

7 Senescence in Mammalian Life History Traits

Jean-Michel Gaillard, Michael Garratt and Jean-François Lemaître

Short Summary

For several decades, senescence was considered as non-existing in free-ranging mammalian populations simply because most animals were expected to die from environmentally driven causes of mortality before the age at which senescence starts. Thanks to an increasing number of long-term individually based monitoring schemes of known-age animals in the wild, evidence of senescence in most life history traits has now been reported in a large number of species across all mammalian orders. From a review of these studies, we found that actuarial senescence is the rule rather than the exception in most mammalian species studied so far. We also found clear evidence for reproductive senescence, especially in long-lived primates and ungulates, in which the oldest individuals show the existence of post-reproductive life. Senescence in life history traits is thus pervasive among mammalian species, and the key topics are now to assess the causes and consequences of senescence in mammalian population dynamics and to understand variation in the magnitude and targets of senescence among and within mammalian species. Published analyses have identified the intensity of sexual selection, the environmental context and some physiological and genetic mechanisms as major structuring factors shaping mammalian senescence within and between species. Although not yet quantified in most studies, the fitness costs of senescence do not appear as negligible as generally assumed and warrant further investigation.

Introduction

From an evolutionary perspective, senescence occurs due to the decrease of the forces of natural selection with increasing age (Hamilton 1966; Medawar 1952; Williams 1957). In his classic paper, Hamilton (1966: 12) concluded that senescence is ‘an inevitable outcome of evolution’ in age-structured populations. Because mammalian species display strongly age-structured demographic parameters (Caughley (1966) for survival, Emlen (1970) for reproduction), we therefore expect, under our current evolutionary theory, that senescence should be universal in mammals. However, the picture is not that clear. Firstly, the theory formulated in the fifties through the seventies focused on senescence in survival (hereafter called ‘actuarial senescence’). Hamilton (1966) himself noticed that the problem of reproductive senescence is more complex than actuarial

senescence and did not address the question of senescence in life history traits other than survival and reproduction such as body mass or body condition, which describe qualitatively the individual phenotype and indirectly shape variation in individual fitness by their influence on demographic parameters. Secondly, mammals in the wild face a high environmentally driven mortality, which allows only a few individuals to reach the old ages at which the negative effects of senescence can be detected (Comfort 1979; Medawar 1952). Lastly, mortality at a given age within a cohort is not a random process, and individuals that survive are often heavier or in better body condition than individuals that die. Such viability selection (*sensu* Fisher 1930) generates an increase in the average individual quality with age, which can prevent senescence from being detected in studies performed at the population level (van de Pol & Verhulst 2006; Vaupel & Yashin 1985). Independently of the mere existence of senescence in mammalian populations, we can thus wonder about our ability to detect actuarial senescence in the wild. In this chapter we review our current knowledge of mammalian senescence in the wild. We first present recent advances in our ability to detect actuarial senescence in the wild and show how the increased abundance of age-specific mortality data is providing an insight into previously unsolved questions related to the proximate and ultimate causes of senescence. Because long-term individual-based monitoring of populations is required to assess reliably actuarial senescence in the wild, our current knowledge is biased towards the most intensively studied groups, such as large herbivores and primates. Then we discuss new findings in the study of mammalian reproductive senescence, and we show how patterns of reproductive senescence can be complex and uncoupled from patterns of actuarial senescence. Finally, we review the few studies that have investigated senescence in traits other than survival and reproduction. We discuss in each of these sections the main questions that further research on mammalian senescence should address to fill gaps in our current knowledge.

Assessing Actuarial Senescence in Wild Mammals

Survival is 'in general the most difficult estimation problem facing the field ecologist' (Hibly & Mullen 1980). Following the pioneering work by Deevey (1947), age-specific survival has been mostly obtained from transversal life tables based on dead recoveries (e.g. Spinage 1972) or sampling of live individuals (e.g. Pielowski 1984). Such information has been repeatedly used to analyse survival patterns in mammals (Lynch & Fagan 2009; Promislow 1991; Sibly et al. 1997) and usually leads to detection of a marked decrease in survival at old ages (Figure 7.1). However, the validity of senescence patterns obtained from transversal life tables is highly questionable. There are problems of estimation of age (Vincent et al. 1994), strong and unrealistic assumptions of stability of demographic parameters and stationarity of population size (McCullough 1979; Menkens & Boyce 1993) and the assumption of a constant detection probability of live or dead animals across ages (Gimenez et al. 2008). This has led to weak accuracy and low precision of survival estimates, which has prevented a reliable assessment of actuarial senescence. Fortunately, since the eighties, there has been an ongoing marked

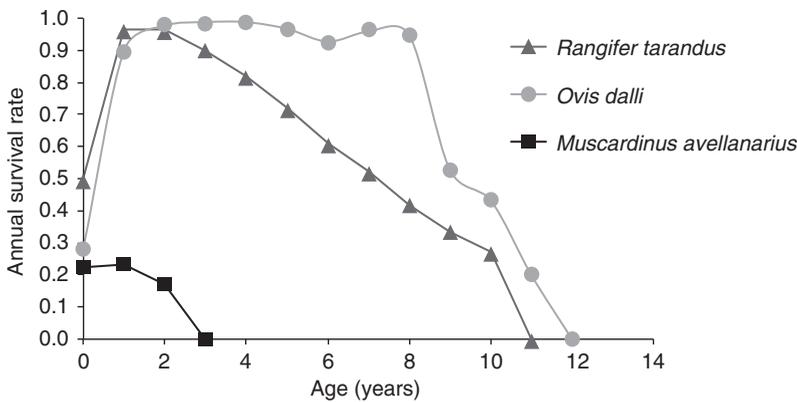


Figure 7.1 Empirical evidence of actuarial senescence across mammalian species based on analyses of transversal life tables. No statistical support for actuarial senescence is available, but most transversal life tables indicate a marked decrease in annual survival rate at old ages. Age-specific variation in survival is displayed for female reindeer (*Rangifer tarandus*) in south Georgia (Leader-Williams 1988), in Dall sheep (*Ovis dalli*) in McKinley Park, Alaska (Murie 1944) and in the common dormouse (*Muscardinus avellanarius*) in Lithuania (Juskaitis 2008).

increase in the availability of age-specific estimates of demographic parameters from intensive monitoring of individually marked animals from birth to death in mammalian populations (Clutton-Brock & Sheldon 2010), which has provided the required empirical information to measure the magnitude of actuarial senescence, often using a capture-recapture sampling design (Lebreton et al. 1992). By accounting for imperfect detection, capture-recapture methods indeed allow accurate age-specific estimates to be obtained (Nichols 1992). From a literature survey (Nussey et al. 2013), there is clear evidence of actuarial senescence in large mammalian species (i.e. ungulates, marine mammals and primates) (Table 7.1). In small mammals, actuarial senescence has been much less studied (but see Millar 1994) and even suggested to be negligible (Slade 1995). However, these species also deserve thorough investigation. In scurids, for example, intensive monitoring has indicated that actuarial senescence might also be pervasive (e.g. Broussard et al. 2003, 2005; Descamps et al. 2008) (Table 7.1).

To measure actuarial senescence, different metrics have been used. In some studies aiming only to provide evidence of senescence, the recorded survival decrease beyond some threshold age has been used. When an exact model of actuarial senescence is looked for, the rate of mortality increase with age is estimated (Jones et al. 2008), most often based on the Gompertz model (Gaillard et al. 2003). Indeed, following Gompertz's (1825) classical work, the increase in mortality with age is estimated from the following equation:

$$\log(\mu) = \alpha + \beta \times \text{age} \quad (7.1)$$

where μ is the annual mortality, α is the baseline mortality and β is the senescence rate. According to the Hamilton's (1966) model, the baseline mortality should be minimal at

Table 7.1 Evidence of Actuarial Senescence in Female Mammals from Long-Term Studies

Species	Reference
Moose (<i>Alces alces</i>)	Ericsson & Wallin (2001)
Pronghorn (<i>Antilocapra americana</i>)	Byers (1997)
Subantarctic fur seal (<i>Arctocephalus tropicalis</i>)	Beauplet et al. (2006)
American bison (<i>Bison bison</i>)	Pyne et al. (2010)
Muriqui (<i>Brachyteles hypoxanthus</i>)	Bronikowski et al. (2011)
Northern fur seal (<i>Callorhinus ursinus</i>)	Lander (1981)
Ibex (<i>Capra ibex</i>)	Toïgo et al. (2007)
Roe deer (<i>Capreolus capreolus</i>)	Gaillard et al. (2004)
White-headed capuchin (<i>Cebus capucinus</i>)	Bronikowski et al. (2011)
Blue monkey (<i>Cercopithecus mitis</i>)	Bronikowski et al. (2011)
Elk (<i>Cervus elaphus canadensis</i>)	Garrott et al. (2003)
Red deer (<i>Cervus elaphus</i>)	Clutton-Brock et al. (1988)
Persian fallow deer (<i>Dama mesopotamica</i>)	Saltz (1996)
Little red kaluta (<i>Dasykaluta rosamondae</i>)	Woolley (1991)
Virginia opossum (<i>Delphinus virginiana</i>)	Austad (1993)
Asian elephant (<i>Elephas maximus</i>)	Robinson et al. (2012)
Sea otter (<i>Enhydra lutris</i>)	Tinker et al. (2006)
Horse (<i>Equus caballus</i>)	Garrott & Taylor (1990)
Short-finned pilot whale (<i>Globicephala macrorhynchus</i>)	Foote (2008)
Long-finned pilot whale (<i>Globicephala melaena</i>)	Foote (2008)
Mountain gorilla (<i>Gorilla beringei</i>)	Bronikowski et al. (2011)
Weddell seal (<i>Leptonychotes weddellii</i>)	Rotella et al. (2012)
African elephant (<i>Loxodonta africana</i>)	Whitehouse & Hall-Martin (2000)
Alpine marmot (<i>Marmota marmota</i>)	Berger et al. (2016)
Badger (<i>Meles meles</i>)	McDonald et al. (2014)
Mediterranean monk seal (<i>Monachus schauinslandii</i>)	Baker & Thompson (2007)
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	Lee & Tietje (2005)
Mule deer (<i>Odocoileus hemionus</i>)	Bishop et al. (2009)
White-tailed deer (<i>Odocoileus virginianus</i>)	DelGiudice et al. (2006)
Killer whale (<i>Orcinus orca</i>)	Foote (2008)
Mountain goat (<i>Oreamnos americana</i>)	Festa-Bianchet et al. (2003)
Soay sheep (<i>Ovis aries</i>)	Catchpole et al. (2000)
Bighorn sheep (<i>Ovis canadensis</i>)	Jorgenson et al. (1997)
Chimpanzee (<i>Pan troglodytes</i>)	Nishida et al. (2003)
Lion (<i>Panthera leo</i>)	Packer et al. (1998)
Yellow baboon (<i>Papio cynocephalus</i>)	Bronikowski et al. (2011)
Hamadryas baboon (<i>Papio hamadryas</i>)	Packer et al. (1998)
White-footed mouse (<i>Peromyscus leucopus</i>)	Millar (1994)
Allied rock-wallaby (<i>Petrogale assimilis</i>)	Delean (2007)
Red-tailed phascogale (<i>Phascogale calura</i>)	Bradley (1997)
New Zealand sea lion (<i>Phocarctos hookeri</i>)	Chilvers et al. (2010)
Harbour porpoise (<i>Phocoena phocoena</i>)	Moore & Read (2008)
Sperm whale (<i>Physeter catodon</i>)	Evans & Hindell (2004)
Eastern pipistrelle (<i>Pipistrellus subflavus</i>)	Davis (1966)
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Richard et al. (2002)
Reindeer (<i>Rangifer tarandus</i>)	Albon et al. (2002)
Chamois (<i>Rupicapra rupicapra</i>)	Loison et al. (1999)

Table 7.1 (cont.)

