Assessing senescence patterns in populations of large mammals

J.–M. Gaillard, A. Viallefont, A. Loison & M. Festa–Bianchet

Abstract

Assessing senescence patterns in populations of large mammals.— Theoretical models such as those of Gompertz and Weibull are commonly used to study senescence in survival for humans and laboratory or captive animals. For wild populations of vertebrates, senescence in survival has more commonly been assessed by fitting simple linear or quadratic relationships between survival and age. By using appropriate constraints on survival parameters in Capture–Mark–Recapture (CMR) models, we propose a first analysis of the suitability of the Gompertz and the two-parameter Weibull models for describing aging–related mortality in free–ranging populations of ungulates. We first show how to handle the Gompertz and the two–parameter Weibull models in the context of CMR analyses. Then we perform a comparative analysis of senescence patterns in both sexes of two ungulate species highly contrasted according to the intensity of sexual selection. Our analyses provide support to the Gompertz model for describing senescence patterns in ungulates. Evolutionary implications of our results are discussed.

Key words: Gompertz model, Two–parameter Weibull model, Ungulates, Survival, Life history, Sexual selection.

Resumen

Evaluación de pautas de senescencia en poblaciones de grandes mamíferos.— Por lo general, para estudiar el papel que desempeña la senescencia en la supervivencia, ya sea en humanos, en animales de laboratorio o en animales cautivos. Se emplean modelos teóricos, como los de Gompertz y Weibull. En el caso de las poblaciones silvestres de vertebrados, dicho papel tiende a evaluarse ajustando relaciones lineales o cuadráticas simples entre la supervivencia y la edad. En el presente estudio proponemos —a partir de la aplicación de constricciones apropiadas en los parámetros de supervivencia empleados en los modelos de captura–marcaje–recaptura (CMR)— un primer análisis de la idoneidad del modelo de Gompertz y del modelo de dos parámetros de Weibull para describir la mortalidad relacionada con el envejecimiento en poblaciones de ungulados criadas en régimen de pasto libre. En primer lugar indicamos cómo emplear el modelo de Gompertz y el modelo de dos parámetros de Weibull en el contexto de los análisis de CMR, para seguidamente llevar a cabo un análisis comparativo de las pautas de senescencia en dos especies de ungulados de sexos opuestos, altamente contrastadas según la intensidad de la selección sexual. Nuestro análisis apoya el modelo de Gompertz para la descripción de pautas de senescencia en ungulados. Se discuten las implicaciones evolutivas de los resultados obtenidos.

Palabras clave: Modelo de Gompertz, Modelo de dos parámetros de Weibull, Ungulados, Supervivencia, Historia vital, Selección sexual.

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Introduction

Senescence, usually defined as a decrease in reproductive output and/or survival with increasing age (Partridge & Barton, 1993), occurs in a large range of organisms ranging from nematodes to humans (Finch, 1990). However, from an evolutionary standpoint, the persistence of senescence over generations despite counter–selective pressures is paradoxical and is yet to be explained. Two main non–exclusive theories have been proposed: the mutation accumulation that involves mutations with deleterious effects during late life (Medawar, 1952) and the antagonistic pleiotropy that involves pleiotropic genes with advantageous effects during early life but detrimental effects during late life (Williams, 1957). Of the two, the theory of antagonistic pleiotropy has received more support (Partridge & Gems, 2002 for a review) although Hughes et al. (2002) have recently provided clear support for the mutation accumulation theory. Both theories assume that there are alleles that are deleterious in old but not in young individuals. However, only the theory of antagonistic pleiotropy assumes that there is a trade–off between performance in early and late life. So far, empirical studies have failed to show whether such a trade–off is likely to occur in natural populations of vertebrates except in humans where the theory of antagonistic pleiotropy has received some support (e. g., Westendorp & Kirkwood, 1998). Senescence is indeed especially difficult to study in the field because it requires a large number of animals to be monitored from birth to death. Thus while senescence has been reported in most captive populations of birds and mammals studied so far (e. g., Ricklefs, 2000; Ricklefs & Scheuerlein, 2001), whether senescence is pervasive among free–ranging populations of the same species has long been a matter of discussion (e. g., Promislow, 1991; Wooler et al., 1992; Gaillard et al., 1994). Comfort (1979) had even suggested that most free–ranging animals die as young or prime–age adults because adverse conditions do not let them survive until old age.

However, the increasing number of studies based on long–term monitoring of known–aged free–ranging animals and the increasing availability of methods to reliably estimate age–specific survival (especially capture–mark–recapture techniques, Schwarz & Seber, 1999) have recently allowed biologists to accumulate empirical evidence showing that senescence is also common in natural populations of large mammals such as ungulates (Loison et al., 1999; Gaillard et al., 2003b). Such a finding has important consequences for our understanding of population dynamics and life history evolution, as neglecting senescence could bias estimates of adult survival (e.g., Festa–Bianchet et al., 2003). Therefore, we need to know how to model senescence, an issue that has rarely been addressed in population studies of vertebrates. Senescence is most often modelled by using either the Gompertz (e. g., Finch & Pike, 1996) or the Weibull (e. g., Ricklefs, 2000) model, but (1) their use has been limited because of the lack of possibilities to implement these models in the analysis of survival data, and (2) consequently, comparative analyses of the adequacy of these models to survival data from free–ranging vertebrates are lacking. Such comparisons are required because Gompertz and Weibull models imply different patterns of senescence (i. e., the effects of senescence on mortality multiply (Gompertz) versus add to (Weibull) the initial mortality rate, Ricklefs, 1998). The following work is intended to fill this gap.

