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# The relationships linking age and body mass to vital rates: a comparative perspective in birds and mammals

Victor Ronget

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**The relationships linking age and body mass  
to vital rates: a comparative perspective in  
birds and mammals**

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# Abstract

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Individuals vary in terms of survival and reproduction. Most of those variations in vital rates can be linked to individual characteristics such as age or body mass. Demographic models were developed to make predictions on those trait-structured populations and are now often used to manage wild populations. However, the amount of data needed to perform those models is not available for every populations. To overcome this issue, I tried in my thesis to assess the general patterns for the relationships linking age and body mass to the vital rates in birds and mammals. By comparing relationships extracted from the literature, I was then able to assess the general effect of body mass or age on vital rates as well as the biological factor explaining the variation of those relationships between species and populations. I first assess how body mass influences vital rates in birds and mammals. I demonstrated the positive effect of offspring body mass on offspring survival and showed how the relative importance of each causes of mortality influence this relationship, with for instance a negative effect of the predation rate on the intensity of the relationship. I also showed that mother body mass is positively related to offspring body mass and that heavier mother are also more likely to reproduce. On a second part I focused on describing the relationship between age and survival for mammals. We built a database Malddaba compiling all relationships linking vital rates to age for wild mammals from life tables reported in the literature. Using life table data compiled in the database I was able to demonstrate that females live on average longer than males in wild populations of mammals. I then critically assess the metrics of longevity and provide new insight to describe the relationship between mortality and age. With my thesis I provided new views on the uses of comparative approaches to highlight the major factors influencing the population dynamic in the wild.

Keywords: heterogeneity, population dynamics, body mass, age, meta-analysis, comparative analysis

# Résumé

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Les individus varient en termes de taux de survie et de taux de reproduction. Les variations de ces taux vitaux peuvent être reliées aux caractéristiques des individus tel que la masse et l'âge. Des modèles démographiques ont été développés pour prendre en compte ces variations dans les populations naturelles et permettre de faire des prédictions pour gérer ces populations naturelles. Cependant, la quantité de données démographiques nécessaire pour construire ces modèles n'est pas disponible dans toutes les populations. Pour surmonter ce problème, j'ai pendant ma thèse, décrit les patrons généraux des relations reliant l'âge et la masse aux taux vitaux chez les mammifères et les oiseaux. En utilisant les données de la littérature, j'ai pu décrire les patrons généraux de ces relations et mis en évidence les facteurs biologiques pouvant expliquer les variations de ces relations entre les espèces et les populations. Dans un premier temps je me suis concentré sur le lien entre la masse des individus et leurs taux vitaux. J'ai montré un effet positif de la masse des jeunes sur la survie des jeunes. J'ai ensuite mis évidence l'effet des différentes causes de mortalité sur cette relation avec par exemple un effet négatif de la prédation sur l'intensité de cette relation. J'ai ensuite montré un effet positif de la masse de la mère sur la masse du jeune et enfin que la probabilité de reproduction d'une femelle est impactée positivement par sa masse. Dans une seconde partie, je me suis concentré sur le lien entre l'âge et la survie chez les mammifères. Pour décrire ce lien, nous avons construit une base de données Malddaba compilant les relations reliant l'âge aux taux vitaux chez les populations naturelles de mammifères que nous avons extraits de tables de vie issues de la littérature. En utilisant ces données, nous avons démontré que les femelles vivent en moyenne plus longtemps que les mâles chez les mammifères. J'ai enfin décrit les avantages et les inconvénients des différentes métriques de longévité et proposé de nouvelles méthodes pour décrire la relation entre l'âge et le taux de mortalité. Avec cette thèse, je mets en avant l'utilisation des approches comparatives pour mieux comprendre quels sont les facteurs qui influence la dynamique des populations naturelles.

Mots-clés : hétérogénéité, dynamique des populations, masse, âge, méta-analyse, analyse comparative



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## APPENDIX 1

**Staerk, J., Conde, D., Ronget, V., Lemaître, J.F., Gaillard, J.M. & Colchero, F. (Under Review) Assessing error in generation time estimates to improve IUCN extinction risk assessments**



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# **Chapter I**

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## **General introduction**

## **Prologue**

Between-individual variation in traits underlying fitness is one of the core assumptions proposed by Darwin to explain the process of natural selection (Darwin, 1859). Differences in vital rates (i.e. survival or reproduction rates) can be thus linked to individual morphological traits in animal populations. Some of those morphological traits explain most of the variation in vital rates and thus major traits explaining the heterogeneity in vital rates can be described for animal populations. Population dynamic studies have developed models to make predictions on changes in population size (Leslie, 1945) and several methodological developments have been proposed to take into account this heterogeneity in vital rates such as the matrix projection models and the integral projections models (Caswell, 2001; Ellner & Rees, 2006). However, all those models for structured populations are based on the existence of heterogeneity of vital rates and include relationships between the morphological traits and the vital rates. To get proper prediction on the evolution of population size from these models it is therefore important to assess these relationships reliably and to identify the biological factors that shape these relationships. In my thesis I will focus on assessing those relationships in bird and mammal populations.

### **1. The relationships between age and vital rates**

The first studies of demographic heterogeneity in population biology focused on the differences in lifespan among individuals within a same population. Indeed, one of the easiest observations you can do when following individuals through their lifetime is that individuals die at different ages. Based on these observations in humans, the first demographic model to take into account this heterogeneity in age at death was developed by Halley for the population of Breslau in 1662 (Bacaër, 2011). The primary goal of the later called ‘life tables’ was to summarize and rank all individuals from birth to death to assess whether observed differences in lifespan correspond to a random process or are responses to some biological or environmental factors.

### 1.1. The life table as a tool to study age-structured populations

The general principle of a life table is to report the number of individuals alive at each age (called  $F_x$  series). From this information, we can derive different statistics to describe age-specific changes in mortality (Caughley, 1966) (see Fig. 1.1 for the construction of life table and definition of the statistics calculated). The key statistic is the mortality rate per age ( $q_x$ ), corresponding to the probability for an individual alive at age  $x$  to die before age  $x+1$ . However, there are major disadvantages in using mortality rates, each mortality rate has a time dimension so that the value of the mortality rate depends on the time interval between two censuses (Ergon *et al.*, 2017). Most often the time interval between two censuses is one year (Millar & Zammuto, 1983). Therefore, life tables are generally the best way to present discrete mortality rates. However, sometimes, the time interval is in month for short-lived species (e.g. Soulsbury *et al.*, 2008 on the Red fox) or can be longer than 1 year if we consider long-lived species such as Killer whales (Olesiuk, Bigg, & M. Ellis, 1990). Moreover, as the mortality rate is a probability, it must be bounded between 0 and 1, which can complexify the expression of the function to model this rate.

This mortality rate was later formalized in demographic modelling using hazard of mortality ( $\mu_x$ ) instead of mortality rate (Makeham, 1867). Instead of considering time as corresponding to a succession of intervals during which mortality is repeatedly measured (i.e. discrete time), mortality can be modelled as a continuous process using continuous distribution. Then,

-  $p_x$  is the continuous distribution of the ages at death, which is the continuous equivalent of the  $d_x$  statistic in life tables,

-  $P_x$  is the cumulative distribution of  $p_x$ , which is the continuous equivalent of the  $1-l_x$  statistic in life tables.

Using these cumulative distribution functions, hazard of mortality also called force of mortality can be described using the same formula as the mortality rate but in a continuous case. Thus, instead of taking a time-step of 1 year, a time-step tending towards 0 is used:

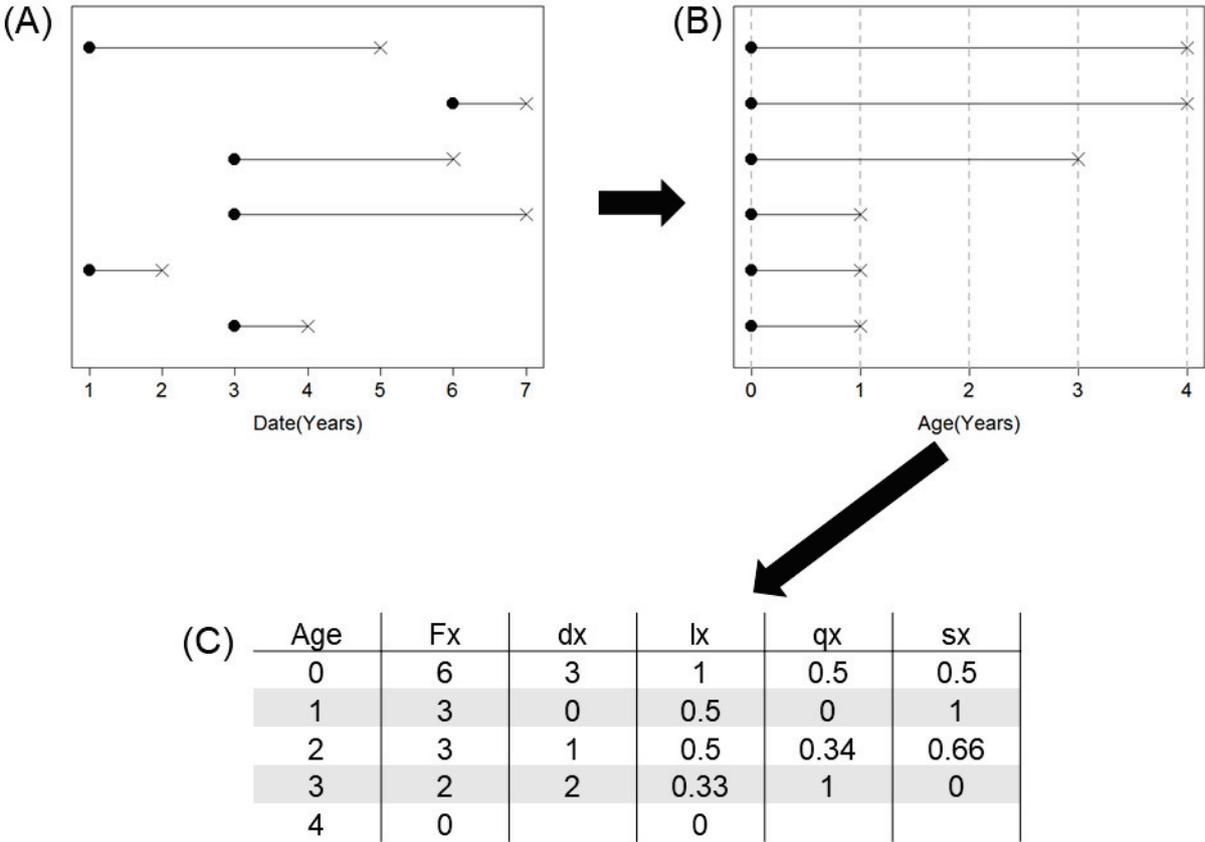
$$\mu(x) = \lim_{dx \rightarrow 0} \frac{Px(x + dx) - Px(x)}{dx(1 - Px(x))} = \frac{Px'(x)}{1 - Px(x)}$$

The benefit of this approach is that hazards of mortality are dimensionless numbers (*sensu* Charnov, 1993) and thus they are easily comparable whatever the time-step used for

the population monitoring. Moreover, hazards of mortality are always positive and boundless making them relatively easier to model than mortality rates. It is also easy to convert mortality rate to hazard of mortality by considering a constant hazard of mortality through the time interval during which the mortality rate is measured:

$$\mu(x) = -\frac{\log(1 - qt1 \rightarrow t2)}{t1 - t2}$$

With  $qt1 \rightarrow t2$  the mortality rate between  $t1$  and  $t2$



**Figure 1.1.** The construction of a life table using hypothetical birth and death records  
 (A) Birth and death records of six hypothetical individuals can be represented graphically, each segment represents the lifespan of an individual with the black circles indicating dates of birth and the black crosses dates of death. Because of their different dates of birth, individuals

cannot be directly compared. They have to be reorganized using their birth as the same starting point for each individual (B). We can thus create the life table (C) to summarize the effect of age on the mortality of individuals for this population by calculating the following statistics for each age:

$F_x$ : number of individuals still alive at age  $x$

$d_x$ : number of individuals that die between age  $x$  and age  $x+1$

$L_x$ : proportion of individuals included in the study which are still alive at age  $x$ , also called cumulative survival

$$l_x = \frac{F_x}{F_0}$$

$q_x$ : probability for an individual alive at age  $x$  to be dead at age  $x+1$ , also called mortality rate

$$q_x = 1 - \frac{l_{x+1}}{l_x}$$

$s_x$ : probability for an individual alive at age  $x$  to be still alive at age  $x+1$ , also called survival rate

$$s_x = \frac{l_{x+1}}{l_x}$$

## 1.2. Modelling the relationship between age and mortality using a Siler Model

One of the most influential work in modelling the mortality hazard of animals through their entire lifetime was made by Siler (1979). Siler was indeed the first to develop the use of bathtub curves to model the mortality hazard using the following equation:

$$\mu(x) = a_0e^{-a_1x} + c_0 + b_0e^{b_1x}$$

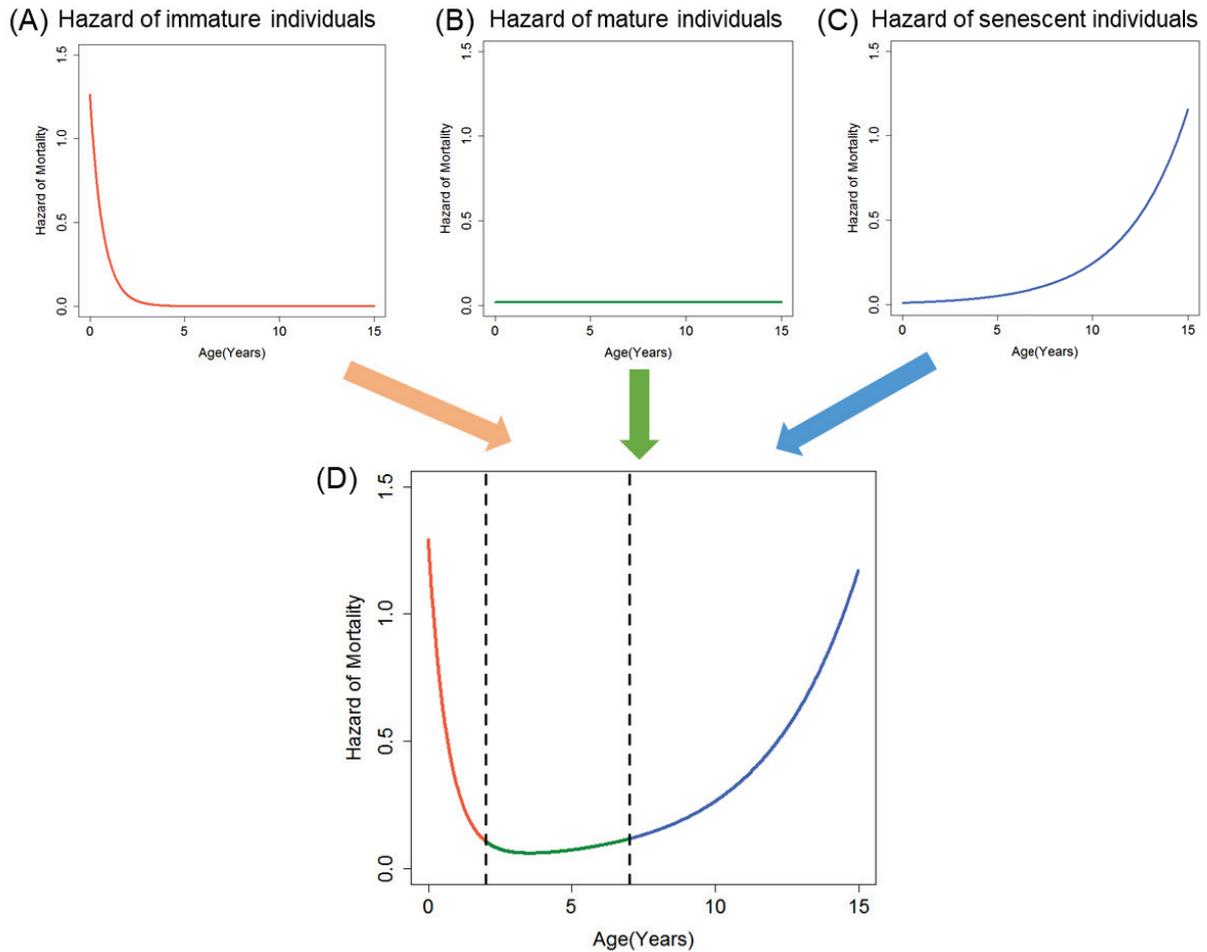
With  $x$  being the age of the individuals and  $a_0$ ,  $a_1$ ,  $c_0$ ,  $b_0$  and  $b_1$  being positive constants

This model is characterized by the addition of three different hazard rates with  $a_0e^{-a_1x}$  corresponding to “hazard of immature individuals” that decreases with increasing age,  $c_0$  corresponding to “hazard mature individuals” constant with age, and  $b_0e^{b_1x}$  corresponding to “hazard of senescent individuals” that increases with age (See Fig. 1.2. for a graphical representation of the Siler function for roe deer females in Trois Fontaines, France). All of these three hazards are higher than zero regardless of the age considered. This implies

that all these three hazard rates consistently have an effect on the total hazard of mortality but with different magnitudes depending on age (i.e. competing risk model). This model is especially well fitted to describe patterns of mortality for animals because it pictures the different phases of the lifetime for birds and mammals (Caughley 1966). At young ages, the immature hazard is the most influential, resulting in a high overall mortality that decreases rapidly with increasing age. This stage represents the juvenile mortality. Around the sexual maturity of the individuals, the mature hazard is the most influential, with a low and relatively constant mortality during adulthood. This stage represents prime-aged adult mortality. At old ages, the senescent hazard is the most influential and leads to an increase of mortality with age. This stage represents the mortality of senescent individuals. In the following, I will explain why this model provides a good fit for all the three stages, according to our current knowledge of the biological cycle of both birds and mammals.

### *1.3. The juvenile stage*

The juvenile stage in mammals and birds is characterized by a high mortality that decreases rapidly with age. Juveniles are the most vulnerable individuals in populations of birds and mammals mostly because of their smaller body size. In ungulates, juveniles are more dependent on changes in environmental conditions than adults (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Gaillard *et al.*, 2000). There are multiple reasons that can explain this highest vulnerability of juveniles. First, they have little or no body reserves and they are thus likely to die from starvation when the amount of resources is low (Linnell *et al.*, 1995). Second, predation often targets juveniles, leading their mortality to be high (Linnell *et al.*, 1995; Martin, 1995). Juveniles have indeed lower evasiveness to predators because they are less developed and they are less experienced (Fu, Cao, & Fu, 2019). Lastly, juveniles are also more likely to die from diseases. They typically suffer from high parasitism intensity because their acquired immunity is not well developed, especially when newborns (Lynsdale *et al.*, 2017).



**Figure 1.2.** Age-specific changes in hazard of mortality fitted using a Siler model to data collected on female roe deer *Capreolus capreolus* in Trois Fontaines, France. (A), (B) and (C) represents the juvenile, mature, and senescent mortality hazard, respectively. The total hazard of mortality (D) results from the interplay of the three hazard rates. We can identify three main life stages from this curve, which characterize most bird and mammal life cycles: the juvenile stage in orange, the adult stage in green, and the senescence stage in blue. For illustrative purpose, I have set the upper limit of the juvenile stage at 2 years of age (age at first reproduction for female roe deer (Gaillard *et al.*, 2003)) and the upper limit of the adult stage at 7 years (onset of senescence for roe deer (Loison *et al.*, 1999)). Note that the Siler model does not include such dichotomies between the different stages in the way it is generally formulated (it rather is a continuous change between each stage). See Chapter VI for the methodology used to fit the Siler model.

Those reasons are likely to account for the peak of mortality found in newborns they and the mortality decrease with increasing age throughout the juvenile stage. With the increase in size generated by the growth process, juveniles store more and more reserves and are thus less likely to die from starvation. They also are less likely to die from predation because they have higher escape capabilities and have gained more experience (Sullivan, 1989; Martin *et al.*, 2018). Growth is not a linear process, and generally decreases in intensity so that individuals grow slower as they age, which leads mortality to decrease also with increasing age before they reach adulthood (Gaillard *et al.*, 1997). The exponential decreasing function from the Siler model reliably accounts this pattern. However, as it is widely accepted that the mortality is highest for newborn and then decrease gradually, the exact form of the relationship between mortality and age in juveniles remains unknown for most species. This lack of knowledge is partly due to the fact that the duration of the juvenile stage is usually short and so difficult to monitor. Indeed, population monitoring in the wild typically involves only one census a year, leading juveniles in species with late maturity to be censused 4 to 5 times but juveniles in species with early sexual maturity to be censused only two times. With this little information it is almost impossible to model the juvenile stage accurately. In fact, for some species it has been demonstrated that most of the juvenile mortality occurred only the first weeks after birth and reached the lowest mortality rate much before sexual maturity (Naef-Daenzer *et al.*, 2001).

#### *1.4. The prime-aged adult stage*

The prime-aged adult stage is characterized by a very low mortality rate constant with age. The mature individuals display the lowest mortality right after the juvenile stage (Gaillard *et al.* 2000). Individuals have reached their maturity and are thus less vulnerable to the different causes of environmentally driven mortality in the wild. As those individuals are not expected to change through the adult stage because individuals have reached their asymptotic size, the risks of mortality are not expected to vary. However, a mortality minimum is expected for this stage, but the duration of this adult stage is debated in the community. There is always a minimum of mortality associated with the adult stage but whether it is associated with a real mortality plateau is questionable (Péron *et al.*, 2010). In some species, the increase of mortality started immediately after the juvenile stage while in others, the mortality increase is delayed (Tidière *et al.*, 2015). In fact, there is no real plateau

expressed in the Siler model, there is just a stage with a minimum mortality of varying duration depending on the hazard rates of both immature and senescent individuals at this age (i.e. longer stage when both hazards are low).

### 1.5. *The senescent stage*

The senescent stage is characterized by an increase in mortality rate with increasing age (i.e. actuarial senescence). This pattern of increase with age was first describe by Gompertz in 1825. Since then the biological process behind this pattern was explained by three main evolutionary theories, “the mutation accumulation”, “the antagonistic pleiotropy“ and the “disposable soma” theories. The “mutation accumulation” theory was first developed by (Medawar, 1952). As demonstrated mathematically later by Hamilton, (1966) the force of natural selection should decrease with age for adults because reproductively active individuals have already reproduced and transmitted their gene pool as they grow older. This decrease of natural selection should lead to the accumulation of deleterious mutations expressed at old ages in the genome. The antagonistic pleiotropy theory developed by (Williams, 1957) is based on the same assumption that the force of natural selection decreases with age and on the existence of pleiotropic genes that are advantageous early in life but have deleterious effect later in life. Those genes, because of the higher force of natural selection early in life than later in life, should be selected. The disposable soma theory (Kirkwood, 1977) states that the individuals have a limited amount of energy that they can allocate throughout their life to growth, reproduction and somatic maintenance. Thus, by allocating resources early in life to growth and reproduction individuals should have less energy to allocate to somatic maintenance later on, which leads to a deterioration in the soma with time. These three theories have been repeatably tested to understand the process of physiological aging, which have demonstrated the that actuarial senescence is ubiquitous in the wild (Durham *et al.*, 2014; Gaillard & Lemaître, 2017). The existence of such pattern of senescence in survival also called actuarial senescence has been widely described in the wild (Nussey *et al.*, 2013; Jones *et al.*, 2014).

However, as the occurrence of senescence pattern across vertebrates appears to be the rule, the detailed modelling of such patterns remains a big issue. The first and one of the most influential models used to describe actuarial senescence is the Gompertz model (Gompertz, 1825):

$$\mu(x) = ae^{bx}$$

with  $a$  the initial hazard of mortality and  $b$  the rate of mortality increase.

The Gompertz mortality model describes an exponential increase in mortality. In other words, the mortality rate increases faster as the individuals age. This model corresponds to the hazard function for the senescent individuals of the Siler model. This exponential increase makes sense if we remember that the senescence pattern is due to the decrease of the force of the natural selection, and we can thus expect that the number of deleterious mutations will increase with age, leading to a gradual increase of the mortality rate. However, the use of the Gompertz model is debated mainly for two main reasons. First, survival patterns at old ages do not follow a Gompertz increase. For instance, in humans, there is a mortality plateau at oldest ages (i.e. beyond 80 years of age), which could be accounted for by using extended Gompertz models including heterogeneity in mortality rates at a given age among individuals (Vaupel, Manton, & Stallard, 1979). Other models were also developed to take in account the existence of a different shape of mortality changes with age among oldest individuals in the wild (i.e. Weibull model (Ricklefs & Scheuerlein, 2001) or Logistic model (Pletcher & Curtsinger, 1998)). The second cause explaining the difficulties to model adequately the senescence curve using the Gompertz model relies on the difficulty to identify the age when senescence begins. Gompertz models imply that the mortality increase begins right after the age at first reproduction, which matches the decline in the force of the natural selection proposed as a mechanism of senescence by Hamilton. However, there is ample evidence in the wild that actuarial senescence begins later than the age of first reproduction (Jones *et al.*, 2008). Several models have been proposed to account for this delayed senescence and to estimate the age of the onset of senescence (e.g. threshold models, non-parametric GAM models, Tidière *et al.*, 2015). There have been lots of methodological advances to adequately model mortality rate, but most of the issues with modelling senescence patterns come in fact from the low amount of data available for older individuals (Nichols, Hines, & Blums, 1997). By definition, senescent individuals are the less numerous in a population and the sample size used is generally very low, making it hard to identify which model is appropriate.

### *1.6. The relationship between reproduction and age*

To understand the dynamics of a population, survival rates are obviously not enough. For instance, to understand how the size of a population changes over time, we need to know

how many individuals survive from one census to another one, but also how many individuals are generated by reproduction. The relationship between reproduction and age is also often reported in life tables by the  $m_x$  statistic, which corresponds to the average number of female offspring produced by a female of age  $x$ . Interestingly, the modelling of the relationship between reproduction and age has not received as much attention as the mortality-age relationship. Most of the studies modeled the reproduction-age relationship as a quadratic one but did only test this relationship against a linear model and thus did only compare one model with a decreasing phase of reproductive performance with age (Derocher & Stirling, 1994). Even though the detailed form of the relationship remains unknown we can identify some of the major typological features associated with this curve (Emlen, 1970). First there is a maximum of reproduction associated with the adult stage. In most of the species studied, this peak of reproduction is delayed from the age at first reproduction with newly reproductive individuals having a lower reproduction (Neuhaus *et al.*, 2004; Zedrosser *et al.*, 2009). Newly reproductive individuals have not yet reached their full adult size and are also less experienced, which explain their relatively lower reproductive rate compared to more mature individuals (Lunn, Boyd, & Croxall, 1994).

One of the other features of this curve is the decrease of reproductive performance at old ages, also named reproductive senescence (Nussey *et al.*, 2013). The reproductive senescence can be explained by using the same theoretical background than actuarial senescence because deleterious mutation affecting reproductive functions are also expected to occur with reproductive age and also because individuals that allocate a lot to growth and early reproduction should be constrained to allocate less and less to the reproduction as they grow older (Lemaître *et al.*, 2015). As well as the actuarial senescence, the existence of a reproductive senescence has been demonstrated to be a widespread pattern in animals (Lemaître & Gaillard, 2017). However, the description of such reproductive senescence patterns remains a big issue and there is a real need of the development of more tools to understand those patterns.

### *1.7. Using Life tables to perform comparative demographic analyses*

In order to understand the factors shaping the different relationships linking age and vital rates, we need to compare the different relationships between species and populations with different characteristics (Pagel, 1994) and thus to compile demographic data over a wide

range of species. Life tables are especially well designed to report the effect of age on survival and reproduction rates in the wild. Most of life tables published for birds and mammals are based on a yearly time scale and, therefore, the description of discrete vital rates for each year provides the most detailed information to describe the effect of heterogeneity in age on vital rates. Life tables also offer a standard presentation of demographic data that could be in theory easily recovered and used to perform comparative analyses of mortality and reproduction patterns because of the standard definitions used for those vital rates. However, demographic data collected in the wild are not always as simple as the one I presented in the Fig. 1.1. In lots of studies in the wild, individuals are not monitored through their entire lifetime. For those studies, different methodologies are used to calculate mortality rates, which include for instance age determination methods (Hamlin *et al.*, 2000) or methods to account for incomplete capture-capture datasets (Choquet *et al.*, 2004). To perform comparative analyses from life tables, we need to do a critical assessment of the different methodologies used in each of the studies reporting life table data and of the quality of these data and to find a way to standardize the different vital rates. Moreover there has been little attempt to date to collect all those data in the literature (but see Millar & Zammuto, 1983; Gaillard *et al.*, 2005; Clutton-Brock & Isvaran, 2007) and until recently there was no compilation of the life tables published in the literature (but see <https://datlife.org/> a new database reporting life tables published for animals). For these reasons, most of the studies performing comparative analyses of senescence patterns have used life tables from captive populations (e.g. generally based on zoo data) instead of wild data because of the greater accuracy of the data coming from daily zoo monitoring (Ricklefs & Scheuerlein, 2001; Tidière *et al.*, 2015). However, I believe that the study of life tables obtained in the wild should markedly improve our knowledge about actuarial senescence because the ecological and evolutionary consequences of natural causes of mortality such as predation are overlooked in life tables coming from zoo data.