Species	Reference
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	Neuhaus & Pelletier (2001)
Richardson's ground squirrel (<i>Spermophilus richardsoni</i>)	Broussard et al. (2005)
Greater kudu (<i>Tragelaphus strepsiceros</i>)	Owen-Smith (1990)
African buffalo (<i>Syncerus caffer</i>)	Sinclair (1977)
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	Descamps et al. (2007)
Common brushtail possum (<i>Trichosurus vulpecula</i>)	Isaac & Johnson (2005)
California sea lion (<i>Zalophus californicus</i>)	Hernandez-Camacho et al. (2008b)

Note: The focal mammalian species and one illustrative reference are provided (from Nussey et al. 2013, modified).

the age of first reproduction, so the senescence rate is generally estimated from the age at first reproduction onwards.

In the context of capture-recapture modelling (which allows accounting for imperfect detection) (Nichols 1992), the Gompertz model can be rewritten as (Gaillard et al. 2004)

$$\log[-\log(\Phi)] = (1 - \alpha) + \beta \times \text{age} \quad (7.2)$$

where Φ is the annual survival, α is the baseline mortality and β is the senescence rate. Fitting this model to survival data of twelve species of large herbivores has revealed strong evidence of actuarial senescence in both sexes (Gaillard et al. 2003). However, detailed analyses of case studies have identified several problems with this approach. Firstly, the theoretical assumption of a minimal mortality at the age of first reproduction does not seem to hold in most cases. For instance, while most ibex (*Capra ibex*) females usually give birth for the first time at two or three years of age (Toïgo et al. 2002), their survival does not show any sign of decline before seven years of age (Toïgo et al. 2007). Such clear evidence for delayed actuarial senescence compared to Hamilton's prediction seems to be the rule rather than the exception in the most intensively monitored populations of mammals (Jones et al. 2008). Secondly, the two parameters of the Gompertz model, the baseline mortality and the rate of senescence, have a strong negative co-variation, meaning that any overestimation of the baseline mortality will lead to underestimation of the rate of senescence. Lastly, because mammals generally display a J- or U-shaped mortality curve involving a decreasing mortality with increasing age in early life, a minimal mortality at some age during adulthood and finally an increasing mortality with age late in life (Caughley 1966), the Gompertz model does not allow the full range of age-specific changes in survival to be modelled. The Siler model (Siler 1979) explicitly accounts for different age-specific changes in survival among early-life, prime-age and late-life stages by involving five parameters to fit three different functions of survival variation. More flexible bathtub models of senescence, which were initially developed to model age-specific changes in human mortality (see e.g. Bebbington et al. 2007), nowadays provide a promising way to get a reliable picture of the full age dependence in survival. These models can be easily implemented in free

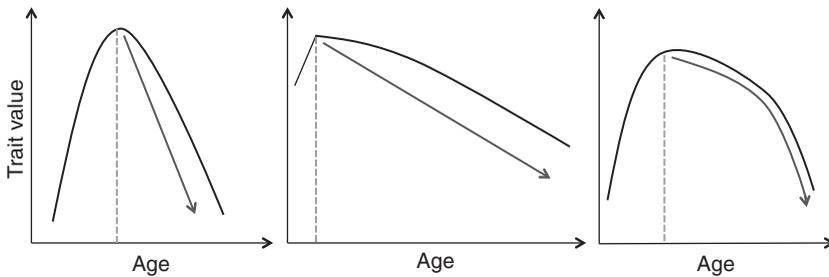


Figure 7.2 Assessing patterns of actuarial senescence in mammals: two metrics instead of one. While most analyses of senescence have focused on the strength of senescence (measured by the rate of senescence), the timing of senescence (measured by the onset of senescence) should also be investigated.

software such as E-Surge (Choquet and Nogué 2011) or BaSTA (Colchero et al. 2012). Bathtub models can be parameterised so as to give an estimate of the onset of senescence, providing information about the timing of senescence in addition to its strength measured by the actuarial senescence rate (Choquet et al. 2011). However, all these models require high-quality data on age-specific changes in survival to provide reliable estimates of senescence rates.

While previous analyses of actuarial senescence have focused almost entirely on the rate of senescence (e.g. Ricklefs 2010), the age at onset of senescence provides a complementary metric for studying senescence that should also be considered (Figure 7.2), especially in the context of comparative analyses of senescence across species. For instance, a recent analysis in wild boar (*Sus scrofa*), a polygynous ungulate species that exhibits a unusual life history combining high fecundity and early age at primiparity with a potentially long life span (Focardi et al. 2008), has shown that the onset of actuarial senescence, rather than the rate of ageing, differs from that of other ungulate species (Gamelon et al. 2014). Comparative analyses of actuarial senescence across mammals in the wild are still very scarce. Since the fifties, most previous comparative inter-specific analyses have focused on longevity (de Magalhaes et al. 2007; Sacher 1959; Stearns 1983; Wilder et al. 2013), likely because of the high availability of these types of data (Carey & Judge 2000; de Magalhaes & Costa 2009). Some studies have been conducted using adult life expectancy (Gaillard et al. 1989) or survival rates (Promislow et al. 1990; Toïgo & Gaillard 2003), and the only few broad-scale studies that analysed the rate of senescence were either based on poor-quality data issued from life tables without accounting for data quality (Promislow 1991) or on heterogeneous data including a mixture of wild and captive populations and/or males and females (Ricklefs 2010). Nowadays, the increasing availability of high-quality estimates of both onset and rate of actuarial senescence should allow comparative analyses that account for phylogenetic inertia to be performed while also controlling for potentially confounding factors such as sex, body mass and diet. For instance, a comparative analysis across twenty-two species of large herbivores showed that captive populations have a lower rate of senescence than their wild counterparts (Lemaître et al. 2013) once correcting for

body mass (to account for decreased rate of senescence with increasing mass) (Jones et al. 2008), diet (measured as the proportion of grass in the natural diet to account for the larger difficulty of maintaining browsers than grazers in optimal conditions in captivity) (Müller et al. 2010) and the quality of the data (to account for higher reliability of capture-recapture estimates compared to simple enumeration) (Péron et al. 2010).

While empirical evidence recently accumulated from long-term detailed studies clearly demonstrates that actuarial senescence is pervasive in mammals, the factors shaping the observed variation in the intensity of senescence, in terms of either strength (rate of senescence) or timing (onset of senescence), remain to be identified. Besides the general influence of body size (with a decreasing intensity of senescence with increasing size) (Ricklefs 2010) and of the pace of life (with an increasing intensity of senescence with a faster pace of life) (Garratt et al. 2013; Jones et al. 2008; Lemaître & Gaillard 2013a; Péron et al. 2010; Ricklefs 2010), one knows very little about the influence of environmental factors (Do mammals living at high elevations have lower intensity of actuarial senescence than those living at low elevations? Do mammals living in the tropics have lower intensity of actuarial senescence than those living in temperate or arctic areas?) or social factors (Do mammals with complex social bonds have lower intensity of actuarial senescence than solitary mammals?) for shaping among-species variation in senescence patterns of mammals. So far, only a few recent studies have started to evaluate the influence of sexual selection on the diversity of senescence patterns currently observed in mammals (e.g. Tidière et al. 2014). For instance, a comparative study based on twenty-four species of large herbivores failed to detect any relationship between measures of male allocation to sexual competition (i.e. sexual size dimorphism, weapon size and relative testes mass) and actuarial senescence rates (Lemaître & Gaillard 2013b). However, this sample of large herbivores included species with relatively similar reproductive tactics, and evidence that male life expectancy is shorter than female life expectancy in polygynous mammals but is not in monogamous mammals (Clutton-Brock & Isvaran 2007) suggests that the role of sexual selection in shaping species-specific patterns of senescence might be detectable only at a very broad scale. There is thus now a great need to target this question using a wide range of contrasted mammals before drawing any definitive conclusion on a possible link between intensity of sexual selection and actuarial senescence patterns across species.

Within a given species, one knows even less about the factors driving variation in senescence among populations. The ecological context could influence the intensity of actuarial senescence. Most captive populations of ruminants enjoy smaller rates of senescence than their wild counterparts (Lemaître et al. 2013), and senescence seems to be slower in island populations than in mainland ones (Austad 1993). Under classical evolutionary theories of senescence, any environmental factor causing increased fecundity associated with increased mortality in early adulthood should lead to accelerated senescence (Hamilton 1966; Williams 1957). Thus, mammals in populations under strong predation pressure or facing especially harsh climatic conditions should senesce faster than their counterparts facing more favourable conditions. There is, to our knowledge, no comparative analyses that have tested this

prediction in mammals, even across species, but recent inter-specific studies of bird longevity have provided supporting evidence (Valcu et al. 2014). However, we still lack a full understanding of the link between the amount of environmentally driven mortality and the intensity of senescence. This relationship might be complex because the type of mortality (i.e. whether mortality is selective or affects equally all individuals within a population) also shapes senescence patterns (Abrams 1993; Chen & Maklakov 2012; Williams et al. 2006). Variation in senescence patterns among individuals within a given population has been neglected for a long time. Detailed analyses of red deer (*Cervus elaphus*) on Rum Island have revealed high individual variation in the intensity of senescence. Females that were born at high population density suffered from earlier and greater actuarial senescence than their conspecifics that were born at low density (Nussey et al. 2007). From the few studies that have looked for among-individual variation in actuarial senescence, it appears that individual mammalian females that allocate more to reproduction early in their adulthood pay the cost at old age in terms of decreased survival, providing support for the disposable soma theory initially proposed by Kirkwood (1977), as recently reviewed by Lemaître et al. (2015). Such delayed reproductive costs in terms of survival have been so far reported in Asian elephants (*Elephas maximus*) (Hayward et al. 2014), red deer (Nussey et al. 2007), Weddell seals (*Leptonychotes weddellii*) (Hadley et al. 2007), Rhesus macaques (*Macaca mulatta*) (Blomquist 2009) and reindeer (*Rangifer tarandus*) (Weladji et al. 2008).