We analysed age–specific variation in survival of both males and females in two contrasted species of large mammals. Indeed we studied roe deer (*Capreolus capreolus*), a long–lived forest dwelling ungulate that is slightly dimorphic in size and weakly polygynous, and bighorn sheep (*Ovis canadensis*), a long–lived mountain–dwelling ungulate that is highly dimorphic in size and strongly polygynous. We performed our comparative analysis of senescence including the two parameter Weibull and Gompertz models within the framework of CMR methods based on two long–term studies (> 20 years). This procedure allowed us to work on unbiased estimates of survival (i. e., taking account of capture rates less than 1, Nichols, 1992) and to benefit from updated procedures of model selection based on information criterion (AIC, Burham & Anderson, 1998). We first developed a new method permitting to estimate the parameters of the Gompertz model and those of the two–parameter Weibull model, directly from CMR data in wild animal populations, based on the use of specific constraints on the survival parameters. According to our current knowledge of senescence patterns in ungulates we expected that (1) senescence would fit the Gompertz model better than the two–parameter Weibull model in both sexes of both species because ungulate mortality rates have generally been reported to increase exponentially with age (Calder, 1982); (2) males would have both lower initial survival and higher senescence rates than females in both species because the sex ratio among adults usually decreases with increasing age in free–ranging ungulates (Clutton–Brock, 1991); (3) bighorns of both sexes would show higher initial survival than roe deer of both sexes because bighorns are larger than roe deer and survival increases allometrically with body size among mammals (Peters, 1983; Calder, 1984); and (4) bighorn males would show higher senescence rates than roe deer males because the intensity of sexual selection is more acute on strongly polygynous bighorn than on weakly polygynous roe deer, the intensity of sexual selection leading to survival cost (Promislow, 1992).

Material and methods

Study areas and populations studied

Bighorn sheep were studied at Ram Mountain (52º N, 115º W), Alberta, from 1975 to 1997. We did not include data collected after 1997 because some ewes were removed that year and mortality was affected by an increase in cougar predation. The number of bighorn sheep in June ranged from 94 to 232. All adult ewes were marked in all years of the study, and resighting probability was over 99%. Over 98% of adult rams were marked, and annual resighting probability exceeded 95% (Jorgenson et al., 1997). From 1972 to 1980, yearly removals of 12–24% of adult ewes (Jorgenson et al., 1993) kept the population at 94–105 sheep. After 1980, ewe removals were discontinued and the population increased. Some males aged 4 years and older were shot by hunters (range 0–6, average 2.4/year), both during and after the period of ewe removals (Jorgenson et al., 1993). Ages of all individuals were known exactly because they were first captured when aged 4 years or younger (almost all as lambs or year-lings), when age can be accurately determined from horn annuli (Geist, 1966). Potential preda-tors of adult bighorns included cougars (*Puma concolor*), wolves (*Canis lupus*) and black bears (*Ursus americanus*).

Roe deer were studied at Chizé (46º N, 0º E), France, from 1978 to 2003. The population is in a 26 km^2 enclosure and about 70% of the adults are marked. Each year, about 50% of adult deer are captured with drive nets (Gaillard et al., 1993). Ages of almost all marked roe deer born during the study were known because they were caught as fawns. Each year, some unmarked deer were removed for release elsewhere in France. Changes in the number of deer removed from the study area led to popula-tion size estimates varying from 157 to 569 deer older than one year in March (therefore excluding fawns born the previous year) (Gaillard et al., 1993). There were no predators of adult roe deer.

Modelling senescence with CMR models

We analysed our data with recent developments of Capture–Mark–Recapture techniques. Because we were interested in natural mortality, all animals that died because of hunting or accidents, or were re-moved from the population, were excluded from our sample in the year of their death or removal (see Loison et al., 1999). As emigration was impossible at Chizé and extremely rare at Ram Mountain (Jorgenson et al., 1997; Loison et al., 1999), we therefore assumed that all disappearances were due to mortality. Recent survival analyses in these populations have shown that the assumptions of CMR models were fulfilled by our data sets, so that the time–dependent model, the so–called Cormack–Jolly–Seber model (Lebreton et al., 1992) can be used as a starting model (Festa–Bianchet et al.,

2003). Recapture probabilities for bighorn sheep were very high and did not vary among years (Jorgenson et al., 1997; Loison et al., 1999). For roe deer, recapture probabilities varied over time (e. g., Gaillard et al., 2003a). We did not include time in the models in either study because, based on earlier studies (e.g., Loison et al., 1999), we did not find any statistical evidence for time–specific variation in adult survival in the two sexes. We therefore started with the model (ϕ, p_t) for roe deer at Chizé and with the model (ϕ, p) for bighorn sheep at Ram Mountain. Similarly to our previous work, the sexes were ana-lysed separately (Gaillard et al., 1993 for roe deer, Jorgenson et al., 1997 for bighorn sheep). We then fitted the following models to assess the effects of senescence on survival:

(1) a 4 age–class model distinguishing yearling (1 to 2 years), prime–aged (2 to 7 years), old adults (8 to 12 years) and senescent adults (13 years and older). Because only a few bighorn males survived past 12 years, we only considered 3 classes of adult males (yearling from 1 to 2 years, prime–aged from 2 to 7 years, and old males of 8 years and more); this model corresponds to the so–called Caughley model (Caughley, 1966; Gaillard et al., 2000) and fits our current knowledge of survival patterns in ungulate populations (Gaillard et al., 2000) and previous analyses on bighorn sheep and roe deer (Loison et al., 1999); we noted this model (ϕ_c).

(2) The Gompertz model (see below) from 2 years onwards. We indeed excluded yearlings that often show lower survival than adults because of their higher susceptibility to environmental variation (see Gaillard et al., 2000, for a review); in this model we considered that senescence should begin at the age of first reproduction as assumed in evolutionary theories of senescence (Hamilton, 1966); this model corresponds to an evolutionary–based model; we noted this Gompertz model (ϕ_g).