### *1.8. The age-structured matrix model*

Once the effect of age on vital rates is assessed, we can make predictions on the evolution over time of the age structure of the population using projection models. The first and most influential model was the matrix projection model developed by Leslie (Leslie, 1945). The core principle for this age-structured model is to predict the asymptotic growth

rate as well as the stable age distribution of the population studied. Since the pioneer contribution from Leslie (1945), matrix projection models (MPM) have become a key tool to analyze wild populations (Caswell, 2001). For instance, these models can be used to get the asymptotic deterministic growth rate of a population that can be decisive in conservation biology to assess the extinction risk of an endangered population (Beissinger & Westphal, 1998). Two databases collecting projections matrices published for plants (COMPADRE, Salguero-Gómez *et al.*, 2015) and animals (COMADRE, Salguero-Gómez *et al.*, 2016) were developed following the great interest in using MPM for conservation biology and well as in comparative demography.

## **2. The relationships between body mass and vital rates**

Age is not the only trait structuring among-individual differences in performances. There is usually a high variance in terms of survival and reproduction within an age class, which suggests the existence of other axes of heterogeneity than age (Wilson & Nussey, 2010). The most studied source of individual heterogeneity acting on populations dynamics is body mass (Vindenes & Langanen, 2015). Individuals of largest body size or mass perform often consistently better in terms of survival and reproduction. The simplest model to take into account this heterogeneity in body mass involves using a generalization of the age-structured matrix population model (Caswell, 2001). Instead of distributing individuals by age they are also distributed into classes based on size or body mass. The projection matrix is thus very similar to the projection matrix of an age-structured model, the only minor differences being that individuals do not necessarily transit to the next class because some individuals can keep the same size or mass. However, this model is in fact very similar to an age-structured one because age is correlated to mass in animal populations (Gaillard *et al.*, 1997) and so this model accounts poorly for the variation in body mass within one age class. To take in account this heterogeneity, a two-layer model is needed to incorporate both an age effect and the heterogeneity in body mass within each of the different age classes.

## 2.1. The integral projection model

Integral Projection Models (Ellner & Rees, 2006; Coulson, 2012; Merow *et al.*, 2014) were developed to take in account variation among individuals in one or more traits, body mass being the most frequently used (Vindenes & Langanen, 2015). IPMs are in fact similar in their goals to the MPMs. MPMs follow changes in the distribution of ages over time in the population while IPMs follow the distribution of the structuring traits (for instance body mass) over time. The biggest difference between these two approaches is that IPMs consider the distribution of the structuring trait as being continuous instead of using discrete age classes for the MPMs. To know how this distribution change with time we need to develop a kernel function that describes how the distribution changes from one time step to the next one. Thus, by using the following formula, we can obtain the distribution of body mass at the next step:

$$N_{t+1}(z') = \int_{\Omega} K(z, z')N_t(z)dz$$

with  $N_{t+1}(z')$  the distribution of the trait (body mass) at time t+1,  $N_t(z)$  the distribution of body mass at time t and  $K(z, z')$  the kernel function describing the change in the mass distribution through survival, reproduction and growth of the different individuals. The kernel function is integrated through all the ranges of size  $\Omega$  that are possible for the organism.

## 2.2. The Kernel Function

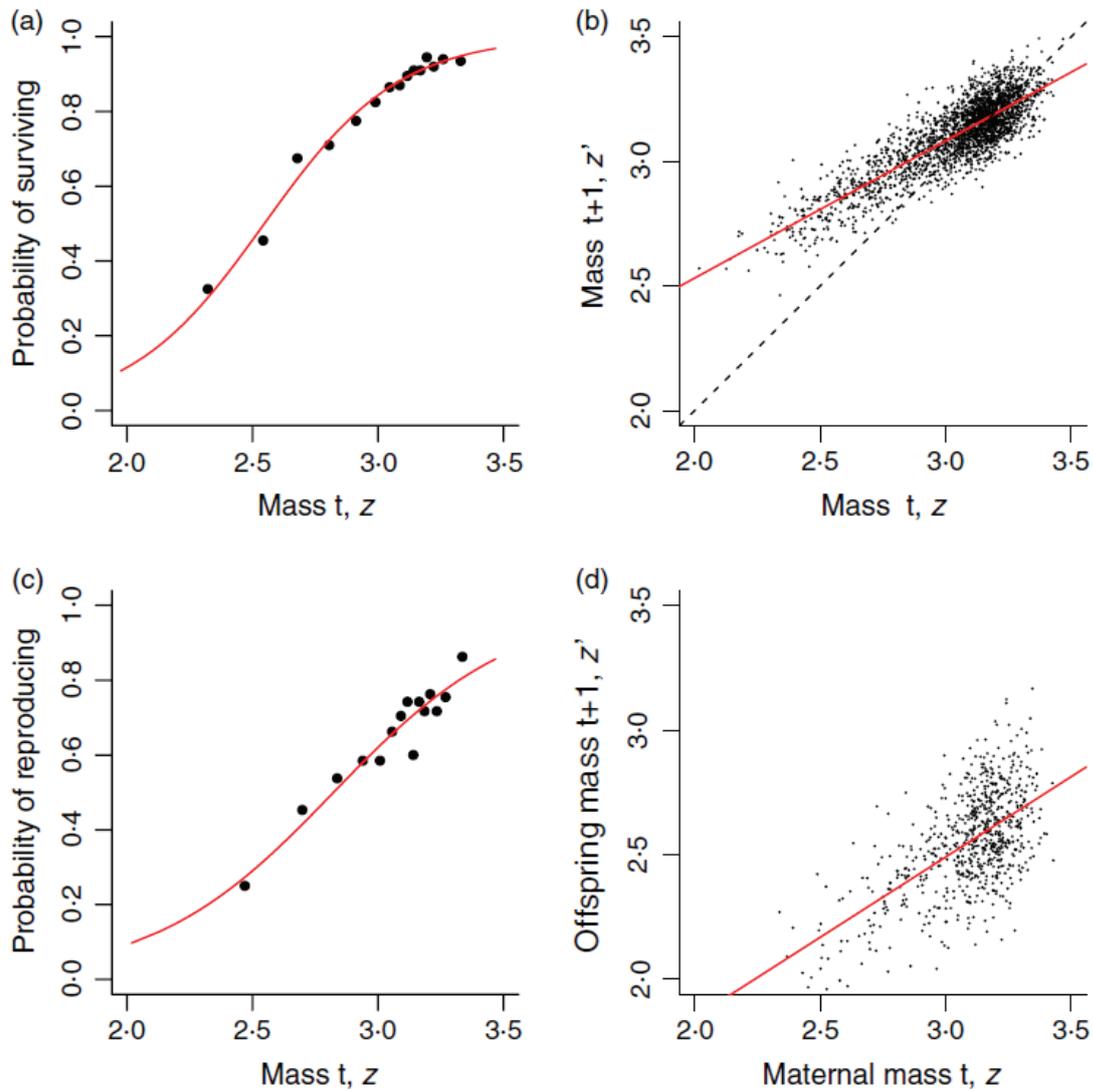
The kernel is the key part when building an IPM, which is highly dependent on the biological cycle of the species studied and on the timing of the census through the year (Merow *et al.*, 2014). This function should describe how an individual of a certain trait value would influence the distribution of body mass at the next time step. Thus, for animals, kernel functions are the addition of two components explaining how reproduction and survival influence the next distribution of the trait. To include these two components, we thus need to establish the 4 main functions describing the link between the demographic parameters and the focal trait for the population (See Fig. 1.3. for an example of the 4 main functions in Soay Sheep, *Ovis aries*). First, the model should take in account how the individuals previously present in the population affect the distribution of the trait. They do that by surviving and by growing. The survival function informs how the mass of an individual affects survival and the

growth function tells us how the surviving individuals change in mass over time. The new recruits in the population also change the distribution of the focal trait. The reproduction function informs the probability that a female reproduces (so its probability to produce new recruits) in function of its mass. Finally, the inheritance (or transmission) function allows predicting the mass of the new recruit from the mass of the mother. IPMs allow estimating key population parameters such as the growth rate of the population, the distribution of the mass or the generation time (Plard *et al.*, 2015). Despite the fact that the theoretical concepts to build IPMs have been extensively developed (e.g. Metcalf *et al.*, 2013), there have been few empirical attempts to date to build such models in birds and mammals (Coulson, 2012; Plard *et al.*, 2015). To model the 4 functions, a long-term monitoring of individuals is required to get information on their survival, reproduction and individual characteristics (Clutton-Brock & Sheldon, 2010). Such extensive amount of data is rarely available for wild populations. To overcome this limitation and find a way to build IPM for a large set of populations, general patterns for the 4 functions are needed.

### *2.3. The survival component of the kernel function*

The survival component of the kernel function explains how surviving individuals change the distribution of the trait. This component includes the survival function as well as the growth function. The survival function linking the survival of adult individuals to their body mass has not received so much attention to date. We saw before that adult survival is expected to be very high compared to juvenile survival and thus we expected the variance of adult survival to be small (Gaillard & Yoccoz, 2003), leading to little or even no effect of the focal trait on adult survival. However, I argue here that when the trait is strongly linked with age as body mass is, the survival-trait relationship captures in fact an effect of age rather than an effect of the trait per se. In survival-trait relationships, only mature individuals are included. Thus, mature individuals of all ages are included from newly recruited to more older ones, although we also know that newly mature individuals should have lower survival but also most of the time did not finish their growth and thereby have a lower body mass than older adults. Age differences alone might lead to a positive relationship between adult survival and the focal trait in birds and mammals. Growth patterns are widely available in the literature for different species of birds and mammals. As previous analyses have reported that the shape of the growth curve strongly depends on the species studied (Gaillard *et al.*, 1997), I

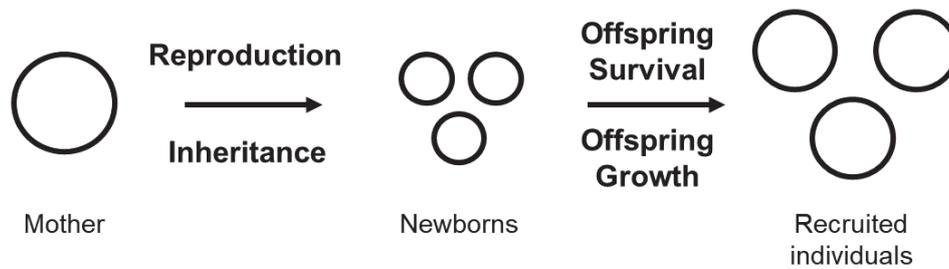
recommend using the species-specific relationship reported in the literature to build reliably the IPM kernel.



**Figure 1.3.** The 4 main function linking the demographic parameters to the structuring trait (body mass here) in a population of Soay sheep (from Rees, Childs, & Ellner, 2014). (a) Survival relationship, (b) Growth relationship, (c) Reproduction relationship and (d) Inheritance relationship.

#### 2.4. The reproductive component of the kernel function

The impact of body mass on reproduction has received even more attention. Depending on the time when individuals are censused the expression of such function should change. We define the reproduction components of the IPM kernel as follows to include most studies that have investigated the effect of body mass on the components of reproduction:



The simplest reproduction function from IPM kernels directly links the mother body mass to the number of recruited individuals. However, we need an intermediate step involving newborns because the relationship linking directly mother mass to recruitment rate of the offspring is rarely provided as such in the literature and also because newborns constitute the vulnerable stage in terms of mortality. Therefore, a higher variance in mortality rate is expected at this early stage. The relationship linking offspring body mass to offspring survival have received much attention (Magrath, 1991; Maness & Anderson, 2013; Monteith *et al.*, 2014). Newborn survival is expected to be highly dependent on their body mass because body mass is linked to individual reserves and reserves are expected provide an advantage for newborns (Lack, 1966; Garnett, 1981). A positive relationship is also expected for the relationship between mother mass and the number of offspring mothers produced (Clutton-Brock *et al.* 1989). As well as reserves should positively impact survival, they should influence positively female reproduction (Schulte-Hostedde, Millar, & Hickling, 2001b). Likewise, the mass of the mother should also positively influence the mass of the offspring because females with higher reserves could allocate more to their offspring (Hamel *et al.* 2012). As the expectations for those three relationships are straightforward, no study to date has tried to compile all the studies presenting these three relationships to test whether there is indeed a positive link on average and whether there are some biological factors that can explain differences between the intensities of these relationships across species.

### **3. Thesis organization**

In this thesis I will present my work on the importance of heterogeneity in vital rates through the two main traits structuring bird and mammal populations: body mass and age. The main goal of my thesis was to compile the different relationships linking body mass or age to the vital rates in animal populations and to assess from all the relationships compiled in the literature whether (1) there is a general pattern and (2) factors shaping those relationships can be identified. The long-term goal is to understand how those different patterns will influence population dynamics.

The first axis of my thesis is to draw the general patterns for the relationships between body mass and the different components of reproduction. Through an extensive review of the literature, I will perform different meta-analyses of each of the relationships to understand what the general pattern is and also what are the factors explaining the diversity of relationships found in the literature. In a first part, I will perform the meta-analysis of the relationships linking body mass to offspring survival and body mass of the mother to body mass of the offspring. In a second part, I will review the importance of the different sources of mortality to shape the relationship between juvenile survival and body mass (or more generally condition indices). I will also highlight the importance of taking into account individual heterogeneity in mortality in evolutionary theories of aging. As a last part I will present the meta-analysis of the relationship linking mother body mass to reproductive rates as well as a meta-analysis of the relationship linking mother body mass to litter size. The goal here is also to identify the biological factors that influence these relationships.

I will then continue by presenting the second axis of my work, which consisted in describing the relationships linking vital rates and age. To do this, along with my supervisors, I performed a review of the different life tables on wild populations of mammals reported in the literature. We thus compiled this information in a demographic database named Malddaba (MAMalian Demographic DATABase). In the first part, I will present the dataset compiled in Malddaba. Then, using some selected case studies I will explain the difficulties to get standardized estimates of vital rates in relation to age. In a second part, I will use the data compiled in Malddaba to perform a comparative analysis of senescence patterns between males and females in wild populations of mammals. I will thus be able to compare differences in terms of longevity or in terms of senescence rate between males and females. In a last part, I will present some new ways to assess senescence patterns in mammals by first assessing the

quality of the different measurement of longevity already used in the literature and by also presenting new ways to analyse the distribution of ages at death in birds and mammals.

I will then finish by discussing some of key results I got from my work and will draw some perspectives for future works using the data already compiled through my thesis.

# Part I

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## **Assessing the general patterns of the relationships between body mass and the different components of reproduction.**

### **Overview**

In this part, I will assess the general patterns for the different relationships linking individual body mass to the different components of reproduction in birds and mammal. I compiled all studies reporting those relationships in the literature. Using a meta-analysis procedure, I first was able to compute the general effect for each of those relationships. The second aim of this part was to identify any biological or environmental factor that could explain the differences in these relationships found between species and populations. This part is composed of three chapters. In the first chapter, I present a meta-analysis of two relationships, the relationship between juvenile survival and juvenile body mass and the relationship between mother mass and offspring mass. In the second chapter, I critically review the importance of integrating the relationship between juvenile survival and juvenile condition when studying dynamics and evolution of wild populations. In the third chapter, I perform a meta-analysis of two relationships linking female body mass to reproduction, the relationship linking female body mass to the pregnancy rate and the relationship linking mother mass to the litter size.

## Chapter II

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# Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals

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# Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals

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## ABSTRACT

Early survival is highly variable and strongly influences observed population growth rates in most vertebrate populations. One of the major potential drivers of survival variation among juveniles is body mass. Heavy juveniles are better fed and have greater body reserves, and are thus assumed to survive better than light individuals. In spite of this, some studies have failed to detect an influence of body mass on offspring survival, questioning whether offspring body mass does indeed consistently influence juvenile survival, or whether this occurs in particular species/environments. Furthermore, the causes for variation in offspring mass are poorly understood, although maternal mass has often been reported to play a crucial role. To understand why offspring differ in body mass, and how this influences juvenile survival, we performed phylogenetically corrected meta-analyses of both the relationship between offspring body mass and offspring survival in birds and mammals and the relationship between maternal mass and offspring mass in mammals. We found strong support for an overall positive effect of offspring body mass on survival, with a more pronounced influence in mammals than in birds. An increase of one standard deviation of body mass increased the odds of offspring survival by 71% in mammals and by 44% in birds. A cost of being too fat in birds in terms of flight performance might explain why body mass is a less reliable predictor of offspring survival in birds. We then looked for moderators explaining the among-study differences reported in the intensity of this relationship. Surprisingly, sex did not influence the intensity of the offspring mass–survival relationship and phylogeny only accounted for a small proportion of observed variation in the intensity of that relationship. Among the potential factors that might affect the relationship between mass and survival in juveniles, only environmental conditions was influential in mammals. Offspring survival was most strongly influenced by body mass in captive populations and wild populations in the absence of predation. We also found support for the expected positive effect of maternal mass on offspring mass in mammals ( $r_{\text{pearson}} = 0.387$ ). As body mass is a strong predictor of early survival, we expected heavier mothers to allocate more to their offspring, leading them to be heavier and so to have a higher survival. However, none of the potential factors we tested for variation in the maternal mass–offspring mass relationship had a detectable influence. Further studies should focus on linking these two relationships to determine whether a strong effect of offspring size on early survival is associated with a high correlation coefficient between maternal mass and offspring mass.

*Key words:* body size, individual heterogeneity, early survival, maternal size, maternal allocation.

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## I. INTRODUCTION

Getting reliable estimates of demographic parameters including survival and reproduction is a major step in assessing population dynamics (Caswell, 2001). Individuals vary greatly in terms of lifespan and reproductive success, which lead them to differ strongly in their contribution to population dynamics. Life-history theory is built on the premise that individual traits that determine reproduction and survival throughout life are shaped by natural selection to maximize individual fitness (Gadgil & Bossert, 1970; Stearns, 1992). It is therefore of crucial importance to assess the relationship among individual traits, demographic parameters, and individual fitness (Cam *et al.*, 2002).

Juvenile survival is an important fitness component because it determines whether or not an individual will reach maturity and therefore reproduce (Lindström, 1999). In long-lived species of mammals and birds the juvenile period is a particularly critical life stage because mortality risks are much higher than after sexual maturity. Since offspring survival often drives population dynamics of long-lived species (Gaillard *et al.*, 2000; Ozgul *et al.*, 2010), it is particularly important to understand the ecological and biological factors that will modulate this fitness component. Numerous studies have investigated the influence of

phenotypic traits on offspring survival, with a particular emphasis on body mass (Magrath, 1991; Maness & Anderson, 2013). Generally, these studies have reported that body mass is a reliable predictor of offspring survival (e.g. Hamel *et al.*, 2009; Mackas *et al.*, 2010).

Body mass is known to be positively correlated with body fat, which represents the main component of body reserves in birds and mammals (Garnett, 1981; Labocha & Hayes, 2012; Monteith *et al.*, 2014; Bennett *et al.*, 2015) and allows large individuals to survive over periods of food shortage. Furthermore, since body mass and body size are generally closely correlated across individuals within a given population, body size also has a positive effect on offspring survival (e.g. McMahon *et al.*, 2015). For instance, in temperate ecosystems, individuals with greater body size survive better than those with low body reserves over the winter (Ringsby, Saether & Solberg, 1998). In addition, energy demands for growth are high during the juvenile stage (Parker, Barboza & Gillingham, 2009) and when food availability is low, body reserves allow growth to continue (Lee, Majluf & Gordon, 1991). However, some studies have failed to detect a positive relationship between offspring body mass and juvenile survival (e.g. Williams & Croxall, 1991; Ylönen, Horne & Luukkonen, 2004; Reading *et al.*, 2009). The most common explanation for these results involves quite constant and abundant food resources during the critical

juvenile stage that lead body reserves, and consequently mass, to have less impact on survival (Van Vuren, Bray & Heltzel, 2013). Likewise, in environments where most juvenile mortality is caused by predation, high individual body mass might not confer a particularly strong survival advantage (Warren, Mysterud & Lynnebakken, 2001). Based on such contrasting results, it remains difficult to infer a general pattern for the effect of body mass on juvenile survival.

Among the factors that influence offspring body mass, maternal condition has been one of the most studied. Maternal body mass is indeed expected to account for a substantial proportion of the variation observed in offspring body mass (Pomeroy *et al.*, 1999; Hamel, Craine & Towne, 2012a) because heavy females can typically allocate more resources to their offspring during both pre- and post-natal stages (e.g. gestation and lactation in mammals), which leads to increased offspring mass and thereby offspring survival. Such relationships between maternal body mass and offspring body mass have been repeatedly documented in the literature (Clutton Brock *et al.*, 1996; Monclús, Pang & Blumstein, 2014). However, some case studies failed to detect such relationships (Campbell & Slade, 1995; Wheatley *et al.*, 2006; Foster & Taggart, 2008). Common explanations for this inconsistency involve the offspring number–size trade-off (Michener, 1989), which appears to be the rule among short-lived species that produce multiple offspring per reproductive attempt (Smith & Fretwell, 1974). Moreover, females of long-lived species often trade current allocation to reproduction for allocation to their own future survival (Tavecchia *et al.*, 2005; Hamel *et al.*, 2010). In harsh years, females of long-lived species are expected to put the emphasis on their own survival, which may produce costs in terms of losing their offspring or of producing offspring of reduced size (Skogland, 1984; Festa-Bianchet & Jorgenson, 1998). Although Lim, Senior & Nakagawa (2014) performed a pioneering meta-analysis to assess the direction of the relationship between mother and offspring body size and found support for an overall positive relationship, they included only a limited number of bird and mammal species (22 birds and 8 mammals) and did not identify the factors driving the observed variation in the strength of that relationship.

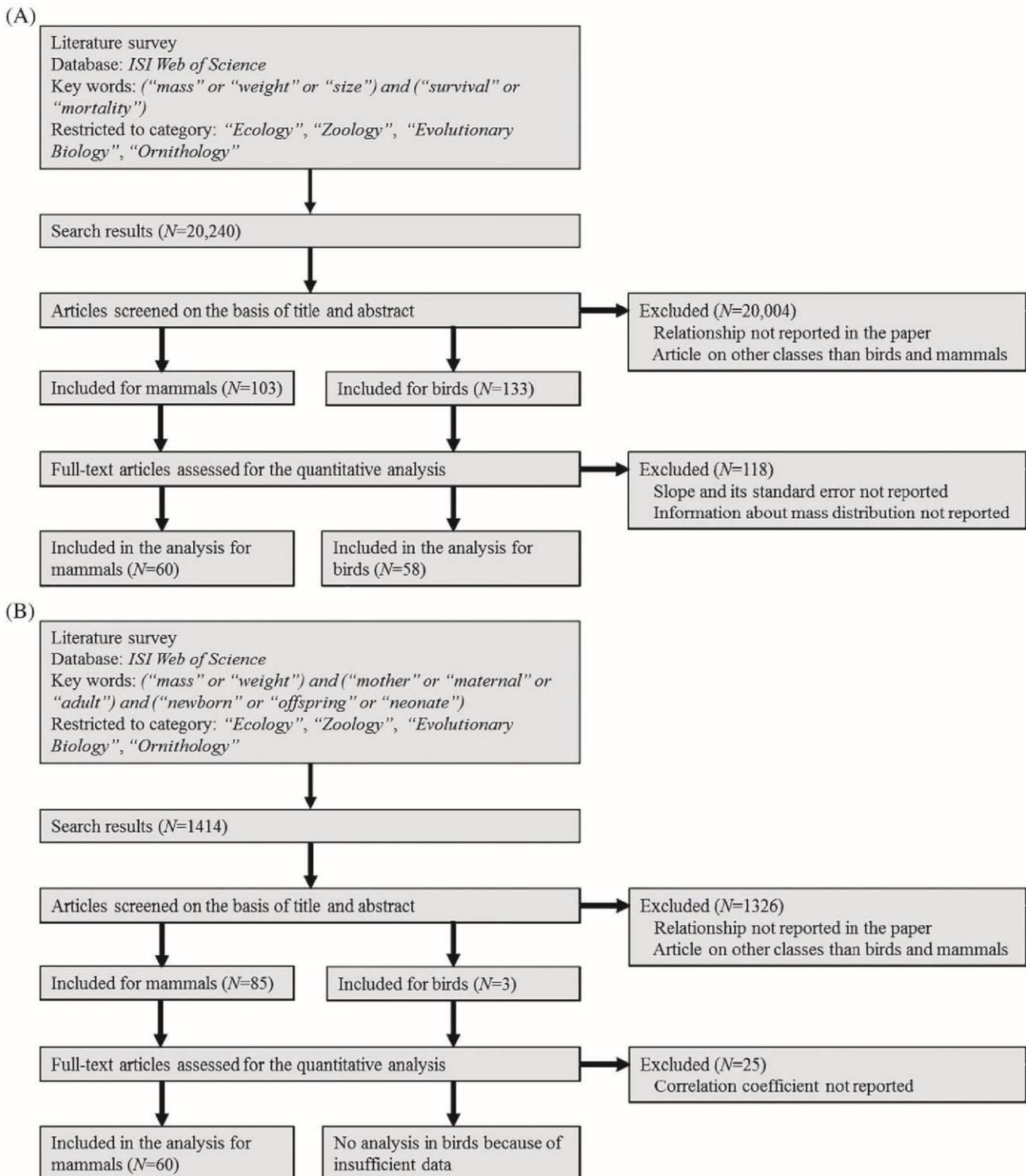
To fill this knowledge gap, we review empirical evidence of the strength of the relationships both between offspring body mass and offspring survival and between offspring mass and maternal body mass from published data. We restricted our analysis to birds and mammals because most detailed studies of free-ranging populations have been performed in these two vertebrate classes (Clutton-Brock & Sheldon, 2010). We first performed two phylogenetically corrected meta-analyses (i.e. one for each relationship) to assess the direction and magnitude of these relationships. In a second step, we looked for biological factors that drive observed variation in each of the two relationships and could explain the conflicting results reported in literature.

We particularly focused on biological moderators that have previously been suggested to influence the relationships between mother and offspring mass, and juvenile survival. Offspring sex was included as one of these because male offspring of dimorphic and polygynous species are more susceptible to harsh conditions than females (Clutton-Brock, Albon & Guinness, 1985). We thus expected that reserves and also body mass will have more influence on male than on female survival, which should ultimately lead to between-sex differences in the relationship between maternal mass and offspring mass. In addition, in polytocous species, the trade-off between offspring mass and offspring number should influence the relationship between offspring mass and maternal mass (Charnov & Ernest, 2006). Thus we accounted for variation in litter size in the analysis of each relationship. Finally, we also tested for an influence of the species mating system because different mating systems lead to different patterns of maternal allocation (Zaveloff & Boyce, 1980) and thereby to expected differences in the relationship between offspring mass and maternal mass.

## II. METHODS

### (1) Literature survey

We collected published papers by using the database of ISI *Web of Science* following a strict search protocol. The key words ('mass' or 'weight' or 'size') and ('survival' or 'mortality') were used to identify studies investigating relationships between offspring survival and mass and the key words ('mass' or 'weight') and ('mother' or 'maternal' or 'adult') and ('newborn' or 'offspring' or 'neonate') were used to identify studies testing for a relationship between maternal mass and offspring mass. The search was conducted in December 2015. We restricted the results to the topics 'Ecology', 'Zoology', 'Ornithology' and 'Evolutionary Biology'. We deliberately used broad key words because much of the required information can be hidden within papers on different topics (e.g. Serra *et al.*, 2012). We identified 20240 papers related to offspring mass and survival and 1414 papers related to maternal mass and offspring mass. We applied a first selection procedure to this list based on the title and only retained papers dealing with mammalian or avian populations. Then, we read all the abstracts to check whether the relationships were explicitly reported in these papers. Finally, we checked the references cited in these articles for any relevant studies missed. A total of 103 papers on mammals and 133 papers on birds were retrieved for the relationship between offspring mass and survival (Fig. 1A). For the relationship between maternal mass and offspring mass we recovered 85 papers on mammals but only three papers on birds (Fig. 1B). We thus did not have enough data on birds to perform a meta-analysis for the relationship between maternal mass and offspring mass. This low amount of published data in birds is discussed in Section IV.



**Fig. 1.** PRISMA flow diagram [search procedure according to the PRISMA statement Liberati *et al.* (2009) and recommended by Nakagawa & Poulin (2012)] for (A) the meta-analysis of the relationship between offspring mass and offspring survival and for (B) the meta-analysis of the relationship between maternal mass and offspring mass.

## (2) Data reported

### (a) Information collected for each case study

For the relationship between offspring mass and survival and for the relationship between maternal mass and offspring mass we retained any relationship including mass or any indicator of mass such as structural size or body condition. When different measurements of mass were used in one paper, we extracted the strict measurement of mass. We did not consider pre-birth measurements such as egg or fetus mass. When the relationship was analysed at different ages (i.e. survival–offspring mass relationship at birth and at weaning), the earliest relationship was retained to avoid pseudo-replication due to repeated measures of the same individuals (Hurlbert, 1984). When the relationship was assessed independently for both sexes, we included sex-specific relationships in the analysis.

All information required for the identification of the paper (i.e. title, first author, year of publication, journal, location and species studied) was recorded. We also reported the timing of offspring measurement, the type of measurement and the data quality (see Section 2.4*b*), which could potentially influence the results of the meta-analysis. We included these factors as moderators in the meta-analysis. We also recorded whether the relationship was assessed for both sexes separately, or for pooled sexes. Lastly we reported whether the focal population was captive or not and if the individuals were subjected to predation.

### (b) Information collected for each species

To assess the potential influence of biological factors on the relationships identified from our meta-analysis, we searched in the literature for information about mating system and litter size (mammal) or brood size (bird) for each species included in our data set (see online Appendices S1, S2 and S3 for all data used for the analysis).