The large amount of evidence for actuarial senescence in mammals has accumulated without accounting for individual heterogeneity in quality. The process of viability selection is expected to remove disproportionately individuals with a selective disadvantage, often characterised by a combination of low reproductive output, low survivorship and low body size. These individuals correspond to poor-quality individuals (*sensu* Wilson & Nussey 2010). Such individual differences are likely to mask senescence and have thus to be accounted for. Since mortality is a unique event in an individual's life, correcting for individual heterogeneity cannot be based on repeated measurements at the individual level. Models including a mixture of high- and low-quality individuals like those used initially by Vaupel and Yashin (1985) offer a promising way to account for individual differences in survivorship. We thus expect the rate of actuarial senescence in mammals to be higher than reported up to now, especially in small species for which a higher magnitude of individual differences in survivorship is expected to occur (Péron et al. 2016). Another way to look for individual heterogeneity in survivorship might involve considering mortality causes. Taking advantage of technological improvements in monitoring individual fates (e.g. radio-telemetry or GPS monitoring) (Cagnacci et al. 2010), we should accumulate knowledge about individual mortality causes and include such heterogeneity to assess actuarial senescence. For instance, a preliminary analysis of age-specific survival in females of an intensively monitored roe deer population has shown that disentangling human-related mortalities and mortalities caused by natural factors led to increases in the rate of actuarial senescence, whereas no age variation occurred in human-related mortality (Koons et al. 2014).

Assessing Reproductive Senescence in Wild Mammals

Compared to actuarial senescence, reproductive senescence has been often overlooked. To the notable exception of humans and a handful of very long-lived species like killer whales, elephants and anthropoid primates, reproductive cessation (*sensu* Packer et al. 1998) is expected to be weak in mammals, and the process of reproductive senescence has not retained much attention. For instance, Caughley (1976) claimed that there is 'no hint of the sharp decrease of fecundity at old age' in large herbivores.

Assessing reproductive senescence in mammals is much easier than assessing actuarial senescence, at least in females. Female reproductive status can be measured at different stages of the reproductive cycle (i.e. at mating, during pregnancy, at birth and at weaning) from captures, hunting or observations. Empirical evidence of reproductive senescence has been reported in two types of studies.

Firstly, the number of female offspring produced per female at different ages has been tabulated (as m_x values) (Seber 1973) in life tables built on data collected through hunting (game species) or trapping (small mammals, small to medium-sized carnivores). Contrary to actuarial senescence, evidence of reproductive senescence from life tables is far from being the rule. In more than half of these case studies, reproductive senescence has simply not been looked for, and the female reproductive output has been assumed to be constant from the mid-adulthood. Only the increase of reproductive output from age of primiparity to prime ages has been reported in such cases (e.g. Slade & Balph (1974) on *Spermophilus armatus*; Rodgers (1984) on *Phacochoerus aethiopicus* or Dinerstein (1991) on *Rhinoceros unicornis*).

Reproductive senescence has also been assessed from detailed individual monitoring of known-age animals from birth to death in a large range of mammals (Table 7.2). From these studies, reproductive senescence displays different patterns according to the reproductive component analysed (Table 7.2). For instance, implantation failure in roe deer increases from a probability of 0.2 in females aged between two and seven years to 0.5 in females older than eight years of age (Hewison & Gaillard 2001), whereas pregnancy rates remain high and constant (>0.95) up to eleven years of age, after which they strongly decrease to below 0.5 from fourteen years onwards (J. M. Gaillard and collaborators, unpublished data). Similar patterns of variation have been reported in reindeer (Milner et al. 2003).

Reproductive senescence thus corresponds to a complex process that involves age-related declines in the efficiency of one or more functions or structures involved in the reproduction process. Thus, different reproductive traits do not consistently show similar senescence patterns across related mammalian species. For example, offspring performance (in terms of birth mass or survival) decreases with increasing female age in Soay sheep (*Ovis aries*) (Hayward et al. 2009), reindeer (Weladji et al. 2010) and white-tailed deer (*Odocoileus virginianus*) (DeGiudice 2007), whereas it does not change with age in bighorn sheep (*Ovis canadensis*) (Bérubé et al. 1999); pregnancy rate decreases with age in baboon (*Papio anubis*) (Packer et al. 1998), red deer (Nussey et al. 2009a), roe deer (J. M. Gaillard and collaborators, unpublished data) and reindeer (*Rangifer*

Table 7.2 Evidence of Reproductive Senescence in Female Mammals from Long-Term Studies

Species	Reference
Moose (<i>Alces alces</i>)	Heard et al. (1997): fertility; Ericsson et al. (2001): litter size/offspring survival
South American fur seal (<i>Arctocephalus australis</i>)	Lima & Paez (1997): reproductive rate
Antarctic fur seal (<i>Arctocephalus gazella</i>)	Lunn et al. (1994): reproductive rate
Sub-Antarctic fur seal (<i>Arctocephalus tropicalis</i>)	Beauplet et al. (2006): reproductive rate
Bison (<i>Bison bison</i>)	Green (1990): breeding proportion; Wilson et al. (2002): reproductive rate
Northern fur seal (<i>Callorhinus ursinus</i>)	Lander (1981): pregnancy rate
Ibex (<i>Capra ibex</i>)	Toigo et al. (2002): reproductive rate
Roe deer (<i>Capreolus capreolus</i>)	Hewison & Gaillard (2001): implantation failure; Gaillard et al. (2003): pregnancy rate/litter size
Elk (<i>Cervus elaphus canadensis</i>)	Flook (1970): pregnancy rate
Red deer (<i>Cervus elaphus</i>)	Clutton-Brock et al. (1982): reproductive rate
Persian fallow deer (<i>Dama mesopotamica</i>)	Saltz (1996): reproductive rate
Virginia opossum (<i>Delphinus virginiana</i>)	Austad (1993): fertility
Asian elephant (<i>Elephas maximus</i>)	Robinson et al. (2012): reproductive rate
Horse (<i>Equus caballus</i>)	Garrott et al. (1991): breeding proportion
Steller sea lion (<i>Eumatopias jubatus</i>)	Holmes et al. (2007): reproductive rate
Short-finned pilot whale (<i>Globicephala macrorhynchus</i>)	Foote (2008): fertility
Long-finned pilot whale (<i>Globicephala melaena</i>)	Foote (2008): fertility
Mountain gorilla (<i>Gorilla beringei</i>)	Robbins et al. (2006): reproductive rate
Gray seal (<i>Halichoerus grypus</i>)	Bowen et al. (2006): birth rate
Ring-tailed lemur (<i>Lemur catta</i>)	Sussman (1991): birth rate/infant mortality
African elephant (<i>Loxodonta africana</i>)	Hanks (1972): reproductive rate
Long-tailed macaque (<i>Macaca fascicularis</i>)	Koyama et al. (1992): reproductive rate
Japanese macaque (<i>Macaca fuscata</i>)	Wolfe & Noyes (1981): birth rate
Rhesus macaque (<i>Macaca mulatta</i>)	Hoffman et al. (2010): interbirth interval/offspring survival
Barbary macaque (<i>Macaca sylvanus</i>)	Paul et al. (1993): reproductive rate
Mandrill (<i>Mandrillus sphinx</i>)	Leigh et al. (2008): reproductive rate
Alpine marmot (<i>Marmota marmota</i>)	Tafari et al. (2013): litter size
Badger (<i>Meles meles</i>)	Dugdale et al. (2011): annual fecundity
Northern elephant seal (<i>Mirounga angustirostris</i>)	Sydeman et al. (1991): reproductive rate
Mediterranean monk seal (<i>Monachus schauinslandii</i>)	Harting et al. (2007): reproductive rate
Mule deer (<i>Odocoileus hemionus</i>)	Lawrence et al. (2004): pregnancy rate
Killer whale (<i>Orcinus orca</i>)	Olesiuk et al. (1990): reproductive rate
Mountain goat (<i>Oreamnos americana</i>)	Bailey (1991): reproductive rate
Soay sheep (<i>Ovis aries</i>)	Robinson et al. (2006): reproductive rate
Bighorn sheep (<i>Ovis canadensis</i>)	Bérubé et al. (1999): birth rate
Chimpanzee (<i>Pan troglodytes</i>)	Sugiyama (1994): birth rate
Lion (<i>Panthera leo</i>)	Packer et al. (1998): birth rate/offspring survival
Hamadryas baboon (<i>Papio hamadryas</i>)	Packer et al. (1998): birth rate
White-footed mouse (<i>Peromyscus leucopus</i>)	Morris (1996): litter size
New Zealand sea lion (<i>Phocarctos hookeri</i>)	Childerhouse et al. (2010): reproductive rate
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Richard et al. (2002): birth rate/offspring survival
Reindeer (<i>Rangifer tarandus</i>)	Adams & Dale (1998): fertility/reproductive pause
Pyrenean chamois (<i>Rupicapra pyrenaica</i>)	Crampe et al. (2006): reproductive rate

Table 7.2 (cont.)

Species	Reference
Chamois (<i>Rupicapra rupicapra</i>)	Tettamanti et al. (2015): reproductive rate
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	Broussard et al. (2003): litter success
Meerkat (<i>Suricata suricatta</i>)	Sharp & Clutton-Brock (2010): litter size/offspring survival
Wild boar (<i>Sus scrofa</i>)	Aumaître et al. (1982): fertility
African buffalo (<i>Syncerus caffer</i>)	Sinclair (1977): pregnancy rate
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	McAdam et al. (2007): reproductive rate
Gelada (<i>Theropithecus gelada</i>)	Dunbar (1980): birth rate
Brown bear (<i>Ursus arctos</i>)	Schwartz et al. (2003): reproductive rate
Polar bear (<i>Ursus maritimus</i>)	Derocher & Stirling (1994): litter size
California sea lion (<i>Zalophus californicus</i>)	Hernandez-Camacho et al. (2008a)

Note: The focal mammalian species, the focal reproductive trait and one illustrative reference are provided (from Nussey et al. 2013, modified).

tarandus) (Milner et al. 2003) but not in white-tailed deer (DelGiudice et al. 2006); and litter size decreases with increasing age from four years onwards in meerkats (*Suricata suricatta*) (Sharp & Clutton-Brock 2010), from six years onwards in roe deer (J. M. Gaillard and collaborators, unpublished data) and from ten years onwards in Alpine marmots (*Marmota marmot*) (Berger et al. 2015) but remains constant with age in white-tailed deer (DelGiudice et al. 2006), mule deer (*Odocoileus hemionus*) (Monteith et al. 2014), pronghorn (*Antilocapra americana*) (Byers 1997) and Soay sheep (Hayward et al. 2009).