(3) The Gompertz model from 8 years onwards. We here excluded yearlings and prime–age adults from the senescence model to account for a possible delayed senescence in longlived species; we chose 8 years of age as a threshold because in both species a marked tooth wear in animals older than 7 allows people to identify them as old individuals; this model corresponds to an empirically–based model; we noted this Gompertz model (ϕ_{g8}).

(4) The two–parameter Weibull model (see be-low) from 2 years onwards; we noted this Weibull model (ϕ_w).

(5) The two–parameter Weibull model from 8 years onwards. We noted this Weibull model (ϕ_{w8}).

And (6) the complete age–dependent model in-volving a specific survival at each age; we noted this model (ϕ_a).

We used the Akaike Information Criterion (AIC) to select the best parsimonious model (Burnham & Anderson, 1998) at each stage of the analysis. Because all models had a high information/param-eter ratio (> 30), we chose to use AIC instead of AICc (Burnham & Anderson, 1998). All parameter estimates are given ± 1 SE.

Method: introducing the two–parameter Weibull and Gompertz models

These two models suppose that the hazard function, i.e., the function of instantaneous risk of death, changes with time following a specific shape. The general shape of the hazard rate for the two–parameter Weibull model is given by the function:

$$h(t) = \frac{\beta}{\alpha}\left(\frac{t}{\alpha}\right)^{\beta-1}$$

where β is a positive real number representing the shape parameter, and α is a positive real number called the scale parameter. When $\beta > 1$, the hazard rate increases with time, whereas it decreases if $\beta < 1$. For $\beta = 1$, the hazard rate is constant, thus the Weibull model is equivalent to the exponential model (see fig. 1 for the shape of the hazard rate function for various values of α and β). For $1 < \beta < 2$, the rate of increase of the hazard rate in this model is larger in the early periods than later; for $\beta = 2$, the rate of increase of the hazard rate is constant over time; and for $\beta > 2$, the rate of increase of the hazard rate is smaller in the early periods than later.

It is important to notice that when the two–parameter Weibull model is used with an increasing hazard rate, the initial hazard rate is null, corresponding to a survival rate equal to one. This is a very strong constraint for the models, since the mortality is naturally never null at any time or age. This will constrain the estimation of β, such as to obtain estimates of survival at early ages that are reasonable. Thus this may induce low estimates of β ($\beta < 2$), whereas the biological hypotheses are more in favour of an increasing increase in the hazard rates with age ($\beta > 2$). To relax this constraint on the initial survival rates, we would have to use the 3–parameter Weibull model, which is more complicated to implement, and less easy to compare to the (two–parameter) Gompertz model.

The general shape of the hazard rate for the Gompertz model is given by the function: $h(t) = \rho.\exp(\sigma.t)$, where ρ and σ are strictly positive real numbers. In this model, the increase in mortality is exponential, i.e. the ageing process is more and more important with time.

The parameter ρ represents the instantaneous risk at time 0, and σ regulates the intensity and delay of the increase in mortality: the higher σ is, the more intense the aging process (fig. 2).

Method: discrete–time two–parameter Weibull and Gompertz models

In CMR experiments, the most usual situation is one when the time is discretised in equal intervals separated by successive capture occasions. Thus, applying Weibull or Gompertz models to CMR data requires the survival to be expressed per time period (usually annual) in function of the model parameters. In the following, $S(a_i)$ represents the probability that an animal survives until age a_i at least, and $\phi(a_i)$ represents the probability that an animal alive at age a_i survives until age a_{i+1}. The function S is called the survival function, whereas ϕ is the conditional survival per time unit. We have:

$$S(a_i) = \exp\left(-\int_0^{a_i} h(u)du\right)$$

and

$$\phi(a_i) = \frac{S(a_{i+1})}{S(a_i)} = \exp\left(-\int_{a_i}^{a_{i+1}} h(u)du\right)$$

Let us denote h_i the hazard rate at age a_i. We assume that this risk is constant over the interval $[a_i; a_{i+1}]$. Then $\phi(a_i) = \exp(-h_i(a_{i+1}-a_i))$. For the two–parameter Weibull model, we have:

$$h_i = \frac{\beta}{\alpha}\left(\frac{a_i}{\alpha}\right)^{\beta-1}$$

thus

$$\phi(a_i) = \exp\left((a_i - a_{i+1})\frac{\beta}{\alpha}\left(\frac{a_i}{\alpha}\right)^{\beta-1}\right)$$

Thus

$$Ln(-Ln(\phi(a_i))) = Ln(a_{i+1}-a_i) + Ln(\beta) - \beta\,Ln(\alpha) + (\beta-1)\,Ln(a_i).$$

If we assume that $a_{i+1}-a_i = 1$ (time unit between two successive occasions of capture), we can write:

$$Loglog(\phi(a_i)) = Ln(\beta) - \beta\,Ln(\alpha) + (\beta - 1)\,Ln(a_i) \quad (1)$$

with $Loglog(x) = -Ln(-Ln(x))$

For the Gompertz model, we have $h_i = \rho.e^{\sigma.a_i}$ thus

$$\phi(a_i) = \exp\left(\rho.e^{\sigma.a_i}(a_{i+1} - a_i)\right)$$

Thus

$$Ln(-Ln(\phi(a_i))) = Ln(a_{i+1} - a_i) + Ln(\rho) + \sigma a_i$$

Assuming that $a_{i+1}-a_i = 1$, we can write:

$$Loglog(\phi(a_i)) = Ln(\rho) + \sigma.a_i \quad\quad (2)$$

Method: implementation of the two–parameter Weibull and Gompertz models into CMR program design

Computer programs that can produce survival estimates from capture–recapture data usually allow to use generalized linear constraints on the parameters. The equation for such constraints is: $f(V) = D.B$, where f is a link function (a strictly monotonous continuous real function), V is the vector of the k parameters to be constrained, D is a k×p–matrix of variables (called the "design matrix" in a software like MARK, White & Burnham, 1999), and B is the p–vector of the "mathematical parameters", i.e. the parameters that are really estimated. The use of such constraints in capture–recapture was first introduced by Clobert & Lebreton (1985) and Pradel et al. (1990).