## (3) Extraction of effect sizes

### (a) Relationship between offspring mass and offspring survival

This relationship was generally reported as a logistic function because survival follows a binomial distribution. The slope of the logistic regression was reported with its standard error. When the slope was not provided but the raw data or the logistic curve were graphically displayed in the paper, we extracted the data from the figure using WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>) and then ran a logistic regression with the package *betareg* in R (version R.3.3.0, R Development Core Team 2015). In cases where the standard error was missing but the Wald statistics was reported, we used the Wald statistics to obtain the standard error. We calculated the Wald statistics as  $(\theta - \theta_0)^2 / \text{var}(\theta)$ , which is to be compared to a  $\chi^2$  distribution with  $\theta_0$  equal to 0. When only the slope of the relationship was reported, the standard error could still be estimated when both the mean and the standard deviation of the offspring body

mass were provided. We thus obtained the standard error by first simulating the survival data for each individual body mass using the published logistic relationship and then re-running a logistic regression (see R code in online Appendix S4). The relationship was sometimes presented with a quadratic term (e.g. Verboven & Visser, 1998) and in such situations, when the raw data were available in the paper, we ran a new logistic regression without the quadratic term. This relationship was also sometimes presented as a linear relationship (e.g. Garnett, 1981). In such cases, we converted the slope of the linear regression to a logistic slope following the procedure given in Hamel, Yoccoz & Gaillard (2012*b*). The linear relationship corresponds to a portion of a logistic that is quasi-linear, and multiplying the linear slope by a factor of 4 allows the slope of a logistic regression to be obtained. Occasionally, especially in old papers, the only results reported were the distributions of body mass with the mean and the standard deviation of the mass of dead and alive individuals. In such cases, we assumed that the masses of the dead individuals and of the live individuals were normally distributed and we simulated two normal distributions (one for each group) and ran a logistic regression. We replicated the procedure 10000 times and retained the mean slope and standard error of this slope (see R code in online Appendix S4).

When performing a meta-analysis, standardized coefficients are required to make results from the compiled studies comparable (Nakagawa & Santos, 2012). Only the measurement of mass was standardized in our data set because the slopes were obtained from very different species that have markedly different distributions of offspring mass. We did not standardize survival because survival is bounded between 0 and 1 across all case studies and species. To standardize body mass, the standard deviation of mass was required. When not available, the range of mass was used to infer the standard deviation. We assumed that mass was normally distributed, so that the range corresponds to 4 standard deviations (because in a normal distribution 95% of the values belong to the interval encompassing approximately two standard deviations). Semi-standard slopes were calculated by multiplying the slope with the standard error of the mass (Menard, 2011), the standard error being calculated in the same way. The effect sizes were reported in terms of odds ratios to facilitate interpretation (Lipsey & Wilson, 2001). The odds ratio is calculated as the exponential of the semi-standardized slope. When mass increases by one standard deviation, the odds of survival (i.e. the ratio between the probability to survive and the probability to die) is multiplied by one semi-standardized odds ratio. Thus, a coefficient greater than 1 corresponds to a positive effect of mass on survival. To assess a potential impact of the data extraction on the results for each effect size we scored the data quality as high when all the required information was reported in the paper and as low when we needed to report the data from the figure or to run simulations to obtain the information (see Tables 1, 2 and 3 for detailed information on the extraction

procedure of data and on the quality assessment of each paper).

(b) *Relationship between maternal mass and offspring mass*

For this relationship, the coefficients extracted were Pearson correlation coefficients or partial correlation coefficients. Correlation coefficients can also be inferred from  $\chi^2$ ,  $t$ , and  $F$  statistics using the formulae provided in Lipsey & Wilson (2001). When only raw data were provided we extracted them with WebPlotDigitizer and ran the R function `cor.test` on the data. For the meta-analysis, all these correlation coefficients were converted into a Fisher  $Z_r$ , which is an unbounded measure of effect size for correlation coefficients (Lipsey & Wilson, 2001). This transformation allows the direct calculation of the standard error when the sample size is known. Following Cohen (1988), we considered that correlation coefficients of 0.1, 0.3, and 0.5 represent low, moderate, and strong effects, respectively. We reported the quality of the effect size as described in Section 2.3a to check whether our transformation had any impact on the results of the meta-analysis.

#### (4) Statistical analysis

(a) *General model*

A multi-level meta-analysis was performed because the effect sizes are not independent from each other. Correlation between the different effect sizes can arise when multiple effect sizes are recorded in one population or on the same species or in studies analysed by the same author. Moreover, the shared history among different species makes them non-independent (Harvey & Pagel, 1991). For such analyses, linear mixed models are recommended (Nakagawa & Santos, 2012). We used the function `MCMCglmm` of the package `MCMCglmm` (Hadfield, 2010; Hadfield & Nakagawa, 2010) to perform our analyses. Bayesian hierarchical models are especially recommended to handle phylogenetic meta-analyses in which several effect sizes are reported for the same species (e.g. Santos & Nakagawa, 2012).

In order to assess phylogenetic relatedness among the different species, we used phylogenetic trees for avian (Jetz *et al.*, 2012) and mammalian (Bininda-Emonds *et al.*, 2007) species. These phylogenies were used in the meta-analyses to correct for non-independence between species-specific data points.

For each meta-analysis, linear mixed models were fitted with the effect size as the dependent variable and the error variance implemented for each effect size (with the `mev` argument in the function `MCMCglmm`). The covariance matrix among the species was extracted from the phylogeny. The phylogeny, species, population and first author were included in the model as random factors. We included another random effect as species independently of phylogeny because individuals from the same species can share characteristics that are independent of phylogeny

(e.g. lifestyle). In the absence of clear *a priori* information, we used a non-informative prior (Inverse Wishart prior with  $\nu=0.02$  and  $V=1$ ). To assess whether the prior impacted the results, we re-ran the analysis using a new parameter expanded prior ( $\nu=1$ ,  $V=1$ ,  $\alpha.\mu=0$ ,  $\alpha.V=1000$ ). This sensitivity analysis did not uncover any difference between the two models, meaning that the results we obtained were not dependent on the prior used. Each model was run with 2000000 iterations. We ran several models and assessed convergence with the Gelmann diagnostic (Gelmann & Rubin, 1992) by using the `Gelmann.diag` function in R. This diagnostic detects statistically significant differences in the MCMC chains that could potentially occur between two models when these models do not converge. However, we did not detect any difference among models.

For each model, the mean of the posterior distribution was reported, which corresponds to the meta-analysis mean. We also reported the 95% credibility interval of the highest posterior density distribution (HPDI). The mean was considered as statistically significant when 0 (for  $Z_r$ ) or 1 (for the odds ratio) was not included in the credibility interval. To quantify the importance of the different random effects,  $I^2$  statistics were calculated for each random effect (Nakagawa & Santos, 2012).  $I^2$  represents the percentage of the total variance that is accounted for by the random effect. Values of 25, 50, and 75% are classically interpreted as a low, moderate, and high percentage of variance explained, respectively (Higgins *et al.*, 2003). The  $I^2$  values are presented with their 95% highest posterior density credibility interval, this interval being bounded between 0 and 1.

(b) *Models with moderators*

To test the effect of moderators we included them with fixed effects in new models. In addition to the biological variables presented in the introduction we included other study-specific variables that could influence the intensity of the relationships. We implemented the following moderators.

- (1) The timing of the measurement, which is the life stage that includes the time elapsed between the offspring mass measurement and the record of offspring survivorship. The timing of the measurement was included in models as a three-level factor (Early, Late and Total). ‘Early’ corresponds to pre-weaning (mammals) or pre-fledging (birds) survival. Mass is then recorded at or right after birth (mammals) or hatching (birds). ‘Late’ corresponds to post-weaning (mammals) or post-fledging (birds) survival before recruitment. Mass is then recorded at or close to weaning (mammals) or fledging (birds). ‘Total’ corresponds to a survival estimate encompassing both pre- and post-weaning (mammals) or fledging (birds). Mass is then recorded at or right after birth (mammals) or hatching (birds). We also used the same kind of metrics for the relationship between offspring mass and maternal mass. We distinguished between pre- and

Table 1. Summary of the statistics and of the potential driving factors compiled in the meta-analysis for the relationship between offspring mass and offspring survival in mammals. For each study the logistic slope (Beta), its standard error (S.E.) and the standard deviation of the mass distribution (S.D. Mass), the standardized logistic slope (standardized Beta) and the standardized standard error (standardized S.E.) are reported. The extraction procedure is reported in parentheses as 1 if the statistic is directly calculated in the study, 2 if data are reported from a figure, and 3 if data are reported from our own simulation. See Section II.3a for further information on the extraction procedure and Section II.4b for explanation of Timing of measurement categories

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<b>CARNIVORA</b>										
<i>Ursus maritimus</i>	Ramsay & Stirling (1988)	0.012 (3)	0.007 (3)	32.1 (3)	0.385	0.225	Mass	Early	Combined	Wild
	Derocher & Stirling (1996)	0.1423 (1)	0.054 (3)	3.02 (3)	0.430	0.163	Mass	Early	Combined	Wild
<i>Ursus arctos</i>	Dahle <i>et al.</i> (2006)	0.089 (1)	0.055 (1)	7.517 (1)	0.669	0.413	Mass	Late	Combined	Wild
<i>Mirounga leonina</i>	McMahon, Burton & Bester (2000)	0.031 (3)	0.018 (3)	5.22 (3)	0.162	0.094	Mass	Total	Female	Wild
	Postma, Bester & de Bruyn (2013)	0.04 (3)	0.015 (3)	6.02 (3)	0.241	0.090	Mass	Total	Male	Wild
		0.024 (1)	0.019 (1)	20.62 (1)	0.495	0.392	Mass	Late	Combined	Wild
<i>Leptonychotes weddellii</i>	Proffitt, Garrott & Rotella (2008)	0.007 (1)	0.003 (1)	21.4 (1)	0.150	0.064	Mass	Late	Combined	Wild
<i>Phoca vitulina</i>	Coltman, Bowen & Wright (1998)	-0.21 (3)	0.36 (3)	1.02 (3)	-0.214	0.367	Mass	Early	Female	Wild
		0.38 (3)	0.38 (3)	1.26 (3)	0.479	0.479	Mass	Early	Male	Wild
<i>Halichoerus grypus</i>	Hall, McConnell & Barker (2001)	0.353 (1)	0.159 (1)	1 (1)	0.353	0.159	Condition	Late	Combined	Wild
	Hall, McConnell & Barker (2002)	0.256 (1)	0.135 (1)	1 (1)	0.256	0.135	Mass	Late	Combined	Wild
<i>Eumetopias jubatus</i>	Maniscalco (2014)	0.097 (3)	0.049 (3)	4.35 (3)	0.422	0.213	Mass	Total	Male	Wild
		0.096 (3)	0.063 (3)	3.75 (3)	0.360	0.236	Mass	Total	Female	Wild
<i>Zalophus californianus</i>	Kraus <i>et al.</i> (2013)	1.804 (1)	0.209 (1)	1.009 (3)	1.820	0.211	Mass	Early	Combined	Wild
<i>Arctocephalus gazella</i>	Hoffman, Forcada & Amos (2006)	0.763 (1)	0.15 (3)	0.64 (3)	0.488	0.096	Mass	Early	Combined	Wild
<b>ARTIODACTYLA</b>										
<i>Vicugna vicugna</i>	Donadio, Buskirk & Novaro (2012)	0.773 (1)	0.269 (1)	0.957 (1)	0.740	0.257	Mass	Early	Combined	Wild
<i>Lama guanicoe</i>	Gustafson <i>et al.</i> (1998)	0.067 (3)	0.114 (3)	2.18 (3)	0.146	0.249	Mass	Early	Combined	Wild
<i>Antilocapra americana</i>	Fairbanks (1993)	-0.01 (3)	0.99 (3)	0.45 (3)	-0.005	0.446	Mass	Early	Combined	Wild
	Van Vuren <i>et al.</i> (2013)	-0.91 (3)	0.61 (3)	0.47 (3)	-0.428	0.287	Mass	Early	Combined	Wild
<i>Cervus elaphus</i>	Blaxter & Hamilton (1980)	0.551 (3)	0.129 (3)	1.25 (3)	0.689	0.161	Mass	Early	Combined	Captive
	Loison, Langvatn & Solberg (1999)	0.237 (1)	0.049 (1)	5 (3)	1.185	0.245	Mass	Total	Combined	Wild
	Barber-Meyer, Mech & White (2008)	-0.001 (3)	0.113 (3)	2.25 (3)	-0.002	0.254	Mass	Total	Female	Wild
	White, Zager & Gratson (2010)	0.001 (3)	0.128 (3)	2.64 (3)	0.003	0.338	Mass	Total	Male	Wild
		0.101 (1)	0.033 (1)	3.71 (3)	0.375	0.122	Mass	Early	Combined	Wild
	Griffin <i>et al.</i> (2011)	0.043 (1)	0.031 (1)	3.97 (3)	0.171	0.123	Mass	Early	Combined	Wild
	Moyes <i>et al.</i> (2011)	0.02 (1)	0.01 (1)	2.6 (3)	0.052	0.026	Mass	Early	Combined	Wild
	Walling <i>et al.</i> (2011)	0.55 (1)	0.06 (1)	0.375 (3)	0.206	0.023	Mass	Total	Combined	Wild
<i>Odocoileus virginianus</i>	Stopher <i>et al.</i> (2014)	0.58 (1)	0.057 (1)	2 (3)	1.160	0.114	Mass	Total	Combined	Wild
	Sams <i>et al.</i> (1996)	0.23 (1)	0.02 (1)	1 (1)	0.230	0.020	Mass	Total	Combined	Wild
		0.596 (1)	0.40 (3)	0.972 (3)	0.579	0.389	Mass	Early	Combined	Wild
<i>Odocoileus hemionus</i>	Ditchkoff <i>et al.</i> (2001)	0.533 (1)	0.335 (1)	2.57 (3)	1.370	0.861	Condition	Early	Combined	Wild
	Carstensen <i>et al.</i> (2009)	1.50 (3)	0.63 (3)	0.77 (3)	1.155	0.485	Mass	Early	Combined	Wild
	White <i>et al.</i> (1987)	0.113 (3)	0.033 (3)	4.22 (3)	0.477	0.139	Mass	Late	Combined	Wild
	Bishop, Unsworth & Garton (2005)	0.195 (1)	0.072 (1)	4.74 (3)	0.924	0.341	Mass	Late	Combined	Wild
	Lomas & Bender (2007)	0.19 (1)	0.04 (1)	0.817 (3)	0.155	0.033	Mass	Early	Combined	Wild
	Bishop <i>et al.</i> (2009)	0.446 (3)	0.145 (3)	0.9 (3)	0.401	0.131	Mass	Early	Combined	Wild
	Hurley <i>et al.</i> (2011)	0.194 (1)	0.113 (1)	1.5 (3)	0.291	0.170	Mass	Early	Combined	Wild
<i>Rangifer tarandus</i>	Whitten <i>et al.</i> (1992)	-0.31 (3)	0.37 (3)	0.989 (3)	-0.307	0.366	Mass	Early	Female	Wild
		0.52 (3)	0.29 (3)	1.247 (3)	0.648	0.362	Mass	Early	Male	Wild

Table 1. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
	Jenkins & Barten (2005)	0.265 (1)	0.248 (1)	0.789 (3)	0.209	0.196	Mass	Early	Combined	Wild
<i>Capreolus capreolus</i>	Plard <i>et al.</i> (2015)	0.53 (1)	0.26 (1)	2 (3)	1.06	0.52	Mass	Total	Combined	Wild
<i>Alces alces</i>	Ericsson <i>et al.</i> (2001)	0.371 (1)	0.113 (1)	1.75 (3)	0.649	0.198	Mass	Early	Combined	Wild
	Keech <i>et al.</i> (2011)	-0.011 (1)	0.066 (1)	2.715 (1)	-0.03	0.179	Mass	Early	Combined	Wild
		0.054 (1)	0.062 (1)	1.837 (1)	0.099	0.114	Mass	Early	Combined	Wild
		0.128 (1)	0.089 (1)	2.945 (1)	0.377	0.262	Mass	Early	Combined	Wild
		0.311 (1)	0.115 (1)	3.08 (1)	0.958	0.354	Mass	Early	Combined	Wild
		0.311 (1)	0.122 (1)	3.317 (1)	1.032	0.405	Mass	Early	Combined	Wild
		0.142 (1)	0.108 (1)	2.952 (1)	0.419	0.319	Mass	Early	Combined	Wild
		0.069 (1)	0.073 (1)	2.433 (1)	0.168	0.178	Mass	Early	Combined	Wild
<i>Gazella subgutturosa</i>	Berger (2012)	0.01 (1)	0.03 (1)	18.828 (3)	0.188	0.565	Mass	Early	Combined	Wild
<i>Oreamnos americanus</i>	Riesch <i>et al.</i> (2013)	2.22 (1)	0.29 (1)	0.35 (3)	0.777	0.102	Mass	Total	Combined	Wild
	Côté & Festa-Bianchet (2001)	0.3 (1)	0.15 (1)	2.5 (3)	0.75	0.375	Mass	Total	Combined	Wild
<i>Ovis canadensis</i>	Festa-Bianchet <i>et al.</i> (1997)	0.139 (3)	0.053 (3)	4.951 (3)	0.688	0.262	Mass	Late	Male	Wild
		0.212 (3)	0.063 (3)	4.745 (3)	1.006	0.299	Mass	Late	Female	Wild
	Feder <i>et al.</i> (2008)	2.529 (1)	1.35 (1)	0.181 (3)	0.458	0.244	Mass	Late	Combined	Wild
	Rioux-Paquette, Festa-Bianchet & Coltman (2011)	0.169 (1)	0.051 (1)	4.5 (3)	0.761	0.230	Mass	Late	Combined	Wild
<i>Ovis vignei</i>	Awan, Festa-Bianchet & Gaillard (2008)	0.759 (1)	0.64 (1)	1.522 (3)	1.155	0.974	Mass	Early	Combined	Wild
<i>Ovis aries</i>	Mukasa-Mugerwa <i>et al.</i> (1994)	3.292 (1)	0.434 (1)	0.83 (1)	2.732	0.36	Mass	Early	Combined	Captive
	Forchhammer <i>et al.</i> (2001)	1.941 (1)	0.176 (1)	0.375 (3)	0.728	0.066	Mass	Early	Combined	Wild
	Jones <i>et al.</i> (2005)	3.591 (3)	0.317 (3)	0.595 (3)	2.137	0.189	Mass	Early	Combined	Wild
	Wilson <i>et al.</i> (2005)	0.807 (1)	0.056 (1)	1 (1)	0.807	0.056	Mass	Total	Combined	Wild
	Casellas <i>et al.</i> (2007)	0.811 (3)	0.133 (3)	0.788 (3)	0.639	0.105	Mass	Total	Combined	Captive
<i>Ovis ammon</i>	Reading <i>et al.</i> (2009)	-0.06 (1)	0.105 (1)	0.831 (1)	-0.050	0.087	Mass	Early	Combined	Wild
<b>PRIMATES</b>										
<i>Saimiri boliviensis</i>	Blomquist & Williams (2013)	0.079 (3)	0.008 (3)	13.76 (3)	1.087	0.110	Mass	Early	Female	Captive
		0.055 (3)	0.006 (3)	14.82 (3)	0.815	0.089	Mass	Early	Male	Captive
<i>Macaca mulatta</i>	Shaughnessy <i>et al.</i> (1978)	0.013 (3)	0.004 (3)	66.94 (3)	0.870	0.268	Mass	Early	Combined	Captive
		0.012 (3)	0.002 (3)	62.7 (3)	0.752	0.752	Mass	Early	Combined	Captive
<b>LAGOMORPHA</b>										
<i>Oryctolagus cuniculus</i>	Rödel <i>et al.</i> (2004)	0.007 (1)	0.001 (3)	309.5 (3)	2.167	0.310	Mass	Early	Combined	Captive
	Rödel <i>et al.</i> (2009)	0.257 (1)	0.106 (1)	7.2 (3)	1.850	0.763	Mass	Late	Combined	Captive
<b>RODENTIA</b>										
<i>Sciurus vulgaris</i>	Wauters, Bijmens & Dhondt (1993)	0.034 (1)	0.011 (1)	8.22 (3)	0.279	0.090	Mass	Total	Combined	Wild
<i>Tamiasciurus hudsonicus</i>	Larivée <i>et al.</i> (2010)	0.031 (3)	0.016 (3)	1.113 (3)	0.035	0.018	Mass	Total	Combined	Wild
<i>Marmota flaviventris</i>	Monclús <i>et al.</i> (2014)	0.0039 (3)	0.0015 (3)	125 (3)	0.488	0.188	Mass	Late	Combined	Wild
<i>Erethizon dorsatum</i>	Mabille & Berteaux (2014)	-0.106 (1)	1 (1)	1 (1)	-0.106	1.000	Mass	Early	Combined	Wild
<i>Peromyscus maniculatus</i>	Myers & Master (1983)	12.13 (3)	1.372 (3)	0.088 (3)	1.067	0.121	Mass	Early	Combined	Captive
<i>Phyllotis darwini</i>	Nespolo & Bacigalupe (2009)	0.465 (3)	0.089 (3)	0.925 (3)	0.430	0.082	Mass	Total	Combined	Captive

post-weaning (mammals) or fledging (birds) periods when possible because the weaning (mammals) and fledging (birds) periods are usually the most critical life stages (Clutton-Brock, 1991). In particular, at weaning, most mammals no longer rely on parental care for survival.

- (2) The type of mass measurement was fitted as a two-level factor (Mass *versus* Condition index). We

included this moderator to assess whether the use of different measures impacted our results. In some cases, condition index and mass can be related to body reserves with different intensities (e.g. Wilder, Raubenheimer & Simpson, 2016).

- (3) The fact that the data were obtained from wild or captive conditions was recorded as a two-level factor (Wild *versus* Captive). We considered a population as

Table 2. Summary of the statistics and potential driving factors compiled in the meta-analysis for the relationship between offspring mass and offspring survival in birds. For each study the logistic slope (Beta), its standard error (S.E.) and the standard deviation of the mass distribution (S.D. Mass), the standardized logistic slope (standardized Beta) and the standardized standard error (standardized S.E.) are reported. The extraction procedure is reported in parentheses as 1 if the statistic is directly calculated in the study, 2 if data are reported from a figure, and 3 if data are reported from our own simulation. See Section II.3a for further information on the extraction procedure and Section II.4b for explanation of Timing of measurement categories

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<b>CORACIIFORMES</b>										
<i>Dacelo novaeguineae</i>	Legge (2002)	0.036 (3)	0.01 (2)	38.7 (3)	1.393	0.387	Mass	Late	Combined	Wild
<b>STRIGIFORMES</b>										
<i>Athene cucularia</i>	Todd <i>et al.</i> (2003)	0.053 (3)	0.032 (2)	14.24 (3)	0.755	0.456	Mass	Late	Combined	Wild
	Davies & Restani (2006)	-0.032 (3)	0.35 (2)	0.99 (3)	-0.032	0.347	Condition	Total	Combined	Wild
<b>FALCONIFORMES</b>										
<i>Accipiter gentilis</i>	Wiens, Noon & Reynolds (2006)	0.01 (1)	0.01 (1)	110 (3)	1.100	1.100	Mass	Total	Combined	Wild
<b>PASSERIFORMES</b>										
<i>Helmitheros vermivorum</i>	Vitz & Rodewald (2011)	1.00 (3)	0.47 (2)	0.81 (3)	0.810	0.381	Condition	Late	Combined	Wild
<i>Seiurus aurocapilla</i>	Vitz & Rodewald (2011)	0.63 (3)	0.42 (2)	0.84 (3)	0.529	0.353	Condition	Late	Combined	Wild
<i>Melospiza melodia</i>	Dybala, Gardali & Eadie (2013)	0.14 (1)	0.036 (1)	1 (1)	0.140	0.036	Mass	Total	Combined	Wild
<i>Junco phaeonotus</i>	Sullivan (1989)	1.096 (2)	0.269 (2)	1.125 (2)	1.233	0.303	Mass	Late	Combined	Wild
<i>Sturnella magna</i>	Kershner, Walk & Warner (2004)	0.175 (3)	0.107 (2)	4.802 (3)	0.840	0.514	Mass	Late	Combined	Wild
	Suedkamp Wells <i>et al.</i> (2007)	0.042 (3)	0.032 (2)	7.085 (3)	0.298	0.227	Mass	Total	Combined	Wild
<i>Spiza americana</i>	Suedkamp Wells <i>et al.</i> (2007)	0.092 (3)	0.064 (2)	2.62 (3)	0.241	0.168	Mass	Total	Combined	Wild
<i>Loxops coccineus</i>	Medeiros & Freed (2009)	0.91 (3)	0.34 (2)	0.88 (3)	0.801	0.299	Mass	Late	Combined	Wild
<i>Passer domesticus</i>	Ringsby <i>et al.</i> (1998)	0.157 (1)	0.045 (1)	6.25 (2)	0.981	0.281	Mass	Late	Combined	Wild
		0.0942 (1)	0.042 (1)	6.25 (2)	0.589	0.263	Mass	Late	Combined	Wild
	Cleasby <i>et al.</i> (2010)	0.002 (1)	0.019 (1)	1 (1)	0.002	0.019	Mass	Total	Combined	Wild
<i>Ficedula albicollis</i>	Lindén, Gustafsson & Part (1992)	0.0231 (1)	0.003 (1)	1 (1)	0.023	0.003	Mass	Late	Combined	Wild
<i>Ficedula hypoleuca</i>	Potti <i>et al.</i> (2002)	0.43 (1)	0.17 (1)	1 (1)	0.430	0.170	Mass	Total	Female	Wild
		0.28 (1)	0.25 (1)	1 (1)	0.280	0.250	Mass	Total	Male	Wild
	Lobato <i>et al.</i> (2005)	-0.31 (3)	0.36 (2)	0.68 (3)	-0.211	0.245	Mass	Total	Combined	Wild
<i>Erythroptgia coryphaeus</i>	Lloyd <i>et al.</i> (2009)	0.39 (1)	0.13 (1)	2.41 (2)	0.940	0.313	Mass	Total	Combined	Wild
<i>Turdus merula</i>	Snow (1958)	0.011 (2)	0.018 (2)	8.01 (2)	0.088	0.144	Mass	Total	Combined	Wild
	Magrath (1991)	0.076 (2)	0.011 (2)	7.38 (2)	0.561	0.081	Mass	Early	Combined	Wild
<i>Hyalocichla mustelina</i>	Brown & Roth (2004)	0.12 (2)	0.077 (2)	1 (1)	0.120	0.077	Mass	Total	Combined	Wild
<i>Cinclus mexicanus</i>	Mackas <i>et al.</i> (2010)	0.208 (2)	0.008 (2)	3.447 (2)	0.717	0.028	Condition	Total	Combined	Wild
<i>Sturnus vulgaris</i>	Serra <i>et al.</i> (2012)	0.056 (3)	0.044 (2)	10.8 (3)	0.605	0.475	Mass	Early	Female	Wild
<i>Parus major</i>	Garnett (1981)	0.165 (1)	0.0468 (1)	1.25 (2)	0.206	0.059	Mass	Total	Combined	Wild
	Smith, Kallander & Nilsson (1989)	0.347 (2)	0.247 (2)	1.192 (2)	0.414	0.294	Mass	Early	Combined	Wild
	Lindén <i>et al.</i> (1992)	0.0047 (1)	0.003 (1)	1 (1)	0.005	0.003	Mass	Late	Combined	Wild
	Verboven & Visser (1998)	0.135 (2)	0.035 (2)	1.44 (2)	0.194	0.050	Mass	Late	Female	Wild
		0.161 (2)	0.069 (2)	1.444 (2)	0.232	0.100	Mass	Late	Female	Wild
		0.244 (2)	0.035 (2)	1.518 (2)	0.370	0.053	Mass	Late	Male	Wild
		0.231 (2)	0.067 (2)	1.494 (2)	0.345	0.100	Mass	Late	Male	Wild
	Naef-Daenzer, Widmer & Nuber (2001)	0.045 (1)	0.012 (1)	15.75 (2)	0.709	0.189	Mass	Late	Combined	Wild
	Monrós, Belda & Barba (2002)	0.14 (1)	0.05 (1)	1 (1)	0.140	0.050	Mass	Late	Combined	Wild
	Greño, Belda & Barba (2008)	0.26 (1)	0.07 (1)	1 (1)	0.260	0.070	Mass	Late	Combined	Wild
<i>Parus ater</i>	Naef-Daenzer <i>et al.</i> (2001)	0.045 (1)	0.012 (1)	15.75 (2)	0.709	0.189	Mass	Late	Combined	Wild
<i>Parus caeruleus</i>	Nur (1984)	0.297 (2)	0.13 (2)	1.02 (2)	0.303	0.133	Mass	Total	Combined	Wild
	Raberg, Stjernman & Nilsson (2005)	0.295 (1)	0.105 (1)	1 (1)	0.295	0.105	Mass	Total	Male	Wild
		0.29 (1)	0.153 (1)	1 (1)	0.290	0.153	Mass	Total	Female	Wild
<i>Corvus frugilegus</i>	Patterson, Dunnet & Goodbody (1988)	0.0084 (3)	0.0013 (2)	46.8 (3)	0.393	0.061	Mass	Late	Combined	Wild