Why do such different patterns of age-specific variation occur among reproductive traits? The reproductive output at each stage of the reproductive cycle is tightly linked with the energy allocated to reproduction, and trade-offs are likely to occur. For instance, the offspring size-number trade-off is one of the most intensively studied trade-offs (Smith & Fretwell 1974; Stearns 1992). According to the Y model proposed by van Noordwijk & de Jong (1986), the direction of the trade-off should depend on the balance between variability in resource acquisition, which includes both resource availability and individual ability to exploit resources, and variability in resource allocation. When allocation is more variable among individuals than acquisition, a trade-off occurs.

Finally, we regret that most published studies so far have focused on females, with only a few investigations of reproductive senescence occurring in mammalian males. Such bias probably arises from the fact that genetic data are required to determine reproductive success in males, while this is not automatically the case for females. However, males also suffer from reproductive senescence, as nicely revealed by a thorough study conducted on male red deer, in which breeding success declines from the age of ten years onwards (Nussey et al. 2009a). Similarly to females, male reproductive senescence can be complex. For instance, senescence in harem size is faster in male red deer that control the largest harems and spend the most time rutting during early adulthood (Lemaître et al. 2014). Male reproductive senescence can also involve an age-dependent decline in secondary

sexual traits, as reported in roe deer, for which antler size (a trait positively associated with reproductive success) (Vanpé et al. 2010) decreases after males reach eight years of age (Vanpé et al. 2007). Note that for red deer, whether antler size decreases with increasing age is not so clear (Myysterud et al. 2005 versus Nussey et al. 2009a).

Alternatively, a decrease in male fertilisation efficiency at old ages might also account for reproductive senescence. Until now, studies that have documented senescence in ejaculate quality in mammals have focused on captive populations (Crosier et al. 2007; Thongtip et al. 2008) because it is particularly challenging to collect longitudinal data on ejaculate quality in the wild. The few published data are thus cross sectional (see Curren et al. (2013) for a study case in spotted hyena, *Crocuta crocuta*), which might explain why senescence in sperm-related traits has not been documented yet in free-ranging mammalian populations.

As virtually all female mammals are iteroparous, reproductive traits can be measured repeatedly over the lifetime of a given individual, which makes it easy to correct for individual heterogeneity using generalised linear mixed models (van de Pol and Verhulst 2006; van de Pol and Wright 2009). However, accounting for confounding effects of selective disappearance requires repeated measures of the same individuals, which are available only from longitudinal studies. Age-specific reproduction assessed from transversal data often collected from reproductive tracts of dead females are likely to underestimate severely the intensity of reproductive senescence and should thus be taken with great caution.

Observed changes in reproductive output between prime-age and old individuals are likely to be shaped by different processes. Senescence is obviously one process, but prime-age and old reproducers might have different strategies of energy allocation to reproduction (Berger et al. 2015). Terminal investment (Clutton-Brock 1984) and terminal allocation (Weladji et al. 2010) have been shown to increase reproductive allocation at old ages and counter-balance thereby the influence of reproductive senescence, even though the two processes co-occur (Hamel et al. 2012; Weladji et al. 2010). Thus, we can expect trade-offs between resource acquisition and allocation to reproduction to vary among ages. Are trade-offs age dependent? Surprisingly, very few empirical studies have tackled this question in mammals or in any other taxonomic group, and further investigation is necessary to understand what is the relative contribution of senescence in age-specific variation of reproductive traits at old ages.

Both the onset and the rate of reproductive senescence isometrically scale with physiological time (*sensu* Linstedt and Calder 1981). In support, available data indicate that both the timing and the strength of senescence strongly depend on generation time (Garratt et al. 2013; Jones et al. 2008), a reliable metric of variation in the pace of life across mammals (Gaillard et al. 2005). For a given pace of life, we thus expect to find only little variation among mammalian orders in either the onset or the rate of senescence.

The rapid increase in age-specific survival and reproductive data is providing the material to test the hypothesis that actuarial and reproductive senescence patterns should be synchronous (Williams 1957). In his thorough review of post-reproductive life span, Cohen (2004) proposed different scenarios of age-specific patterns in reproduction and survival to assess when post-reproductive life span might evolve (Figure 7.2). However,

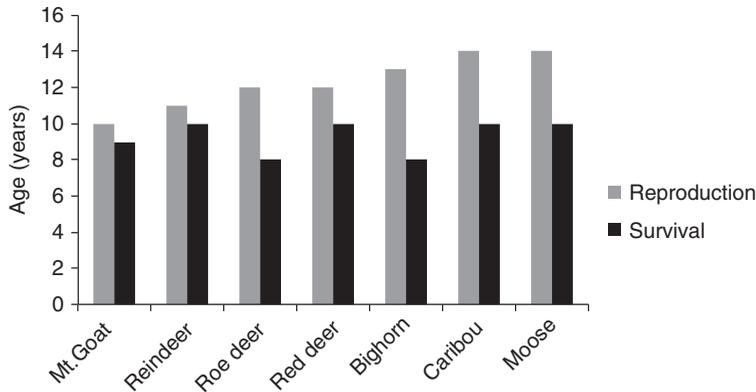


Figure 7.3 Onsets of actuarial and reproductive senescence estimated in a selected set of large herbivore species for which an intensive individual monitoring was available.

Mt goat (*Oreamnos americana*): Festa-Bianchet and Côté (2008)

Reindeer (*Rangifer tarandus*): Albon et al. (2002)

Roe deer (*Capreolus capreolus*): Gaillard et al. (1998)

Red deer (*Cervus elaphus*): Clutton-Brock et al. (1982)

Bighorn sheep (*Ovis canadensis*): Jorgenson et al. (1997) and Bérubé et al. (1999)

Caribou (*Rangifer tarandus*): Adams and Dale (1998) and Thomas and Barry (1990)

Moose (*Alces alces*): Ericsson and Wallin (2001) and Ericsson et al. (2001)

the link between post-reproductive life span and age-specific variation in reproduction is more complex than expected. Indeed, an earlier age of reproductive cessation could involve either earlier or stronger reproductive senescence. As most studies (including Cohen's (2004) scenarios displayed in Figure 7.2) focused on the rate of senescence and have neglected the onset of senescence, the interplay between the onset and the rate of reproductive senescence is still poorly understood. Although evidence from laboratory studies suggests that patterns of senescence across life history traits are uncoupled (Nussey et al. 2013; Promislow et al. 2006; Walker & Herndon 2010), few studies have yet directly targeted this question in the wild (but see Hayward et al. (2015) for a notable recent exception in Soay sheep). Nonetheless, results from separate studies but published on the same species might provide a few elements to tackle this question, although it is noteworthy that data sets used in these studies are evidently not strictly identical. So far, preliminary results in large herbivores suggest that the onset of reproductive senescence occurs later than the onset of actuarial senescence (Figure 7.3).

Evidence of Senescence in Other Mammalian Life History Traits

Body Mass in Wild Mammals

When looking for the underlying factors potentially explaining actuarial and reproductive senescence in wild mammals, the most obvious trait is probably the loss of body

mass. The strength of the relationship between body mass and body condition varies a lot across species. For instance, while body condition is almost perfectly measured using body mass in roe deer (Toïgo et al. 2006), a larger variation in mass at a given size occurs in the Columbian ground squirrel, *Spermophilus columbianus* (Dobson 1992). However, body mass and body condition are positively correlated in all mammals studied so far, and as a rule, heavier mammalian females survive better, give birth at an earlier age and produce more and larger offspring than lighter females (Clutton-Brock 1988; Gaillard et al. 2000; Sadleir 1969). Therefore, patterns of actuarial and reproductive senescence reported in the wild (Nussey et al. 2013) might be, in mammals, explained by a senescence in body condition. So far, senescence in body mass has already been documented in several species, principally large herbivores (e.g. Mysterud et al. (2001) in red deer; Weladji et al. (2010) in reindeer; and Nussey et al. (2011) in Soay sheep, roe deer and bighorn sheep) or seals (e.g. Proffitt et al. 2007). However, most of the published studies did not disentangle between-individual selective disappearance and within-individual changes in body mass in their analyses and thus potentially underestimated the magnitude of the body-mass decline with age. Indeed, if light individuals are more likely to die during early adulthood, old age classes will be constituted by the heaviest individuals of the population, which can make senescence more difficult to detect.

Interestingly, studies controlling for selective disappearance processes have revealed contrasted patterns of senescence in body mass. For example, Nussey and colleagues found that the decrease in body mass accelerates with increasing age in roe deer, while body mass declines steadily only two years before individuals die in Soay sheep (Nussey et al. 2011). If the exact nature of these differences remains unknown, the authors suggested that possible interactions between phenotypic attributes and environmental conditions might play an important role. To go one step further, to understand the origin of body-mass senescence requires comparing patterns between males and females from the same species. Indeed, selective pressures are different between the sexes, which might ultimately lead to divergent patterns of senescence. For instance, in polygynous mammals, males allocate substantially to sexual competition through the defence of females or of territories and in some species through the growth of conspicuous weapons. It is thus possible to predict that in these species males should suffer from a much steeper decline in body mass than females, while in monogamous species, senescence patterns are expected to be similar between the sexes. To date, only a few detailed studies of sex-specific senescence in mass have been performed. Senescence patterns in mass of the grey mouse lemur (*Microcebus murinus*), a sexually monomorphic primate, did not differ between the sexes in either captive or wild populations (Hämäläinen et al. 2015), in support of the expectation. On the contrary, in the socially monogamous Alpine marmots (*Marmota marmota*), senescence in body mass was only observed in males. Male body mass declined from the age of eight years in association with an acceleration of the mass loss the year before death, but female body mass remained constant across the whole life (Tafani et al. 2013). In the European badger (*Meles meles*), males also showed stronger senescence in mass than females, likely in relation to intra-sexual competition during early life (Beirne et al. 2015). These results

suggest that the factors underpinning senescence in body condition are likely to be complex and are yet to be understood. Obtaining longitudinal measures of body mass in the wild is difficult, especially for large species. However, such data are badly required to investigate at a broad scale the relationship between senescence in body condition and senescence in fitness-related traits.