Implementing the two–parameter Weibull or Gompertz model into CMR programs is fairly
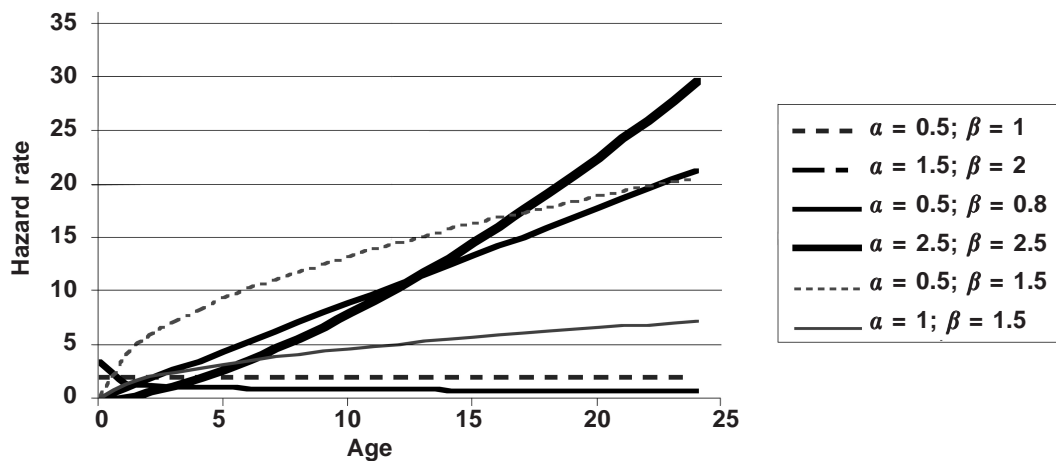
Fig. 1. Hazard function of the two–parameter Weibull model for various values of α and β.

Fig. 1. Función de riesgo del modelo de dos parámetros de Weibull para diversos valores de α y β.
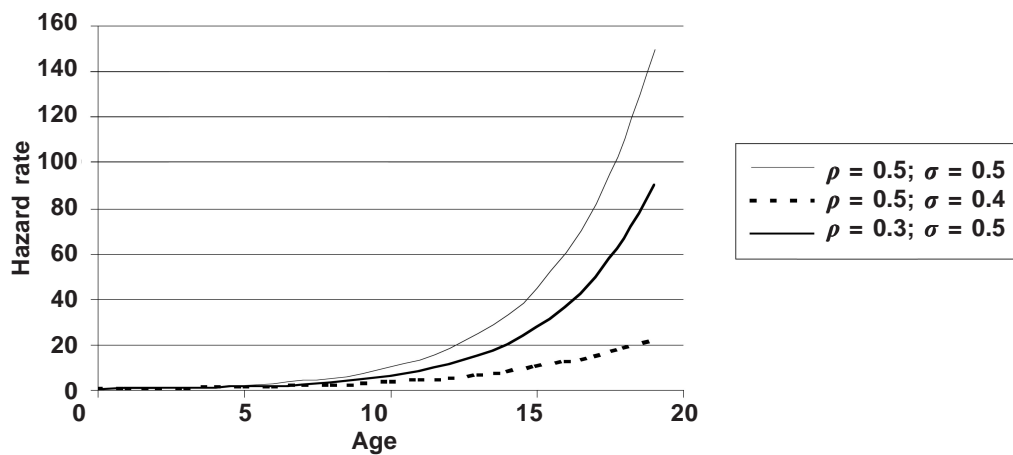
Fig. 2. Hazard function of the Gompertz model for various values of ρ and σ.

Fig. 2. Función de riesgo del modelo de Gompertz para diversos valores de ρ y σ.

straightforward when using this framework. The vector V is the vector of the survival parameters according to age (i.e. the i–th element of V is the probability of surviving from age i to age i+1, $\phi(a_i)$).

For the two–parameter Weibull model we have:

$$Loglog(\phi(a_i)) = Ln(\beta) - \beta\,Ln(\alpha) + (\beta - 1)\,Ln(a_i) \quad (1)$$

that we can also write:

$$f(\phi(a_i)) = B_0 + B_1\,Ln(a_i) \quad (3)$$

where the link function is $f = Loglog$, $B_0 = Ln(\beta) - \beta\,Ln(\alpha)$, and $B_1 = \beta - 1$.

Thus, to fit the two–parameter Weibull model we must use the link function Loglog, and a matrix D constituted of a column of 1's (intercept), and a column of the $Ln(a_i)$'s. In other words the second column of D is the vector of the natural logarithms of ages.

Fitting a model with this constraint will produce the estimated parameters $\hat{B}_0$ and $\hat{B}_1$, from which we can reconstitute the estimates of the parameters of the Weibull model, as:

$$\hat{\alpha} = \exp\left(\frac{Ln(\hat{B}_1 + 1) - \hat{B}_0}{\hat{B}_1 + 1}\right)$$

$$\hat{\beta} = \hat{B}_1 + 1$$

Table 1. Model selection for the senescence of adult bighorn sheep males at Ram Mountain, Canada. Selected models are (2) and (4). Capture probability is constant in all models (p). Models fitted include: (1) a two age class dependent survival (ϕ, yearling and older); (2) a yearling survival and a Gompertz model of senescence from 2 years onwards (ϕ_g); (3) a yearling survival, a prime–age adult survival and a Gompertz model of senescence from 8 years onwards (ϕ_{g8}); (4) a yearling survival and a Weibull model of senescence from 2 years onwards (ϕ_w); (5) a yearling survival, a prime–age survival and a Weibull model of senescence from 8 years onwards (ϕ_w); (6) a three age class dependent survival (ϕ_c, yearling, 2 to 7, and older) that correspond to the Caughley model; and (7) a complete age–dependent survival (ϕ_a); ΔAIC corresponds to the difference of AIC between a given model and the selected model (i.e., 0 for the selected model).

Tabla 1. Selección de modelos para el estudio de la senescencia en el cordero cimarrón macho, de edad adulta, de Ram Mountain, Canadá. Modelos seleccionados son (2) y (4). La probabilidad de captura es constante en todos los modelos (p). Los modelos ajustados incluyen: (1) una supervivencia dependiente de dos clases de edad (ϕ, de 1 año de edad y más); (2) una supervivencia de 1 año de edad y un modelo de senescencia de Gompertz que abarca desde los 2 años de edad en adelante (ϕ_g); (3) una supervivencia de 1 año de edad, una supervivencia en el período de plenitud de la edad adulta y un modelo de senescencia de Gompertz que abarca desde los 8 años de edad en adelante (ϕ_{g8}); (4) una supervivencia de 1 año de edad y un modelo de senescencia de Weibull que abarca desde los 2 años de edad en adelante (ϕ_w); (5) una supervivencia de 1 año de edad, una supervivencia en el período de plenitud la edad adulta y un modelo de senescencia de Weibull que abarca desde los 8 años de edad en adelante (ϕ_w); (6) una supervivencia dependiente de tres clases de edad (ϕ_c: de 1 año de edad, de 2 a 7 años, y más), correspondiente al modelo de Caughley; y (7) una supervivencia dependiente por completo de la edad (ϕ_a); ΔAIC corresponde a la diferencia de AIC entre un modelo determinado y el modelo seleccionado (es decir, 0 para el modelo seleccionado).

Model	Parameter	Deviance	ΔAIC
(1) (ϕ, p)	3	393.404	1.990
(2) (ϕ_g, p)	4	389.480	0.066
(3) (ϕ_{g8}, p)	5	390.603	3.189
(4) (ϕ_w, p)	4	389.414	0
(5) (ϕ_{w8}, p)	5	390.870	3.456
(6) (ϕ_c, p)	4	391.710	2.296
(7) (ϕ_a, p)	13	385.616	14.202

For the Gompertz model we have:

$$\text{Loglog}(\phi(a_i)) = \text{Ln}(\rho) + \sigma.a_i \qquad (2)$$

that we can also write:

$$f(\phi(a_i)) = B_0 + B_1.a_i \qquad (4)$$

where the link function is f = Loglog, B_0 = Ln(ρ), and $B_1 = \sigma$.

Thus, to fit the Gompertz model we must use the link function Loglog, and a matrix D constituted of a column of 1's (intercept), and a column of the ages a_i's.

Fitting a model with this constraint will produce the estimated parameters $\hat{B}_0$ and $\hat{B}_1$, from which we can reconstitute the estimates of the parameters of the Gompertz model, as:

$$\hat{\rho} = \exp(\hat{B}_0)$$
$$\hat{\sigma} = \hat{B}_1$$

The variances of the reconstituted parameters (α and β for the Weibull model, ρ and σ for the Gompertz model) can finally be computed from those of the estimated parameters B_0 and B_1, using the "delta–method" (e. g., Seber 1982, pp. 8–9). For the Gompertz model the obtained formulas are quite simple:

$$\text{Var}(\hat{\rho}) = \hat{\rho}\exp(\hat{B}_0), \ \text{Var}(\hat{\sigma}) = \text{Var}(\hat{B}_1).$$

Method: application to real data

For computational reasons the link function called "Loglog" in software MARK (White & Burnham, 1999) is in fact the opposite of the function Loglog: $f(x) = - \text{Ln}(-\text{Ln}(x))$, which is an increasing function,
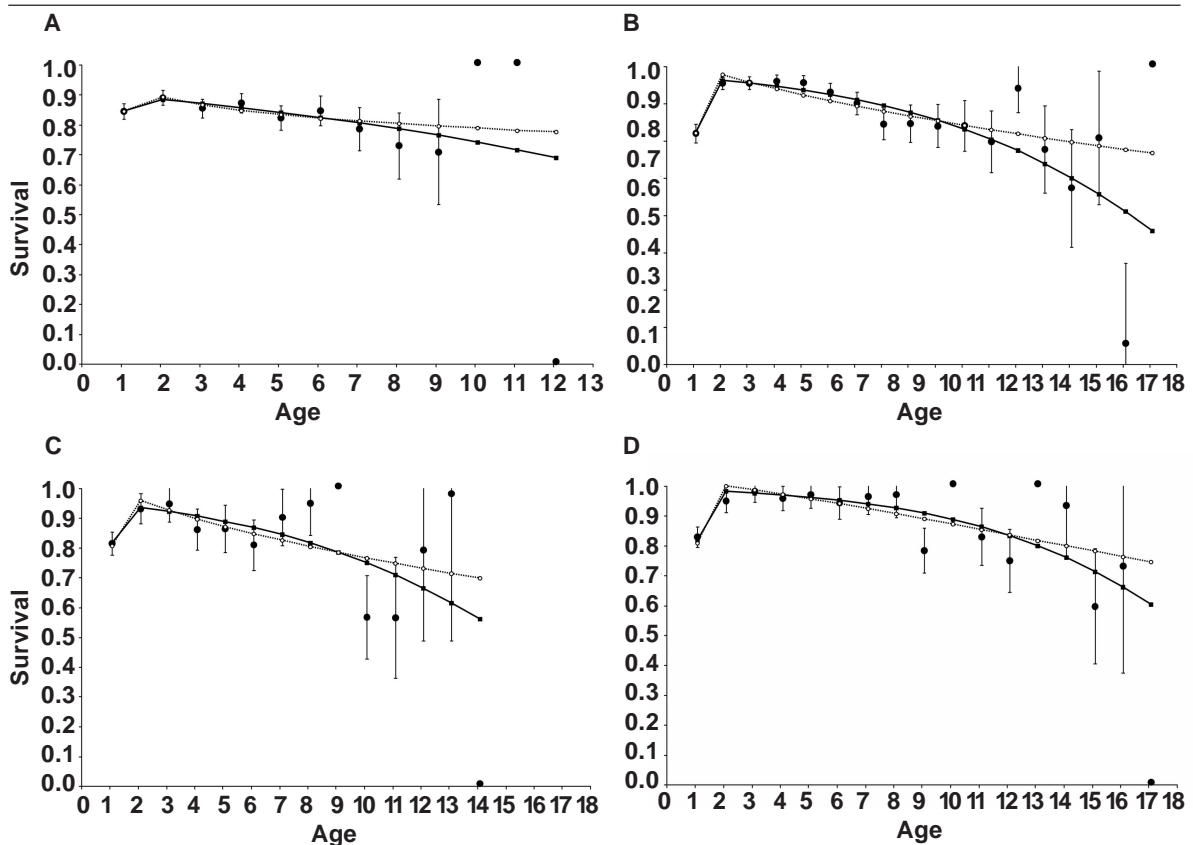
Fig. 3. Age–dependent survival modelled by using a complete age–dependent model (filled symbols with ± 1 SE), a Gompertz function (full line) and a Weibull function (dotted line) in: A. Bighorn sheep males at Ram Mountain, Canada; B. Bighorn sheep females at Ram Mountain, Canada; C. Roe deer males at Chizé, France; D. Roe deer females at Chizé, France.