Table 2. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<i>Pica pica</i>	Husby & Slagsvold (1992)	0.03 (3)	0.015 (2)	33.17 (3)	0.995	0.498	Mass	Total	Combined	Wild
	Ponz Miranda, Gil-Delgado Alberti & López Iborra (2007)	0.039 (1)	0.018 (1)	22.5 (2)	0.765	0.360	Mass	Total	Combined	Wild
<i>Aphelocoma coerulescens</i>	Mumme <i>et al.</i> (2015)	0.069 (2)	0.006 (2)	6.99 (2)	0.482	0.042	Mass	Total	Combined	Wild
<i>Acanthiza pusilla</i>	Green & Cockburn (2001)	1.7 (2)	0.783 (2)	0.35 (2)	0.595	0.274	Mass	Total	Male	Wild
<i>Tyrannus tyrannus</i>	Dolan <i>et al.</i> (2009)	0.661 (2)	0.562 (2)	0.43 (2)	0.284	0.242	Mass	Total	Female	Wild
		0.022 (1)	0.062 (1)	2.483 (1)	0.055	0.154	Mass	Total	Male	Wild
<i>Platycercus elegans</i>	Krebs (1999)	-0.076 (1)	0.08 (1)	2.5 (1)	-0.190	0.200	Mass	Total	Female	Wild
<i>Clamator glandarius</i>	Solcr, Palomino & Martinec (1994)	0.138 (3)	0.162 (2)	2.12 (3)	0.293	0.343	Mass	Total	Male	Wild
<b>CHARADRIIFORMES</b>	Morrison <i>et al.</i> (2009)	0.187 (3)	0.067 (2)	11.45 (3)	2.141	0.767	Mass	Late	Combined	Wild
		<i>Fratrercula cirrhata</i>	0.0012 (1)	0.0039 (1)	62.5 (2)	0.075	0.244	Mass	Late	Combined
<i>Fratrercula arctica</i>	Harris & Rothery (1985)	-0.002 (3)	0.0054 (2)	27.456 (3)	-0.055	0.148	Mass	Late	Combined	Wild
<i>Uria aalge</i>	Hedgren (1981)	-0.002 (2)	0.002 (2)	24.87 (2)	-0.050	0.050	Mass	Late	Combined	Wild
<i>Alca torda</i>	Lloyd (1979)	0.11 (3)	0.07 (2)	6.15 (3)	0.677	0.431	Mass	Total	Combined	Wild
		0.19 (3)	0.11 (2)	6.45 (3)	1.226	0.710	Mass	Total	Combined	Wild
<i>Synthliboramphus antiquus</i>	Gaston (1997)	0.239 (1)	0.103 (1)	2 (3)	0.478	0.206	Mass	Late	Combined	Wild
<i>Sterna dougallii</i>	Monticelli & Ramos (2012)	0.52 (3)	0.24 (2)	0.47 (3)	0.244	0.113	Condition	Total	Combined	Wild
<i>Sterna hirundo</i>	Schauroth & Becker (2008)	0.19 (3)	0.07 (2)	13.3 (3)	2.527	0.931	Mass	Late	Male	Wild
		0.1 (3)	0.06 (2)	10.5 (3)	1.050	0.630	Mass	Late	Female	Wild
<i>Sterna sandvicensis</i>	Braasch, Schauroth & Becker (2009)	0.023 (1)	0.014 (1)	12.506 (3)	0.288	0.175	Mass	Late	Combined	Wild
		-0.80 (3)	1.11 (2)	0.184 (3)	-0.147	0.204	Condition	Late	Combined	Wild
<i>Larus fuscus</i>	Stienen & Brenninkmeijer (2002)	0.081 (3)	0.044 (2)	6.41 (3)	0.519	0.282	Mass	Early	Combined	Wild
<i>Haemotopus ostralegus</i>	Bolton (1991)	0.0065 (1)	0.005 (1)	27.5 (2)	0.179	0.138	Mass	Late	Combined	Wild
<i>Charadrius montanus</i>	Kersten & Brenninkmeijer (1995)	0.77 (1)	0.265 (1)	1 (1)	0.77	0.265	Mass	Total	Combined	Wild
<b>OTIDIFORMES</b>	Dinsmore, White & Knopf (2003)	0.0012 (2)	0.00035 (2)	500 (2)	0.600	0.175	Mass	Late	Male	Wild
		0.0012 (2)	0.0004 (2)	500 (2)	0.600	0.200	Mass	Late	Female	Wild
<i>Otis tarda</i>	Martin <i>et al.</i> (2007)	0.41 (1)	0.18 (1)	1 (1)	0.410	0.180	Mass	Late	Combined	Wild
<b>SPHENISCIFORMES</b>	Horswill <i>et al.</i> (2014)	0.51 (1)	0.072 (1)	0.594 (3)	0.303	0.043	Mass	Late	Combined	Wild
<i>Eudypetes chrysolophus</i>	McClung <i>et al.</i> (2004)	0.074 (3)	0.17 (2)	2.29 (3)	0.169	0.389	Mass	Total	Combined	Wild
<i>Megadyptes antipodes</i>	Olsson (1997)	0.007 (3)	0.003 (2)	132 (3)	0.924	0.396	Mass	Late	Combined	Wild
<i>Aptenodytes patagonicus</i>	Williams & Croxall (1991)	0.007 (3)	0.003 (2)	132 (3)	0.924	0.396	Mass	Late	Combined	Wild
<b>PROCELLARIIFORMES</b>	Diomedea exulans	0.011 (3)	0.003 (2)	63.38 (3)	0.697	0.190	Mass	Late	Combined	Wild
<i>Puffinus puffinus</i>	Perrins, Harris & Britton (1973)	0.0034 (3)	0.0012 (2)	166.3 (3)	0.565	0.200	Mass	Late	Combined	Wild
<i>Puffinus griseus</i>	Sagar & Horning (1998)	0.004 (3)	0.005 (2)	60.5 (1)	0.242	0.303	Mass	Total	Male	Wild
<i>Diomedea exulans</i>	Weimerskirch, Barbraud & Lys (2000)	0.075 (3)	0.039 (2)	32 (1)	2.400	1.248	Mass	Total	Female	Wild
<b>SULIFORMES</b>	<i>Sula granti</i>	0.000247 (2)	0.000219 (2)	236.702 (1)	0.058	0.052	Mass	Late	Male	Wild
<i>Sula granti</i>	Maness & Anderson (2013)	0.000261 (2)	0.000264 (2)	234.526 (1)	0.061	0.062	Mass	Late	Female	Wild
<b>ANSERIFORMES</b>	<i>Aythya valisineria</i>	0.113 (1)	0.091 (1)	0.165 (2)	0.019	0.015	Mass	Total	Combined	Wild
<i>Aythya valisineria</i>	Anderson, Lindberg & Emery (2001)	0.45 (1)	0.24 (1)	1 (1)	0.450	0.240	Mass	Total	Female	Wild
<i>Aythya affinis</i>	Rotella, Clark & Afron (2003)									

Table 2. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<i>Aix sponsa</i>	Davis <i>et al.</i> (2007)	0.083 (1)	0.031 (1)	1.5 (2)	0.125	0.047	Mass	Early	Combined	Wild
<i>Melanitta fusca</i>	Traylor & Alisauskas (2006)	0.2 (1)	0.077 (1)	1 (1)	0.200	0.077	Condition	Early	Combined	Wild
<i>Chen caerulescens</i>	Cooch (2002)	0.004 (2)	0.001 (2)	78 (3)	0.312	0.078	Mass	Total	Female	Wild
	Souchay, Gauthier & Pradel (2013)	1.66 (1)	0.898 (1)	0.5 (2)	0.830	0.449	Condition	Late	Female	Wild
<i>Chen canagica</i>	Schmutz (1993)	0.002 (3)	0.001 (2)	122.7 (3)	0.245	0.123	Mass	Total	Female	Wild
		0.002 (3)	0.00084 (2)	143.2 (3)	0.286	0.120	Mass	Total	Male	Wild
<i>Branta leucopsis</i>	Owen & Black (1989)	0.005 (3)	0.001 (2)	166.5 (3)	0.833	0.167	Mass	Late	Combined	Wild
	Van der Jeugd & Larsson (1998)	0.00176 (2)	0.000832 (2)	211.7 (1)	0.373	0.176	Mass	Late	Combined	Wild
<b>GALLIFORMES</b>										
<i>Colinus virginianus</i>	Lusk <i>et al.</i> (2005)	0.014 (2)	0.002 (2)	47.57 (2)	0.666	0.095	Mass	Early	Combined	Wild

being captive when the individuals were kept in an enclosure and artificially fed. Captive animals do not display the same mortality patterns as free-ranging animals (e.g. Lemaître *et al.*, 2013; Tidière *et al.*, 2016). In particular, captive individuals have access to veterinary care that can markedly influence the magnitude of the offspring mass–survival relationship. As all bird populations included in the meta-analysis were free-living, we only tested an effect of captive *versus* wild conditions in mammals.

- (4) The occurrence of predation in the studied population was implemented as a two-level factor (Predation *versus* No predation) for the analysis of the relationship between offspring survival and body mass. We first considered the information provided in the paper about the occurrence of predation. When no information about the causes of mortality was reported, we searched for other papers about the same population to find out whether the focal population was subjected to predation. We expected that predation should decrease the effect of body mass on offspring survival because predators generally prey upon juveniles independently from their mass (Hurley *et al.*, 2011; Keech *et al.*, 2011). This moderator was only tested for mammalian populations because all of the bird populations included in our data set were subjected to predation. We did not report any information about hunting in populations because juveniles are typically not hunted.
- (5) Offspring sex was included as a three-level factor (Female, Male or Combined). ‘Combined’ corresponds to studies in which individuals from both sexes were pooled within the same relationship. ‘Male’ and ‘Female’ correspond to studies in which sex-specific relationships were provided. We looked for potential sex differences in the effect sizes of the relationships.
- (6) The influence of species-specific mating system was tested differently in mammals and birds. As

only two mating systems occurred in our set of mammalian species, we included this moderator as a two-level factor (Polygynous *versus* Promiscuous). Our bird species were principally socially monogamous, although a high rate of extra-pair paternities occurred in several species (Garamszegi *et al.*, 2005). As the degree of monogamy can impact the amount of parental care and thereby influence the offspring mass–survival relationship (Jašarević *et al.*, 2013) we distinguished between strict monogamy and other mating systems. We defined species as being strictly monogamous when the rate of extra-pair paternities was lower than 5%. As the magnitude of between-sex differences might differ in relation to mating systems, we included a test of the interaction between mating system and sex in our analyses.

- (7) Litter size was implemented as a two-level factor in mammals (Monotocous *versus* Polytocous). Monotocous species have a mean litter size of one, whereas polytocous species produce more than one offspring per litter. Brood size in birds was measured as the average clutch size for each species (i.e. a continuous variable). Litter (mammals) or clutch (birds) size could influence the offspring mass–survival relationship because of the expected offspring size–number trade-off (Smith & Fretwell, 1974). We also tested for the interaction between litter size and mating system for mammals because siblings in species displaying a promiscuous mating system are expected to face higher sibling competition than siblings in species with other mating systems (Forstmeier *et al.*, 2014; Garratt *et al.*, 2014).
- (8) Data quality was implemented as a two-level factor (High quality *versus* Low quality). Data were considered as high quality when all data required for the analysis were explicitly reported. Low-quality data corresponded to case studies for which the required data were extracted from graphs or obtained from simulations. We thus tested whether the data-extraction

Table 3. Summary of the statistics and potential driving factors compiled in the meta-analysis for the relationship between offspring mass and maternal mass in mammals. Pearson correlation coefficient and sample size are reported. The extraction procedure is reported in parentheses as 1 if the statistic is directly calculated in the study, and 2 if data are reported from a figure. See Section 2.3*b* for more information on the extraction procedure and Section II.4*b* for explanation of Mass or other relationships and Offspring age categories

Species	Study	Pearson's $r$	$N$	Fisher $\tilde{z}r$	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive	
<b>DASYUROMORPHIA</b>										
<i>Phascogale calura</i>	Foster & Taggart (2008)	0.494 (2)	16	0.541	0.277	Mass	Weaning	Male	Captive	
		0.554 (2)	13	0.624	0.316	Mass	Weaning	Female	Captive	
<b>DIPROTODONTIA</b>										
<i>Phascogale cinereus</i>	Tobey <i>et al.</i> (2006)	0.259 (1)	27	0.265	0.204	Mass	Weaning	Female	Captive	
		0.298 (1)	27	0.307	0.204	Mass	Weaning	Male	Captive	
<b>CHIROPTERA</b>										
<i>Eptesicus fuscus</i>	Booher (2008)	0.458 (1)	10	0.495	0.378	Mass	Birth	Combined	Captive	
		0.854 (1)	9	1.271	0.408	Mass	Birth	Combined	Captive	
<b>CARNIVORA</b>										
<i>Mungo mungo</i>	Hodge <i>et al.</i> (2009)	0.481 (2)	39	0.524	0.167	Mass	Birth	Combined	Wild	
<i>Suricata suricatta</i>	Russell <i>et al.</i> (2003)	0.469 (1)	37	0.509	0.171	Mass	Weaning	Combined	Wild	
<i>Ursus maritimus</i>	Derocher & Stirling (1994)	0.84 (1)	27	1.221	0.204	Mass	Birth	Combined	Wild	
<i>Ursus arctos</i>	Noyce, Coy & Garshelis (2002)	0.624 (1)	59	0.732	0.134	Mass	Birth	Combined	Wild	
	Dahle <i>et al.</i> (2006)	0.232 (1)	224	0.236	0.067	Mass	Birth	Combined	Wild	
	Gonzalez <i>et al.</i> (2012)	0.173 (1)	254	0.175	0.063	Other	Birth	Combined	Wild	
<i>Mirounga leonina</i>	Robbins <i>et al.</i> (2012)	0.775 (1)	18	1.033	0.258	Mass	Birth	Combined	Wild	
	McCann, Fedak & Harwood (1989)	0.812 (1)	13	1.133	0.316	Mass	Birth	Female	Wild	
		0.332 (1)	16	0.345	0.277	Mass	Birth	Male	Wild	
	Fedak, Arnbohm & Boyd (1996)	0.701 (1)	12	0.869	0.333	Mass	Birth	Male	Wild	
<i>Mirounga angustirostris</i>	Arnbohm <i>et al.</i> (1997)	0.552 (1)	15	0.621	0.289	Mass	Birth	Female	Wild	
		0.146 (2)	74	0.147	0.119	Mass	Birth	Female	Wild	
		0.141 (2)	63	0.142	0.129	Mass	Birth	Male	Wild	
<i>Mirounga angustirostris</i>	Crocker <i>et al.</i> (2001)	0.57 (1)	16	0.648	0.277	Other	Weaning	Combined	Wild	
<i>Leptonychotes weddellii</i>	Wheatley <i>et al.</i> (2006)	0.768 (2)	47	1.015	0.151	Mass	Weaning	Combined	Wild	
<i>Phoca vitulina</i>	Bowen <i>et al.</i> (1994)	0.42 (1)	124	0.448	0.091	Mass	Birth	Female	Wild	
		0.32 (1)	134	0.332	0.087	Mass	Birth	Male	Wild	
	Coltman <i>et al.</i> (1998)	0.13 (1)	60	0.131	0.132	Mass	Birth	Combined	Wild	
	Ellis <i>et al.</i> (2000)	0.41 (1)	118	0.436	0.093	Mass	Birth	Male	Wild	
		0.5 (1)	126	0.549	0.090	Mass	Birth	Female	Wild	
	Bowen <i>et al.</i> (2001 <i>a</i> )	0.51 (1)	100	0.563	0.102	Mass	Weaning	Combined	Wild	
	Bowen <i>et al.</i> (2001 <i>b</i> )	0.28 (1)	30	0.288	0.192	Mass	Birth	Combined	Wild	
	<i>Halichoerus grypus</i>	Iverson <i>et al.</i> (1993)	0.567 (2)	9	0.643	0.408	Mass	Birth	Combined	Wild
	Pomeroy <i>et al.</i> (1999)	0.316 (1)	95	0.327	0.104	Mass	Birth	Combined	Wild	
	<i>Phocarcus hookeri</i>	Chilvers <i>et al.</i> (2007)	0.543 (1)	98	0.608	0.103	Mass	Birth	Combined	Wild
<i>Arctocephalus gazella</i>	Boyd & McCann (1989)	0.028 (2)	35	0.028	0.177	Mass	Birth	Female	Wild	
		0.42 (1)	40	0.448	0.164	Mass	Birth	Male	Wild	
	Lunn & Boyd (1993)	0.09 (1)	32	0.090	0.186	Mass	Birth	Male	Wild	
		0.251 (1)	17	0.256	0.267	Mass	Birth	Male	Wild	
		0.597 (1)	14	0.688	0.302	Mass	Birth	Male	Wild	
		0.386 (1)	54	0.407	0.140	Mass	Birth	Female	Wild	
		0.637 (1)	17	0.753	0.267	Mass	Birth	Female	Wild	
		0.162 (1)	19	0.163	0.250	Mass	Birth	Female	Wild	
	McDonald <i>et al.</i> (2012)	0.469 (1)	49	0.509	0.147	Mass	Birth	Combined	Wild	
	<i>Callorhinus ursinus</i>	Boltnev & York (2001)	0.287 (2)	137	0.295	0.086	Mass	Birth	Female	Wild
		0.329 (2)	106	0.342	0.099	Mass	Birth	Male	Wild	
<b>ARTIODACTYLA</b>										
<i>Dama dama</i>	Birgersson & Ekvall (1997)	0.61 (1)	138	0.709	0.086	Mass	Birth	Combined	Captive	

Table 3. Continued

Species	Study	Pearson's $r$	$N$	Fisher $Z_r$	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive
<i>Cervus elaphus</i>	Clutton-Brock, Albon & Guinness (1986)	0.455 (1)	104	0.491	0.100	Mass	Birth	Combined	Wild
	Moore, Littlejohn & Cowie (1988)	0.437 (1)	143	0.469	0.085	Mass	Birth	Combined	Captive
	Bonenfant <i>et al.</i> (2003)	0.436 (1)	46	0.467	0.152	Mass	Weaning	Combined	Wild
	Landete-Castillejos <i>et al.</i> (2003)	0.39 (1)	24	0.412	0.218	Mass	Birth	Combined	Captive
	Landete-Castillejos <i>et al.</i> (2005)	0.46 (1)	91	0.497	0.107	Mass	Birth	Combined	Captive
<i>Odocoileus virginianus</i>	Michel <i>et al.</i> (2015)	0.318 (1)	229	0.329	0.067	Mass	Birth	Combined	Captive
<i>Rangifer tarandus</i>	Rognmo <i>et al.</i> (1983)	0.752 (2)	39	0.978	0.167	Mass	Birth	Combined	Captive
	Eloranta & Nieminen (1986)	0.58 (1)	70	0.662	0.122	Mass	Birth	Combined	Captive
	Kojola (1993)	0.656 (1)	65	0.786	0.127	Mass	Weaning	Female	Captive
		0.657 (1)	55	0.788	0.139	Mass	Weaning	Male	Captive
	Holand <i>et al.</i> (2004)	0.607 (1)	52	0.704	0.143	Mass	Birth	Combined	Captive
	Adams (2005)	0.47 (1)	46	0.510	0.152	Mass	Birth	Combined	Wild
	Holand <i>et al.</i> (2006)	0.249 (1)	66	0.254	0.126	Mass	Birth	Combined	Captive
	Mysterud <i>et al.</i> (2009)	0.29 (1)	88	0.299	0.108	Mass	Birth	Combined	Captive
	Taillon <i>et al.</i> (2012)	0.55 (2)	48	0.618	0.149	Mass	Birth	Combined	Wild
		0.272 (2)	48	0.279	0.149	Mass	Birth	Combined	Wild
<i>Capreolus capreolus</i>	Hewison <i>et al.</i> (2005)	0.476 (1)	35	0.518	0.177	Mass	Weaning	Female	Wild
		0.259 (1)	38	0.265	0.169	Mass	Weaning	Male	Wild
		0.482 (1)	38	0.526	0.169	Mass	Weaning	Female	Wild
		0.366 (1)	36	0.384	0.174	Mass	Weaning	Male	Wild
<i>Alces alces</i>	Keech <i>et al.</i> (2000)	0.458 (1)	37	0.495	0.171	Mass	Birth	Combined	Wild
<i>Bison bison</i>	Hamel <i>et al.</i> (2012a)	0.374 (2)	316	0.393	0.057	Mass	Weaning	Male	Wild
		0.267 (2)	302	0.274	0.058	Mass	Weaning	Female	Wild
<i>Oreamnos americanus</i>	Côté & Festa-Bianchet (2001)	0.412 (1)	32	0.438	0.186	Mass	Birth	Combined	Wild
<i>Ovis canadensis</i>	Festa-Bianchet & Jorgenson (1998)	0.289 (1)	231	0.297	0.066	Mass	Weaning	Combined	Wild
<i>Ovis aries</i>	Clutton-Brock <i>et al.</i> (1996)	0.266 (1)	350	0.273	0.054	Mass	Birth	Combined	Wild
		0.045 (1)	120000	0.045	0.003	Mass	Weaning	Combined	Captive
<b>PRIMATES</b>									
<i>Macaca mulatta</i>	Bercovitch, Widdig & Nürnberg (2000)	0.289 (1)	97	0.297	0.103	Mass	Weaning	Combined	Wild
<i>Mandrillus sphinx</i>	Setchell <i>et al.</i> (2001)	0 (1)	65	0.000	0.127	Mass	Birth	Combined	Captive
<b>RODENTIA</b>									
<i>Sciurus vulgaris</i>	Wauters <i>et al.</i> (1993)	0.49 (1)	57	0.536	0.136	Mass	Weaning	Combined	Wild
		0.64 (1)	28	0.758	0.200	Mass	Weaning	Combined	Wild
<i>Spermophilus richardsonii</i>	Dobson & Michener (1995)	0.31 (1)	51	0.321	0.144	Other	Birth	Combined	Wild
		0.53 (1)	38	0.590	0.169	Other	Birth	Combined	Wild
<i>Spermophilus columbianus</i>	Skibiél, Dobson & Murie (2009)	0.37 (1)	66	0.388	0.126	Other	Weaning	Combined	Wild
		0.34 (1)	28	0.354	0.200	Other	Weaning	Combined	Wild
		0.37 (1)	93	0.388	0.105	Other	Weaning	Combined	Wild
<i>Marmota flaviventris</i>	Monclús <i>et al.</i> (2014)	0.253 (2)	82	0.259	0.113	Mass	Weaning	Combined	Wild
		-0.183 (2)	70	-0.185	0.122	Mass	Weaning	Combined	Wild
<i>Cavia aperea</i>	Kasparian, Geißler & Trillmich (2005)	0.37 (1)	81	0.388	0.113	Mass	Birth	Combined	Captive
		0.184 (1)	117	0.186	0.094	Mass	Birth	Combined	Captive
		0.464 (1)	35	0.502	0.177	Mass	Birth	Combined	Captive
		0.335 (1)	10	0.348	0.378	Mass	Birth	Combined	Captive
<i>Microtus pennsylvanicus</i>	Dobson & Myers (1989)	0.11 (1)	135	0.110	0.087	Mass	Birth	Combined	Captive
<i>Microtus agrestis</i>	Koskela <i>et al.</i> (2004)	0.218 (2)	83	0.222	0.112	Other	Birth	Male	Captive
		0.419 (2)	88	0.446	0.108	Other	Birth	Female	Captive

Table 3. Continued

Species	Study	Pearson's $r$	$N$	Fisher $\tilde{z}$	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive
	Helle, Laaksonen & Huitu (2013)	0.066 (1)	67	0.066	0.125	Mass	Birth	Female	Captive
<i>Peromyscus maniculatus</i>	Myers & Master (1983)	0.479 (1)	53	0.522	0.141	Mass	Birth	Male	Captive
		0.245 (1)	393	0.250	0.051	Mass	Birth	Combined	Captive
<i>Sigmodon hispidus</i>	Campbell & Slade (1995)	0.48 (1)	29	0.523	0.196	Mass	Birth	Combined	Captive
<i>Mus musculus</i>	Krackow (1997)	0.506 (1)	83	0.557	0.112	Mass	Weaning	Male	Captive
		0.479 (1)	71	0.522	0.121	Mass	Weaning	Female	Captive
<i>Apodemus argentus</i>	Shibata & Kawamichi (2009)	0.292 (2)	53	0.301	0.141	Mass	Birth	Male	Wild
		0.197 (2)	58	0.200	0.135	Mass	Birth	Female	Wild

procedure had any detectable impact on the results.

To assess the impact of these different moderators on the relationships of interest, we reported the mean difference between the groups with the 95% highest posterior density interval (the odds ratios were log-transformed to obtain a meaningful mean difference between groups). The mean difference was considered as statistically significant when 0 did not fall within the credibility interval.

### (5) Publication bias

If studies with no detectable effects are less likely to be published (Rosenthal, 1979), the meta-analysis performed from published information would lead to an overestimate of the true effect. To test whether such a publication bias was present in our data, funnel plots were built. The standard diagram plots the precision of the study (measured as the inverse of the standard error) against the mean of the study (Egger *et al.*, 1997). The closer the mean is to the meta-analysis mean, the greater the precision. In the absence of any bias the diagram should be perfectly symmetrical around the mean. To test the symmetry of the diagram a linear regression of the means of each study as a function of their precision is performed. This test is known as the Egger regression (Egger *et al.*, 1997). However, the means are not independent from each other, leading a key assumption of linear regression to be violated. The only values that were independent between the different effect sizes were the residuals of the meta-analysis (Nakagawa & Santos, 2012), which correspond to the variance that is not explained by the different random factors. The residuals should be symmetrically distributed around 0. A linear regression of residuals on the precision of the study was performed. A publication bias occurs when the intercept of the regression is statistically different from 0. To assess the influence of publication bias, the trim and fill method of the package metafor (Viechtbauer, 2010) was

used. This method provides an estimate of the number of studies that are absent on one side of the funnel plot and adjusts the meta-analysis mean accordingly. It should not be interpreted as an exact correcting factor of the publication bias but rather provides an assessment of the magnitude of the publication bias.

## III. RESULTS

### (1) Relationship between offspring mass and offspring survival

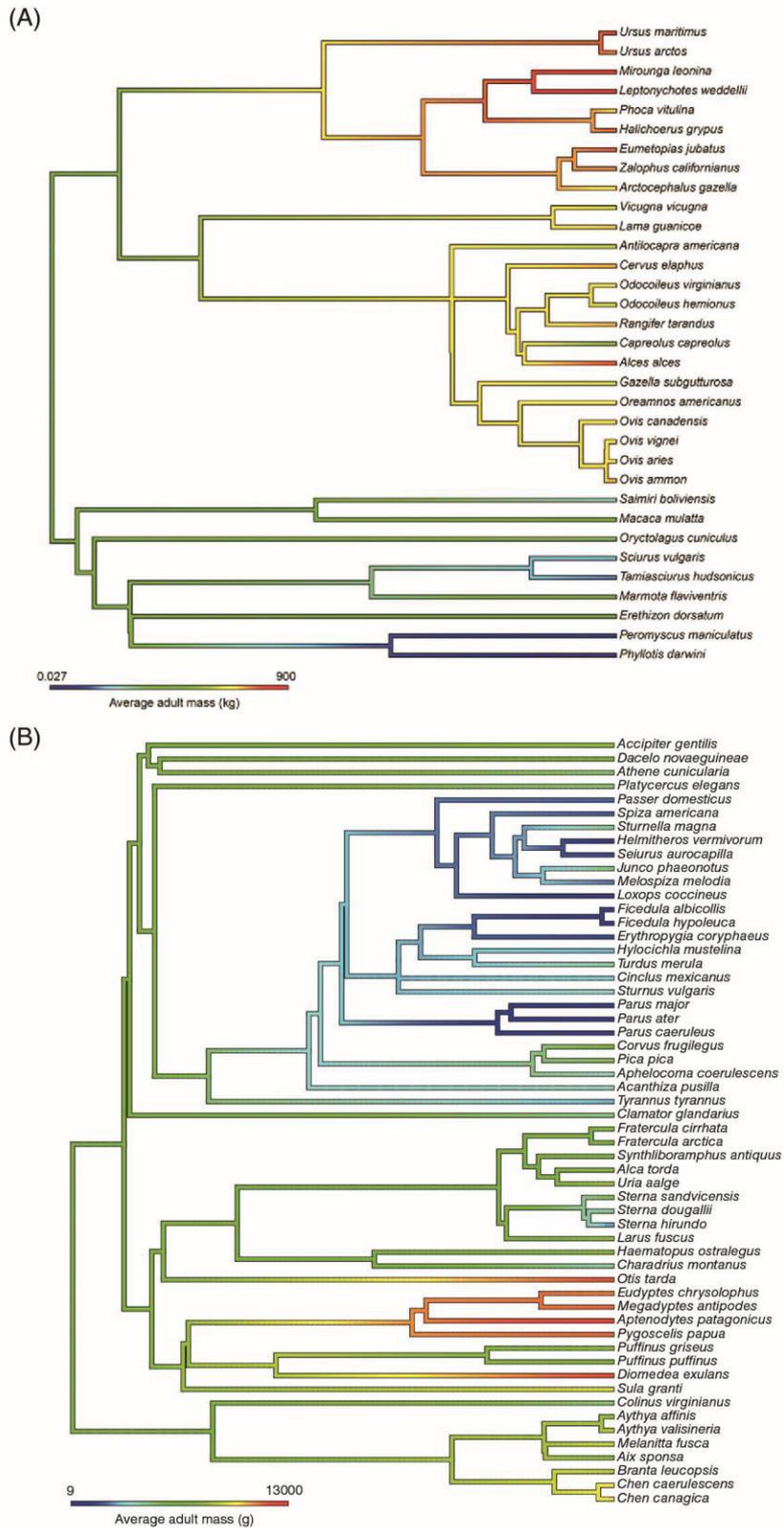
#### (a) Data set

In mammals, we extracted 75 effect sizes from 60 published papers. These effect sizes came from 33 different species. Overall, Carnivora (9 species), Artiodactyla (15 species) and Rodentia (6 species) were the most represented mammalian orders (Table 1; Fig. 2A). In birds, we extracted 86 effect sizes from 58 published studies. These effect sizes corresponded to 56 different species, mostly Passeriformes (25 species), Charadriiformes (11 species) and Anseriformes (7 species) (Table 2; Fig. 2B).