Physiological Parameters in Wild Mammals

Studies of senescence in physiological parameters in wild mammals are beginning to increase and offer an insight into mechanistic causes for increased mortality rates with age and further validation of the presence of senescence in the wild. Examination of physiological traits in wild animals is not easy, however, and is often restricted to biological markers that can be assayed in blood (Selman et al. 2012). Much of this work to date has been preliminary and has involved cross-sectional comparisons of individuals of different ages in a particular population. Limited information can be gained from studies of animals of only two age groups, such as between young and adults or young and old individuals, because it is not possible to determine those changes that occur as a consequence of senescence and those that change simply as a side effect of animals getting older. Perhaps more importantly, correlations between age and physiological trait expression can be generated by differential survival rates of animals of different genotypes and phenotypes in the wild, as was the case for a positive correlation between the concentration of anti-nuclear antibodies and age in wild Soay sheep (Graham et al. 2010).

Target parameters for physiological senescence in wild mammals are usually based on those that have been implicated in ageing in laboratory and domesticated populations of animals, particularly mice and rats, the model mammalian organisms for biomedical science. Assessments of muscle physiology in wild animals of various age groups has confirmed that animals survive to an age where senescence can be detectable in aspects of muscle physiology, and these changes are largely consistent with muscle senescence reported in non-wild animals. In a range of wild cetacean species, animals judged to be approaching senescence via visual morphology show a change to slower muscle phenotype, which is largely consistent with the physiological muscle alterations observed in elderly humans – although the authors also point out that such alterations might be adaptive if they facilitate more prolonged underwater diving (Sierra et al. 2013). A more detailed analysis of muscle samples across forty-seven Weddell seals classified as ‘adult’ or ‘old’ further documented a range of changes in muscle physiology with age, including increased collagen build-ups, which the authors speculated might affect sprint capacity and contractile efficiency of these old individuals (Hindle et al. 2009a). Young-adult and prime-aged wild-caught individuals of two shrew species (*Blarina brevicauda* and *Sorex palustris*) confirmed age-related increases in collagen content in wild small mammals, highlighting that similar age-related changes are observed in shorter-lived terrestrial species (Hindle et al. 2009b).

Changes in aspects of the immune system are known to occur with senescence in laboratory rodents, domesticated mammals and also humans. In the wild, where

parasites and pathogens are prevalent, senescence in the immune system could conceivably have a substantial impact on health and mortality (Maizels & Nussey 2013). Cross-sectional analysis of young, adult and old-aged wild Soay sheep have supported the notion that the immune system is impaired in senescent individuals in the wild, with alterations in T-cell subsets in old-age sheep largely mirroring the changes observed in laboratory rodents (Nussey et al. 2012). These age-related changes in the immune system might be a contributing factor to the elevation in rates of parasitism that occurs in sheep of this population as they age, demonstrated through a rare longitudinal analysis (Hayward et al. 2009). Ageing of the immune system and the potential costs of this in terms of parasite and pathogen burden might be one substantial factor contributing to increased rates of mortality in old-aged mammals living in the wild.

Oxidative stress and an impaired ability to regulate defence mechanisms that protect against this are a central feature of senescence in laboratory rodents (Fraga et al. 1990; Sohal et al. 1995; Stadtman 1992), and there has been much investigation and discussion of the potential role of oxidative stress as a public cause of senescence across animals (Kirkwood & Austad 2000). Studies of oxidative stress and its relation to senescence in the wild are beginning to emerge, although the methodological issues in collection samples and their interpretation are numerous (Selman et al. 2012). Studies of wild Soay sheep and Eastern chipmunks (*Tamias striatus*) have explored the cross-sectional relationship between age and a marker of oxidative stress in blood. Surprisingly, while both studies noted an elevation in serum oxidative stress in young animals, old-aged individuals had similar levels of a serum marker of oxidative stress to middle-aged adults (Bergeron et al. 2011; Nussey et al. 2009b). In a more detailed analysis of oxidative stress in the muscles of wild-caught shrews, no consistent change in oxidative stress was observed: one marker increased with age, while another decreased (Hindle et al. 2010). Despite this, the activity of several antioxidants was consistently elevated in old individuals, which also occurs in the muscles of old laboratory rodents and is thought to be related to impaired transcriptional regulation and altered physiological responses to bouts of muscle exercise (Vasilaki et al. 2006). Thus, although the very limited assessment of oxidative stress to date has not revealed large increases in oxidative stress with old age, a more detailed analysis of redox function across a greater variety of tissues may prove enlightening.

Changes in physiological parameters with age are detectable in wild populations of mammals (e.g. see Jégo et al. (2014) for a recent case study in roe deer), although research in this area is still in its infancy. In contrast to research in wild birds, which have been studied more intensively, some key aspects of physiology linked to senescence have not yet been assessed in wild mammals, including telomere attrition and production of inflammatory cytokines. Moving forward, it will be important to understand whether senescence-related changes in these physiological traits also occur in wild mammals. It is notable, however, that there is a growing appreciation that assessment of individual markers of physiological traits does not capture the complexity of physiological decline and loss of condition in wild animals (Cohen 2015; Milot et al. 2014), particularly since different markers of traits such as oxidative stress and inflammation can be uncorrelated (see Christensen et al

(2015) for a recent example in Soay sheep). A more comprehensive approach of assessing multiple different markers of multiple aspects of physiology may provide a more robust and repeatable means to assess physiological dysregulation and identify senescent individuals in the wild and could include those aspects of physiology yet to be assessed. Once a broader understanding of the patterns of physiological deterioration in wild animals has been made, we may be able to move to the more complicated issue of which of these changes is causally involved in generating decreased reproduction and increased mortality with age.

Conclusion

Empirical evidence clearly demonstrates that senescence is pervasive in most mammalian species studied to date. Patterns of senescence are trait dependent but seem to be shaped by the same major sources of variation. The intensity of sexual selection, the environmental context and some physiological and genetic mechanisms are the most structuring factors shaping mammalian senescence within and between species. Senescence is expected to have strong implications for conservation and management of mammalian populations. In particular, the occurrence of actuarial and reproductive senescence is expected to lead to a decrease in individual fitness and population growth rates, which has to be accounted for when modelling populations. Thus, thirty years ago, Lee Eberhardt (1985) stressed the need of including senescence when assessing population dynamics. However, to date, the fitness loss due to actuarial and reproductive senescence, and thus the costs of senescence in terms of population dynamics, remains poorly understood. A pioneering study on thirteen populations of twelve species of birds and mammals indicates that the senescence costs could be far from negligible (Bouwhuis et al. 2012). Future studies will be required to measure the impact of senescence on population dynamics in a wide range of mammals and to identify potential drivers of such senescence costs.

References

- Abrams, P. A. (1993). Does increased mortality favor the evolution of more rapid senescence? *Evolution*, **47**, 877–87.
- Adams, L. G. & Dale, B. W. (1998). Reproductive performance of female Alaskan caribou. *Journal of Wildlife Management*, **62**, 1184–95.
- Albon, S. D., Stien, A., Irvine, R. J., et al. (2002). The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **269**, 1625–32.
- Aumaître, A., Morvan, C., Quéré, J. P., et al. (1982). Productivité potentielle et reproduction hivernale chez la laie (*Sus scrofa scrofa*) en milieu sauvage. *Journée de la Recherche Porcine*, **14**, 109–24.

- Austad, S. N. (1993). Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *Journal of Zoology*, **229**, 695–708.
- Baker, J. D. & Thompson, P. M. (2007). Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **274**, 407–15.
- Bailey, J. A. (1991). Reproductive success in female mountain goats. *Canadian Journal of Zoology*, **69**, 2956–61.
- Beauplet, G., Barbraud, C., Dabin, W., Kussener, C. & Guinet, C. (2006). Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos*, **112**, 430–41.
- Bebbington, M., Lai, C. & Zitikis, R. (2007). Modeling human mortality using mixtures of bathtub shaped failure distributions. *Journal of Theoretical Biology*, **245**, 528–38.
- Beirne, C., Delahay, R. & Young, A. (2015). Sex differences in senescence: the role of intra-sexual competition in early adulthood. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **282**, 20151086.
- Berger, V., Lemaître, J. F., Gaillard, J.-M. & Cohas, A. (2015). How do animals optimize the size-number trade-off when aging? Insights from reproductive senescence patterns in marmots. *Ecology*, **96**, 46–53.
- Berger, V., Lemaître, J. F., Gaillard, J.-M. & Cohas, A. (2016). Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence. *Journal of Mammalogy* **97**, 992–1000.
- Bergeron, P., Careau, V., Humphries, M. M., et al. (2011). The energetic and oxidative costs of reproduction in a free-ranging rodent. *Functional Ecology*, **25**, 1063–71.
- Bérubé, C. H., Festa-Bianchet, M. & Jorgenson, J. T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, **80**, 2555–65.
- Bishop, C. J., White, G. C., Freddy, D. J., et al. (2009). Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs*, **172**, 1–28.
- Blomquist, G. E. (2009). Trade-off between age of first reproduction and survival in a female primate. *Biology Letters*, **5**, 339–42.
- Bouwhuis, S., Choquet, R., Sheldon, B. C. & Verhulst, S. (2012). The forms and fitness cost of senescence: age-specific recapture, survival, reproduction, and reproductive value in a wild bird population. *American Naturalist*, **179**, E15–27.
- Bowen, W. D., Iverson, S. J., McMillan, J. I. & Boness, D. J. (2006). Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology*, **75**, 1340–51.
- Bradley, A. J. (1997). Reproduction and life history in the red-tailed phascogale, *Phascogale calura* (Marsupialia: Dasyuridae): the adaptive-stress senescence hypothesis. *Journal of Zoology*, **241**, 739–55.
- Bronikowski, A. M., Altmann, J., Brockman, D. K., et al. (2011). Aging in the natural world: comparative data reveal similar mortality patterns across primates. *Science*, **331**, 1325–8.
- Broussard, D. R., Michener, G. R., Risch, T. S. & Dobson, F. S. (2005). Somatic senescence: evidence from female Richardson's ground squirrels. *Oikos*, **108**, 591–601.
- Broussard, D. R., Risch, T. S., Dobson, F. S. & Murie, J. O. (2003). Senescence and age-related reproduction of female Columbian ground squirrels. *Journal of Animal Ecology*, **72**, 212–19.

