassed a large range of taxonomic orders and included many more species than our study focusing on a single order of mammals.

Mating tactics did not influence male and sex bias in actuarial intensity of senescence. This is surprising regarding the fact that the intensity of sexual competition is expected to be stronger in female defense group. However, this result is in accordance with Toïgo and Gaillard (2003) who did not report any difference in male-biased prime-age mortality between species with distinct mating tactics. High plasticity in male mating tactics (Lott 1991) might also explain our results. For instance, red deer males can shift from defense of harem to defense of territories according to the presence of defendable resources in the environment (Carranza et al. 1995; see also Apollonio et al. 1992 for an example in fallow deer, *D. dama*), which makes it difficult to relate an ungulate species with a clearly defined mating tactic. However, the use of mating tactic rather than mating system is justified in ungulates because in this group, most species are polygynous (Clutton-Brock 1989). Thus, the level of male allocation to sexual competition might be less variable between mating tactics than between mating systems, which might explain why we did not detect an effect of mating tactic on male and sex bias in median lifespan or intensity of senescence. The same reasoning can be applied to the absence of relationship between sex-biased survival and SSD. Indeed, sexual dimorphism is high and much less variable among polygynous mammals than across all mammals. In other words, allocation to sexual competition might have different costs between monogamous and polygynous species (although this was not supported by data on mammal and bird mating systems provided in Clutton-Brock and Isvaran 2007), but within a given mating system other ecological factors might be better predictors of sex-specific survival or intensity of senescence (see also Plard et al. 2011). For instance, sex bias in median lifespan and intensity of senescence might be caused by susceptibility to high population density in males but not in females (Leblanc et al. 2001; Bonenfant et al. 2009).

Finally, we found higher sex bias in median lifespan in Cervidae than in Bovidae but the male median lifespan did not differ between these 2 groups. This suggests that female median lifespan might be higher in Cervidae than in Bovidae. However, sample size differed strongly between these 2 groups (7 Cervidae and 17 Bovidae) and in the Yellowstone population of elk (*Cervus canadensis*) used in our study (Houston 1982), females survived extremely well (compared with other ungulate populations), which might explain our results.

CONCLUSION

Overall, our study reveals that males have a lower median lifespan and a stronger actuarial intensity of senescence than females. However, these differences were not explained by male allocation to sexual competition, which questions the idea that allocation to these phenotypic attributes constitutes a substantial investment (sensu Trivers 1972), which has often been assumed in sexual selection studies but seldom documented in vertebrates (Kotiaho 2001). Indirectly, our results provide no convincing support to the disposable soma theory (Kirkwood 1977) because our findings do not support

a trade-off between an allocation to sexual competition and an early death or stronger senescence. However, it is possible that physiological costs of reproduction (not encompassed by our measure of sexual competition) or sensitivity to environmental conditions might be responsible for the differences in survival and senescence intensity found between males and females in large herbivores.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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