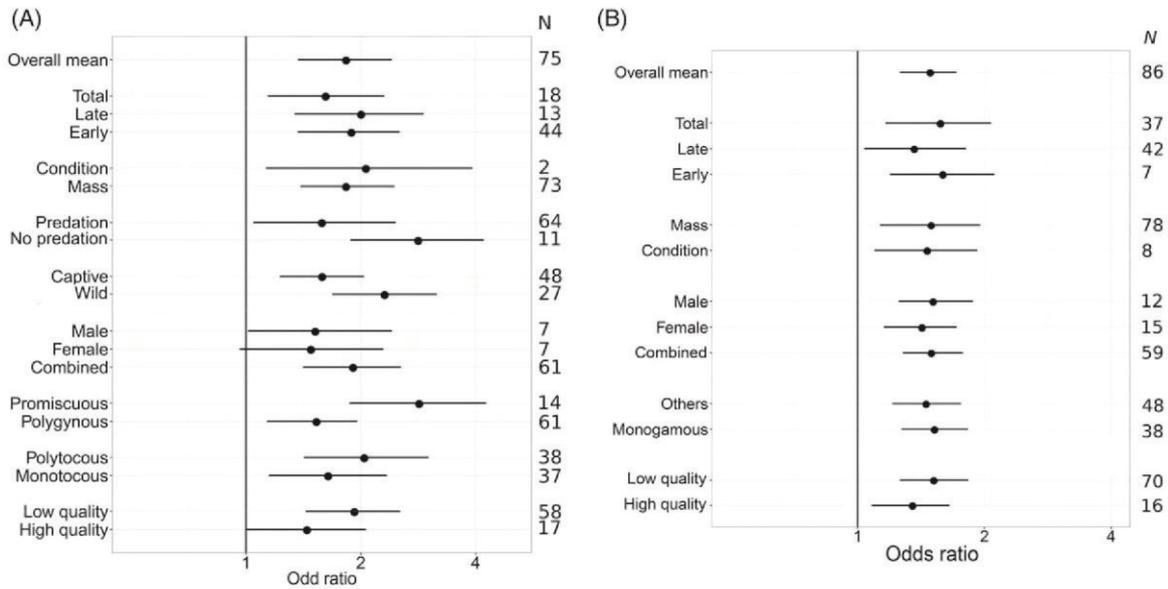
#### (b) Results from general meta-analyses

In mammals, offspring mass positively influenced offspring survival with a meta-analysis mean of 1.82. This effect was statistically significant because the highest posterior density interval of the odds ratio did not overlap 1 [HPDI = (1.37; 2.41)] (Fig. 3A). In birds, the same positive effect of mass occurred for offspring survival (meta-analysis mean = 1.48). This effect was also statistically significant [HPDI = (1.26; 1.72)] (Fig. 3B).

The heterogeneity analysis in mammals indicated that each random effect (the effect of phylogeny, of species independently of phylogeny, of population and of first author) included in our meta-analysis only accounted for a weak but similar proportion of heterogeneity among studies, with an



**Fig. 2.** Phylogenies of (A) mammal (from Bininda-Emonds *et al.*, 2007) and (B) bird (from Jetz *et al.*, 2012) species included in the meta-analyses. The colours indicate the average adult body mass of the species.



**Fig. 3.** Meta-analysis means of each moderator (see Section II.4b) for (A) mammals and (B) birds for the relationship between offspring mass and offspring survival. Meta-analysis overall means are also provided. All means are presented with their 95% highest posterior density intervals and sample size is provided (*N*).

Table 4.  $I^2$  value associated with random effect of phylogeny, species, population, and author included when modelling the relationship between offspring mass and offspring survival in mammals and birds. For each value, the lower and upper high posterior density intervals (HPDI) limits of the credibility interval are reported

Mammals	Mean	Lower HPDI	Upper HPDI
$I^2$ Phylogeny	18.64	0.44	47.44
$I^2$ Species	18.43	0.73	44.92
$I^2$ Population	10.29	0.54	30.66
$I^2$ Author	39.74	4.02	72.24
$I^2$ Residuals	10.95	0.47	34.11

Birds	Mean	Lower HPDI	Upper HPDI
$I^2$ Phylogeny	26.11	2.97	54.45
$I^2$ Species	20.26	2.24	46.39
$I^2$ Population	16.39	1.92	40.00
$I^2$ Author	26.40	2.98	56.16
$I^2$ Residuals	10.13	1.63	24.08

$I^2$  near to 25% for each effect (Table 4). In birds, results were similar with all  $I^2$  near 25%, which indicates that each random effect included in our meta-analysis accounted for an equal and weak part of the heterogeneity among studies (Table 4). The credibility intervals were large for all the values, preventing us from relying on the exact  $I^2$  value.

(c) *Assessing the effects of moderators on the strength of the offspring mass–survival relationship*

The age at which mass was measured, the type of mass measurement, data quality and sex did not have any

detectable effect on the relationship between offspring mass and survival in either birds or mammals (Fig. 3, Table 5). Clutch/litter size did not influence the slope of the relationship either in birds [linear regression slope =  $-0.010$ , HPDI =  $(-0.040; 0.021)$ ] or in mammals (Table 5). The meta-analysis mean was higher in captive than in wild mammals, and in mammal populations with no predation than in populations subjected to predation. We did not detect any influence of the mating system in birds but promiscuous mammals had a higher meta-analysis mean than polygynous ones, this difference being statistically significant (Table 5). The mating system was not independent from environmental conditions, since 97% of studies on polygynous species lived in the wild while 64% of studies on promiscuous species lived in captivity. This prevented us from reaching a firm conclusion on whether mating system influences the offspring mass–survival relationship, because polygynous species in this data set were virtually all from the wild, and our analysis indicated that living in the wild weakens the relationship between offspring mass and survival (see Section IV). Including an interaction between mating system and sex did not reveal any detectable effect either in mammals [ $\text{mean}_{\text{male vs female promiscuous}} = 0.276$ , HPDI =  $(-0.394; 0.973)$ ;  $\text{mean}_{\text{male vs female polygynous}} = -0.142$ , HPDI =  $(-0.535; 0.222)$ ] or in birds [ $\text{mean}_{\text{male vs female monogamous}} = 0.013$ , HPDI =  $(-0.232; 0.251)$ ;  $\text{mean}_{\text{male vs female othermating}} = -0.100$ , HPDI =  $(-0.264; 0.086)$ ]. Likewise, we did not find any detectable interaction between litter size and mating system in mammals [ $\text{mean}_{\text{monotocous vs polytocous promiscuous}} = 0.181$ , HPDI =  $(-0.735; 1.067)$ ;  $\text{mean}_{\text{monotocous vs polytocous polygynous}} = 0.085$ , HPDI =  $(-0.307; 0.454)$ ].

Table 5. Difference between the log-transformed mean of each moderator for the relationship between offspring mass and offspring survival in mammals and birds with their 95% high posterior density intervals (HPDI). Values in bold are statistically significant

Mammals	Mean difference	Lower HPDI	Upper HPDI
Early <i>versus</i> late	0.058	-0.341	0.439
Early <i>versus</i> total	-0.155	-0.502	0.200
Mass <i>versus</i> condition	0.120	-0.480	0.765
<b>Captive <i>versus</i> wild</b>	<b>-0.582</b>	<b>-0.993</b>	<b>-0.133</b>
<b>No predation <i>versus</i> predation</b>	<b>-0.378</b>	<b>-0.629</b>	<b>-0.123</b>
Combined sex <i>versus</i> female	-0.255	-0.682	0.186
Combined sex <i>versus</i> male	-0.228	-0.632	0.238
<b>Polygynous <i>versus</i> promiscuous</b>	<b>0.620</b>	<b>0.202</b>	<b>1.027</b>
Monotocous <i>versus</i> polytocous	0.218	-0.144	0.608
High quality <i>versus</i> low quality	0.292	-0.103	0.645
Birds	Mean difference	Lower HPDI	High HPDI
Early <i>versus</i> late	-0.013	-0.311	0.265
Early <i>versus</i> total	-0.156	-0.427	0.128
Condition <i>versus</i> mass	0.022	-0.256	0.291
Both sex <i>versus</i> female	-0.051	-0.257	0.139
Both sex <i>versus</i> male	0.010	-0.177	0.229
Monogamous <i>versus</i> other mating	-0.046	-0.229	0.146
High quality <i>versus</i> low quality	0.116	-0.066	0.306

*(d) Publication bias*

The intercept of the Egger regression was statistically different from zero in mammals [intercept = 0.077, HPDI = (0.004, 0.152)]. The publication bias diagram was not symmetrical (Fig. 4A), indicating that a publication bias towards positive effects was likely. The trim and fill method indicated a lack of 18 studies on the left side of the funnel plot. The meta-analytic mean should thus be adjusted by -0.062, which results in a value of 1.71. In birds the intercept of the Egger regression also differed from 0 on statistical grounds [intercept = 0.156, HPDI = (0.065; 0.246)] (Fig. 4B). The trim and fill method indicated a lack of 15 studies on the left side of the funnel plot. The meta-analytic mean should thus be adjusted by -0.027, which results in a value of 1.44. Therefore, the slight publication bias we detected did not influence our conclusions.

**(2) Relationship between maternal mass and offspring mass***(a) Data set*

For this meta-analysis, we extracted 96 effect sizes from 60 published papers. We collected effect sizes for 38 different mammalian species with Carnivora (12 species), Rodentia (11 species) and Artiodactyla (10 species) as the most represented mammalian orders (Fig. 5; Table 3). This meta-analysis was performed in mammals only (see Section II.1).

*(b) Results from the general meta-analysis*

A positive relationship occurred between offspring and maternal mass (mean meta-analysis = 0.408, which is equivalent to a Pearson correlation coefficient of 0.387).

This effect was statistically significant because the highest posterior density interval did not overlap 0 [HPDI = (0.223; 0.580)] (Fig. 6).

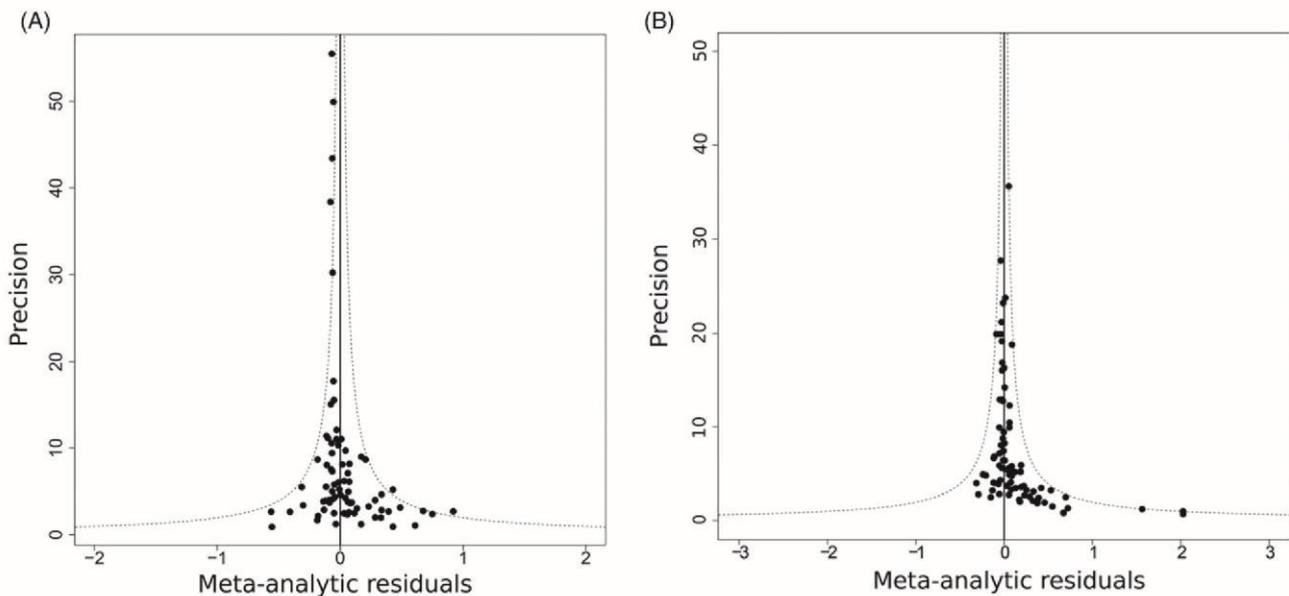
The heterogeneity analysis showed that all the random effects included in our meta-analysis contributed equally but weakly to the overall heterogeneity across studies, with an  $I^2$  less than 25% (Table 6).

*(c) Assessing the effects of moderators on the strength of the maternal mass-offspring mass relationship*

The age at which offspring mass was measured, the type of mass measurement, sex, whether animals were captive or not, litter size, data quality, and mating system did not have any detectable effect on the magnitude of the relationship (Fig. 6; Table 7). Likewise, we did not detect any effect of interactions both between mating system and sex [mean<sub>male vs female promiscuous</sub> = -0.064, HPDI = (-0.343; 0.247); mean<sub>male vs female polygynous</sub> = 0.016, HPDI = (-0.010; 0.148)] and between litter size and mating system [mean<sub>monotocous vs polytocous promiscuous</sub> = -0.050, HPDI = (-0.596; 0.523); mean<sub>monotocous vs polytocous polygynous</sub> = 0.044, HPDI = (-0.151; 0.248)].

*(d) Publication bias*

The intercept of the Egger regression was almost statistically different from zero [intercept = 0.037, HPDI = (-0.001; 0.075)]. A direct inspection of the diagram suggests that some studies might be lacking on the left side since the funnel plot is not symmetrical (Fig. 7). This indicates that a small publication bias might exist. However, the results of the Egger regression indicate that our results are robust to such a small bias.



**Fig. 4.** Funnel plots of the different effect sizes in (A) mammals and (B) birds for the relationship between offspring mass and survival. The precision is plotted as a function of the meta-analysis residuals, as recommended by Nakagawa & Santos (2012). The vertical solid line corresponds to 0.

#### IV. DISCUSSION

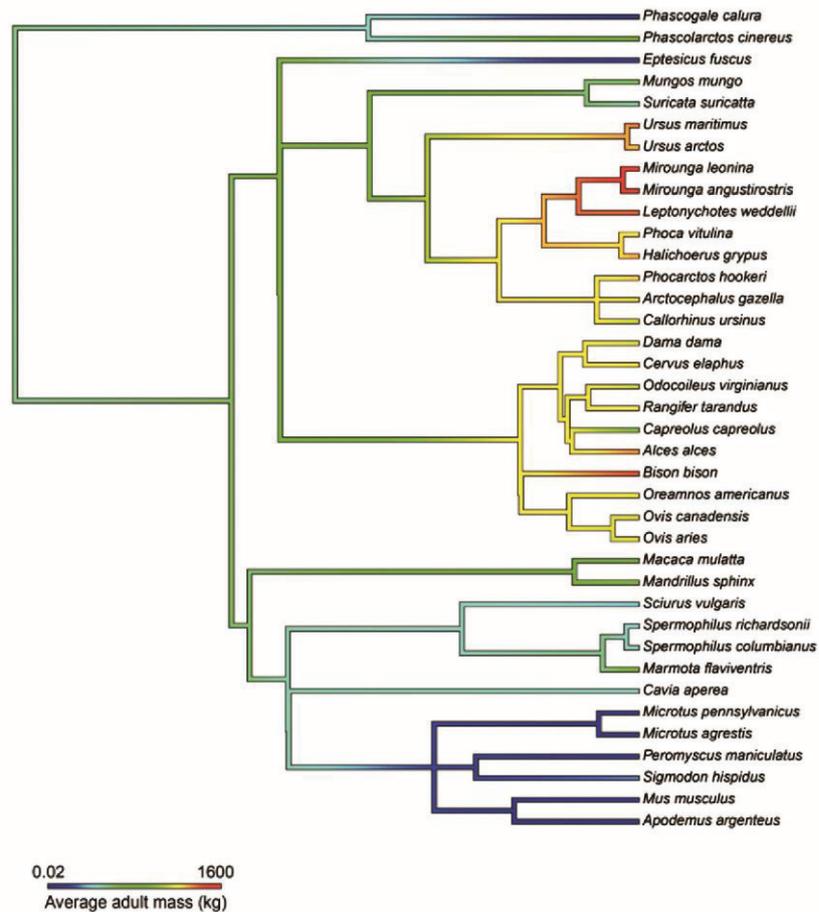
We assessed the sign and the magnitude of the relationships between offspring mass and offspring survival in mammals and birds and between maternal and offspring mass in mammals. The meta-analyses we performed provided strong support for positive relationships in all cases.

In mammals, on average, when offspring mass increases by 1 standard deviation of the offspring body mass distribution in the population, the odds of offspring survival increase by 71%. We also highlighted the existence of a positive relationship between offspring mass and survival in birds. On average, when offspring mass increases by one standard deviation of the early mass distribution the odds of offspring survival increase by 44%. Overall, these positive relationships support our expectation that offspring mass is a reliable proxy of individual survival in birds and mammals (e.g. Hamel *et al.*, 2009). The magnitude of the relationship was slightly weaker in birds. This difference might be due to the fact that birds and mammals are not subject to the same constraints. As 92% of our effect sizes were measured on post-fledging survival, flight constraints are likely involved. The advantages of a greater body mass in birds might be not so strong because a high body mass increases the wing loading (Chandler & Mulvihill, 1992) and affects birds in terms of flying performance (Norberg, 1995). There is an extensive literature about the cost of being too fat, especially when individuals need high flight performance to escape predators (e.g. Gosler, Greenwood & Perrins, 1995; Bonter *et al.*, 2013; Rogers, 2015). In birds, there is clearly a trade-off between the advantage of being fat to avoid starvation and its costs in terms of predation. Alternatively, a methodological

issue might account for the weaker influence of mass on juvenile survival in birds compared to mammals. In bird studies, it is especially difficult to distinguish between death and emigration from the study site (Lebreton *et al.*, 1992; Lebreton, Pradel & Clobert, 1993; Gilroy *et al.*, 2012). When the probability of emigration increases with body mass, the relationship between resighting rate (often used as a proxy of survival) and mass is weaker than the relationship between true survival and mass (Stoleson & Beissinger, 1997; Barbraud, Johnson & Bertault, 2003).

From the heterogeneity analysis, we found weak effects of phylogeny, of species independent of phylogeny, and of population. As neither among-species nor among-population differences accounted for a substantial proportion of the variation observed in the strength of the relationship between offspring survival and body mass, we can generalize our results to all mammals and birds. The absence of any detectable random effect to explain part of the heterogeneity highlights the importance of environmental variation on shaping these relationships. Juveniles from the same species can die from different causes and, even within the same population, juveniles born in different cohorts do not face the same environment (e.g. Keech *et al.*, 2011; Garratt *et al.*, 2015). In both birds and mammals, data quality did not influence our finding because we did not detect any difference between the mean of low-quality data and that of high-quality data. While a publication bias was detected in birds and to a lesser extent in mammals, it only involved a negligible decrease of the overall effect size, which left our conclusions unchanged.

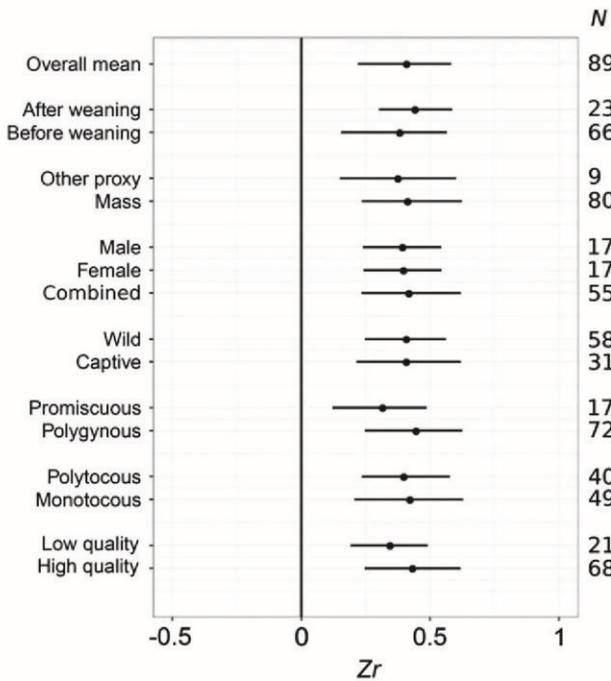
To find potential major drivers explaining the variation in slopes reported in the literature for the offspring



**Fig. 5.** Phylogeny of mammal species included in the analysis of the relationship between offspring mass and maternal mass (from Bininda-Emonds *et al.*, 2007). The colours indicate the average adult body mass of the species.

mass–survival relationship, we tested potential effects of the timing of the measurement. We examined three periods, including the period with high parental care from birth to weaning/fledging, the period of juvenile independence from weaning/fledging to adult stage, and the overall juvenile survival from birth to adult stage. A general objective behind this analysis was to assess in which period juvenile survival is most dependent on body mass. We did not identify a critical period likely because such effects could be masked by dominant mortality causes like predation, which is often less body-mass dependent than other causes of mortality such as starvation (Monteith *et al.*, 2014). A negative effect of predation on the strength of the offspring mass–survival relationship is confirmed by our findings in mammals that offspring survival in populations subjected to predation is less closely associated with body mass. However, the effective predation rate might strongly influence the strength of condition-dependence, which is expected to peak at some intermediate value of predation rate. Unfortunately, predation rates for the mammalian populations considered in our meta-analysis were not provided and it was thus impossible to assess accurately how predation affects the

mass–survival relationship. It is also noteworthy that absolute body mass as analysed here might not reflect condition-dependent mortality through predation. Indeed, if we assume the existence of a limited mass range over which predators are able to prey upon juveniles, all juveniles in a population will be susceptible to predation initially, but the duration of the vulnerability period will be much lower for fast-growing juveniles. In such cases, which encompass most ungulates (Byers, 1997), condition-dependent mortality is weak when using absolute body mass but could be much stronger when using individual growth rate instead of mass. In birds, several studies have reported that the critical period in terms of survival occurs just after fledging because the newly independent juveniles have little experience in foraging and so have to rely on their body reserves, which could be expected to strengthen the relationship between mass and survival (e.g. Sullivan, 1989; Stienen & Brenninkmeijer, 2002). However, fledging in birds also corresponds to a period when other causes of mortality occur, such as predation, likely explaining why late survival is not strongly associated with condition (Davies & Restani, 2006). The relationship between offspring survival and offspring body mass is driven



**Fig. 6.** Meta-analysis means of each moderator (see Section II.4*b*) in mammals for the relationship between offspring mass and maternal mass. Meta-analysis overall means are also provided. All means are presented with their 95% highest posterior density intervals and sample size is provided (*N*).

**Table 6.**  $I^2$  value associated with random effect of phylogeny, species, population, and author when modelling the relationship between offspring mass and maternal mass in mammals. For each value, the lower and upper high posterior density interval (HPDI) limits of the credibility interval are reported

Mammals	Mean	Lower HPDI	High HPDI
$I^2$ Phylogeny	24.15	3.39	47.72
$I^2$ Species	16.10	2.92	34.79
$I^2$ Population	14.19	2.98	31.28
$I^2$ Author	19.58	3.20	39.71
$I^2$ Residuals	16.73	3.08	34.21

by two parameters: the proportion of total mortality that is condition-independent or weakly condition-dependent and the strength of the relationship for each type of condition-dependent mortality. Condition-dependent mortality is mainly caused by starvation in relation to the depletion of body reserves of the juveniles (Williams & Croxall, 1991). As we compiled studies over a large range of environmental conditions and mortality causes, the absence of any influence of the juvenile period studied is not so surprising.

Surprisingly, survival of captive mammals was more dependent on body mass than that of wild mammals. Wild animals have to face a much larger range of mortality factors,

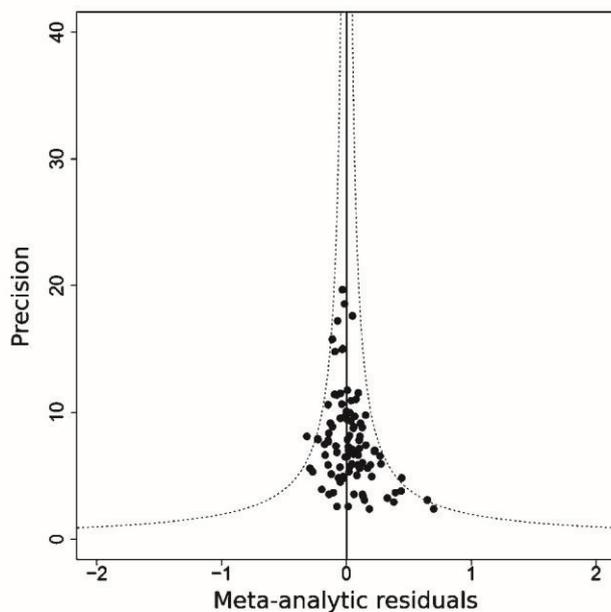
such as predation, which is often a major cause of offspring mortality (e.g. Linnell, Aanes & Andersen, 1995 in ungulates). Although accurate estimates of predation rates in the wild are generally lacking, it seems likely that predation, which is likely to be the highest during a limited time window of the juvenile stage, is only weakly related to absolute juvenile body mass. On the contrary, juveniles in captive populations are not subjected to predation and mostly die from infectious diseases or starvation, which can occur over the entire juvenile stage and are highly associated with absolute body mass (Yapi, Yapi, Boylan & Robinson, 1990; Mandal *et al.*, 2007). To assess the offspring mass–survival relationship in multiple case studies, different measures of mass were included. The most commonly used metric other than mass was body condition (i.e. mass corrected for size; Schulte-Hostedde *et al.*, 2005). Such heterogeneity in mass measurements could have led to an increase in variance across studies. However, a relatively low number of studies based on body condition were included in our analyses (two out of 75 for mammals and eight out of 86 for birds). Using other phenotypic traits to assess condition, such as growth rate, would improve our understanding of condition-dependent juvenile mortality.

We did not find any effect of sex on the magnitude of the relationship in mammals or birds. In particular, we did not find any evidence for disproportionately larger survival or mass advantage of increasing offspring mass in males than in females during early stages of life even when we accounted for the potential confounding effect of mating systems. However, these results do not necessarily contradict the Trivers–Willard Hypothesis (Trivers & Willard, 1973) because we only looked at the early stages of life, whereas, as recently demonstrated, sex-specific reproductive value across the whole life course has to be considered to predict reliably a selective pressure for sex-biased allocation, even in the most sexually dimorphic and polygynous species (Schindler *et al.*, 2015). Among the species-specific reproductive life-history traits, we considered only the mating system in mammals, which had a detectable influence on the offspring mass advantage. Offspring survival was more strongly mass-dependent in promiscuous species than in polygynous species. However, as the mating system had a confounding effect with environmental conditions, we cannot firmly conclude which of these factors generated the observed relationship. Furthermore, we did not find a higher effect of offspring body mass in polytocous and promiscuous mammal species for which we expected high sibling competition due to the existence of multi-paternity within litters.

In mammals, maternal mass was positively correlated to offspring mass with a mean correlation coefficient of 0.387, which corresponds to a moderate effect (*sensu* Cohen, 1988). This finding matches the expectation that heavier mothers in a given population allocate more to their offspring than lighter ones, by allowing offspring to reach higher body mass and thereby higher survival. Interestingly, this finding supports recent results reported by Lim *et al.* (2014) who found a correlation coefficient of 0.414 between maternal size and offspring size for a wider set of taxonomic groups.

Table 7. Difference between the mean of each moderator for the relationship between offspring mass and maternal mass in mammals with their 95% high posterior density interval (HPDI)

Mammals	Mean difference	Lower HPDI	Upper HPDI
Before <i>versus</i> after weaning	0.060	-0.078	0.203
Mass <i>versus</i> other proxy	-0.038	-0.259	0.188
Both sex <i>versus</i> female	-0.021	-0.173	0.125
Both sex <i>versus</i> male	-0.025	-0.176	0.125
Captive <i>versus</i> wild	-0.001	-0.156	0.154
Polygynous <i>versus</i> promiscuous	-0.123	-0.322	0.041
Monotocous <i>versus</i> polytocous	-0.025	-0.185	0.154
High quality <i>versus</i> low quality	-0.087	-0.237	0.059



**Fig. 7.** Funnel plots of the different effect sizes in mammals for the relationship between offspring mass and maternal mass. The precision is plotted as a function of the meta-analysis residuals, as recommended by Nakagawa & Santos (2012). The vertical solid line corresponds to 0.

The generally strong size–mass relationship explains the consistency of results across studies (e.g. Dahle, Zedrosser & Swenson, 2006).