- Byers, J. A. (1997). *American Pronghorn: Social Adaptations and the Ghosts of Predators Past* (University of Chicago Press).
- Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **365**, 2157–62.
- Carey, J. R. & Judge, D. S. (2000). *Longevity Records: Life Spans of Mammals, Birds, Reptiles, Amphibians and Fish* (Odense Monographs on Population Aging) (Odense University Press).
- Catchpole, E. A., Morgan, B. J. T., Coulson, T. N., et al. (2000). Factors influencing Soay sheep survival. *Journal of the Royal Statistical Society Series C: Applied Statistics*, **49**, 453–72.
- Caughley, G. (1966). Mortality patterns in mammals. *Ecology*, **47**, 906–18.
- Caughley, G. (1976). Wildlife management and the dynamics of ungulate populations. In *Applied Biology*, Vol. 1 (pp. 183–246), ed. T. H. Coaker (London: Academic Press).
- Chen H. Y. & Maklakov A. A. (2012). Longer life span evolves under high rates of condition-dependent mortality. *Current Biology*, **22**, 2140–3.
- Childerhouse, S. J., Dawson, S. M., Fletcher, D. J., et al. (2010). Growth and reproduction of female New Zealand sea lions. *Journal of Mammalogy*, **91**, 165–76.
- Chilvers, B. L., Wilkinson, I. S. & Mackenzie, D. I. (2010). Predicting life-history traits for female New Zealand sea lions, *Phocarctos hookeri*: integrating short-term mark-recapture data and population modeling. *Journal of Agricultural Biological and Environmental Statistics*, **15**, 259–78.
- Choquet, R. & Nogu e, E. (2011). *E-SURGE 1–8 User’s Manual* (CEFE, UMR 5175, Montpellier, France), available at <http://ftp.cefe.cnrs.fr/biom/soft-cr/>.
- Choquet, R., Viallefont, A., Rouan, L., et al. (2011). A semi-Markov model to assess reliably survival patterns from birth to death in free-ranging populations. *Methods in Ecology and Evolution*, **2**, 383–9.
- Christensen, L. L., Selman, C., Blount, J. D., et al. (2015). Plasma markers of oxidative stress are uncorrelated in a wild mammal. *Ecology and Evolution*, **5**, 5096–5108.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red Deer: Ecology and Behaviour of Both Sexes* (University of Chicago Press).
- Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–29.
- Clutton-Brock, T. H. (1988). *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (University of Chicago Press).
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1988). Reproductive success in male and female red deer. In *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (pp. 325–43), ed. T. H. Clutton-Brock (University of Chicago Press).
- Clutton-Brock, T. H. & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **274**, 3097–3310.
- Clutton-Brock, T. H. & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution*, **25**, 562–73.

- Cohen, A. A. (2004). Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*, **79**, 733–50.
- Cohen, A. A. (2015). Complex systems dynamics in aging: new evidence, continuing questions. *Biogerontology*, **17**, 1–16.
- Colchero, F., Jones, O. R. & Rebke, M. (2012). BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. *Methods in Ecology and Evolution*, **3**, 466–70.
- Comfort, A. (1979). *The Biology of Senescence* (London: Churchill Livingstone).
- Crampe, J. P., Loison, A., Gaillard, J.-M., et al. (2006). Monitoring of the reproduction in isard females (*Rupicapra pyrenaica pyrenaica*) in a non-hunted population and demographic consequences. *Canadian Journal of Zoology*, **84**, 1263–8.
- Crosier, A. E., Marker, L., Howard, J., et al. (2007). Ejaculate traits in the Namibian cheetah (*Acinomyx jubatus*): influence of age, season and captivity. *Reproduction Fertility and Development*, **19**, 370–82.
- Curren, L. J., Weldele, M. L. & Holekamp, K. E. (2013). Ejaculate quality in spotted hyenas: intraspecific variation in relation to life-history traits. *Journal of Mammalogy*, **94**, 90–9.
- Davis, W. H. (1966). Population dynamics of bat *Pipistrellus subflavus*. *Journal of Mammalogy*, **47**, 383.
- Deevey, E. S. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology*, **22**, 283–314.
- Delean, J. S. C. (2007). Longitudinal Population Demography of the Allied Rock Wallaby, *Petrogale assimilis*. Unpublished PhD dissertation, James Cook University, Australia.
- de Magalhaes, J. P. & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology*, **22**, 1770–4.
- de Magalhaes, J. P., Costa, J. & Church, G. M. (2007). Analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *Journals of Gerontology Series A*, **62**, 149–60.
- Delgiudice, G. D., Fieberg, J., Riggs, M. R., et al. (2006). A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management*, **70**, 1556–68.
- DelGiudice, G. D., Lenarz, M. S. & Powell, M. C. (2007). Age-specific fertility and fecundity in northern free-ranging white-tailed deer: evidence for reproductive senescence? *Journal of Mammalogy*, **88**, 427–35.
- Derocher, A. E. & Stirling, I. (1994). Age-specific reproductive performance of female polar bears (*Ursus maritimus*). *Journal of Zoology*, **234**, 527–36.
- Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.-M. (2007). Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. *Journal of Animal Ecology*, **76**, 1192–1201.
- Dinerstein, E. (1991). Demography and habitat use by greater one-horned rhinoceros in Nepal. *Journal of Wildlife Management*, **55**, 401–11.
- Dobson, F. S. (1992). Body mass, structural size, and life-history patterns of the Columbian ground squirrel. *American Naturalist*, **140**, 109–25.
- Dugdale, H. L., Pope, L. C., Newman, C., et al. (2011). Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology*, **20**, 3261–74.

- Dunbar, R. I. M. (1980). Demographic and life-history variables of a population of Gelada baboons (*Theropithecus gelada*). *Journal of Animal Ecology*, **49**, 485–506.
- Eberhardt, L. L. (1985). Assessing the dynamics of wild populations. *Journal of Wildlife Management*, **49**, 997–1012.
- Emlen, J. M. (1970). Age specificity and ecological theory. *Ecology*, **51**, 588–601.
- Ericsson, G. & Wallin, K. (2001). Age-specific moose (*Alces alces*) mortality in a predator-free environment: evidence for senescence in females. *Ecoscience*, **8**, 157–63.
- Ericsson, G., Wallin, K., Ball, J. P. & Broberg, M. (2001). Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology*, **82**, 1613–20.
- Evans, K. & Hindell, M. A. (2004). The age structure and growth of female sperm whales (*Physeter macrocephalus*) in southern Australian waters. *Journal of Zoology*, **263**, 237–50.
- Festa-Bianchet, M., Gaillard, J.-M. & Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, **72**, 640.
- Festa-Bianchet, M. & Côté, S. D. (2008). *Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate* (Washington, DC: Island Press).
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press).
- Flook, D. R. (1970). Causes and implications of an observed sex differential in the survival of wapiti. *Canadian Wildlife Service Report*, **11**, 1–70.
- Focardi, S., Gaillard, J.-M., Ronchi, F. & Rossi, S. (2008). Survival of wild boars in variable environments: unexpected life-history variation in an unusual ungulate. *Journal of Mammalogy*, **89**, 1113–23.
- Footo, A. D. (2008). Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biology Letters*, **4**, 189–91.
- Fraga, C. G., Shigenaga, M. K., Park, J. W., et al. (1990). Oxidative damage to DNA during aging: 8-hydroxy-2'-deoxyguanosine in rat organ DNA and urine. *Proceedings of the National Academy of Sciences of the United States of America*, **87**, 4533–7.
- Gaillard, J.-M., Pontier, D., Allainé, D., et al. (1989). An analysis of demographic tactics in birds and mammals. *Oikos*, **56**, 59–76.
- Gaillard, J.-M., Liberg, O., Andersen, R., et al. (1998). Population dynamics of roe deer. In *European Roe Deer: The Biology of Success* (pp. 309–35), ed. R. Andersen, P. Duncan & J. D. C. Linnell (Oslo: Scandinavian University Press).
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., et al. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–93.
- Gaillard, J.-M., Duncan, P., Delorme, D., et al. (2003). Effects of hurricane Lothar on the population dynamics of European roe deer. *Journal of Wildlife Management*, **67**, 767–73.
- Gaillard, J.-M., Loison, A., Festa-Bianchet, M., et al. (2003). Ecological correlates of life span in populations of large herbivorous mammals. *Population & Development Review*, **29**, 39–56.

- Gaillard, J.-M., Viallefont, A., Loison, A. & Festa-Bianchet, M. (2004). Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation*, **27**, 47–58.
- Gaillard, J.-M., Yoccoz, N. G., Lebreton, J.-D., et al. (2005). Generation time: a reliable metric to measure life-history variation among mammalian populations. *American Naturalist*, **166**, 119–23.
- Gaillard, J.-M., Hewison, A. J. M., Klein, F., et al. (2013). How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecology Letters*, **16**, 48–57.
- Gamelon, M., Focardi, S., Gaillard, J.-M., et al. (2014). Do age-specific survival patterns of wild boar fit current evolutionary theories of senescence? *Evolution*, **68**, 3636–43.
- Garratt, M., Gaillard, J.-M., Brooks, R. C. & Lemaître, J. F. (2013). Diversification of the eutherian placenta is associated with changes in the pace of life. *Proceedings of the National Academy of Sciences of the United States*, **110**, 7760–5.
- Garrott, R. A. & Taylor, L. (1990). Dynamics of a feral horse population in Montana. *Journal of Wildlife Management*, **54**, 603–12.
- Garrott, R. A., Eagle, T. C. & Plotka, E. D. (1991). Age-specific reproduction in feral horses. *Canadian Journal of Zoology*, **69**, 738–43.
- Garrott, R. A., Eberhardt, L. L., White, P. J. & Rotella, J. (2003). Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology*, **81**, 33–45.
- Gimenez, O., Viallefont, A., Charmantier, A., et al. (2008). The risk of flawed inference in evolutionary studies when detectability is less than one. *American Naturalist*, **172**, 441–8.
- Gompertz, B. (1825). On the nature of the function expressive of the law of human mortality and on a new model of determining life contingencies. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **115**, 513–85.
- Graham, A. L., Hayward, A. D., Watt, K. A., et al. (2010). Fitness correlates of heritable variation in antibody responsiveness in a wild mammal. *Science*, **330**, 662–5.
- Green, W. C. H. (1990). Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? *Behavioral Ecology*, **1**, 148–60.
- Hadley, G. L., Rotella, J. J. & Garrott, R. A. (2007). Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology*, **76**, 448–58.
- Hämäläinen, A., Dammhahn, M., Aujard, F., et al. (2015). Senescence or selective disappearance? Age trajectories of body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **281**, 20140830.
- Hamel, S., Craine, J. M. & Towne, E. G. (2012). Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications*, **22**, 1628–39.
- Hamilton, W. D. (1966). Moulding of senescence by natural selection. *Journal of Theoretical Biology*, **12**, 12–45.
- Hanks, J. (1972). Reproduction of elephant, *Loxodonta africana*, in Luangwa Valley, Zambia. *Journal of Reproduction and Fertility*, **30**, 13–26.
- Harting, A. L., Baker, J. D. & Johanos, T. C. (2007). Reproductive patterns of the Hawaiian monk seal. *Marine Mammal Science*, **23**, 553–73.

