



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



Morgane Tidière^{a,*}, Jean-Michel Gaillard^{a,b}, Dennis W.H. Müller^c, Laurie Bingaman Lackey^d, Olivier Gimenez^e, Marcus Clauss^f, Jean-François Lemaître^{a,b}

^a Université de Lyon, F-69000 Lyon, France

^b Université Lyon 1, CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France

^c National Park "Bavarian Forest", Freyunger Str. 2, 94481 Grafenau, Germany

^d 1230 Oakland Street, Hendersonville, NC, USA

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

^f Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland

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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.

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1. Introduction

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 (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.

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