Both the species and the population random effects only accounted for a weak proportion of observed heterogeneity in our meta-analysis, which indicates that the positive effect we highlighted is consistent across mammalian species. As we included a large diversity of mammals, we can safely generalize our findings to the entire class of mammals. The type of data used did not influence the results and the publication bias we detected had only a very weak effect on the final result. We were not able to perform this analysis for birds because of insufficient data. In birds more effort has been allocated to studying the relationship between maternal mass and egg mass, which is likely to be positive (Wiggins, 1990; Budden & Beissinger, 2005). Egg mass also relates

to neonatal mass in birds (Krist, 2011), which leads us to expect that the relationship we identified in mammals also holds in birds. The few studies that assessed the maternal mass–offspring mass relationship in birds supported the existence of a positive relationship between maternal mass and offspring mass (Blums, Clark & Mednis, 2002; Parker, 2002; Newbrey & Reed, 2009).

We checked whether the timing of the offspring measurement could impact the magnitude of the mother–offspring mass relationship. Measuring offspring before weaning or after weaning led to similar results. Maternal mass thus provides a reliable predictor of both offspring birth mass and weaning mass in mammals. This result is not surprising because weaning mass is highly related to birth mass in mammals, with weaning mass being about four times the birth mass in pinnipeds, primates, and ungulates (Lee *et al.*, 1991). As in the analysis of the offspring mass–survival relationship, the use of different types of measurement did not have any impact on this meta-analysis. Likewise, wild and captive mammalian females allocate to their offspring with the same intensity at a given size. This is quite surprising when considering that body mass is more closely related to offspring survival in captive than in wild populations. However, we expect that females should increase their offspring body mass relative to their own mass only if an increase of the offspring body mass can give a sufficient increase in offspring survival compared to lighter ones. In captivity offspring body mass is more closely related to survival than in the wild but average offspring survival is typically higher in captivity than in the wild (Littleton, 2005). Because offspring survival is already high in captivity, any increase in offspring body mass might not provide additional survival benefits.

The absence of any sex difference on the maternal–offspring mass relationship was an unexpected result, which indicates that mothers allocate the same relative amount of energy to male and female offspring irrespective of their body mass. Similar results were found in birds with no sex-biased allocation to egg size (Rutkowska, Dubiec & Nakagawa, 2014). In polygynous species the disproportionate mass or size advantage of offspring males is expected to be higher than in promiscuous species (Clutton-Brock, 1991) but we did not find any interaction between offspring sex

and mating system. However, a similar correlation coefficient does not imply that there is no differential allocation between sexes. For a given mass, mothers can produce heavier male than female offspring. We did not detect any difference between the correlation coefficients but the intercept of the relationship was generally higher in males, indicating that mothers allocate more to male than to female offspring (e.g. Foster & Taggart, 2008). Furthermore, the mother can also allocate more toward males by biasing offspring sex ratio instead of increasing male mass, explaining why in some cases maternal mass can be related to offspring sex ratio (Arnbom, Fedak & Boyd, 1997). In addition, as recently pointed out by Schindler *et al.* (2015), the full sex-specific reproductive value has to be considered before stating that there are adaptive sex differences in maternal care. In 11 of our 17 studies that tested such differences, offspring mass was measured at birth, meaning that all the maternal allocation after birth was not accounted for.

Interestingly we did not find any difference in female allocation to offspring mass between monotocous and polytocous mammals. Mammals that produce multiple offspring can modify maternal allocation *via* two pathways: the offspring mass or the offspring number. We thus expected females of polytocous mammals to allocate less to offspring mass than females of monotocous species. However, in most cases, the expected offspring size–number trade-off does not show up among females within a population and both the mean mass of offspring and litter size increase with maternal mass (reviewed by Lim *et al.*, 2014). The mating system does not seem to impact this relationship. This is not so surprising because the difference between promiscuous and polygynous mating systems is only expected to impact paternal allocation (Adrian *et al.*, 2005). As the degree of paternity certainty is lower in promiscuous species than in polygynous species, promiscuous fathers should allocate less than polygynous fathers (Wright & Cotton, 1994), whereas such differences are not expected for maternal allocation.

## V. CONCLUSIONS

(1) Using meta-analyses we provide strong evidence of a positive relationship between offspring mass and offspring survival in birds and mammals. Our main finding shows the importance of considering body mass when analysing variation in early survival. Offspring mass offers a reliable indicator of offspring survival in both birds and mammals. However, the magnitude of the relationship was weaker for birds, likely because of flight constraints.

(2) We did not identify biological drivers that explained the differences we observed in the magnitude of the offspring mass–survival relationship across studies. We propose that this is because the offspring mass–survival relationship is highly dependent on the mortality causes in the focal populations. When most individuals die from weakly condition-dependent factors such as predation, a low magnitude of the relationship is expected, whereas when

condition-dependent factors such as starvation mostly cause mortality, a higher magnitude of the relationship is expected.

(3) Offspring body mass, which drives individual differences in survival among offspring, is positively correlated with maternal body mass in mammals. This correlation was not quantitatively tested in birds due to a lack of data. However, from the limited information collected so far, there is support for a positive relationship. Further work, when sufficient data are available, should assess the correlation coefficient in birds for comparison with the coefficient obtained here for mammals. Because offspring survival is less related to offspring mass in birds, we expect a smaller coefficient of correlation in birds than in mammals.

(4) We did not identify any major driver that could explain the observed variability in the relationship between maternal mass and offspring mass. As we found large variation in condition-dependent survival in mammals in relation to variation in environmental conditions, we expected also to find large variation in the relationship between offspring and maternal mass. The link between the two relationships studied here is not clear and is worth further investigation.

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## VII. REFERENCES

- \*References marked with an asterisk have been included in the meta-analyses.
- \*ADAMS, L. G. (2005). Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. *Journal of Mammalogy* **86**, 506–513.
- ADRIAN, O., BROCKMANN, I., HOHOFF, C. & SACHSER, N. (2005). Paternal behaviour in wild guinea pigs: a comparative study in three closely related species with different social and mating systems. *Journal of Zoology* **265**, 97–105.
- \*ANDERSON, M. G., LINDBERG, M. S. & EMERY, R. B. (2001). Probability of survival and breeding for juvenile female canvasbacks. *Journal of Wildlife Management* **65**, 385–397.
- \*ARNBOM, T., FEDAK, M. A. & BOYD, I. L. (1997). Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* **78**, 471–483.
- \*AWAN, G. A., FESTA-BIANCHET, M. & GAILLARD, J. M. (2008). Early survival of Punjab urial. *Canadian Journal of Zoology* **86**, 394–399.
- \*BARBER-MEYER, S. M., MECH, L. D. & WHITE, P. J. (2008). Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* **169**, 1–30.
- BARBRAUD, C., JOHNSON, A. R. & BERTAULT, G. (2003). Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. *Journal of Animal Ecology* **72**, 246–257.
- BENNETT, K. A., HUGHES, J., STAMATAS, S., BRAND, S., FOSTER, N. L., MOSS, S. E. & POMEROY, P. P. (2015). Adiponectin and insulin in gray seals during suckling and fasting: relationship with nutritional state and body mass during nursing in mothers and pups. *Physiological and Biochemical Zoology* **88**, 295–310.
- \*BERGOVITCH, F. B., WIDDIG, A. & NÜRNBERG, P. (2000). Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons. *Behavioral Ecology and Sociobiology* **48**, 1–11.
- \*BERGER, J. (2012). Estimation of body-size traits by photogrammetry in large mammals to inform conservation. *Conservation Biology* **26**, 769–777.
- BININDA-EMONDS, O. R. P., CARDILLO, M., JONES, K. E., MACPHEE, R. D. E., BECK, R. M. D., GRENYER, R., PRICE, S. A., VOS, R. A., GITTELMAN, J. L. & PURVIS, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507–512.

- \*BIRGERSSON, B. & EKVALL, K. (1997). Early growth in male and female fallow deer fawns. *Behavioral Ecology* **8**, 493–499.
- \*BISHOP, C. J., UNSWORTH, J. W. & GARTON, E. O. (2005). Mule deer survival among adjacent populations in southwest Idaho. *Journal of Wildlife Management* **69**, 311–321.
- \*BISHOP, C. J., WHITE, G. C., FREDDY, D. J., WATKINS, B. E. & STEPHENSON, T. R. (2009). Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* **177**, 1–28.
- \*BLAXTER, K. L. & HAMILTON, W. J. (1980). Reproduction in farmed red deer. II. Calf growth and mortality. *Journal of Agricultural Science* **95**, 275–284.
- \*BLOMQUIST, G. E. & WILLIAMS, L. E. (2013). Quantitative genetics of costly neonatal sexual size dimorphism in squirrel monkeys (*Saimiri boliviensis*). *Journal of Evolutionary Biology* **26**, 756–765.
- BLUMS, P., CLARK, R. G. & MEDNIS, A. (2002). Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. *Journal of Animal Ecology* **71**, 280–295.
- \*BOLTNEV, A. I. & YORK, A. E. (2001). Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. *Journal of Zoology* **254**, 219–228.
- \*BOLTON, M. (1991). Determinants of chick survival in the lesser Black-Backed Gull: relative contributions of egg size and parental quality. *Journal of Animal Ecology* **60**, 949–960.
- \*BONENFANT, C., GAILLARD, J. M., LOISON, A. & KLEIN, F. (2003). Sex-ratio variation and reproductive costs in relation to density in a forest-dwelling population of red deer (*Cervus elaphus*). *Behavioral Ecology* **14**, 862–869.
- BONTER, D. N., ZUCKERBERG, B., SEDGWICK, C. W. & HOCHACHKA, W. M. (2013). Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20123087.
- \*BOOHER, C. M. (2008). Effects of calcium availability on reproductive output of big brown bats. *Journal of Zoology* **274**, 38–43.
- \*BOWEN, W. D., ELLIS, S. L., IVERSON, S. J. & BONESS, D. J. (2001a). Maternal effects on offspring growth rate and weaning mass in harbour seals. *Canadian Journal of Zoology* **79**, 1088–1101.
- \*BOWEN, W. D., IVERSON, S. J., BONESS, D. J. & OFTEDAL, O. T. (2001b). Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* **15**, 325–334.
- \*BOWEN, W. D., OFTEDAL, O. T., BONESS, D. J. & IVERSON, S. J. (1994). The effect of maternal age and other factors on birth mass in the harbour seal. *Canadian Journal of Zoology* **72**, 8–14.
- \*BOYD, I. L. & MCCANN, T. S. (1989). Pre-natal investment in reproduction by female Antarctic fur seals (*Arctophthalus gazella*). *Behavioral Ecology and Sociobiology* **24**, 377–385.
- \*BRAASCH, A., SCHAUROTH, C. & BECKER, P. H. (2009). Post-fledging body mass as a determinant of subadult survival in common terns *Sterna hirundo*. *Journal of Ornithology* **150**, 401–407.
- \*BROWN, W. P. & ROTH, R. R. (2004). Juvenile survival and recruitment of wood thrushes *Hylocichla mustelina* in a forest fragment. *Journal of Avian Biology* **35**, 316–326.
- BUDDEN, A. E. & BEISSINGER, S. R. (2005). Egg mass in an asynchronously hatching parrot: does variation offset constraints imposed by laying order? *Oecologia* **144**, 318–326.
- BYERS, J. A. (1997). *American Pronghorn. Social Adaptations and the Ghosts of Predators Past*. The University of Chicago Press, Chicago & London.
- CAM, E., LINK, W. A., COOCH, E. G., MONNAT, J. Y. & DANCHIN, E. (2002). Individual covariation in life-history traits: seeing the trees despite the forest. *The American Naturalist* **159**, 96–105.
- \*CAMPBELL, M. T. & SLADE, N. A. (1995). The effect of maternal mass on litter size and offspring survival in the hispid cotton rat (*Sigmodon hispidus*). *Canadian Journal of Zoology* **73**, 133–140.
- \*CARSTENSEN, M., DELGIUDICE, G. D., SAMPSON, B. A. & KUEHN, D. W. (2009). Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *Journal of Wildlife Management* **73**, 175–183.
- \*CASELLAS, J., CAJA, G., SUCH, X. & PIEDRAFITA, J. (2007). Survival analysis from birth to slaughter of Ripollés lambs under semi-intensive management. *Journal of Animal Science* **85**, 512–517.
- CASWELL, H. (2001). *Matrix Population Models*. John Wiley & Sons, Ltd, Chichester.
- CHANDLER, C. R. & MULVHILL, R. S. (1992). Effects of age, sex, and fat level on wing loading in dark-eyed juncos. *The Auk* **109**, 235–241.
- CHARNOV, E. L. & ERNEST, S. K. M. (2006). The offspring-size/clutch-size trade-off in mammals. *The American Naturalist* **167**, 578–582.
- \*CHILVERS, B. L., ROBERTSON, B. C., WILKINSON, I. S. & DUGNAN, P. J. (2007). Growth and survival of New Zealand sea lions, *Phocartos hookeri*: birth to 3 months. *Polar Biology* **30**, 459–469.
- \*CLEASBY, I. R., NAKAGAWA, S., GILLESPIE, D. O. S. & BURKE, T. (2010). The influence of sex and body size on nestling survival and recruitment in the house sparrow. *Biological Journal of the Linnean Society* **101**, 680–688.
- CLUTTON-BROCK, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton.
- CLUTTON-BROCK, T. H., ALBON, S. D. & GUINNESS, F. E. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**, 131–133.
- \*CLUTTON-BROCK, T. H., ALBON, S. D. & GUINNESS, F. E. (1986). Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour* **34**, 460–471.
- 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 & Evolution* **25**, 562–573.
- \*CLUTTON-BROCK, T. H., STEVENSON, I. R., MARROW, P., MACCOLL, A. D., HOUSTON, A. I. & MCNAMARA, J. M. (1996). Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology* **65**, 675–689.
- COHEN, J. (1988). *Statistical Power Analysis for the Behavioral Studies*. Academic Press, New York.
- \*COLTMAN, D. W., BOWEN, W. D. & WRIGHT, J. M. (1998). Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. *Proceedings of the Royal Society B: Biological Sciences* **265**, 803–809.
- \*COOCH, E. G. (2002). Fledging size and survival in snow geese: timing is everything (or is it?). *Journal of Applied Statistics* **29**, 143–162.
- \*CÔTÉ, S. D. & FESTA-BIANCHET, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230–238.
- \*CROCKER, D. E., WILLIAMS, J. D., COSTA, D. P. & LE BOEUF, B. J. (2001). Maternal traits and reproductive effort in northern elephant seals. *Ecology* **82**, 3541–3555.
- \*DAHLE, B., ZEDROSSER, A. & SWENSON, J. E. (2006). Correlates with body size and mass in yearling brown bears (*Ursus arctos*). *Journal of Zoology* **269**, 273–283.
- \*DAVIES, J. M. & RESTANI, M. (2006). Survival and movements of juvenile burrowing owls during the postfledging period. *The Condor* **108**, 282–291.
- \*DAVIS, J. B., COX, R. R. J., KAMINSKI, R. M. & LEOPOLD, B. D. (2007). Survival of wood duck ducklings and broods in Mississippi and Alabama. *Journal of Wildlife Management* **71**, 507–517.
- \*DEROCHER, A. E. & STIRLING, I. (1994). Age-specific reproductive performance of female polar bears (*Ursus maritimus*). *Journal of Zoology* **234**, 527–536.
- \*DEROCHER, A. E. & STIRLING, I. (1996). Aspects of survival in juvenile polar bears. *Canadian Journal of Zoology* **74**, 1246–1252.
- \*DINSMORE, S. J., WHITE, G. C. & KNOPF, F. L. (2003). Annual survival and population estimates of mountain plovers in southern Phillips County, Montana. *Ecological Applications* **13**, 1013–1026.
- \*DITCKHOFF, S. S., SAMS, M. G., LOCHMILLER, R. L. & LESLIE, D. M. JR. (2001). Utility of tumor necrosis factor- $\alpha$  and interleukin-6 as predictor of neonatal mortality in white-tailed deer. *Journal of Mammalogy* **82**, 239–245.
- \*DOBSON, F. S. & MICHENER, G. R. (1995). Maternal traits and reproduction in Richardson's ground squirrels. *Ecology* **76**, 851–862.
- \*DOBSON, F. S. & MYERS, P. (1989). The seasonal decline in the litter size of meadow voles. *Journal of Mammalogy* **70**, 142–152.
- \*DOLAN, A. C., MURPHY, M. T., REDMOND, L. J. & DUFFIELD, D. (2009). Maternal characteristics and the production and recruitment of sons in the eastern kingbird (*Tyrannus tyrannus*). *Behavioral Ecology and Sociobiology* **63**, 1527–1537.
- \*DONADIO, E., BUSKIRK, S. W. & NOVARO, A. J. (2012). Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population. *Journal of Mammalogy* **93**, 1536–1544.
- \*DYBALA, K. E., GARDALI, T. & EADIE, J. M. (2013). Dependent vs. independent juvenile survival: contrasting drivers of variation and the buffering effect of parental care. *Ecology* **94**, 1584–1593.
- EGGER, M., DAVEY SMITH, G., SCHNEIDER, M. & MINDER, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal* **315**, 629–634.
- \*ELLIS, S. L., BOWEN, W. D., BONESS, D. J. & IVERSON, S. J. (2000). Maternal effects on offspring mass and stage of development at birth in the harbor seal, *Phoca vitulina*. *Journal of Mammalogy* **81**, 1143–1156.
- \*ELORANTA, E. & NIEMINEN, M. (1986). Calving of the experimental reindeer herd in Kaamanen during 1970–1985. *Rangifer* **1**, 115–121.
- \*ERICSSON, G., WALLIN, K., BALL, J. P. & BROBERG, M. (2001). Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* **82**, 1613–1620.
- \*FAIRBANKS, W. S. (1993). Birthdate, birthweight, and survival in pronghorn fawns. *Journal of Mammalogy* **74**, 129–135.
- \*FEDAK, M., ARNBOM, T. & BOYD, I. (1996). The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat, and protein during lactation. *Physiological Zoology* **69**, 887–911.
- \*FEDER, C., MARTIN, J. G. A., FESTA-BIANCHET, M., BÉRUBÉ, C. & JORGENSEN, J. (2008). Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia* **156**, 773–781.
- \*FESTA-BIANCHET, M. & JORGENSEN, J. T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology* **9**, 144–150.
- \*FESTA-BIANCHET, M., JORGENSEN, J. T., BÉRUBÉ, C. H., PORTIER, C. & WISHART, W. D. (1997). Body mass and survival of bighorn sheep. *Canadian Journal of Zoology* **75**, 1372–1379.

- \*FORCHHAMMER, M. C., CLUTTON-BROCK, T. H., LINDSTRÖM, J. & ALBON, S. D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**, 721–729.
- FORSTMEIER, W., NAKAGAWA, S., GRIFFITH, S. C. & KEMPENAERS, B. (2014). Female extra-pair mating: adaptation or genetic constraint? *Trends in Ecology & Evolution* **29**, 456–464.
- \*FOSTER, W. K. & TAGGART, D. A. (2008). Gender and parental influences on the growth of a sexually dimorphic carnivorous marsupial. *Journal of Zoology* **275**, 221–228.
- GADGIL, M. & BOSSERT, W. H. (1970). Life historical consequences of natural selection. *The American Naturalist* **104**, 1–24.
- GAILLARD, J. M., FESTA-BIANCHET, M., YOCOZ, N., LOISON, A. & TOIGO, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology, Evolution, and Systematics* **31**, 367–393.
- GARAMSZEGI, L., EENS, M., HURTREZBOUSSES, S. & MOLLER, A. (2005). Testosterone, testes size, and mating success in birds: a comparative study. *Hormones and Behavior* **47**, 389–409.
- \*GARNETT, M. C. (1981). Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis* **123**, 31–41.
- GARRATT, M., BROOKS, R. C., LEMAÎTRE, J. F. & GAILLARD, J. M. (2014). Female promiscuity and maternally dependent offspring growth rates in mammals. *Evolution* **68**, 1207–1215.
- GARRATT, M., LEMAÎTRE, J. F., DOUHARD, M., BONENFANT, C., CAPRON, G., WARNANT, C., KLEIN, F., BROOKS, R. C. & GAILLARD, J. M. (2015). High juvenile mortality is associated with sex-specific adult survival and lifespan in wild roe deer. *Current Biology* **25**, 759–763.
- \*GASTON, A. J. (1997). Mass and date at departure affect the survival of ancient murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* **139**, 673–678.
- GELMANN, A. & RUBIN, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science* **7**, 457–511.
- GILROY, J. J., VIRZI, T., BOULTON, R. L. & LOCKWOOD, J. L. (2012). A new approach to the 'apparent survival' problem: estimating true survival rates from mark–recapture studies. *Ecology* **93**, 1509–1516.
- \*GONZALEZ, O., ZEDROSSER, A., PELLETIER, F., SWENSON, J. E. & FESTA-BIANCHET, M. (2012). Litter reductions reveal a trade-off between offspring size and number in brown bears. *Behavioral Ecology and Sociobiology* **66**, 1025–1032.
- GOSLER, A. G., GREENWOOD, J. J. D. & PERRINS, C. (1995). Predation risk and the cost of being fat. *Nature* **377**, 621–623.
- \*GREEN, D. J. & COCKBURN, A. (2001). Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* **70**, 505–514.
- \*GREÑO, J. L., BELDA, E. J. & BARBA, E. (2008). Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. *Journal of Avian Biology* **39**, 41–49.
- \*GRIFFIN, K. A., HEBBLEWHITE, M., ROBINSON, H. S., ZAGER, P., BARBER-MEYER, S. M., CHRISTIANSON, D., CREE, S., HARRIS, N. C., HURLEY, M. A., JACKSON, D. H., JOHNSON, B. K., MYERS, W. L., RAITHEL, J. D., SCHLEGEL, M., SMITH, B. L., WHITE, C. & WHITE, P. J. (2011). Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology* **80**, 1246–1257.
- \*GUSTAFSON, L. L., FRANKLIN, W. L., JOHNSON, W. E., BEHL, M. J., SARNO, R. J., HUNTER, R. L. & YOUNG, K. M. (1998). Predicting early mortality of newborn guanacos by birth mass and hematological parameters: a provisional model. *Journal of Wildlife Management* **62**, 24–35.
- HADFIELD, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22.
- HADFIELD, J. D. & NAKAGAWA, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* **23**, 494–508.
- \*HALL, A. J., MCCONNELL, B. J. & BARKER, R. (2001). Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* **70**, 138–149.
- \*HALL, A. J., MCCONNELL, B. J. & BARKER, R. J. (2002). The effect of total immunoglobulin levels, mass and condition on the first-year survival of Grey Seal pups. *Functional Ecology* **16**, 462–474.
- \*HAMEL, S., CRAINE, J. M. & TOWNE, E. G. (2012a). Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications* **22**, 1628–1639.
- HAMEL, S., YOCOZ, N. G. & GAILLARD, J. M. (2012b). Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. *Methods in Ecology and Evolution* **3**, 731–742.
- HAMEL, S., GAILLARD, J. M., FESTA-BIANCHET, M. & CÔTÉ, S. D. (2009). Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* **90**, 1981–1995.
- HAMEL, S., GAILLARD, J. M., YOCOZ, N. G., LOISON, A., BONENFANT, C. & DESCAMPS, S. (2010). Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecology Letters* **13**, 915–935.
- \*HARRIS, M. P. & ROTHERY, P. (1985). The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* **127**, 243–250.
- HARVEY, P. H. & PAGEL, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- \*HEDGREN, S. (1981). Effects of fledging weight and time of fledging on survival of guillemot *Uria aalge* chicks. *Ornis Scandinavica* **12**, 51–54.
- \*HELLE, S., LAARSONEN, T. & HUITTU, O. (2013). Sex-specific offspring growth according to maternal testosterone, corticosterone, and glucose levels. *Behavioral Ecology* **24**, 205–212.
- \*HEWISON, A. J. M., GAILLARD, J. M., KJELLANDER, P., TOIGO, C., LIBERG, O. & DELORME, D. (2005). Big mothers invest more in daughters – reversed sex allocation in a weakly polygynous mammal. *Ecology Letters* **8**, 430–437.
- HIGGINS, J. P. T., THOMPSON, S. G., DEEKS, J. J. & ALTMAN, D. G. (2003). Measuring inconsistency in meta-analyses. *British Medical Journal* **327**, 557–560.
- \*HODGE, S. J., BELL, M. B. V., MWANGUHYA, F., KYABULIMA, S., WALDICK, R. C. & RUSSELL, A. F. (2009). Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behavioral Ecology* **20**, 729–735.
- \*HOFFMAN, J. I., FORCADA, J. & AMOS, W. (2006). No relationship between microsatellite variation and neonatal fitness in Antarctic fur seals, *Arctocepalus gazella*. *Molecular Ecology* **15**, 1995–2005.
- \*HOLAND, O., MYSTERUD, A., ROED, K. H., COULSON, T., GJØSTEIN, H., WELADJI, R. B. & NIEMINEN, M. (2006). Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society B: Biological Sciences* **273**, 293–299.
- \*HOLAND, O., WELADJI, R. B., GJØSTEIN, H., KUMPULA, J., SMITH, M. E., NIEMINEN, M. & RØED, K. H. (2004). Reproductive effort in relation to maternal social rank in reindeer (*Rangifer tarandus*). *Behavioral Ecology and Sociobiology* **57**, 69–76.
- \*HORSWILL, C., MATTHIOPOULOS, J., GREEN, J. A., MEREDITH, M. P., FORCADA, J., PEAT, H., PRESTON, M., TRATHAN, P. N. & RATCLIFFE, N. (2014). Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *Journal of Animal Ecology* **83**, 1057–1067.
- HURLBERT, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187.
- \*HURLEY, M. A., UNSWORTH, J. W., ZAGER, P., HEBBLEWHITE, M., GARTON, E. O., MONTGOMERY, D. M., SKALSKI, J. R. & MAYCOCK, C. L. (2011). Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs* **178**, 1–33.
- \*HUSBY, M. & SLAGSVOLD, T. (1992). Post-fledging behavior and survival in male and female behaviour Magpies *Pica pica*. *Ornis Scandinavica* **23**, 483–490.
- \*IVERSON, S. J., BOWEN, W. D., BONESS, D. J. & OFTEDAL, O. T. (1993). The effects of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* **66**, 61–88.
- JASAREVIĆ, E., BAILEY, D. H., CROSSLAND, J. P., DAWSON, W. D., SZALAI, G., ELLERSIECK, M. R., ROSENFELD, C. S. & GEARY, D. C. (2013). Evolution of monogamy, paternal investment, and female life history in *Peromyscus*. *Journal of Comparative Psychology* **127**, 91–102.
- \*JENKINS, K. J. & BARTEN, N. L. (2005). Demography and decline of the Mentasta caribou herd in Alaska. *Canadian Journal of Zoology* **83**, 1174–1188.
- JEITZ, W., THOMAS, G. H. H., JOY, J. B. B., HARTMANN, K. & MOOERS, A. O. O. (2012). The global diversity of birds in space and time. *Nature* **491**, 1–5.
- \*JONES, O. R., CRAWLEY, M. J., PILKINGTON, J. G. & PEMBERTON, J. M. (2005). Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proceedings of the Royal Society B: Biological Sciences* **272**, 2619–2625.
- \*KASPARIAN, K., GEISSLER, E. & TRILLMICH, F. (2005). Optimal offspring size in a small mammal: an exception to the tradeoff invariant life-history rule. *Oikos* **111**, 271–278.
- \*KEECH, M. A., BOWYER, R. T., HOEF, J. M. V., BOERTJE, R. D., DALE, B. W. & STEPHENSON, T. R. (2000). Life-history consequences of maternal condition in Alaskan Moose. *Journal of Wildlife Management* **64**, 450.
- \*KEECH, M. A., LINDBERG, M. S., BOERTJE, R. D., VALKENBURG, P., TARAS, B. D., BOUDREAU, T. A. & BECKMEN, K. B. (2011). Effects of predator treatments, individual traits, and environment on moose survival in Alaska. *Journal of Wildlife Management* **75**, 1361–1380.
- \*KERSHNER, E. L., WALK, J. W. & WARNER, R. E. (2004). Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. *The Auk* **121**, 1146–1154.
- \*KERSTEN, M. & BRENNINKMEIJER, A. (1995). Growth, fledging success and post-fledging survival of juvenile oystercatchers *Haematopus ostralegus*. *Ibis* **137**, 396–404.
- \*KOJOLA, I. (1993). Early maternal investment and growth in reindeer. *Canadian Journal of Zoology* **71**, 753–758.
- \*KOSKELA, E., HUITTU, O., KOIVULA, M., KORPIMAKI, E. & MAPPES, T. (2004). Sex-biased maternal investment in voles: importance of environmental conditions. *Proceedings of the Royal Society B: Biological Sciences* **271**, 1385–1391.
- \*KRACKOW, S. (1997). Maternal investment, sex-differential prospects, and the sex ratio in wild house mice. *Behavioral Ecology and Sociobiology* **41**, 435–443.
- \*KRAUS, C., MUELLER, B., MEISE, K., PIEDRAHITA, P., PÖRSCHMANN, U. & TRILLMICH, F. (2013). Mama's boy: sex differences in juvenile survival in a highly dimorphic large mammal, the Galapagos sea lion. *Oecologia* **171**, 893–903.