Fig. 3. Supervivencia dependiente de la edad, modelada empleando un modelo dependiente por completo de la edad (símbolos complementados con ± 1 EE), una función de Gompertz (línea continua) y una función de Weibull (línea discontinua) en: A. Cordero cimarrón macho de Ram Mountain, Canadá; B. Cordero cimarrón hembra de Ram Mountain, Canadá; C. Corzo macho de Chizé, Francia; D. Corzo hembra de Chizé, Francia.

contrary to the "true" Loglog that is decreasing. Thus when using this software it is important to know that the parameter estimates obtained are in fact $(-\hat{B}_0)$ and $(-\hat{B}_v)$. The following steps are identical to those described above.

Results

Male bighorn sheep (table 1, fig. 3A)

The Caughley model provided a similar fit as the constant survival model (i.e., models $[\phi_c, p]$ and $[\phi, p]$ with very close AIC). As expected survival first slightly increased from yearlings (0.837 ± 0.025) to prime–aged adults (0.850 ± 0.014) and then decreased from prime–aged adults to old ones (0.752 ± 0.082). This model

accounted for age–dependence in survival (i.e., model $[\phi_c, p]$ with a much lower AIC than model $[\phi_a, p]$). Both the Weibull and the Gompertz models performed better than the Caughley model (i.e., models $[\phi_w, p]$ and $[\phi_g, p]$ with a lower AIC than model $[\phi_c, p]$), indicating that senescence of male bighorn is better fitted by using a continuous model than a threshold model. Modelling senescence from 2 years onwards provided a better fit than modelling senescence from 8 years. For the same number of parameters, both evolutionary–based models provided the same fit. According to our first prediction, we selected the Gompertz model from 2 years onwards to describe senescence of male bighorns. From this model, the initial mortality (ρ) was estimated to be 0.121 (± 0.024) and the rate of senescence (σ) to be 0.105 (± 0.052).

Table 2. Model selection for the senescence of adult bighorn sheep females at Ram Mountain, Canada. The selected model is (2). Capture probability is constant in all models (p): P. Parameter; D. Deviance. (See table 1 for more information on models fitted.)

Tabla 2. Selección de modelos para el estudio de la senescencia en el cordero cimarrón hembra, de edad adulta, de Ram Mountain, Canadá. El modelo seleccionado es el (2). La probabilidad de captura es constante en todos los modelos (p): P. Parámetro; D. Desviación. (Para más información sobre los modelos ajustados, ver tabla 1.)

Model	P	D	ΔAIC
(1) (ϕ, p)	3	314.543	33.886
(2) (ϕ_g, p)	4	278.657	0
(3) (ϕ_{g8}, p)	5	279.736	3.079
(4) (ϕ_w, p)	4	284.015	5.358
(5) (ϕ_{w8}, p)	5	280.932	4.275
(6) (ϕ_c, p)	5	281.297	4.640
(7) (ϕ_a, p)	19	267.495	18.838

Table 3. Model selection for the senescence of adult roe deer males at Chizé, France. The selected models are (2), (3) and (5). Capture probability is time–dependent in all models (p_t): P. Parameter; D. Deviance. (See table 1 for more information on models fitted.)

Tabla 3. Selección de modelos para el estudio de la senescencia en el corzo macho, de edad adulta, de Chizé, Francia. Los modelos seleccionados son el (2), (3) y (5). La probabilidad de captura es dependiente del tiempo en todos los modelos (p_t): P. Parámetro; D. Desviación. (Para más información sobre los modelos ajustados, ver tabla 1.)

Model	P	D	ΔAIC
(1) (ϕ, p_t)	27	950.840	17.160
(2) (ϕ_g, p_t)	28	931.993	0.313
(3) (ϕ_{g8}, p_t)	29	930.027	0.347
(4) (ϕ_w, p_t)	28	935.391	3.711
(5) (ϕ_{w8}, p_t)	29	929.680	0
(6) (ϕ_c, p_t)	29	934.766	5.086
(7) (ϕ_a, p_t)	39	919.100	9.420

Female bighorn sheep (table 2, fig. 3B)

The Caughley model provided a much better fit than the constant survival model (i.e., model [ϕ_c, p] with a much lower AIC than model [ϕ, p]). Survival first increased from yearlings (0.813 ± 0.025) to prime–aged adults (0.940 ± 0.008) and then decreased first from prime–aged adults to old ones (0.832 ± 0.025), and then from old adults to senescent ones (0.776 ± 0.062). This model accounted for age–dependence in survival (i.e., model [ϕ_c, p] with a much lower AIC than model [ϕ_a, p]).

While the Weibull model did not outperform the Caughley model (i.e., model [ϕ_c, p] with a lower AIC than model [ϕ_w, p]), the Gompertz model did (i.e., model [ϕ_g, p] with a much lower AIC than model [ϕ_c, p] or [ϕ_w, p]). The Gompertz model with the onset of senescence at 2 years of age outperformed the Gompertz model with the onset of senescence at 8 years of age (i. e., model [ϕ_g, p] with a lower AIC than model [ϕ_{g8}, p]) and was finally selected to model senescence of female bighorns. From this model, the initial mortality (ρ) was estimated to be 0.039 (± 0.007) and the rate of senescence (σ) to be 0.161 (± 0.025).

Male roe deer (table 3, fig. 3C)

The Caughley model provided a much better fit than either the constant or the complete age–dependent model (i.e., model [ϕ_c, p_t] with a much lower AIC than both models [ϕ, p_t] and [ϕ_a, p_t]). Survival first increased from yearlings (0.826 ± 0.037) to prime–aged adults (0.887 ± 0.017) and then decreased first from prime–aged adults to old adults (0.804 ± 0.046), and then from old to senescent adults (0.383 ± 0.167). Both the Weibull and the Gompertz models performed better than the Caughley model (i.e., models [ϕ_w, p] and [ϕ_g, p] with a lower AIC than model [ϕ_c, p]), indicating that senescence of male roe deer is better fitted by using a continuous model than a threshold model.

For the same number of parameters, the Gompertz model provided a much better fit than the Weibull model when senescence was assumed to occur from 2 years of age whereas both models performed very well and similarly when senescence occurred from 8 years of age. From a statistical viewpoint, we cannot choose among both evolutionary– and empirically–based Gompertz models and the evolutionary–based Weibull model (differences of AIC among these

Table 4. Model selection for the senescence of adult roe deer females at Chizé, France. The selected models are (2) and (3). Capture probability is time–dependent in all models (p_t): P. Parameter; D. Deviance. (See table 1 for more information on models fitted.)

Tabla 4. Selección de modelos para el estudio de la senescencia en el corzo hembra, de edad adulta, de Chizé, Francia. Los modelos seleccionados son (2) y (3). La probabilidad de captura es dependiente del tiempo en todos los modelos (p_t): P. Parámetro; D. Desviación. (Para más información sobre los modelos ajustados, ver tabla 1.)

Model	P	D	ΔAIC
(1) (ϕ, p_t)	27	1483.662	39.638
(2) (ϕ_g, p_t)	28	1442.024	0
(3) (ϕ_{g8}, p_t)	29	1440.580	0.556
(4) (ϕ_w, p_t)	28	1449.892	7.868
(5) (ϕ_{w8}, p_t)	29	1444.284	4.260
(6) (ϕ_c, p_t)	29	1447.714	7.690
(7) (ϕ_a, p_t)	43	1421.735	9.711

three models within 1). For comparative purposes, we selected the evolutionary–based Gompertz to model senescence of male roe deer. From this model, the initial mortality (ρ) was estimated to be 0.064 (± 0.017) and the rate of senescence (σ) to be 0.171 (± 0.039).

Female roe deer (table 4, fig. 3D)

As for males, the Caughley model provided a much better fit than the constant survival model (i.e., model [ϕ_c, p] with a much lower AIC than model [ϕ, p]). Survival first increased from yearlings (0.818 ± 0.032) to prime–aged adults (0.957 ± 0.010) and then decreased first from prime–aged adults to old adults (0.886 ± 0.023), and then from old adults to senescent ones (0.725 ± 0.054). This model accounted for age–dependence in survival (i. e., model [ϕ_c, p] with a much lower AIC than model [ϕ_a, p]). While the Weibull model did not outperform the Caughley model (i.e., model [ϕ_c, p] with similar AIC as model [ϕ_w, p]), the Gompertz model did (i.e., model [ϕ_g, p] with a much lower AIC than model [ϕ_c, p]). The Gompertz model with the onset of senescence at 2 years of age performed closely to the Gompertz model with the onset of senescence at 8 years of age (i.e., model [ϕ_g, p] with similar AIC as model

[ϕ_{g8}, p]). We selected the evolutionary–based Gompertz to model senescence of female roe deer. From this model, the initial mortality (ρ) was estimated to be 0.021 (± 0.006) and the rate of senescence (σ) to 0.199 (± 0.031).

Discussion

The results reported here on senescence of survival in both sexes of two contrasted ungulate populations monitored over the long–term using a new methodology revealed some consistent patterns that allow us to discuss whether or not the predictions we set either from theoretical or empirical knowledge so far accumulated are supported.

Comparison with the existing methodology

Ad hoc methods mostly based on life tables have often been used to assess senescence in mammals (e.g., Nesse, 1988; Promislow, 1991). By allowing to account for capture rates less than one (Nichols, 1992), CMR methods offer a promising way to reliably estimate the rate of senescence and thereby to test current theories about senescence patterns. To date, CMR analyses have aimed to assess whether or not survival decreases with increasing age but no study to date has yet tried to fit various theoretical models of senescence directly from capture–recapture data, and thus to make comparisons between these models. However, previous CMR studies have already approximated the Gompertz model either by fitting a logit–linear relationship between estimates of survival and age of ungulates (Loison et al., 1999), a linear relationship between the logarithm of the "instantaneous force of mortality" μ (estimated by the Kaplan–Meier method) and age of captive animals (McDonald et al., 1996), or by regressing the Log of mortality estimates ($1 - \phi(a_i)$) on age in ungulates (Gaillard et al., 2003b). These approaches were in fact very close to the models presented here. The (–Loglog) link used here is almost equal to the Logit link used by Loison et al. (1999) when survival rates are greater than 0.75 as is usually observed for large mammals such as ungulates. In the model used by McDonald et al. (1996), μ is defined as: $\mu \approx - Ln(\phi(a_i))$, which means a Loglog relationship between $\hat{\phi}$ and age, exactly like in the Gompertz model implemented here. Lastly, the approximation used by Gaillard et al. (2003b) is also very close to ours, especially when survival is high, as can be seen by comparing the graphical representations of functions "complementary–Log" ($f(\phi) = Ln(1-\phi)$) and of the –Loglog functions. However, when dealing with CMR data, the method described in this paper, fitting the model with a built–in constraint on the parameters, should be preferred because the estimates obtained for various ages in an unconstrained CMR model are not independent of each other, thus not suitable for the estimation of regression parameters (Lebreton et al., 1992). Moreover, our procedure also allowed us

to implement the two–parameter Weibull model for the first time in a CMR context. By allowing us to compare between senescence models, the approach presented here appears as the most efficient and reliable to date to assess senescence from CMR data.

Modelling senescence by Gompertz or Weibull models

In females of both species, the Gompertz model provided the best fit whereas in males, both the two–parameter Weibull and Gompertz models provided the same fit. We therefore found support to our first empirically–based prediction that mammalian senescence can be reliably modelled by using Gompertz model. The multiplicative effects of senescence on mortality might be caused by a degeneration of vital functions when ageing, predicted by both theories of senescence ("mutation accumulation" and "antagonistic pleiotropy"). That the Gompertz model is suitable to describe senescence in ungulates supports previous works performed on more usual material for studying senescence such as drosophilae, nematodes, medfly and humans (Finch & Pike, 1996; Olshanski & Carnes, 1997). However, these works did not provide information on the suitability of other senescence models. The apparent difference between ungulates (that seem to follow better the Gompertz model, this study, Gaillard et al., 2003) and birds (that seem to follow better the Weibull model, Ricklefs, 2000; Ricklefs & Scheuerlein, 2001) in the shape of the senescence curve could account for the much longer longevity of birds despite similar rates of initial mortality (typically less than 0.10). However, such a hypothesis would warrant further investigation. Both models predict an increase of mortality rates with increasing age and only differ according to the shape of the increase (additive vs multiplicative). To address the question, Ricklefs (1998) used regression on survival estimates to fit a three–parameter version of the Gompertz model, and the three parameter Weibull model. Ricklefs & Scheuerlain (2002) reported a reasonably good fit of both Gompertz and Weibull models. In our present analyses, we failed to conclude whether the Gompertz or the two–parameter Weibull model better describe senescence for males of both species for which data spanned over a lower range of ages because of shorter lifespan compared to females. Distinguishing the Gompertz model from the three–parameter Weibull model would probably be more appropriate, but it would not be an easy task because of (1) the usual lack of data for very old individuals, and (2) the difficulty in implementing the three–parameter Weibull model in capture–recapture software. Our modelling did not allow us to assess whether antagonistic pleiotropy or mutation accumulation better accounted for observed senescence patterns in the two ungulate populations we studied. Such an issue is however of major importance and has not yet been satisfactorily solved, especially in natural populations. We feel that having reliable methods for modelling senescence is a prerequisite for any progress in this area.

Between–sex differences in initial mortality and rate of senescence

Senescence patterns reported for bighorn sheep partly supported our second prediction based on current theories of sexual selection. As expected, initial mortality was higher in males than in females in both species. Costly mating tactics of males and between–sex differences in the timing of energy expenditures might account for these results. Highly polygynous bighorn males compete intensively during the mating period at the end of the autumn and almost stop to feed (Ruckstuhl, 1998). At the same time, females spend most time feeding in order to recover body condition after the costly lactation period (Festa–Bianchet et al., 1998). Therefore, males enter winter in much poorer condition than females and are more susceptible to mortality factors (winter severity, predation or diseases, Jorgenson et al., 1997). Results reported for roe deer also supported higher vulnerability of males for initial mortality. Despite slight sexual dimorphism in size and low level of polygyny (Andersen et al., 1998), roe deer males are much more vulnerable to harsh conditions than females. Territory defence over half the year by male roe deer could be involved.

Contrary to the second prediction, however, senescence rates were not higher in males than in females in either species, females showing an even slightly higher rate. Low numbers of old males could be involved in this surprising result.

Allometric effects in senescence patterns

We did not find any support for the third prediction based on allometry according to which larger bighorn should enjoy lower initial mortality than smaller roe deer. Contrary to the expectations, initial mortality rates were higher in bighorn than in roe deer in both sexes. Survival of adult ungulates is high (typically around 0.90, Gaillard et al., 2000) in all species irrespective of their size, likely because of a risk adverse strategy of adults (Gaillard & Yoccoz, 2003). Such a life history tactic is expected to dampen among–species variation in survival. Alternatively, sampling error of survival estimates might mask any existing allometric effect.

Between–species differences in male senescence rate

As expected from our fourth prediction based on current theories of sexual selection, male bighorn sheep tended to show a higher rate of senescence than male roe deer. Such a result supports the hypothesis that males of highly polygynous and dimorphic species exhibit a high risk–high benefit tactic from birth onwards: they usually are born

heavier, grow faster, have higher juvenile mortality, allocate more energy to growth and reproduction than to maintenance, and spend more time in aggressive contests with conspecifics than females (Clutton–Brock, 1991; Short & Balaban, 1994). Although male roe deer differ from females by spending time to defend territories against conspecifics, they are born at the same size, have similar growth rates, and similar juvenile survival as females (Gaillard et al., 1998), likely accounting for the lower rate of senescence observed in male roe deer.

Acknowledgments

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