- Hayward, A. D., Wilson, A. J., Pilkington, J. G., et al. (2009). Ageing in a variable habitat: environmental stress affects senescence in parasite resistance in St Kilda Soay sheep. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **276**, 3477–85.
- Hayward, A. D., Wilson, A. J., Pilkington, J. G., et al. (2013). Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. *Functional Ecology*, **27**, 184–95.
- Hayward, A. D., Mar, K. U., Lahdenperä, M. & Lummaa, V. (2014). Early reproductive investment, senescence and lifetime reproductive success in female Asian elephants. *Journal of Evolutionary Biology*, **27**, 772–83.
- Hayward, A. D., Moorad, J., Regan, C. E., et al. (2015). Asynchrony of senescence among phenotypic traits in a wild mammal population. *Experimental Gerontology*, **71**, 56–68.
- Heard, D., Barry, S., Watts, G. & Child, K. (1997). Fertility of female moose (*Alces alces*) in relation to age and body composition. *Alces*, **33**, 165–76.
- Hernandez-Camacho, C. J., Auriolles-Gamboa, D. & Gerber, L. R. (2008a). Age-specific birth rates of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. *Marine Mammal Science*, **24**, 664–76.
- Hernandez-Camacho, C. J., Auriolles-Gamboa, D., Laake, J. & Gerber, L. R. (2008b). Survival rates of the California sea lion, *Zalophus californianus*, in Mexico. *Journal of Mammalogy*, **89**, 1059–66.
- Hewison, A. J. M. & Gaillard, J.-M. (2001). Phenotypic quality and senescence affect different components of reproductive output in roe deer. *Journal of Animal Ecology*, **70**, 600–8.
- Hibly, A. R. & Mullen, A. J. (1980). Simultaneous determination of fluctuating age structure and mortality from field data. *Theoretical Population Biology*, **18**, 192–203.
- Hindle, A. G., Horning, M., Mellish, J.-A. E. & Lawler, J. M. (2009a). Diving into old age: muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). *Journal of Experimental Biology*, **212**, 790–6.
- Hindle, A. G., Lawler, J. M., Campbell, K. L. & Horning, M. (2009b). Muscle senescence in short-lived wild mammals, the soricine shrews *Blarina brevicauda* and *Sorex palustris*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, **311A**, 358–67.
- Hindle, A. G., Lawler, J. M., Campbell, K. L. & Horning, M. (2010). Muscle aging and oxidative stress in wild-caught shrews. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, **155**, 427–34.
- Hoffman, C. L., Higham, J. P., Mas-Rivera, A., et al. (2010). Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behavioral Ecology*, **21**, 972–8.
- Holmes, E. E., Fritz, L. W., York, A. E. & Sweeney, K. (2007). Age-structured modeling reveals long-term declines in the natality of western Steller sea lions. *Ecological Applications*, **17**, 2214–32.
- Isaac, J. L. & Johnson, C. N. (2005). Terminal reproductive effort in a marsupial. *Biology Letters*, **1**, 271–5.
- Jégo, M., Lemaître, J. F., Bourgoïn, G., et al. (2014). Haematological parameters do senesce in the wild: evidence from different populations of a long-lived mammal. *Journal of Evolutionary Biology*, **27**, 2745–52.

- Jones, O. R., Gaillard, J.-M., Tuljapurkar, S., et al. (2008). Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters*, **11**, 664–73.
- Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J.-M. & Wishart, W. D. (1997). Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology*, **78**, 1019–32.
- Juškaitis, R. (2008). *The Common Dormouse Muscardinus avellanarius: Ecology, Population Structure and Dynamics* (Institute of Ecology of Vilnius University).
- Kirkwood, T. B. L. (1977). Evolution of ageing. *Nature*, **270**, 301–4.
- Kirkwood, T. B. L. & Austad, S. N. (2000). Why do we age? *Nature*, **408**, 233–8.
- Koons, D. N., Gamelon, M., Gaillard, J.-M., et al. (2014). Methods for studying cause-specific senescence in the wild. *Methods in Ecology and Evolution*, **5**, 924–33.
- Koyama, N., Takahata, Y., Huffman, M. A., et al. (1992). Reproductive parameters of female Japanese macaques: 30 years data from the Arashiyama troops, Japan. *Primates*, **33**, 33–47.
- Lander, R. H. (1981). A life table and biomass estimate for Alaskan fur seals. *Fisheries Research*, **1**, 55–70.
- Lawrence, R. K., Demarais, S., Relyea, R. A., et al. (2004). Desert mule deer survival in southwest Texas. *Journal of Wildlife Management*, **68**, 561–9.
- Leader-Williams, N. (1988). *Reindeer on South Georgia* (Cambridge University Press).
- Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lee, D. E. & Tietje, W. D. (2005). Dusky-footed woodrat demography and prescribed fire in a California oak woodland. *Journal of Wildlife Management*, **69**, 1211–20.
- Leigh, S. R., Setchell, J.-M., Charpentier, M., et al. (2008). Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). *Journal of Human Evolution*, **55**, 75–85.
- Lemaître, J. F. & Gaillard, J.-M. (2013a). Polyandry has no detectable mortality cost in female mammals. *PloS ONE*, **8**, e66670.
- Lemaître, J. F. & Gaillard, J.-M. (2013b). Male survival patterns do not depend on male allocation to sexual competition in large herbivores. *Behavioral Ecology*, **24**, 421–8.
- Lemaître, J. F., Gaillard, J.-M., Lackey, L. B., et al. (2013). Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Experimental Gerontology*, **48**, 162–7.
- Lemaître, J. F., Gaillard, J.-M., Pemberton, J. M., et al. (2014). Early life expenditure in sexual competition is associated with increased reproductive senescence in male red deer. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20140792.
- Lemaître, J. F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., et al. (2015). Early-late life trade-offs and the evolution of ageing in the wild. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **282**, 20150209.
- Lima, M. & Paez, E. (1997). Demography and population dynamics of South American fur seals. *Journal of Mammalogy*, **78**, 914–20.
- Lindstedt, S. L. & Calder, W. A. (1981). Body size, physiological time, and longevity of homeothermic animals. *Quarterly Review of Biology*, **56**, 1–16.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., et al. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, **80**, 2539–54.

- Lunn, N. J., Boyd, I. L. & Croxall, J. P. (1994). Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, **63**, 827–40.
- Lynch, H. J. & Fagan, W. F. (2009). Survivorship curves and their impact on the estimation of maximum population growth rates. *Ecology*, **90**, 1116–24.
- Maizels, R. M. & Nussey, D. H. (2013). Into the wild: digging at immunology's evolutionary roots. *Nature Immunology*, **14**, 879–83.
- McAdam, A. G., Boutin, S., Sykes, A. K. & Humphries, M. M. (2007). Life histories of female red squirrels and their contributions to population growth and lifetime fitness. *Ecoscience*, **14**, 362–9.
- McCullough, D. R. (1979). *The George Reserve Deer Herd: Population Ecology of a K-Selected Species* (Ann Arbor: University of Michigan Press).
- McDonald, J. L., Smith, G. C., McDonald, R. A., et al. (2014). Mortality trajectory analysis reveals the drivers of sex-specific epidemiology in natural wildlife-disease interactions. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **281**, 20140526.
- Medawar, P. B. (1952). *An Unsolved Problem of Biology* (London: Lewis).
- Menkens, G. E. & Boyce, M. S. (1993). Comments on the use of time-specific and cohort life tables. *Ecology*, **74**, 2164–8.
- Millar, J. S. (1994). Senescence in a population of small mammals? *Ecoscience*, **1**, 317–21.
- Milner, J. M., Stien, A., Irvine, R. J., et al. (2003). Body condition in Svalbard reindeer and the use of blood parameters as indicators of condition and fitness. *Canadian Journal of Zoology*, **81**, 1566–78.
- Milot, E., Cohen, A. A., Vézina, F., et al. (2014). A novel integrative method for measuring body condition in ecological studies based on physiological dysregulation. *Methods in Ecology and Evolution*, **5**, 146–55.
- Monteith, K. L., Bleich, V. C., Stephenson, T. R., et al. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs*, **186**, 1–62.
- Moore, J. E. & Read, A. J. (2008). A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. *Ecological Applications*, **18**, 1914–31.
- Morris, D. W. (1996). State-dependent life history and senescence of white-footed mice. *Ecoscience*, **3**, 1–6.
- Müller, D. W. H., Gaillard, J.-M., Lackey, L. B., et al. (2010). Comparing life expectancy of three deer species between captive and wild populations. *European Journal of Wildlife Research*, **56**, 205–8.
- Murie, A. (1944). *The Wolves of Mount McKinley* (Washington, DC: US Department Interior, National Park Service).
- Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. (2001). Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependence. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **268**, 911–19.
- Mysterud, A., Meisingset, E., Langvatn, R., et al. (2005). Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos*, **111**, 245–52.

- Neuhaus, P. & Pelletier, N. (2001). Mortality in relation to season, age, sex, and reproduction in Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology*, **79**, 465–70.
- Nichols, J. D. (1992). Capture-recapture models. *Bioscience*, **42**, 94–102.
- Nishida, T., Corp, N., Hamai, M., et al. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, **59**, 99–121.
- Nussey, D. H., Kruuk, L. E. B., Morris, A. & Clutton-Brock, T. H. (2007). Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology*, **17**, R1000–1.
- Nussey, D. H., Kruuk, L. E. B., Morris, A., et al. (2009a). Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *American Naturalist*, **174**, 342–57.
- Nussey, D. H., Pemberton, J. M., Pilkington, J. G. & Blount, J. D. (2009b). Life history correlates of oxidative damage in a free-living mammal population. *Functional Ecology*, **23**, 809–17.
- Nussey, D. H., Coulson, T., Delorme, D., et al. (2011). Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology*, **92**, 1936–47.
- Nussey, D. H., Watt, K., Pilkington, J. G., et al. (2012). Age-related variation in immunity in a wild mammal population. *Aging Cell*, **11**, 178–80.
- Nussey, D. H., Froy, H., Lemaitre, J. F., et al. (2013). Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, **12**, 214–25.
- Oleziuk, P. F., Bigg, M. A. & Ellis, G. M. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, **12**, 209–43.
- Owen-Smith, N. (1990). Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology*, **59**, 893–913.
- Packer, C., Tatar, M. & Collins, A. (1998). Reproductive cessation in female mammals. *Nature*, **392**, 807–11.
- Paul, A., Kuester, J. & Podzuweit, D. (1993). Reproductive senescence and terminal investment in female Barbary macaques (*Macaca sylvanus*) at Salem. *International Journal of Primatology*, **14**, 105–24.
- Péron, G., Gimenez, O., Charmantier, A., et al. (2010). Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **277**, 2849–3285.
- Péron, G., Gaillard, J.-M., Barbraud, C., Bonenfant, C., Charmantier, A., et al. (2016). Evidence of reduced heterogeneity in adult survival of long-lived species. *Evolution*, **70**, 2909–2914.
- Pielowski, Z. (1984). Some aspects of population structure and longevity of field roe deer. *Acta Theriologica*, **29**, 17–33.
- Proffitt, K. M., Garrott, R. A., Rotella, J. J. & Wheatley, K. E. (2007). Environmental and senescent related variations in Weddell seal body mass: implications for age-specific reproductive performance. *Oikos*, **116**, 1683–90.
- Promislow, D. E. L. (1991). Senescence in natural populations of mammals: a comparative study. *Evolution*, **45**, 1869–87.

- Promislow, D. E. L. & Harvey, P. H. (1990). Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology*, **220**, 417–37.
- Promislow, D. E. L., Fedorka, K. M. & Burger, J. M. S. (2006). Evolutionary biology of aging: future directions. In *Handbook of the Biology of Aging*, eds. E. J. Masoro & S. N. Austad (pp. 217–42). (Burlington, MA: Academic Press).
- Pyne, M. I., Byrne, K. M., Holfelder, K. A., et al. (2010). Survival and breeding transitions for a reintroduced bison population: a multistate approach. *Journal of Wildlife Management*, **74**, 1463–71.
- Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, **256**, 421–36.
- Ricklefs, R. E. (2010). Life-history connections to rates of aging in terrestrial vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 10314–19.
- Robbins, A. M., Robbins, M. M., Gerald-Steklis, N. & Steklis, H.D. (2006). Age-related patterns of reproductive success among female mountain gorillas. *American Journal of Physical Anthropology*, **131**, 511–21.
- Robinson, M. R., Pilkington, J. G., Clutton-Brock, T. H., et al. (2006). Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. *Evolution*, **60**, 2168–81.
- Robinson, M. R., Mar, K. U. & Lummaa, V. (2012). Senescence and age-specific trade-offs between reproduction and survival in female Asian elephants. *Ecology Letters*, **15**, 260–6.
- Rotella, J. J., Link, W. A., Chambert, T., et al. (2012). Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark-recapture data. *Journal of Animal Ecology*, **81**, 162–73.
- Rodgers, W. A. (1984). Warthog ecology in South East Tanzania. *Mammalia*, **48**, 327–50.
- Sacher, G. A. (1959). Relation of life span to brain weight and body weight in mammals. In *The Lifespan of Animals* (CIBA Foundation: Colloquia on Aging, Vol. 5, pp. 115–33) (Hoboken, NJ: Wiley).
- Sadleir, R. M. F. S. (1969). *The Ecology of Reproduction in Wild and Domestic Animals* (London: Methuen).
- Saltz, D. (1996). Minimizing extinction probability due to demographic stochasticity in a reintroduced herd of Persian fallow deer *Dama dama mesopotamica*. *Biological Conservation*, **75**, 27–33.
- Schwartz, C. C., Keating, K. A., Reynolds, H. V., et al. (2003). Reproductive maturation and senescence in the female brown bear. *Ursus*, **14**, 109–19.
- Seber, G. A. F. (1973). *The Estimation of Animal Abundance and Related Parameters* (London: Griffin).
- Selman, C., Blount, J. D., Nussey, D. H. & Speakman, J. R. (2012). Oxidative damage, ageing, and life-history evolution: where now? *Trends in Ecology and Evolution*, **27**, 570–7.
- Sharp, S. P. & Clutton-Brock, T. H. (2010). Reproductive senescence in a cooperatively breeding mammal. *Journal of Animal Ecology*, **79**, 176–83.
- Sibly, R. M., Collett, D., Promislow, D. E. L., et al. (1997). Mortality rates of mammals. *Journal of Zoology*, **243**, 1–12.

- Sierra, E., Fernandez, A., de los Monteros, A. E., et al. (2013). Muscular senescence in cetaceans: adaptation towards a slow muscle fibre phenotype. *Scientific Reports*, **3**, 1795.
- Siler, W. (1979). Competing-risk model for animal mortality. *Ecology*, **60**, 750–7.
- Sinclair, A. R. E. (1977). *The Africa Buffalo: A Study of Resource Limitation of Populations* (University of Chicago Press).
- Slade, N. A. (1995). Failure to detect senescence in persistence of some grassland rodents. *Ecology*, **76**, 863–70.
- Slade, N. A. & Balph, D. F. (1974). Population ecology of Uinta ground squirrels. *Ecology*, **55**, 989–1003.
- Smith, C. C. & Fretwell, S. D. (1974). Optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.
- Sohal, R. S., Agarwal, S. & Sohal, B. H. (1995). Oxidative stress and aging in the Mongolian gerbil (*Meriones unguiculatus*). *Mechanisms of Ageing and Development*, **81**, 15–25.
- Spinage, C. A. (1972). African ungulates life tables. *Ecology*, **53**, 645–52.
- Stadtman, E. R. (1992). Protein oxidation and aging. *Science*, **257**, 1220–4.
- Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**, 173–87.
- Stearns, S. C. (1992). *The Evolution of Life Histories* (Oxford University Press).
- Sugiyama, Y. (1994). Age-specific birth rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *American Journal of Primatology*, **32**, 311–18.
- Sussman, R. W. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza-Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology*, **84**, 43–58.
- Sydeman, W. J., Huber, H. R., Emslie, S. D., et al. (1991). Age-specific weaning success of Northern elephant seals in relation to previous breeding experience. *Ecology*, **72**, 2204–17.
- Tafari, M., Cohas, A., Bonenfant, C., et al. (2013). Decreasing litter size of marmots over time: a life history response to climate change? *Ecology*, **94**, 580–6.
- Tettamanti, F., Grignolio, S., Filli, F., et al. (2015). Senescence in breeding success of Alpine chamois (*Rupicapra rupicapra*): the role of female quality and age. *Oecologia*, **178**, 187–95.
- Thomas, D. C. & Barry, S. J. (1990). A life table for female barren-ground caribou in North Central Canada. *Rangifer*, **3**, 177–84.
- Thongtip, N., Saikhun, J., Mahasawangkul, S., et al. (2008). Potential factors affecting semen quality in the Asian elephant (*Elephas maximus*). *Reproductive Biology and Endocrinology*, **6**, 9.
- Tidière, M., Gaillard, J.-M., Muller, D. W. H., et al. (2014). Males do not senesce faster in large herbivores with highly seasonal rut. *Experimental Gerontology*, **60**, 167–72.
- Tinker, M. T., Doak, D. F., Estes, J. A., et al. (2006). Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. *Ecological Applications*, **16**, 2293–2312.
- Toïgo, C., Gaillard, J.-M., Gauthier, D., et al. (2002). Female reproductive success and costs in a temperate capital breeder: the effect of contrasting environmental conditions. *Ecoscience*, **9**, 427–33.

- Toïgo, C. & Gaillard, J.-M. (2003). Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environmental harshness? *Oikos*, **101**, 376–84.
- Toïgo, C., Gaillard, J.-M., van Laere, G., et al. (2006). How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography*, **29**, 301–8.
- Toïgo, C., Gaillard, J.-M., Festa-Bianchet, M., et al. (2007). Sex- and age-specific survival of the highly dimorphic alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology*, **76**, 679–86.
- Valcu, M., Dale, J., Griesser, M., Nakagawa, S. & Kempenaers, B. (2014). Global gradients of avian longevity support the classic evolutionary theory of ageing. *Ecography*, **37**, 930–8.
- Van Noordwijk, A. J. & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist*, **128**, 137–42.
- van de Pol, M. & Verhulst, S. (2006). Age-dependent traits: a new statistical model to separate within- and between-individual effects. *American Naturalist*, **167**, 766–73.
- van de Pol, M. & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, **77**, 753–8.
- Vanpé, C., Gaillard, J.-M., Kjellander, P., et al. (2007). Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist*, **169**, 481–93.
- Vanpé, C., Gaillard, J.-M., Kjellander, P., et al. (2010). Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic species? *Oikos*, **119**, 1484–92.
- Vasilaki, A., McArdle, F., Iwanejko, L. M. & McArdle, A. (2006). Adaptive responses of mouse skeletal muscle to contractile activity: the effect of age. *Mechanisms of Ageing and Development*, **127**, 830–9.
- Vaupel, J. W. & Yashin, A. I. (1985). Heterogeneity's ruses: some surprising effects of selection on population dynamics. *American Statistician*, **39**, 176–85.
- Vincent, J. P., Angibault, J. M., Bideau, E. & Gaillard, J.-M. (1994). Problem of age determination: overlooked source of error in vertical life table calculations [in French]. *Mammalia*, **58**, 293–9.
- Walker, M. L., & Herndon, J. G. (2010). Mosaic aging. *Medical Hypotheses*, **74**, 1048–51.
- Weladji, R. B., Loison, A., Gaillard, J.-M., et al. (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, **156**, 237–47.
- Weladji, R. B., Holand, O., Gaillard, J.-M., et al. (2010). Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia*, **162**, 261–71.
- Whitehouse, A. M. & Hall-Martin, A. J. (2000). Elephants in Addo Elephant National Park, South Africa: reconstruction of the population's history. *Oryx*, **34**, 46–55.
- Wilder, S. M., Le Couteur, D. G. & Simpson, S. J. (2013). Diet mediates the relationship between longevity and reproduction in mammals. *Age*, **35**, 921–7.
- Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. *Evolution*, **11**, 398–411.
- Williams, P. D., Day, T., Fletcher, Q. & Rowe, L. (2006). The shaping of senescence in the wild. *Trends in Ecology and Evolution*, **21**, 458–63.

- Wilson, A. J. & Nussey, D. N. (2010). What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution*, **25**, 207–14.
- Wilson, G. A., Olson, W. & Strobeck, C. (2002). Reproductive success in wood bison (*Bison bison athabasca*) established using molecular techniques. *Canadian Journal of Zoology*, **80**, 1537–48.
- Wolfe, L. D. & Noyes, M. J. S. (1981). Reproductive senescence among female Japanese macaques (*Macaca fuscata fuscata*). *Journal of Mammalogy*, **62**, 698–705.
- Woolley, P. A. (1991). Reproduction in *Dasykaluta rosamondae* (Marsupiala, Dasyuridae): field and laboratory observations. *Australian Journal of Zoology*, **39**, 549–68.