- \*KREBS, E. A. (1999). Last but not least: nestling growth and survival in asynchronously hatching crimson rosellas. *Journal of Animal Ecology* **68**, 266–281.
- \*KRIST, M. (2011). Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews* **86**, 692–716.
- \*LABOCHA, M. K. & HAYES, J. P. (2012). Morphometric indices of body condition in birds: a review. *Journal of Ornithology* **153**, 1–22.
- \*LANDETE-CASTILLEJOS, T., GARCÍA, A., GÓMEZ, J. Á., MOLINA, A. & GALLEGO, L. (2003). Subspecies and body size allometry affect milk production and composition, and calf growth in red deer: comparison of *Cervus elaphus hispanicus* and *Cervus elaphus scoticus*. *Physiological and Biochemical Zoology* **76**, 594–602.
- \*LANDETE-CASTILLEJOS, T., GARCÍA, A., LÓPEZ-SERRANO, F. R. & GALLEGO, L. (2005). Maternal quality and differences in milk production and composition for male and female Iberian red deer calves (*Cervus elaphus hispanicus*). *Behavioral Ecology and Sociobiology* **57**, 267–274.
- \*LARIVÉE, M. L., BOUTIN, S., SPEAKMAN, J. R., MCADAM, A. G. & HUMPHRIES, M. M. (2010). Associations between over-winter survival and resting metabolic rate in juvenile North American red squirrels. *Functional Ecology* **24**, 597–607.
- \*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.
- \*LEBRETON, J. D., PRADEL, R. & CLOBERT, J. (1993). The statistical analysis of survival in animal populations. *Trends in Ecology & Evolution* **8**, 91–95.
- \*LEE, P. C., MAJLUF, P. & GORDON, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology* **225**, 99–114.
- \*LEGGE, S. (2002). Siblicide, starvation and nestling growth in the laughing kookaburra. *Journal of Avian Biology* **33**, 159–166.
- \*LEMAÎTRE, J. F., GAILLARD, J. M., LACKEY, L. B., CLAUSSE, M. & MÜLLER, D. W. H. (2013). Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Experimental Gerontology* **48**, 162–167.
- \*LIBERATI, A., ALTMAN, D. G., TETZLAFF, J., MULROW, C., GOTZSCHE, P. C., IOANNIDIS, J. P. A., CLARKE, M., DEVEREAUX, P. J., KLEIJNEN, J. & MOHER, D. (2009). The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate healthcare interventions: explanation and elaboration. *British Medical Journal* **339**, b2700.
- \*LIM, J. N., SENIOR, A. M. & NAKAGAWA, S. (2014). Heterogeneity in individual quality and reproductive trade-offs within species. *Evolution* **68**, 2306–2318.
- \*LINDÉN, M., GUSTAFSSON, L. & PART, T. (1992). Selection on fledging mass in the collared flycatcher and the great tit. *Ecology* **73**, 336.
- \*LINDSTRÖM, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* **14**, 343–348.
- \*LINNELL, J. D. C., AANES, R. & ANDERSEN, R. (1995). Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* **1**, 209–223.
- \*LIPSEY, M. W. & WILSON, D. B. (2001). *Practical Meta-analysis*. Sage Publications, Thousand Oaks.
- \*LITTLETON, J. (2005). Fifty years of Chimpanzee demography at Taronga Park Zoo. *American Journal of Primatology* **67**, 281–298.
- \*LLOYD, C. S. (1979). Factors affecting breeding of razorbills *Alca torda* on Skokholm. *Ibis* **121**, 165–176.
- \*LLOYD, P., ANDREW, T. W., DU PLESSIS, M. A. & MARTIN, T. E. (2009). Females increase reproductive investment in response to helper-mediated improvements in allo-feeding, nest survival, nestling provisioning and post-fledging survival in the Karoo scrub-robin *Cercotrichas coryphaeus*. *Journal of Avian Biology* **40**, 400–411.
- \*LOBATO, E., MORENO, J., MERINO, S., SANZ, J. J. & ARRIERO, E. (2005). Haematological variables are good predictors of recruitment in nestling pied flycatchers (*Ficedula hypoleuca*). *Ecoscience* **12**, 27–34.
- \*LOISON, A., LANGVATN, R. & SOLBERG, E. J. (1999). Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22**, 20–30.
- \*LOMAS, L. A. & BENDER, L. C. (2007). Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *Journal of Wildlife Management* **71**, 884–894.
- \*LUNN, N. J. & BOYD, I. L. (1993). Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology* **229**, 55–67.
- \*LUSK, J. J., GUTHERY, F. S., COX, S. A., DEMASO, S. J. & PEOPLES, A. D. (2005). Survival and growth of northern bobwhite chicks in western Oklahoma. *The American Midland Naturalist* **153**, 389–395.
- \*MABILLE, G. & BERTEAUX, D. (2014). Hide or die: use of cover decreases predation risk in juvenile North American porcupines. *Journal of Mammalogy* **95**, 992–1003.
- \*MACKAS, R. H., GREEN, D. J., WHITEHORNE, I. B. J., FAIRHURST, E. N., MIDDLETON, H. A. & MORRISSEY, C. A. (2010). Altitudinal migration in American Dipper (*Cinclus mexicanus*): do migrants produce higher quality offspring? *Canadian Journal of Zoology* **88**, 369–377.
- \*MAGRATH, R. D. (1991). Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* **60**, 335–351.
- \*MANDAL, A., PRASAD, H., KUMAR, A., ROY, R. & SHARMA, N. (2007). Factors associated with lamb mortalities in Muzaffarnagari sheep. *Small Ruminant Research* **71**, 273–279.
- \*MANESS, T. J. & ANDERSON, D. J. (2013). Predictors of juvenile survival in birds. *Ornithological Monographs* **78**, 1–55.
- \*MANISCALCO, J. M. (2014). The effects of birth weight and maternal care on survival of juvenile Steller sea lions (*Eumetopias jubatus*). *PLoS ONE* **9**, e96328.
- \*MARTÍN, C. A., ALONSO, J. C., ALONSO, J. A., PALACÍN, C., MAGAÑA, M. & MARTÍN, B. (2007). Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *Journal of Avian Biology* **38**, 335–346.
- \*McCANN, T. S., FEDAK, M. A. & HARWOOD, J. (1989). Parental investment in southern elephant seals, *Mirounga leonina*. *Behavioral Ecology and Sociobiology* **25**, 81–87.
- \*McCLUNG, M. R., SEDDON, P. J., MASSARO, M. & SETIAWAN, A. N. (2004). Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect fledging weight and juvenile survival? *Biological Conservation* **119**, 279–285.
- \*McDONALD, B. I., GOEBEL, M. E., CROCKER, D. E. & COSTA, D. P. (2012). Dynamic influence of maternal and pup traits on maternal care during lactation in an income breeder, the Antarctic fur seal. *Physiological and Biochemical Zoology* **85**, 243–254.
- \*McMAHON, C. R., BURTON, H. R. & BESTER, M. N. (2000). Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* **12**, 149–153.
- \*McMAHON, C. R., NEW, L. F., FAIRLEY, E. J., HINDELL, M. A. & BURTON, H. R. (2015). The effects of body size and climate on post-weaning survival of elephant seals at Heard Island. *Journal of Zoology* **297**, 301–308.
- \*MEDEIROS, M. C. & FREED, L. A. (2009). A fledging-mass threshold greatly affects juvenile survival in the Hawaii akepa (*Loxops coccyzus coccyzus*). *The Auk* **126**, 319–325.
- \*MENARD, S. (2011). Standards for standardized logistic regression coefficients. *Social Forces* **89**, 1409–1428.
- \*MICHEL, E. S., DEMARAIS, S., STRICKLAND, B. K. & BELANT, J. L. (2015). Contrasting the effects of maternal and behavioral characteristics on fawn birth mass in white-tailed deer. *PLoS ONE* **10**, e0136034.
- \*MICHENER, G. R. (1989). Reproductive effort during gestation and lactation by Richardson's ground squirrels. *Oecologia* **78**, 77–86.
- \*MONCLÚS, R., PANG, B. & BLUMSTEIN, D. T. (2014). Yellow-bellied marmots do not compensate for a late start: the role of maternal allocation in shaping life-history trajectories. *Evolutionary Ecology* **28**, 721–733.
- \*MONRÓS, J. S., BELDA, E. J. & BARBA, E. (2002). Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* **99**, 481–488.
- \*MONTEITH, K. L., BLEICH, V. C., STEPHENSON, T. R., PIERCE, B. M., CONNER, M. M., KIE, J. G. & BOWYER, R. T. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* **186**, 1–62.
- \*MONTICELLI, D. & RAMOS, J. A. (2012). Laying date, body mass and tick infestation of nestling tropical Roseate Terns *Sterna dougallii* predict fledging success, first-year survival and age at first return to the natal colony. *Ibis* **154**, 825–837.
- \*MOORE, G. H., LITTLEJOHN, R. P. & COWIE, G. M. (1988). Factors affecting live weight gain in red deer calves from birth to weaning. *New Zealand Journal of Agricultural Research* **31**, 279–283.
- \*MORRISON, K. W., HIPFNER, J. M., GJERDRUM, C. & GREEN, D. J. (2009). Wing length and mass at fledging predict local juvenile survival and age at first return in tufted puffins. *The Condor* **111**, 433–441.
- \*MOYES, K., NUSSEY, D. H., CLEMENTS, M. N., GUINNESS, F. E., MORRIS, A., MORRIS, S., PEMBERTON, J. M., KRUK, L. E. B. & CLUTTON-BROCK, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology* **17**, 2455–2469.
- \*MUKASA-MUGERWA, E., SAID, A. N., LAHLOU-KASSI, A., SHERINGTON, J. & MUTIGA, E. R. (1994). Birth weight as a risk factor for perinatal lamb mortality, and the effects of stage of pregnant ewe supplementation and gestation weight gain in Ethiopian Menz sheep. *Preventive Veterinary Medicine* **19**, 45–56.
- \*MUMME, R. L., BOWMAN, R., PRUETT, M. S. & FITZPATRICK, J. W. (2015). Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub-Jay. *The Auk* **132**, 634–646.
- \*MYERS, P. & MASTER, L. L. (1983). Reproduction by *Peromyscus maniculatus*: size and compromise. *Journal of Mammalogy* **64**, 1–18.
- \*MYSTERUD, A., RØED, K. H., HOLAND, O., Yoccoz, N. G. & NIEMINEN, M. (2009). Age-related gestation length adjustment in a large iteroparous mammal at northern latitude. *Journal of Animal Ecology* **78**, 1002–1006.
- \*NAEF-DAENZER, B., WIDMER, F. & NUBER, M. (2001). Differential post fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**, 730–738.
- \*NAKAGAWA, S. & POULIN, R. (2012). Meta-analytic insights into evolutionary ecology: an introduction and synthesis. *Evolutionary Ecology* **26**, 1085–1099.
- \*NAKAGAWA, S. & SANTOS, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274.
- \*NESPOLO, R. F. & BACIGALUPE, L. D. (2009). Viability selection on early body mass and the effect of female body size on fecundity: a study on the leaf-eared mouse *Phyllotis darwini*. *Ecological Research* **24**, 997–1002.
- \*NEWBREY, J. L. & REED, W. L. (2009). Growth of yellow-headed blackbird *Xanthocephalus xanthocephalus* nestlings in relation to maternal body condition, egg mass, and yolk carotenoids concentrations. *Journal of Avian Biology* **40**, 419–429.

- NORBERG, U. M. (1995). How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* **9**, 48.
- \*NOYCE, V., COY, L. & GARSHELIS, L. (2002). Bone prominence and skin-fold thickness as predictors of body fat and reproduction in American black bears. *Ursus* **13**, 275–284.
- \*NUR, N. (1984). The consequences of brood size for breeding blue tits II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology* **53**, 497–517.
- \*OLSSON, O. (1997). Effects of food availability on fledging condition and post-fledging survival in king penguin chicks. *Polar Biology* **18**, 161–165.
- \*OWEN, B. Y. M. & BLACK, J. M. (1989). Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal of Animal Ecology* **58**, 603–617.
- OZGUL, A., CHILDS, D. Z., OLI, M. K., ARMITAGE, K. B., BLUMSTEIN, D. T., OLSON, L. E., TULJAPURKAR, S. & COULSON, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485.
- PARKER, T. H. (2002). Maternal condition, reproductive investment, and offspring sex ratio in captive red junglefowl (*Gallus gallus*). *The Auk* **119**, 840.
- PARKER, K. L., BARBOZA, P. S. & GILLINGHAM, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology* **23**, 57–69.
- \*PATTERSON, I. J., DUNNET, G. M. & GOODBODY, S. R. (1988). Body weight and juvenile mortality. *Journal of Animal Ecology* **57**, 1041–1052.
- \*PERRINS, C. M., HARRIS, M. P. & BRITTON, C. K. (1973). Survival of Manx shearwaters. *Ibis* **115**, 535–548.
- \*PLARD, F., GAILLARD, J. M., COULSON, T., HEWISON, M. A. J., DOUHARD, M., KLEIN, F., DELORME, D., WARNANT, C. & BONENFANT, C. (2015). The influence of birth date via body mass on individual fitness in a long-lived mammal. *Ecology* **96**, 1516–1528.
- \*POMEROY, P. P., FEDAK, M. A., ROTHERY, P. & ANDERSON, S. (1999). Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology* **68**, 235–253.
- \*PONZ MIRANDA, A., GIL-DELGADO ALBERTI, J. A. & LÓPEZ IBORRA, M. (2007). Survival rates of young magpies *Pica pica* in a mountain population of eastern Spain. *Acta Ornithologica* **42**, 63–68.
- \*POSTMA, M., BESTER, M. N. & DE BRUYN, P. J. N. (2013). Age-related reproductive variation in a wild marine mammal population. *Polar Biology* **36**, 719–729.
- \*POTTI, J., DÁVILA, J. A., TELLA, J. L., FRÍS, O. C. & VILLAR, S. (2002). Gender and viability selection on morphology in fledgling pied flycatchers. *Molecular Ecology* **11**, 1317–1326.
- \*PROFFITT, K. M., GARROTT, R. A. & ROTELLA, J. J. (2008). Long-term evaluation of body mass at weaning and postweaning survival rates of Weddell seals in Erebus Bay, Antarctica. *Marine Mammal Science* **24**, 677–689.
- \*RABERG, L., STJERNMAN, M. & NILSSON, J. (2005). Sex and environmental sensitivity in blue tit nestlings. *Oecologia* **145**, 496–503.
- R Core Development Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org/>.
- \*RAMSAY, M. A. & STIRLING, I. (1988). Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of the Zoology* **214**, 601–634.
- \*READING, R. P., KENNY, D., AMGALANBAATAR, S., DENICOLA, A. & WINGARD, G. (2009). Argali lamb (*Ovis ammon*) morphometric measurements and survivorship in Mongolia. *Mammalia* **73**, 98–104.
- \*RIESCH, R., MARTIN, R. A., LERP, H., PLATH, M. & WRONSKI, T. (2013). Size and sex matter: reproductive biology and determinants of offspring survival in *Gazella marica*. *Biological Journal of the Linnean Society* **110**, 116–127.
- \*RINGSBY, T. H., SAETHER, B. E. & SOLBERG, E. J. (1998). Factors affecting juvenile survival in house sparrow *Passer domesticus*. *Journal of Avian Biology* **29**, 241.
- \*RIOUX-PAQUETTE, E., FESTA-BIANCHET, M. & COLTMAN, D. W. (2011). Sex-differential effects of inbreeding on overwinter survival, birth date and mass of bighorn lambs. *Journal of Evolutionary Biology* **24**, 121–131.
- \*ROBBINS, C. T., BEN-DAVID, M., FORTIN, J. K. & NELSON, O. L. (2012). Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy* **93**, 540–546.
- \*RÖDEL, H. G., BORA, A., KAETZKE, P., KHASCHEI, M., HUTZELMEYER, H. & VON HOLST, D. (2004). Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. *Oecologia* **140**, 566–576.
- \*RÖDEL, H. G., STARKLOFF, A., SELTMANN, M. W., PRAGER, G. & VON HOLST, D. (2009). Causes and predictors of nest mortality in a European rabbit population. *Mammalian Biology* **74**, 198–209.
- ROGERS, C. M. (2015). Testing optimal body mass theory: evidence for cost of fat in wintering birds. *Ecosphere* **6**, 1–12.
- \*ROGNMO, A., MARKUSSEN, K. A., JACOBSEN, E., GRAV, H. J. & BLIX, A. S. (1983). Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth, and mortality. *Rangifer* **3**, 10–18.
- ROSENTHAL, R. (1979). The file drawer problem and tolerance for null results. *Psychological Bulletin* **86**, 638–641.
- \*ROTELLA, J. J., CLARK, R. G. & AFRON, A. D. (2003). Survival of female lesser scaup: effects of body size, age, and reproductive effort. *The Condor* **105**, 336–347.
- \*RUSSELL, A. F., BROTHERTON, P. N. M., MCILRATH, G. M., SHARPE, L. L. & CLUTTON-BROCK, T. H. (2003). Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology* **14**, 486–492.
- RUTKOWSKA, J., DUBIEG, A. & NAKAGAWA, S. (2014). All eggs are made equal: meta-analysis of egg sexual size dimorphism in birds. *Journal of Evolutionary Biology* **27**, 153–160.
- \*SAGAR, P. M. & HORNING, D. S. (1998). Mass-related survival of fledgling Sooty shearwaters *Puffinus griseus* at The Snares, New Zealand. *Ibis* **140**, 329–331.
- \*SAMS, M. G., LOCHMILLER, R. L., QUALLS, C. W. J., LESLIE, D. M. J. & PAYTON, M. E. (1996). Physiological correlates of neonatal mortality in an overpopulated herd of white tailed deer. *Journal of Mammalogy* **77**, 179–190.
- SANTOS, E. S. A. & NAKAGAWA, S. (2012). The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology* **25**, 1911–1917.
- \*SCHAUROTH, C. & BECKER, P. H. (2008). Post-fledging body mass increase in common terns *Sterna hirundo*: influence of age, sex and year. *Ibis* **150**, 50–58.
- SCHINDLER, S., GAILLARD, J. M., GRÜNING, A., NEUHAUS, P., TRAILL, L. W., TULJAPURKAR, S. & COULSON, T. (2015). Sex-specific demography and generalization of the Trivers-Willard theory. *Nature* **526**, 249–252.
- \*SCHMUTZ, J. A. (1993). Survival and pre-fledging body mass in juvenile emperor geese. *The Condor* **95**, 222–225.
- SCHULTE-HOSTEDDE, A. I., ZINNER, B., MILLAR, J. S. & GRAHAM, J. H. (2005). Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**, 155–163.
- \*SERRA, L., PIRRELLO, S., CAPRIOLI, M., GRIGGIO, M., ANDREOTTI, A., ROMANO, A., PILASTRO, A., SAINO, N., SACCHI, R., GALEOTTI, P., FASOLA, M., SPINA, F. & RUBOLINI, D. (2012). Seasonal decline of offspring quality in the European starling *Sturnus vulgaris*: an immune challenge experiment. *Behavioral Ecology and Sociobiology* **66**, 697–709.
- \*SETCHELL, J. M., LEE, P. C., WICKINGS, E. J. & DIXSON, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology* **115**, 349–360.
- \*SHAUGHNESSY, P. W., DIGIACOMO, R. F., MARTIN, D. P. & VALERIO, D. A. (1978). Prematurity and perinatal mortality in the rhesus (*Macaca mulatta*): relationship to birth weight and gestational age. *Neonatology* **34**, 129–145.
- \*SHIBATA, F. & KAWAMICHI, T. (2009). Female-biased sex allocation of offspring by an *Apodemus* mouse in an unstable environment. *Behavioral Ecology and Sociobiology* **63**, 1307–1317.
- \*SKIBIEL, A. L., DOBSON, F. S. & MURIE, J. O. (2009). Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* **79**, 325–341.
- SKOGLAND, T. (1984). The effects of food and maternal conditions in fetal growth and size in wild reindeer. *Rangifer* **4**, 39.
- SMITH, C. C. & FRETWELL, S. D. (1974). The optimal balance between size and number of offspring. *The American Naturalist* **108**, 499–506.
- \*SMITH, H., KALLANDER, H. & NILSSON, J.-A. (1989). The trade-off between offspring number and quality in the great tit *Parus major*. *Journal of Animal Ecology* **58**, 383–401.
- \*SNOW, D. W. (1958). The breeding of the Blackbird *Turdus merula* at Oxford. *Ibis* **100**, 1–30.
- \*SOLER, M., PALOMINO, J. & MARTINEZ, J. G. (1994). Activity, survival, independence and migration of fledging great spotted cuckoos. *The Condor* **96**, 802–805.
- \*SOUGHAY, G., GAUTHIER, G. & PRADEL, R. (2013). Temporal variation of juvenile survival in a long-lived species: the role of parasites and body condition. *Oecologia* **173**, 151–160.
- STEARNS, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press, Oxford.
- \*STEINHEIM, G., MYSTERUD, A., HOLAND, Ø., BAKKEN, M. & ADNOY, T. (2002). The effect of initial weight of the ewe on later reproductive effort in domestic sheep (*Ovis aries*). *Journal of Zoology* **258**, 515–520.
- \*STIENEN, E. W. M. & BRENNINKMEIJER, A. (2002). Variation in growth in sandwich tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality. *Ibis* **144**, 567–576.
- STOLESON, S. H. & BEISSINGER, S. R. (1997). Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecological Monographs* **67**, 131–154.
- \*STOPHER, K. V., BENTO, A. I., CLUTTON-BROCK, T. H., PEMBERTON, J. M. & KRULK, L. E. B. (2014). Multiple pathways mediate effects of climate change on maternal reproductive traits in a red deer population. *Ecology* **95**, 3124–3138.
- \*SUEBKAMP WELLS, K. M., RYAN, M. R., MILLSPAUGH, J. J., THOMPSON, F. R. & HUBBARD, M. W. (2007). Survival of postfledging grassland birds in Missouri. *The Condor* **109**, 781.
- \*SULLIVAN, K. A. (1989). Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology* **58**, 275–286.
- \*TAILLON, J., BRODEUR, V., FESTA-BIANCHET, M. & CÔTÉ, S. D. (2012). Is mother condition related to offspring condition in migratory caribou (*Rangifer tarandus*) at calving and weaning? *Canadian Journal of Zoology* **90**, 393–402.

- TAVECCHIA, G., COULSON, T., MORGAN, B. J. T., PEMBERTON, J. M., PILKINGTON, J. C., GULLAND, F. M. D. & CLUTTON-BROCK, T. H. (2005). Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology* **74**, 201–213.
- TIDIÈRE, M., GAILLARD, J. M., BERGER, V., MÜLLER, D. W. H., BINGAMAN LACKEY, L., GIMENEZ, O., CLAUSS, M. & LEMAÎTRE, J. F. (2016). Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific Reports* **6**, 36361.
- \*TOBEY, J. R., ANDRUS, C. H., DOYLE, L., THOMPSON, V. D. & BERGOVITCH, F. B. (2006). Maternal effort and joey growth in koalas (*Phascolarctos cinereus*). *Journal of Zoology* **268**, 423–431.
- \*TODD, L. D., POULIN, R. G., WELLCOME, T. I. & BRIGHAM, R. M. (2003). Post-fledging survival of burrowing owls in Saskatchewan. *Journal of Wildlife Management* **67**, 512–519.
- \*TRAYLOR, J. J. & ALISAUSKAS, R. T. (2006). Effects of intrinsic and extrinsic factors on survival of white-winged scoter (*Melanitta fusca deglandi*) ducklings. *The Auk* **123**, 67–81.
- TRIVERS, R. L. & WILLARD, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–92.
- \*VAN DER JEUGD, H. & LARSSON, K. (1998). Pre-breeding survival of barnacle geese *Brantha leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology* **67**, 953–966.
- \*VAN VUREN, D. H., BRAY, M. P. & HELTZEL, J. M. (2013). Differential investment in twin offspring by female pronghorns (*Antilocapra americana*). *Journal of Mammalogy* **94**, 155–161.
- \*VERBOVEN, N. & VISSER, M. E. (1998). Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* **81**, 511–524.
- VIECHTBAUER, W. (2010). Conducting meta-analyses in R with the metafor Package. *Journal of Statistical Software* **36**, 1–48.
- \*VITZ, A. C. & RODEWALD, A. D. (2011). Influence of condition and habitat use on survival of post-fledging songbirds. *The Condor* **113**, 400–411.
- \*WALLING, C. A., NUSSEY, D. H., MORRIS, A., CLUTTON-BROCK, T. H., KRUIK, L. E. & PEMBERTON, J. M. (2011). Inbreeding depression in red deer calves. *BMC Evolutionary Biology* **11**, 318.
- WARREN, J. T., MYSTERUD, I. & LYNNEBAKKEN, T. (2001). Mortality of lambs in free-ranging domestic sheep (*Ovis aries*) in northern Norway. *Journal of Zoology* **254**, 195–202.
- \*WAUTERS, L., BIJNENS, L. & DHONDT, A. A. (1993). Body mass at weaning and juvenile recruitment in the red squirrel. *Journal of Animal Ecology* **62**, 280–286.
- \*WEIMERSKIRCH, H., BARBRAUD, C. & LYS, P. (2000). Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. *Ecology* **81**, 309–318.
- \*WHEATLEY, K. E., BRADSHAW, C. J. A., DAVIS, L. S., HARCOURT, R. G. & HINDELL, M. A. (2006). Influence of maternal mass and condition on energy transfer in Weddell seals. *Journal of Animal Ecology* **75**, 724–733.
- \*WHITE, G. C., GARROTT, R. A., BARTMANN, R. M. & CARPENTER, L. H. (1987). Survival of mule deer in northwest Colorado. *Journal of Wildlife Management* **51**, 852–859.
- \*WHITE, C. G., ZAGER, P. & GRATSON, M. W. (2010). Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management* **74**, 355–369.
- \*WHITTEN, K., GARNER, G., MAUER, F. & HARRIS, R. (1992). Productivity and early calf survival in the Porcupine caribou herd. *Journal of Wildlife Management* **56**, 201–212.
- \*WIENS, J. D., NOON, B. R. & REYNOLDS, R. T. (2006). Post-fledging survival of northern Goshawks: the importance of prey abundance, weather, and dispersal. *Ecological Applications* **16**, 406–418.
- WIGGINS, D. A. (1990). Sources of variation in egg mass of tree swallows *Tachycineta bicolor*. *Ornis Scandinavica* **21**, 157.
- WILDER, S. M., RAUBENHEIMER, D. & SIMPSON, S. J. (2016). Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Functional Ecology* **30**, 108–115.
- \*WILLIAMS, T. D. & CROXALL, J. P. (1991). Chick growth and survival in gentoo penguins (*Pygoscelis papua*): effect of hatching asynchrony and variation in food supply. *Polar Biology* **11**, 197–202.
- \*WILSON, A. J., PILKINGTON, J. G., PEMBERTON, J. M., COLTMAN, D. W., OVERALL, A. D. J., BYRNE, K. A. & KRUIK, L. E. B. (2005). Selection on mothers and offspring: whose phenotype is it and does it matter? *Evolution* **59**, 451–463.
- WRIGHT, J. & COTTON, P. A. (1994). Experimentally induced sex differences in parental care: an effect of certainty of paternity? *Animal Behaviour* **47**, 1311–1322.
- YAPI, C. V., BOYLAN, W. J. & ROBINSON, R. A. (1990). Factors associated with causes of preweaning lamb mortality. *Preventive Veterinary Medicine* **10**, 145–152.
- YLÖNEN, H., HORNE, T. J. & LUUKKONEN, M. (2004). Effect of birth and weaning mass on growth, survival and reproduction in the bank vole. *Evolutionary Ecology Research* **6**, 433–442.
- ZEVELOFF, S. I. & BOYCE, M. S. (1980). Parental investment and mating systems in mammals. *Evolution* **34**, 973–982.

## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Data used for the analysis of the relationship between offspring body mass and offspring survival in mammals.

**Appendix S2.** Data used for the analysis of the relationship between offspring body mass and offspring survival in birds.

**Appendix S3.** Data used for the analysis of the relationship between maternal mass and offspring mass in mammals.

**Appendix S4.** R code for the extraction of the effect size for the relationship between offspring mass and offspring survival.

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## Chapter III

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# The ‘Evo-Demo’ Implications of Condition-Dependent Mortality

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## Review

## The 'Evo-Demo' Implications of Condition-Dependent Mortality

Victor Ronget,<sup>1,\*</sup> Michael Garratt,<sup>2</sup> Jean-François Lemaître,<sup>1</sup> and Jean-Michel Gaillard<sup>1</sup>

Animals in the wild die from a variety of different mortality sources, including predation, disease, and starvation. Different mortality sources selectively remove individuals with different body condition in different ways, and this variation in the condition dependence of mortality has evolutionary and demographic implications. Subsequent population dynamics are influenced by the strength of condition-dependent mortality during specific periods, with population growth impacted in different ways in short- versus long-lived species. The evolution of lifespan is strongly influenced by condition-dependent mortality, with strikingly different outcomes expected in senescence rates when the relationship between condition and mortality is altered. A coupling of field and laboratory studies is now required to further reveal the evolutionary implications of condition-dependent mortality.

**What Is Condition Dependence?**

Within a given population, individuals display marked differences in phenotype. The most obvious difference occurs in body size, a trait that often varies with a few orders of magnitude within a population. For instance, in a brown bear (*Ursus arctos*) population, newborns are approximately 1200 times lighter than the heaviest adult males. Such individual differences mostly result from differences in age, sex, and population density [1]. However, for a given combination of age, sex, and density, both temporal (i.e., in response to birth date and among-cohort or among-year variation in resources) and spatial (i.e., in response to spatial heterogeneity in resources) variation still occurs in body size among individuals. This residual individual variation in size, mass, or body condition [either assessed directly from physiological measurements (e.g., [2]) or indirectly from the size–mass allometric relationship (e.g., [3])] provides the most commonly used metric in empirical studies of condition dependence. The definition of condition in relation to body mass, size, or broader metrics of individual quality has varied (see Box 1 for a discussion of mean condition and condition dependence in evolutionary ecology) and a general consensus is yet to be reached ([4] versus [5]).

The role of condition in the dynamics of ecological and evolutionary processes has received interest from both theoreticians and empiricists. Condition dependence influences evolutionary processes when individuals of different classes of condition have different reproductive success, because they are either more attractive or more fecund, or have more-viable offspring. Condition dependence has been intensively studied in the context of sexual selection as a process influencing the maintenance of high genetic variance in sexually selected traits (e.g., [4]). In addition, it also provides the mechanism involved in the process of individual

## Trends

Mortality in the wild is strongly influenced by individual condition.

Mortality from predation versus starvation shows different relationships with body mass.

The relative condition dependence of different mortality sources will impact population dynamics and life-history evolution in diverse and even opposing ways.

A coupling of field and laboratory studies is now required to understand the evolutionary implications of condition-dependent selection by different mortality sources.

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#### Box 1. From Condition to Condition Dependence: Definitions and Metrics from Both Empirical and Theoretical Viewpoints

While the term 'condition' has been increasingly used in ecology and evolution over the past 50 years, its use is sometimes vague and can encompass different metrics [5]. From its original definition restricted to the measure of body condition, 'condition' is now used to refer to within or between individual differences in a large range of variables, including state (*sensu* [12]), phenotypic attributes (e.g., age, mass, or size), dominance status, home range quality, resource acquisition, Darwinian fitness, or even genotype (although genotype has never been explicitly considered as a condition metric to the best of our knowledge). Thus, condition is often used as a generic term to rank individuals within a given population along a continuum, from frail individuals at one end to robust individuals at the other end. This continuum of individual quality strongly covaries with individual fitness [13]. In empirical studies that attempt to measure condition in a sample of individuals from a given population, a narrow-sensed definition of condition is required. Clancey and Byers [5] recommend the use of body reserves as a relevant measure of condition in that context. By contrast, when assessing condition dependence in a biological process, such as mortality, from a theoretical viewpoint (as we do here), a broader definition of condition is required. From a theoretical viewpoint, condition-dependent mortality does not refer to any specific trait, but simply corresponds to the amount of variation in mortality risk across individuals. Thus, in the context of condition-independent mortality, when all individuals have the same mortality risk, this means that the individual heterogeneity in mortality is null and mortality occurs randomly. When individual heterogeneity occurs in the mortality risk, frail individuals have a higher mortality risk than robust individuals, leading condition dependence to occur whatever the factor causing differential mortality risk across individuals. Individual heterogeneity in mortality (and in any trait) can be generated by myriad traits, which include all variables that have been interpreted as condition metrics. Given that it is impossible to measure all traits shaping individual heterogeneity in mortality, three main approaches have been used to analyse condition-dependent mortality.

The first approach assumes that the distribution of individual mortality risk matches a distribution of latent condition that cannot be directly measured. The concept of frailty [14] we used here to assess the differential influence of condition-dependent mortality between organisms with slow versus fast pace of life (see Box 2 in the main text) is a classic example of that approach.

A second approach assumes that the focal population corresponds to a mixture of frail and robust individuals, which display different mortality risk. This approach, first proposed by Vaupel and Yashin [11], has been used in experimental evolutionary studies. For instance, in an elegant experiment on *Caenorhabditis elegans*, Lind *et al.* [15] simulated condition-dependent mortality by imposing a heat shock at 40 °C and then varying the time of exposure to obtain low (70 min) and high (110 min) mortality rates; they simulated condition-independent mortality by removing randomly a proportion of worms corresponding to the low and high mortality rates. However, the traits resulting in the highest susceptibility of frail individuals to heat shocks compared with robust individuals were not identified in this study.

A last approach is to identify a priori the best candidate trait to account for observed individual heterogeneity in mortality. Depending on the trait that is selected, this approach can be similar to the first approach. For instance, Rowe and Houle [4] analysed condition-dependent sexual selection by using individual resource acquisition, which cannot be measured in practice. The authors assumed the pool of resources available to a given individual to be strongly and positively correlated with individual fitness, and thereby to latent individual quality and frailty. When measurable traits are selected, this latter approach is often used in empirical studies to test whether body condition is associated to individual mortality risk (see Table 1 in the main text). Trait-based studies have the potential to identify the mechanisms involved in condition-dependent mortality. In that context, condition dependence exactly corresponds to viability selection because the trait distribution will change after mortality will occur [9]. However, trait-based studies cannot provide a reliable way of quantifying condition-dependent mortality in all cases because a strong individual heterogeneity in mortality risk can occur in a given population independently of individual traits (e.g., spatial variation in predation risk).

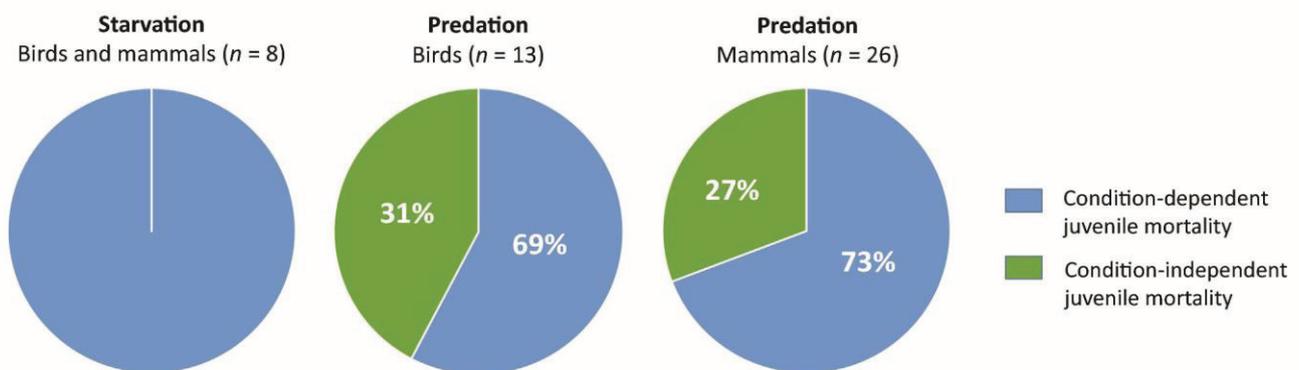
optimization of clutch size [6] and, more recently, a large body of work has pointed out the existence of condition-dependent dispersal (e.g., [7]). Condition dependence in mortality has also been reported in a variety of species [8], but, surprisingly, its ecological, evolutionary, and demographic consequences remain poorly investigated. The role of condition-dependent mortality in shaping trait distribution over time was first recognised by Fisher [9], who coined the term 'viability selection'. As a general rule, for a given sex and age, individuals that are heavy, large, or have good body condition outlive individuals that are light, small, or have poor body condition. This selective disappearance can influence a variety of evolutionary processes, such as population persistence [10] or the strength of senescence [11].

### Evidence for Condition-Dependent Mortality

Condition-dependent mortality has been extensively studied for animals in the juvenile stage. In the wild, juveniles are expected to suffer the highest rate of mortality and, therefore, to be the most susceptible to viability selection [16]. Most studies have shown that body condition is positively linked to juvenile survival in insects [17] and also in birds and mammals [8], leading body condition to be frequently used as a proxy of fitness [13]. However, there are caveats to this use, because the relationship between body condition and fitness is not always straightforward [18]. Sometimes, a positive relationship does not exist and, where it does, the relationship does not account for the complexity of the link between body condition and survival, which can vary in intensity (e.g., strong versus weak) and shape (e.g., linear versus nonlinear) [19]. Moreover, the use of different metrics to measure body condition can also generate variation in the intensity and the shape of condition-dependent mortality [18]. Survival (or mortality) rates offer a general metric to summarise all deaths occurring in a population between two time steps. However, individuals in the wild die from different causes. Besides human-related mortalities, the three major causes of mortality in the wild reported in birds and mammals are predation, starvation (or malnutrition), and disease [20]. The relative importance of each of these causes to the total mortality is highly variable across species, populations, and different age brackets. For instance, juveniles face higher predation risk in some populations than in others and, even within juveniles for a given population, the predation risk varies according to their age [21]. Moreover, different types of mortality occurring in a population usually display different levels of condition-dependent mortality (Figure 1, Table 1). Thus, exposure to different types of mortality is likely to have a major impact on the resultant demographic processes linked to condition-dependent mortality.

### Impact of Body Reserves on Juvenile Survival

Mass-based indices are frequently used to describe condition in birds and mammals [8]. Direct measures of body reserves have also been used (e.g., fat scores in birds [22] and mammals [3]). Given that body reserves allow juveniles to survive over periods of food shortage, a strong link between condition and survival is expected in food limited conditions [23]. High body reserves should be favourable in a low-resource environment because individuals with high reserves can use them to avoid dying from starvation, especially juveniles that have to use resources for not only maintenance but also growth. In this case, we expect a strong link between body condition and the probability of dying from starvation. For individuals dying from malnutrition or starvation (Table 1) and when starvation is the main cause of mortality, juvenile mortality is condition



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Figure 1. Proportion of Studies Reporting Condition-Dependent versus -Independent Juvenile Mortality According to Two of the Main Mortality Factors Occurring in the Wild. We only included studies that tested condition-dependent juvenile mortality and reported the main causes of mortality. For starvation mortality, we combined birds and mammals because the sample size was low and the patterns were similar. All references and the methodology for the iterative research are listed in the supplemental information online.

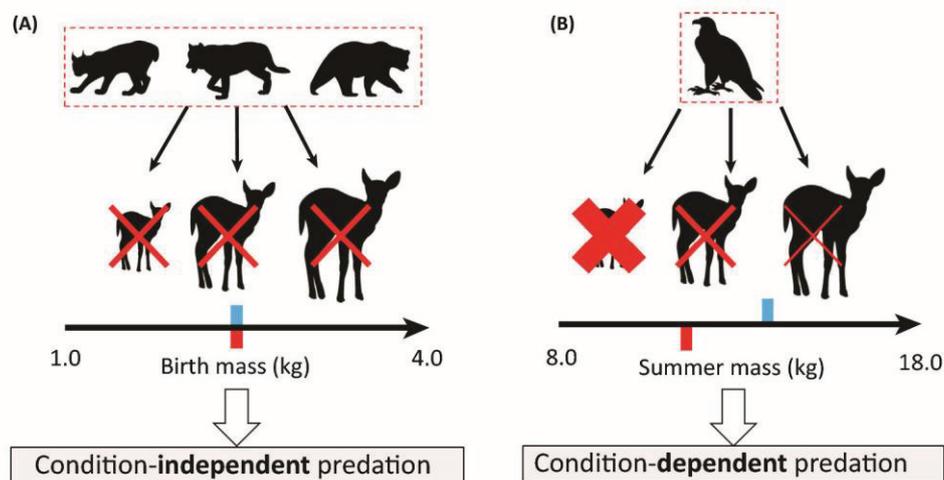
Table 1. Studies of Mortality Cause-Specific Relationships between Body Condition and Mortality of Juveniles in Birds and Mammals

Species	Causes of mortality	Results	Conclusion	Refs
Mammals				
<i>Alces alces</i>	Predation	Lower condition dependence in years when predators are removed	Condition-independent mortality	[26]
<i>Cervus elaphus</i>	Predation	No difference in condition dependence between years with and without predators	Condition-dependent mortality	[27]
		Predated fawns have a lower mass than survivors	Condition-dependent mortality	[28]
<i>Odocoileus hemionus</i>	Malnutrition	Probability of being starved related to mass	Condition-dependent mortality	[21]
	Predation	Probability of being predated unrelated to mass	Condition-independent mortality	
	Predation	No difference in condition dependence between years with and without predators	Condition-dependent mortality	[29]
	Malnutrition	Starved fawns have lower mass than other fawns	Condition-dependent mortality	[30]
	Predation	Predated fawns have same mass as survivors	Condition-independent mortality	
<i>Odocoileus virginianus</i>	Predation	Predated fawns have same mass as survivors	Condition-independent mortality	[31]
<i>Oryctolagus cuniculus</i>	Malnutrition	Probability of suffering from malnutrition mortality related to mass	Condition-dependent mortality	[32]
	Cooling mortality	Probability of suffering from cooling mortality related to mass	Condition-dependent mortality	
	Predation	Probability of being predated unrelated to mass	Condition-independent mortality	
<i>Rangifer tarandus</i>	Predation	Predated fawns have lower mass than survivors	Condition-dependent mortality	[33]
Birds				
<i>Eudypetes chrysolophus</i>	Predation	Intensity of predation pressure has no effect on condition dependence	Condition-independent mortality	[34]
<i>Falco mexicanus</i>	Predation	Predated fledglings have same mass as survivors	Condition-independent mortality	[35]
	Parasitism	Fledglings dying from ectoparasites have lower mass than survivors	Condition-independent mortality	
<i>Cyanistes caeruleus</i>	Predation	Higher condition dependence in years when predators present	Condition-dependent mortality	[36]
		Lower condition dependence in years when predators present	Condition-independent mortality	[37]

dependent (Figure 1). By contrast, in high-resource environments (i.e., no mortality by starvation), mortality is lower and more random [24,25] such that body reserves provide less of a survival advantage. This likely explains why starvation-based mortality has never been reported as condition independent (Table 1). When most mortality events are not attributed to starvation, the relationship between body condition and survival is more difficult to predict.

### Predation, Diseases, Body Condition, and Juvenile Survival

Predation is one of the major causes of mortality in the wild and, unlike starvation mortality, is expected to have a different impact on condition-dependent mortality depending on the '(multi) prey-(multi) predator(s)' system under study. The predator:prey size ratio sets accurate predictions about the strength of condition-dependent mortality, because small predators can handle only small prey, while large predators can handle prey irrespective of their size [38]. For instance, pronghorn (*Antilocapra americana*) fawns are typically heavily preyed upon by coyotes (*Canis latrans*). Coyotes are small predators that cannot handle big individuals, such as adult pronghorn. Thus, they target newborns, which are the most vulnerable individuals [39]. In such cases, there appears to be no selection based on body condition for the young and thus, no condition-dependent mortality. However, selection for reaching the threshold size beyond which juveniles will escape from coyote predation favours faster-growing individuals [40] (Figure 2A). Similarly, in nidicolous birds, chicks are highly dependent on parental feeding and are vulnerable to predators when in the nest, independently of their body condition [41]. Likewise, when individuals are subjected to predation by predators much larger than them, predation is size independent and no size-based selection occurs, also leading to condition-independent predation [42]. In accordance with this prediction, many studies have reported that the probability of juveniles being preyed upon is independent of condition (Table 1). However, as individuals grow, they become less vulnerable to small predators and might even reach a threshold size when they are no longer under threat from these predators. As a consequence, it



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Figure 2. Impact of Predation on Juveniles from Two Populations of Mammals. The thickness of the crosses represents the intensity of predation, the axes represent juvenile mass, the red graduation represents the mean mass of juveniles killed by predators, and the blue graduation represents the mean mass of juveniles that survived. (A) Mule deer (*Odocoileus hemionus*) newborns preyed upon by bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and black bear (*Ursus americanus*) with no selection, which results in condition-independent predation [21]. In this case, there is no selective disappearance and the mean birth mass of juveniles that survived does not differ from the mean mass of juveniles that were killed by predators. (B) Reindeer (*Rangifer tarandus*) juveniles preyed upon by golden eagles (*Aquila chrysaetos*), which cannot handle heavy prey. This results in condition-dependent predation [33]. In this case, the smallest juveniles in summer are more vulnerable to predation, resulting in the mean mass of juveniles killed by eagles to be less than that of surviving juveniles. Such a selective disappearance should lead to an increase in mass of older individuals compared with a population without predation.

has been suggested that condition is a proxy of the time of exposure to a certain predator [43], because small or slow-growing individuals should grow for longer to reach the threshold mass that renders them less vulnerable to predators. However, we can expect condition-dependent predation when some individuals have an advantage in avoiding predators compared with conspecifics of the same age and sex classes by being larger, for example [44] (Figure 2B). This is why some studies suggest that predation on juveniles is sometimes condition dependent (Table 1), and also accounts for several studies that reported condition-dependent juvenile mortality when predation was identified as the main cause of mortality (Figure 1). The impact of body mass on the probability of evading predators has been extensively studied in birds [45,46]. In some cases, high body mass can even be a disadvantage in terms of flight performance, leading the heaviest individuals to have low survival rates. This typically leads to a complex condition-survival relationship, including quadratic effects, in birds (e.g., [47,48]).

Compared with starvation or predation, whether disease-mediated mortality is condition-dependent in free-ranging populations has been less investigated (but note that infection might, in some cases, make juveniles more vulnerable to starvation or predation). The most-detailed studies we compiled revealed that the probability of dying from an infection early in life is related to body condition (Table 1 and [49] for a captive species).

Empirical evidence reported so far shows that different sources of mortality lead to different intensities of condition-dependent mortality. However, in the wild, condition-dependent mortality is most often related to overall mortality because of the difficulty in identifying the exact causes of mortality. Overall mortality is the compound of different competing mortality risks [50]. To know the exact shape of the condition-dependent mortality function, and its resulting evolutionary consequences, we need to assess and then combine the different relationships linking the present mortality causes and condition. However, this requires information on not only the intensity of condition dependence but also the relative importance of mortality causes (Figure 3). This likely explains the occurrence of condition-dependent juvenile mortality found in the literature even when predation is the main cause of mortality (Figure 1). By only considering the main causes of mortality, the effects of minor causes of mortality on condition are lost. For instance, even if predation is condition independent and accounts for most of the juvenile mortality, overall juvenile mortality can be condition dependent if all the minor causes of mortality are condition (dependent Figure 3C).

### Taking into Account Individual Heterogeneity in Population Dynamics

Lomnicki [51] was one of the first to draw the attention of ecologists to the fact that individual heterogeneity (which he called 'individual differences') can strongly influence population dynamics. He made the important but mostly overlooked key point that individual differences should be small when resources are abundant and increase when resources become scarce. His pioneer observation provides a suitable explanation of the higher condition-dependent mortality in food-limited populations (i.e., mortality by starvation) compared with predation-limited populations (Table 1). Despite this early evidence that individual heterogeneity should be accounted for when studying population dynamics, it remained neglected until recently, likely because of a lack of both statistical procedures to handle individual heterogeneity and appropriate empirical data. The development of statistical tools that enable one to account for possible confounding effects of individual heterogeneity when estimating demographic parameters (e.g., [52]) and assessing age dependence in life-history traits (e.g., [53,54]), associated with a concomitant increase in the number of long-term population studies based on individual monitoring (e.g., [55]), have provided a framework to analyse how individual heterogeneity influences population dynamics (Box 1). Thus, while temporal variation in demographic parameters generally has a negative impact on the population growth rate [56], individual heterogeneity can have a positive influence on the population growth rate

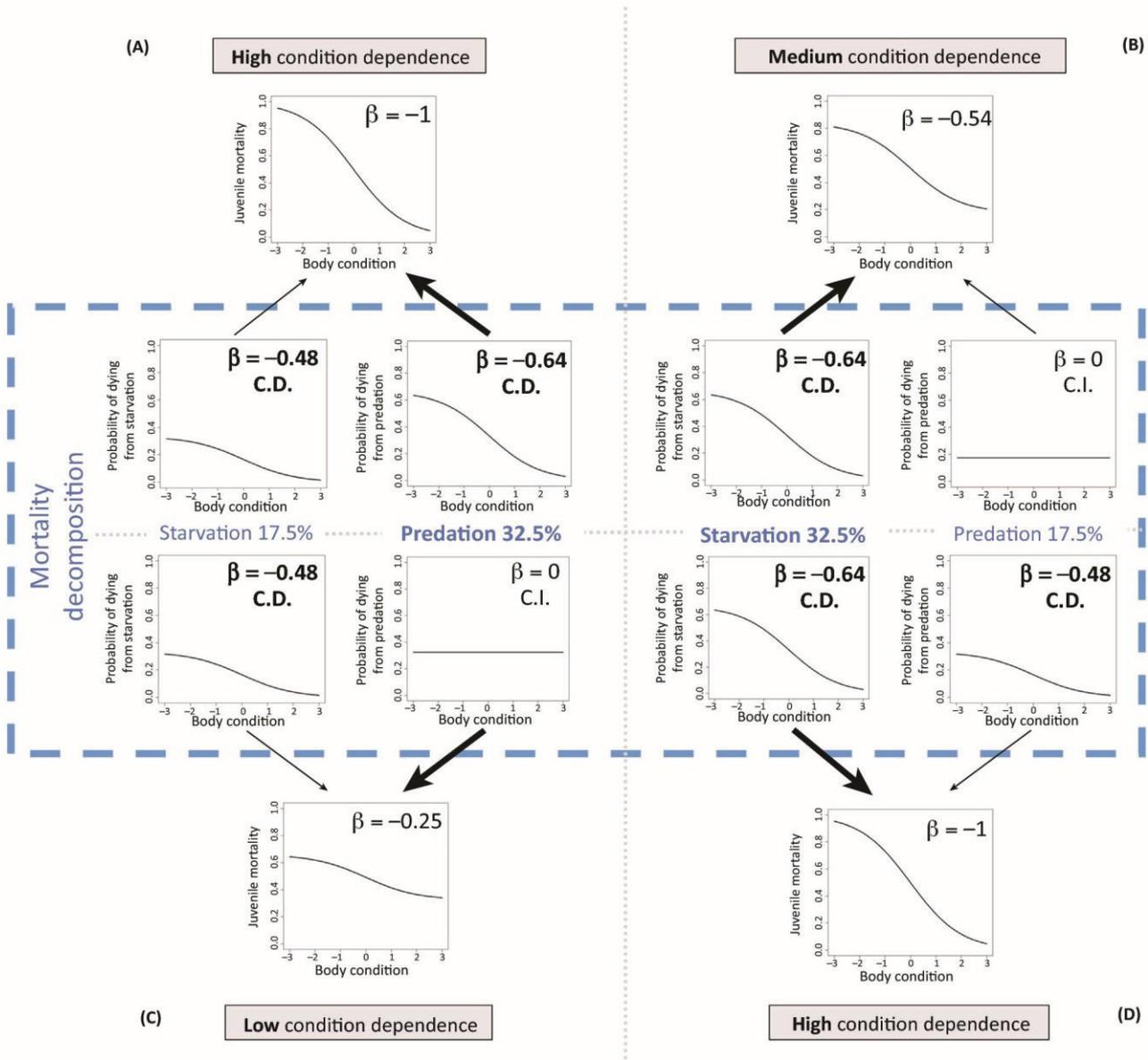


Figure 3. Four Hypothetical Situations Displaying Contrasting Intensity of Condition Dependence on Juvenile Survival in a Population Subjected to the Same Intensity of Mortality but to Differences in the Main Causes of Mortality. In each situation, mortality is caused by a combination of starvation and predation, which are subjected to different condition dependence. (A) Most of the juvenile mortality is due to predation and both causes of mortality are condition dependent. (B) Most of the juvenile mortality is due to starvation and predation is condition independent. (C) Most of the juvenile mortality is due to predation and predation is condition independent. (D) Most of the juvenile mortality is due to starvation and both causes of mortality are condition dependent. For each curve, the slope  $\beta$  of the logistic regression is reported. Abbreviations: C.D. condition-dependent mortality curve; C.I. condition-independent mortality curve.

[57], especially when individual heterogeneity involves condition-dependent mortality (Box 2). There is also clear evidence that the effects of individual heterogeneity on population growth rate and other demographic outputs differ strongly in magnitude in short-versus long-lived species, being more important in short-lived than in long-lived life histories [58] (see Box 2 in the case of condition-dependent mortality). This might explain why observed individual heterogeneity in early adulthood mortality is larger in short-lived than in long-lived species

Box 2. Frailty, Condition Dependence, and Actuarial Senescence

The concept of frailty [14] refers to the heterogeneity in mortality risk among individuals in a population. Each individual is given a frailty value at birth that remains constant throughout its lifespan and measures its mortality risk at a given age relative to the average mortality risk of all individuals in the population at the same age. Thus, an individual with a frailty of 0.5 has a probability of dying twice lower than the average individual in the population and an individual with a frailty of 2 has a probability of dying twice higher than the average individual. Assuming that the frailty value of a given individual is only determined by its body condition, the frailty concept allows the demographic consequences of condition-dependent mortality to be assessed.

To assess the impact of condition dependence on population dynamics, we performed simulations for two life histories (Figure I). We first considered a typical long-lived life history that follows a Gompertz mortality law [with  $\mu(x)$  being the mortality rate at age  $x$ ] according to Equation I:

$$\mu(x) = 0.02e^{0.05x} \quad [I],$$

from 1 year of age onwards, with a mortality of 0.3 during the first year of life. Then, we considered a typical short-lived life history that follows a Gompertz mortality law according to Equation II:

$$\mu(x) = 0.4e^{0.15x} \quad [II],$$

from 1 year of age onwards with a mortality of 0.6 during the first year.

For each life history, we performed 10 000 simulations using three different distributions of frailty [i.e., no frailty, low frailty (using a gamma distribution with  $k = 16$ ), and high frailty (using a gamma distribution with  $k = 4$ )]. The values of  $k$  were chosen so as to obtain a high ( $k = 16$ ) and a low ( $k = 4$ ) variation of frailties among individuals. We displayed the mortality curve for each frailty distribution. For each case, we calculated the 90% longevity of the population, as the age at which 90% of individuals in a given cohort have died (i.e., only 10% of individuals are still alive beyond that age) [62]. We also displayed the stable age structures. These age structures were calculated using age-specific fecundities leading to a stationary population (i.e., a population with  $\lambda$  of 1 for the case with no frailty). We kept the same age-specific fecundities for low- and high-frailty cases to assess the impact of frailty only on survival. For each case the growth rate of the population,  $\lambda$  was calculated.

For the long-lived life history (Figure IA), the increase of frailty has a high impact at old ages. Thus, high frailty increases the proportion of individuals surviving to old age and the longevity of the population, but also decreases the rate of actuarial senescence. Individuals with high frailty (i.e., high mortality risk) die young and only individuals with low frailty (i.e., low mortality risk) reach an old age. However, in our simulation, frailty does not have a great impact on population dynamics, with no major change in the stable age structure or the population growth rate.

For the short-lived life history (Figure IB), the increase of frailty also increases the longevity of the population and decreases the rate of actuarial senescence. However, increasing frailty in the short-lived life history also impacts population dynamics, with a high frailty increasing both population growth rate and the mean age of individuals in the population at equilibrium.

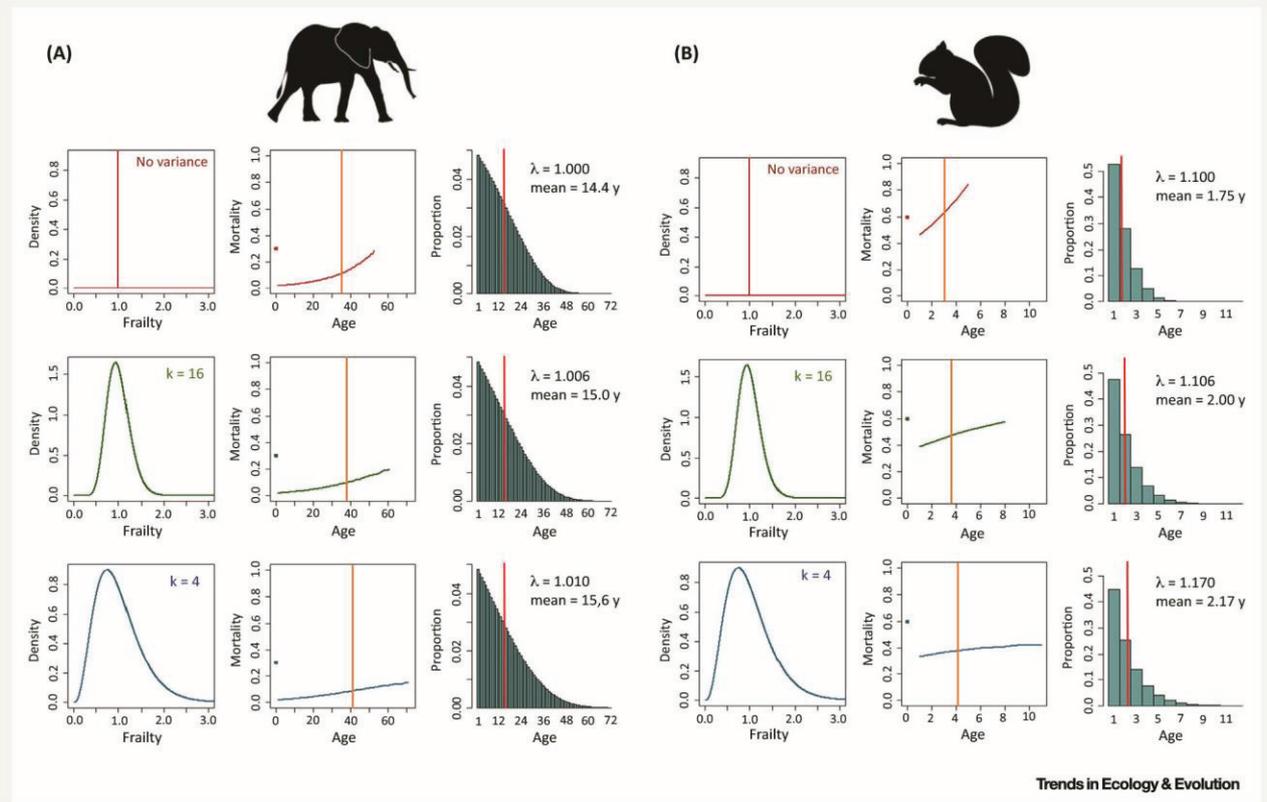


Figure I. Effect of Frailty Distribution (No Frailty, Low Frailty, and High Frailty Variance) on Mortality Curve and Stable Age Structure for Two Life History Cases: (A) Long-Lived Species (B) Short-Lived Species. