



Contents lists available at ScienceDirect

Experimental Gerontology

journal homepage: [www.elsevier.com/locate/expgero](http://www.elsevier.com/locate/expgero)

# Males do not senesce faster in large herbivores with highly seasonal rut

**Q1** Morgane Tidière <sup>a,\*</sup>, Jean-Michel Gaillard <sup>a,b</sup>, Dennis W.H. Müller <sup>c</sup>, Laurie Bingaman Lackey <sup>d</sup>, Olivier Gimenez <sup>e</sup>,  
**3** Marcus Clauss <sup>f</sup>, Jean-François Lemaître <sup>a,b</sup>

**Q2** <sup>a</sup> Université de Lyon, F-69000 Lyon, France

<sup>b</sup> Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France

<sup>c</sup> National Park "Bavarian Forest", Freyunger Str. 2, 94481 Grafenau, Germany

<sup>d</sup> 1230 Oakland Street, Hendersonville, NC, USA

<sup>e</sup> UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, campus CNRS, 1919 route de Mende, 34293, Montpellier Cedex 5, France

**Q3** <sup>f</sup> Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland

## ARTICLE INFO

### Article history:

Received 21 May 2014

Received in revised form 3 November 2014

Accepted 4 November 2014

Available online xxxx

Section Editor: Holly M Brown-Borg

### Keywords:

Aging

Captivity

Ruminants

Mating season

Sexual selection

## ABSTRACT

Patterns of actuarial senescence vary among long-lived species. A proposed explanation of the evolution of species-specific senescence patterns is that increased levels of energy allocation to intra-male competition decrease the amount of energy available for somatic maintenance, leading to earlier or faster actuarial senescence. Previous studies did not provide support for such relationships, but did not focus on the intensity of allocation likely to shape inter-specific variation in actuarial senescence in males. Here, by analyzing data from 56 species of captive large herbivores, we tested whether actuarial senescence is more pronounced in species displaying a well-defined 'rut' period than in species with year-round reproduction. Using an original quantitative metric of the annual duration of reproductive activity, we demonstrated that the length of the mating season has no detectable effect on actuarial senescence. On the other hand, both diet and body mass are important factors shaping actuarial senescence patterns in male captive herbivores.

© 2014 Published by Elsevier Inc.

## 1. Introduction

**Q4** Recent long-term studies have reported evidence of actuarial senescence (i.e. the decrease in survival with increasing age) in most species of vertebrates analyzed to date (Nussey et al., 2013). However, such senescence patterns are highly variable across species (Péron et al., 2010; Ricklefs, 2010; Lemaître et al., 2013) and identifying the factors shaping inter-specific variation in senescence patterns has become a key issue in evolutionary biology (Jones et al., 2014). For instance, it has been shown that species with a slow pace of life have slower senescence than species with a fast pace of life (Jones et al., 2008; Péron et al., 2010; Ricklefs, 2010). However, only a few studies have investigated species-specific variation in actuarial senescence patterns *sensu stricto*. Instead the majority of studies have looked at between-species variation in longevity (e.g. De Magalhães and Costa, 2009; Stuart and Page, 2010;

Bro-Jørgensen, 2012; Wilder et al., 2012; Healy et al., 2014). Although such studies have provided important insights into the ecological and physiological factors leading to substantive mortality costs, they do not shed light on how such factors impact the progressive decline in survival with increasing age.

Ecological factors or evolutionary processes such as sexual selection have been suggested to shape between-species differences of actuarial senescence. In polygynous species of vertebrates, the intensity of sexual selection is expected to be stronger in males than in females. While most adult females of these species produce offspring during their lifetime, a much lower proportion of adult males mate during their lifetime (Clutton-Brock, 1988; Shuster and Wade, 2003) because males face strong competition in securing mating opportunities (Andersson, 1994). In mammals, the allocation of resources to sexual competition by males can occur through different pathways. For example, the growth of secondary sexual traits such as weapons, that generally involves increased body mass (Lemaître et al., 2014) and associated behaviors increase success in intra-sexual competition, and are thereby subject to strong sexual selection pressures (Weckerly, 1998; Bro-Jørgensen, 2007; Lindenfors, 2007; Plard et al., 2011). Males sexually selected to allocate heavily

\* Corresponding author.

E-mail address: [morgane.tidiere@univ-lyon1.fr](mailto:morgane.tidiere@univ-lyon1.fr) (M. Tidière).

to intra-sexual competition should increase their chances of reproducing, but in return are expected to experience an earlier or faster senescence (Bonduriansky et al., 2008).

In large herbivores, neither sexual size dimorphism, mating system, or weapon or testes size relative to body mass have been reported to influence between-species differences in actuarial senescence (Lemaître and Gaillard, 2013). Thus, there is yet no published evidence that variation in male allocation in sexual competition across species accounts for species-specific adult survival and intensity of actuarial senescence in mammals.

Until now, only costs associated with expressing primary (testes) or secondary (body mass dimorphism, weapons/ornaments) sexual traits and the effects of mating systems (i.e. polygyny vs. monogamy) have been investigated. However, the physiological adaptations linked to time constraints of the mating season could also play an important role in shaping senescence patterns. Indeed, a short and well-defined rut may be associated with a disproportionately high energetic allocation to mating activities, which might translate into a faster senescence. In support of the existence of time constraints, Clutton-Brock and Isvaran (2007) showed that the duration of 'effective breeding' (measured as the number of years over which individual males can mate successfully) was shortest in polygynous species with a shorter longevity compared to males of monogamous species. However, this measurement did not account for possible time constraints within the yearly reproductive cycle. The duration of the species-specific mating season provides a relevant measure to define intensity of energy allocation to mating. In species with short mating seasons, male breeding behavior including fights between males are concentrated, potentially leading to a rapid accumulation of physical damage causing an immediate decrease in a male's ability to win male-male competition and a possible progressive decrease in survival probabilities over life (Bonduriansky et al., 2008). The length of the mating season varies widely across mammal species, from a short and well-defined rut (e.g. caribou *Rangifer tarandus*) to year-round mating with no clear 'rutting period' (e.g. American bison *Bison bison*) (Zerbe et al., 2012). Typically, in species with a short rut, males utilize all energy required for mating within a few weeks, rapidly losing body reserves accumulated prior to the rut (McElligott et al., 2003; Mysterud et al., 2003). For instance, Bobek et al. (1990) reported a 40% decrease in total body mass during the 30 days rut in red deer (*Cervus elaphus*). If rutting takes place in the dormant vegetation period (winter), as it does for mountain ungulates in temperate ecosystems such as chamois (*Rupicapra rupicapra*) or ibex (*Capra ibex*), body reserves accumulated prior to the rut have to be large enough to cover not only the costs of rutting but also to allow survival over the critical winter season. If not, losing body mass prior to the winter in temperate ecosystems is likely to lead to the death of many males at the end of the winter (Clutton-Brock et al., 1982). Moreover, males in species with short ruts cease foraging during the rut (French et al., 1960; Clutton-Brock et al., 1982) due to hormonal changes, of which inappetence is a side effect (e.g. McMillin et al., 1980, for White-tailed deer *Odocoileus virginianus*; Suttie and Kay, 1985, for Red deer *C. elaphus*; Miquelle, 1990, for moose *Alces alces*; Suttie et al., 1992, for Reindeer *R. tarandus*; Newman et al., 1998; Apollonio and Di Vittorio, 2004, for Fallow deer *Dama dama*). Thus, a short and intense rutting period is expected to be associated with metabolic costs for males that, when averaged over the year, surpass those of males from species with extended mating periods. Males of the former species should then pay the cost by showing faster senescence.

We aimed to test this hypothesis of faster actuarial senescence of males in species with short rut periods using data for 56 species of large herbivores kept in captivity. The protected conditions of life in captivity should minimize mortality due to environmental causes such as predation and climatic harshness (Bro-Jørgensen, 2012; Valcu et al., 2014) as well as mortality due to intra-specific

aggression, and may thereby better allow identifying differences in senescence caused by species-specific seasonal metabolic programs. In addition, the mating season length is highly constrained within species. Indeed, several studies have shown that the mating season was of similar length in captive and free-ranging populations of the same species. Thus, Zhang et al. (2000) demonstrated that several years after being brought into captivity, Sichuan Golden monkeys (*Rhinopithecus roxellana*) continued to mate and give birth at the same time as free-ranging populations. Likewise, Urian et al. (1996) reported that the seasonality of reproduction of bottlenose dolphins (*Tursiops truncatus*) was not affected by captivity, De Vleeschouwer et al. (2003) found the same peak of births in September–October in both captive- and wild-born females of Golden-Headed Lion Tamarins (*Leontopithecus chrysomelas*), and Spady et al. (2007) did not find any difference between the mean or median dates of parturition between captive and wild females in eight species of Ursidae. For ruminants, Zerbe et al. (2012) demonstrated that captivity did not convert seasonal breeders into aseasonal ones, and that the difference in the timing of the rut between free-ranging and captive populations corresponded to the mean difference in photoperiod between the zoos and the natural habitat. The available evidence clearly indicates that reproductive seasonality is not markedly modified by captivity in ruminants, which allows us to reliably use data from captive populations to assess the length of the mating season. We thus tested the expectation that, across species, senescence should speed up with decreasing length of the mating season due to increased metabolic costs putatively associated with short rutting periods.

## 2. Material and methods

### 2.1. Dataset

We obtained data on survival and seasonal timing of the rut for males of 56 species of ruminants living in captivity from the database International Species Information System (see also Müller et al., 2011; Lemaître et al., 2013), which collects data since 1973, from 850 member institutions (zoos, national parks) in over 80 countries. Information such as sex and dates of birth and death are available for each individual. Assuming that the total number of individuals living in zoos for a given species corresponds to a worldwide meta-population, we computed population parameters for species living in captivity. We only used cohorts of animals for which both dates of birth and death were known, which implies that animals were born in captivity. Importantly, although differences in veterinary care might differ between zoos, several different species are kept at any one institution, and all species are kept at more than one institution, which buffers the effect of health care provided on animals in the following inter-specific analyses. The complete dataset included data for 95 species of ruminants; however, we kept only species for which at least 25 individuals were alive at 1 year of age ( $N = 56$  species) to get accurate estimates of age-specific survival during adulthood.

### 2.2. Metrics

We measured species-specific patterns of actuarial senescence for males by using two metrics; the age at the onset of senescence and the rate of senescence (all data are provided in Table A). The age at the onset of senescence was estimated as the age at which mortality rate was the lowest (Jones et al., 2008). However, to avoid biased estimates caused by a small number of old individuals, we restricted the range of ages to the first two thirds of the maximum lifespan recorded for a male in a given species (see Fig. A for an example). Then, we measured the actuarial senescence rate as the proportional decrease of survival between 6 and 9 years of age. 201

**Table 1**

Parameter estimates from the models selected to account for among-species variation observed in the onset and rate of actuarial senescence in male captive ungulates. For the rate of senescence  $\lambda$  was statistically different from 0, so parameters were estimated with models accounting for phylogeny. For the onset of senescence, phylogeny had no statistically significant effects and parameters were thus estimated without any phylogenetic correction.

	Variables	$\beta$	95% CI	t	Adjusted R <sup>2</sup>	$\lambda$
Onset of senescence (N = 56)	Body mass	0.096	0.021; 0.170	2.51	0.088	<0.001
Rate of senescence between 6 and 9 year-olds (N = 55)	Body mass	−0.033	−0.059; −0.006	−2.40	0.084	0.910*

$\beta$ , estimate; CI, confidence interval;  $\lambda^*$ , significantly different from 0.

We chose these age thresholds based on detailed analyses of age-specific variation in intensively monitored populations of large herbivores (e.g. Loison et al., 1999; Festa-Bianchet et al., 2003; Gaillard et al., 2004; Toigo et al., 2007). As male Saiga (*Saiga tatarica*) had all died by 9 years of age, our dataset for the rate of actuarial senescence between 6 and 9 years of age included 55 species. Moreover, we assessed the robustness of our results to age thresholds by testing the potential effect of mating season length on senescence rates between 9 and 12 years of age as well as between 6 and 12 years of age. Results based on these latter thresholds were similar to those obtained when using 6 and 9 years of age and are reported in Table B.

The length of the mating season was obtained using the birth timing period in days (the time during which 80% of births occur, data from Zerbe et al., 2012) as a proxy, assuming that gestation time is constant for a given species (see Table C). In addition, to account for the possibility that mating costs are restricted to a shorter period around the rut peak, we performed the analyses using the time during which 50% of births occurred (Zerbe et al., 2012). The results remained unchanged, indicating our results are reliable (See results on Tables D and E). Lastly, to check whether the care provided in captivity via feeding and health influenced the results we reported, we replicated the analyses using information from 16 free-ranging populations of large herbivores from which data were available (see data on Table F and Lemaître et al., 2013).

In the analyses described below, we controlled for possible confounding factors previously reported to influence actuarial senescence in captive large herbivores. First, we included body mass as a covariate to control for the allometric relationship linking body mass and senescence in large herbivores. The average species-specific body mass was recovered from the literature (see Table C). Second, we included the species-specific percentage of grass in the natural diet (extracted from Zerbe et al., 2012) that has been shown to be negatively associated with the rate of senescence across species of captive ruminants (Müller et al., 2010; Lemaître et al., 2013; See Table C). Moreover, including diet as a covariate in the analyses controls for the effect of captivity, possibly also including veterinary treatment (Lemaître et al., 2013).

### 2.2.1. Statistical analysis and phylogeny

To avoid biased assessment of the focal relationships due to phylogenetic dependence among species, we controlled for in all analyses the non-independence between species due to shared ancestry using phylogenetic generalized least-squares (PGLS) models. The PGLS method provides an estimate of phylogenetic signal “ $\lambda$ ”, which in most cases, varies between 0 (phylogenetic independence) and 1 (species' traits co-vary in direct proportion to their shared evolutionary history). When  $\lambda$  is not statistically different from 0, the phylogeny does not have any effect on the focal relationships and a linear regression without correcting for phylogeny can be safely used instead (Revell, 2010). In this study, we built a phylogeny of 56 species of large herbivores using a phylogenetic super-tree of mammals (see Fig. B) published by Bininda-Emonds et al. (2007, 2008). To confirm the accuracy of our

results, we performed all analyses with another phylogenetic tree (Agnarsson and May-Collado, 2008) and results were qualitatively similar (not shown). We performed these analyses using the R-package *caper* (Orme, 2012).

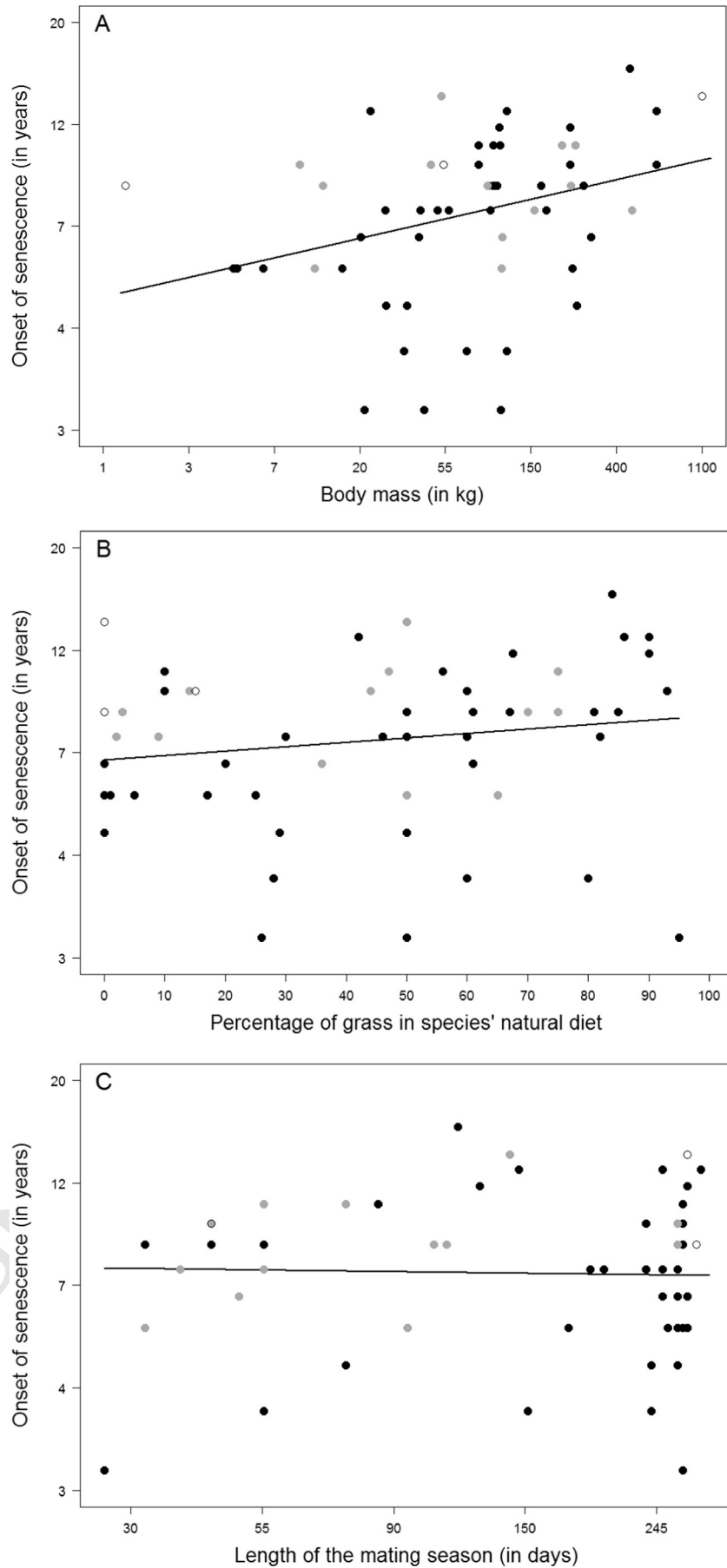
Finally, to select the best model for each metric of actuarial senescence, we used a model selection procedure based on Akaike Information Criterion (AIC, Burnham and Anderson, 2002). Dependent variables included the onset of senescence and the rate of senescence measured between 6 and 9 years of age. The full models included diet, body mass, and the length of the mating season as independent variables. Log-transformation (on a neperian scale) was applied to all variables except diet to improve the normality of the distribution. Moreover, as male American bison (*B. bison*) displayed a rate of senescence of zero (i.e. no individual died between 6 and 9 years of age), we used the log-transformation of (rate of senescence + 1) for all species. For each dependent variable, we retained the model with the lowest AIC. However, when the difference of AIC between competing models was less than 2, we retained the simplest model to satisfy parsimony rules (Burnham and Anderson, 2002). In addition, we calculated the AIC weight ( $w_i$ ) to measure the relative likelihood of each model to be the best among the set of fitted models. We performed these analyses with R version 2.14.0 (R Development Core Team, 2011) and parameter estimates are given  $\pm$  SE.

## 3. Results

We found a strong phylogenetic signal in the rate of male actuarial senescence between 6 and 9 years of age ( $\lambda = 0.91$ ; Table 1). We thus used a PGLS method to analyze variation in the rate of senescence. We did not find any phylogenetic signal in the onset of senescence (Table 1) and we thus used linear regressions without phylogenetic correction for this trait.

The model selected for the onset of actuarial senescence included only body mass ( $w_i = 0.45$ ; Table G). As expected, the onset of male actuarial senescence was delayed in larger species (Table 1, Fig. 1A). However, the model with a difference of 1.86 units of AIC ( $w_i = 0.18$ ; Table G) included additional positive effects of diet ( $\beta = 0.0006 \pm 0.0001$ ) indicating that male actuarial senescence was also delayed when the percentage of grass in the natural diet was higher (Fig. 1B). In contrast, the length of mating season did not influence the onset of actuarial senescence ( $\beta = 0.007 \pm 0.068$ ; Fig. 1C).

The selected model for variation in the rate of actuarial male senescence only included body mass ( $w_i = 0.22$ ; Table G). The senescence rate decreased with increasing body mass (Fig. 2A). However, the model including additional effects of diet consistently had the highest AIC weights ( $w_i = 0.38$ ; Table G), indicating a strong trend for male actuarial senescence to be faster in species incorporating only a small quantity of grass in their natural diet ( $\beta = -0.0011 \pm 0.0006$ ; Fig. 2B). The length of the mating period did not have any effect on the rate of male actuarial senescence across species ( $\beta = 0.001 \pm 0.028$ ; Fig. 2C). Results remained qualitatively unchanged when we used the number of days around the peak during which 50% of birth





occurred instead of the number of days during which 80% of birth occurred in our analyses (see Tables D and E). Similarly, results obtained from free-ranging populations of ruminants supported results obtained from captive populations (Tables H and I).

As bovids and cervids allocate differently to reproduction traits (Kiltie, 1985), we analyzed bovids separately. As for the entire dataset, the length of the mating season did not have any effect on any senescence metric, while body mass and diet showed similar effects (see Table J).

#### 4. Discussion

Most ungulate species display a clear seasonal pattern of mating, with marked differences in intensity. Likewise, actuarial senescence has been reported repeatedly to occur in ungulates (Nussey et al., 2013). However, whether the length of the mating period influences male actuarial senescence across ruminant species has remained unexplored.

We chose to measure the rate of male actuarial senescence for a given species as the mortality rate between two ages for males to make estimates comparable among species, because survival starts to decrease between 6 and 9 years of age in most species included in our dataset (Gaillard et al., 2000). There are many other ways to measure the rate of actuarial senescence, for example by using the Gompertz rate, which corresponds to the exponential rate of mortality with increasing age (Gaillard et al., 2004). Currently, there is no consensus metric of the rate of actuarial senescence. In fact, in a study of the relationship between predation pressure and senescence in guppies (Reznick et al., 2004), three indices of senescence rates calculated using different methods led to different conclusions (Williams et al., 2006). In contrast, all metrics we used to measure species-specific patterns of actuarial senescence in males of large herbivores provided remarkably similar results, demonstrating the high quality of metrics selected and the robustness of our findings.

Contrary to our predictions, the length of the mating season did not influence male actuarial senescence across species of large herbivores living in captivity. Allocating energy to intra-male competition over a short and intense rut period, therefore, does not lead to a decrease in the quantity of energy available for somatic maintenance. A possible explanation of this result could be that males of seasonal species allocated energy to mate not throughout all the mating season but only during the peak season in order to minimize the overall cost of reproduction. However, analyses made on the number of days during which 50% of births occur, instead of 80%, provided the same results, which suggests no systematic difference in the allocation of energy to reproduction when averaged over a whole year between seasonal and aseasonal breeders. With respect to studies linking senescence to life history (Jones et al., 2008; Péron et al., 2010; Ricklefs, 2010), this result also suggests that the evolution of seasonal reproduction – which has been considered to be a derived trait in ruminants (Zerbe et al., 2012) – is not linked with a change in the overall pace of life in this group. Several other studies have previously failed to detect a cost of displaying sexually selected traits in terms of longevity or adult mortality (Owens and Bennett, 1994; Toigo and Gaillard, 2003) or actuarial senescence (Lemaître and Gaillard, 2013). Therefore, it seems that neither the intensity nor the constraint on the period of energy allocation in intra-male competition has any effect on male patterns of actuarial senescence.

In captivity, year-round ad libitum provision of food and preventive health care could at first sight account for the absence of any effect of male's energy allocation to mating on actuarial senescence. Nevertheless, variation in food intake due to rutting may be also observed in captivity under ad libitum feeding conditions (Suttie and Kay, 1985; Suttie et al., 1992; Newman et al., 1998). If such an influence was found in free-ranging populations, this would have suggested that differences in actuarial senescence between captive and free-ranging populations is due to actual intraspecific male encounters, rather than to physiological mechanisms. However, our results indicate that the same patterns occurred in free-ranging populations of ruminants. Therefore, the absence of costly physiological mechanisms linked to the mating season length on male's actuarial senescence appears as a general pattern in populations of ruminants, whether captive or free-ranging. Actually, although there is evidence for physiological mechanisms that lead to the cessation of food intake during the rut in some seasonally reproducing ruminant species (McMillin et al., 1980; Suttie and Kay, 1985; Miquelle, 1990; Suttie et al., 1992; Newman et al., 1998; Apollonio and Di Vittorio, 2004), investigations performed so far on seasonally reproducing species have reported either a cessation of food intake in relation to the time constraint during the rut (Pelletier et al., 2009; Brivio et al., 2010; Guan et al., 2012; Corlatti and Bassano, 2014; Xia et al., 2014) or no change at all in food intake during the rut (Ding et al., 2012). Thus, the potential absence of a general physiological mechanism across ruminants that regulates food intake during the rut could explain the lack of an effect of the intensity of seasonal reproduction on senescence patterns.

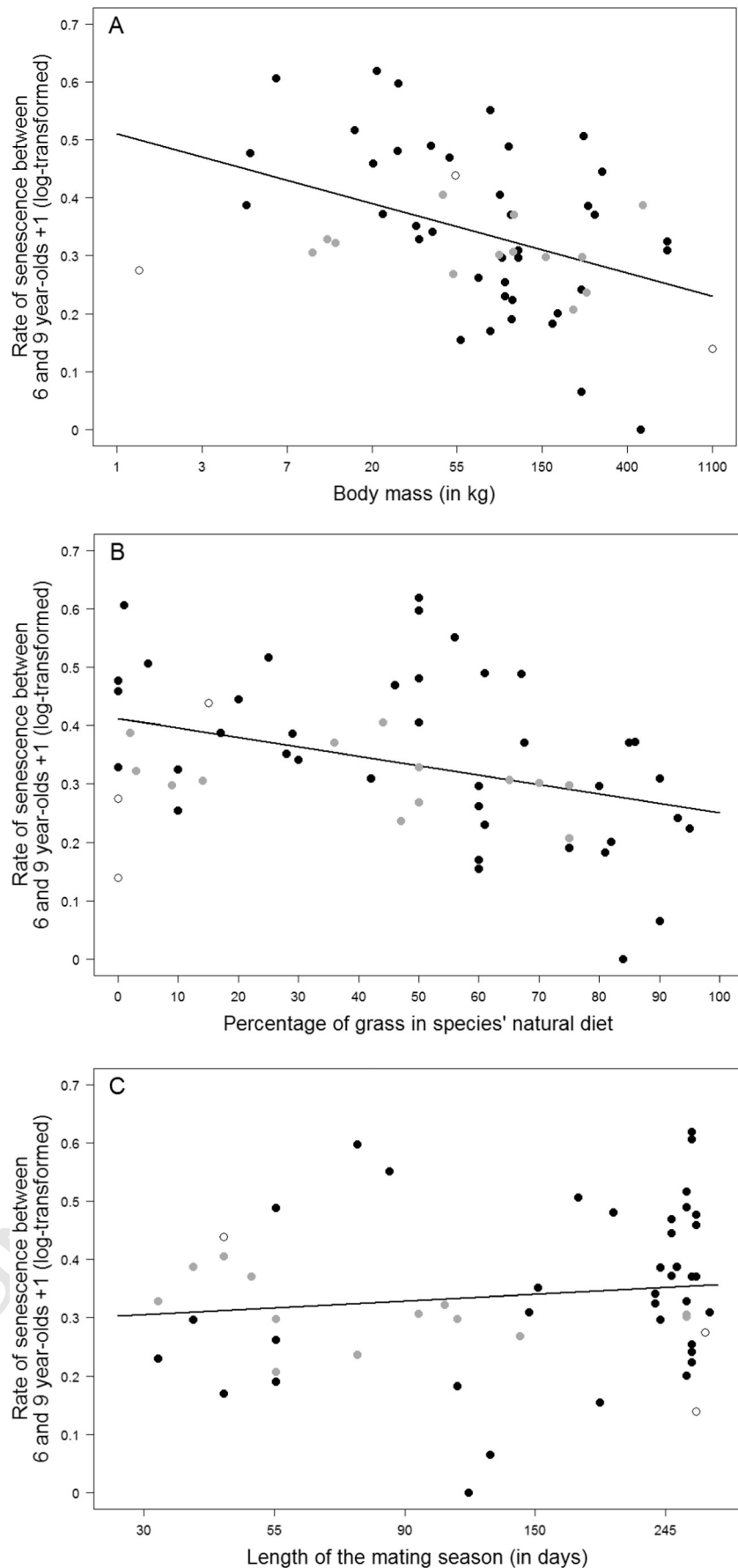
As previously reported, we found that diet tends to influence consistently both the onset and the rate of actuarial senescence in males of captive ungulates. Thus, males of browser species naturally consuming diets with little or no grass tended to senesce faster in captivity than males of grazer species eating mainly grass in natural conditions. This finding mirrors those of Müller et al. (2011) and Lemaître et al. (2013) and suggests that browsers are more difficult to feed and maintain in optimal conditions in captivity. We also found strong evidence that actuarial senescence in males slowed down with increasing body mass across species of large herbivores. This finding is in agreement with Jones et al.'s (2008) results, who reported a direct link between body mass and the intensity of senescence across a selected set of bird and mammal species intensively studied. Our ability to detect previously demonstrated effects of body mass and, to a lesser extent, of diet on actuarial senescence in males across species of ungulates living in captivity, while no influence of the length of the mating season could be detected, allows discarding limitations of our dataset or related to the metrics we used. We can thereby safely conclude that marked among-species differences reflected in the length of the mating season do not influence patterns of male actuarial senescence, at least in this taxonomic group.

According to the findings reported in this study, as well as to results from previous studies (Owens and Bennett, 1994; Toigo and Gaillard, 2003; Lemaître and Gaillard, 2013), the prediction that the intensity of sexual selection pressure should drive observed variation in male actuarial senescence across mammalian species is not supported by currently available data.

#### Acknowledgments

M. Tidière is funded by the Ministry of Education and Research. We are grateful to I. Agnarsson from providing us access to an unpublished

**Fig. 1.** Relationships between the age at the onset of male actuarial senescence and the body mass (A), the percentage of grass in the species' natural diet (B) and the length of the mating season (C) across 56 species of large herbivores in captivity. Bovidæ are indicated in black, Cervidæ in gray and other species (belonging to families of Antilocapridæ, Giraffidæ and Tragulidæ) with an open circle.



phylogenetic tree of ruminants. We warmly thank an anonymous referee for helpful and constructive comments that markedly improved our paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.exger.2014.11.003>.

## References

- Agnarsson, I., May-Collado, L.J., 2008. The phylogeny of Cetartiodactyla: the importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species-level phylogenies. *Mol. Phylogenet. Evol.* 48, 964–985. <http://dx.doi.org/10.1016/j.ympev.2008.05.046>.
- Andersson, M.B., 1994. *Sexual Selection*. Princeton University Press.
- Apollonio, M., Di Vittorio, I., 2004. Feeding and reproductive behaviour in fallow bucks (*Dama dama*). *Naturwissenschaften* 91, 579–584. <http://dx.doi.org/10.1007/s00114-004-0574-0>.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2007. The delayed rise of present-day mammals. *Nature* 446, 507–512. <http://dx.doi.org/10.1038/nature05634>.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2008. The delayed rise of present-day mammals. *Nature* 456, 274. <http://dx.doi.org/10.1038/nature07347>.
- Bobek, B., Perzanowski, K., Weiner, J., 1990. Energy expenditure for reproduction in male red deer: J. Mammal. 71, 230–232. <http://dx.doi.org/10.2307/1382171>.
- Bonduriansky, R., Maklakov, A., Zajitschek, F., Brooks, R., 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol.* 22, 443–453. <http://dx.doi.org/10.1111/j.1365-2435.2008.01417.x>.
- Brivio, F., Grignolio, S., Apollonio, M., 2010. To feed or not to feed? Testing different hypotheses on rut-induced hypophagia in a Mountain ungulate. *Ethology* 116, 406–415. <http://dx.doi.org/10.1111/j.1439-0310.2010.01753.x>.
- Bro-Jørgensen, J., 2007. The intensity of sexual selection predicts weapon size in male bovids. *Evolution* 61, 1316–1326. <http://dx.doi.org/10.1111/j.1558-5646.2007.00111.x>.
- Bro-Jørgensen, J., 2012. Longevity in bovids is promoted by sociality, but reduced by sexual selection. *PLoS One* 7, e45769. <http://dx.doi.org/10.1371/journal.pone.0045769>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, Second edition. Springer.
- Clutton-Brock, T.H., 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. University of Chicago Press.
- Clutton-Brock, T.H., Ivaran, K., 2007. Sex differences in ageing in natural populations of vertebrates. *Proc. R. Soc. B Biol. Sci.* 274, 3097–3104. <http://dx.doi.org/10.1098/rspb.2007.1138>.
- Clutton-Brock, T.H., Albon, S.D., Guinness, F.E., 1982. *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press.
- Corlatti, L., Bassano, B., 2014. Contrasting alternative hypotheses to explain rut-induced hypophagia in territorial male Chamois. *Ethology* 120, 32–41. <http://dx.doi.org/10.1111/eth.12177>.
- De Magalhães, J.P., Costa, J., 2009. A database of vertebrate longevity records and their relation to life-history traits. *J. Evol. Biol.* 22, 1770–1774. <http://dx.doi.org/10.1111/j.1420-9101.2009.01783.x>.
- De Vleeschouwer, K., Leus, K., Van Elsacker, L., 2003. Characteristics of reproductive biology and proximate factors regulating seasonal breeding in captive golden-headed lion tamarins (*Leontopithecus chrysomelas*). *Am. J. Primatol.* 60, 123–137. <http://dx.doi.org/10.1002/ajp.10100>.
- Ding, J., Liu, Z., Song, Y., Zeng, Z., Zhang, Q., Bravery, B.D., 2012. Rut-induced changes in the activity budgets of male tropical ungulates: eld's deer on Hainan Island. *Curr. Zool.* 58, 536–540.
- Festa-Bianchet, M., Gaillard, J.-M., Côté, S.D., 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *J. Anim. Ecol.* 72, 640–649. <http://dx.doi.org/10.1046/j.1365-2656.2003.00735.x>.
- French, C.E., McEwen, L.C., Magruder, N.D., Rader, T., Long, T.A., Swift, R.W., 1960. Responses of white-tailed bucks to added artificial light. *J. Mammal.* 41, 23–29. <http://dx.doi.org/10.2307/1376513>.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toigo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393. <http://dx.doi.org/10.1146/annurev.ecolsys.31.1.367>.
- Gaillard, J.-M., Viallefont, A., Loison, A., Festa-Bianchet, M., 2004. Assessing senescence patterns in populations of large mammals. *Anim. Biodivers. Conserv.* 27, 47–58.
- Guan, T.P., Ge, B.M., Powell, D.M., McShea, W.J., Li, S., Song, Y.L., 2012. Does a temperate ungulate that breeds in summer exhibit rut-induced hypophagia? Analysis of time budgets of male takin (*Budorcas taxicolor*) in Sichuan, China. *Behav. Process.* 89, 286–291. <http://dx.doi.org/10.1016/j.beproc.2011.12.008>.
- Healy, K., Guilleme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D., Kelly, D.J., Donohue, I., Jackson, A.L., Cooper, N., 2014. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B Biol. Sci.* 281, 20140298.

- Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P., Brommer, J., Charmanier, A., Charpentier, M., Clutton-Brock, T., Dobson, F.S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C.G., Lillandt, B.-G., McCleery, R., Merilä, J., Neuhaus, P., Nicoll, M.A.C., Norris, K., Oli, M.K., Pemberton, J., Pietiäinen, H., Ringsby, T.H., Roulin, A., Saether, B.-E., Setchell, J.M., Sheldon, B.C., Thompson, P.M., Weimerskirch, H., Jean Wickings, E., Coulson, T., 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecol. Lett.* 11, 664–673. <http://dx.doi.org/10.1111/j.1461-0248.2008.01187.x>.
- Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren, J.P., Ehrlén, J., García, M.B., Menges, E.S., Quintana-Ascencio, P., Caswell, H., Baudisch, A., Vaupel, J.W., 2014. Diversity of ageing across the tree of life. *Nature* 505, 169–173. <http://dx.doi.org/10.1038/nature12789>.
- Kiltie, R.A., 1985. Evolution and function of horns and hornlike organs in female ungulates. *Biol. J. Linn. Soc.* 24, 299–320. <http://dx.doi.org/10.1111/j.1095-8312.1985.tb00377.x>.
- Lemaître, J.-F., Gaillard, J.-M., 2013. Male survival patterns do not depend on male allocation to sexual competition in large herbivores. *Behav. Ecol.* 24, 421–428. <http://dx.doi.org/10.1093/beheco/ars179>.
- Lemaître, J.-F., Gaillard, J.-M., Bingham Lackey, L., Clauss, M., Müller, D.W.H., 2013. Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Exp. Gerontol.* 48, 162–167. <http://dx.doi.org/10.1016/j.exger.2012.12.004>.
- Lemaître, J.-F., Vanpe, C., Plard, F., Gaillard, J.M., 2014. The allometry between secondary sexual traits and body size is nonlinear among cervids. *Biol. Lett.* 10. <http://dx.doi.org/10.1098/rsbl.2013.0869> (20130869-20130869).
- Lindfors, P., 2007. *Sexual size dimorphism in mammals. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford University Press, Oxford, pp. 16–26.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., Jullien, J.-M., 1999. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80, 2539–2554. [http://dx.doi.org/10.1890/0012-9658\(1999\)080\[2539:ASSIFP\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1999)080[2539:ASSIFP]2.0.CO;2).
- McElligott, A.G., Naulty, F., Clarke, W.V., Hayden, T.J., 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* 5, 1239–1250.
- McMillin, J.M., Seal, U.S., Karns, P.D., 1980. Hormonal correlates of hypophagia in white-tailed deer. *Proc. R. Soc. B Biol. Sci.* 209, 2964–2968.
- Miquelle, D.G., 1990. Why don't Bull moose eat during the rut? *Behav. Ecol. Sociobiol.* 27, 145–151. <http://dx.doi.org/10.1007/BF00168458>.
- Müller, D.W.H., Gaillard, J.-M., Bingham Lackey, L., Hatt, J.-M., Clauss, M., 2010. Comparing life expectancy of three deer species between captive and wild populations. *Eur. J. Wildl. Res.* 56, 205–208. <http://dx.doi.org/10.1007/s10344-009-0342-8>.
- Müller, D.W.H., Bingham Lackey, L., Streich, W.J., Fickel, J., Hatt, J.-M., Clauss, M., 2011. Mating system, feeding type and ex situ conservation effort determine life expectancy in captive ruminants. *Proc. R. Soc. B Biol. Sci.* 278, 2076–2080. <http://dx.doi.org/10.1098/rspb.2010.2275>.
- Mysterud, A., Holand, Ø., Røed, K.H., Gjøstein, H., Kumpula, J., Nieminen, M., 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer tarandus*). *J. Zool.* 261, 341–344. <http://dx.doi.org/10.1017/S0952836903004114>.
- Newman, R.E., McConnell, S.J., Weston, R.H., Reeves, M., Bernasconi, C., Baker, P.J., Wynn, P.C., 1998. The relationship between plasma testosterone concentrations and the seasonal variation in voluntary feed intake in fallow bucks (*Dama dama*). *J. Agric. Sci.* 130, 357–366.
- Nussey, D.H., Froy, H., Lemaître, J.-F., Gaillard, J.-M., Austad, S.N., 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Res. Rev.* 12, 214–225. <http://dx.doi.org/10.1016/j.arr.2012.07.004>.
- Orme, D., 2012. *The Caper Package: Comparative Analysis of Phylogenetics and Evolution in R*.
- Owens, I.P.F., Bennett, P.M., 1994. Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. B Biol. Sci.* 257, 1–8. <http://dx.doi.org/10.1098/rspb.1994.0086>.
- Pelletier, F., Mainguy, J., Côté, S.D., 2009. Rut-induced hypophagia in male Bighorn sheep and Mountain goats: foraging under time budget constraints. *Ethology* 115, 141–151. <http://dx.doi.org/10.1111/j.1439-0310.2008.01589.x>.
- Péron, G., Gimenez, O., Charmanier, A., Gaillard, J.-M., Crochet, P.-A., 2010. Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proc. R. Soc. B Biol. Sci.* 277, 2849–2856. <http://dx.doi.org/10.1098/rspb.2010.0530>.
- Plard, F., Bonenfant, C., Gaillard, J.-M., 2011. Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos* 120, 601–606. <http://dx.doi.org/10.1111/j.1600-0706.2010.18934.x>.
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*.
- Revell, L.J., 2010. Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* 1, 319–329. <http://dx.doi.org/10.1111/j.2041-210X.2010.00044.x>.
- Reznick, D.N., Bryant, M.J., Roff, D., Ghalambor, C.K., Ghalambor, D.E., 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* 431, 1095–1099. <http://dx.doi.org/10.1038/nature03042>.
- Ricklefs, R.E., 2010. Life-history connections to rates of aging in terrestrial vertebrates. *Proc. Natl. Acad. Sci.* 107, 10314–10319. <http://dx.doi.org/10.1073/pnas.1005862107>.
- Shuster, S.M., Wade, M.J., 2003. *Mating Systems and Strategies*. Princeton University Press.

**Fig. 2.** Relationship between rate of actuarial senescence and body mass (A), diet (B) and length of the mating season (C) in males across species of large herbivores in captivity. Bovidae are indicated in black, Cervidae in gray and other species (belonging to families of Antilocapridae, Giraffidae and Tragulidae) with an open circle.

- Spady, T.J., Lindburg, D.G., Durrant, B.S., 2007. Evolution of reproductive seasonality in bears. *Mammal Rev.* 37, 21–53. <http://dx.doi.org/10.1111/j.1365-2907.2007.00096.x>.
- Stuart, J.A., Page, M.M., 2010. Plasma IGF-1 is negatively correlated with body mass in a comparison of 36 mammalian species. *Mech. Ageing Dev.* 131, 591–598. <http://dx.doi.org/10.1016/j.mad.2010.08.005>.
- Suttie, J.M., Kay, R.N.B., 1985. Influence of plane of winter nutrition on plasma concentrations of prolactin and testosterone and their association with voluntary food intake in red deer stags (*Cervus elaphus*). *Anim. Reprod. Sci.* 8, 247–258. [http://dx.doi.org/10.1016/0378-4320\(85\)90030-2](http://dx.doi.org/10.1016/0378-4320(85)90030-2).
- Suttie, J.M., White, R.G., Littlejohn, R.P., 1992. Pulsatile growth hormone secretion during the breeding season in male reindeer and its association with hypophagia and weight loss. *Gen. Comp. Endocrinol.* 85, 36–42. [http://dx.doi.org/10.1016/0016-6480\(92\)90169-K](http://dx.doi.org/10.1016/0016-6480(92)90169-K).
- Toigo, C., Gaillard, J.-M., 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos* 101, 376–384. <http://dx.doi.org/10.1034/j.1600-0706.2003.12073.x>.
- Toigo, C., Gaillard, J.-M., Festa-Bianchet, M., Largo, E., Michallet, J., Maillard, D., 2007. Sex- and age-specific survival of the highly dimorphic *Alpine ibex*: evidence for a conservative life-history tactic. *J. Anim. Ecol.* 76, 679–686. <http://dx.doi.org/10.1111/j.1365-2656.2007.01254.x>.
- Urian, K.W., Duffield, D.A., Read, A.J., Wells, R.S., Shell, E.D., 1996. Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. *J. Mammal.* 77, 394. <http://dx.doi.org/10.2307/1382814>.
- Valcu, M., Dale, J., Griesses, M., Nakagawa, S., Kempenaers, B., 2014. Global gradient of avian longevity support the classic evolutionary theory of ageing. *Ecography* 37, 930–938. <http://dx.doi.org/10.1111/ecog.00929>.
- Weckerly, F.W., 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 79, 33–52. <http://dx.doi.org/10.2307/1382840>.
- Wilder, S.M., Couteur, D.G., Simpson, S.J., 2012. Diet mediates the relationship between longevity and reproduction in mammals. *Age* 35, 921–927. <http://dx.doi.org/10.1007/s11357-011-9380-8>.
- Williams, P.D., Day, T., Fletcher, Q., Rowe, L., 2006. The shaping of senescence in the wild. *Trends Ecol. Evol.* 21, 458–463.
- Xia, C., Liu, W., Xu, W., Yang, W., Xu, F., Blank, D., 2014. The energy-maintenance strategy of goitered gazelles *Gazella subgutturosa* during rut. *Behav. Process.* 103, 5–8. <http://dx.doi.org/10.1016/j.beproc.2013.10.009>.
- Zerbe, P., Claus, M., Codron, D., Bingaman Lackey, L., Rensch, E., Streich, J.W., Hatt, J.-M., Müller, D.W.H., 2012. Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. *Biol. Rev.* 87, 965–990. <http://dx.doi.org/10.1111/j.1469-185X.2012.00238.x>.
- Zhang, S., Liang, B., Wang, L., 2000. Seasonality of matings and births in captive Sichuan golden monkeys (*Rhinopithecus roxellana*). *Am. J. Primatol.* 51, 265–269. [http://dx.doi.org/10.1002/1098-2345\(200008\)51:4<265::AID-AJP6>3.0.CO;2-8](http://dx.doi.org/10.1002/1098-2345(200008)51:4<265::AID-AJP6>3.0.CO;2-8).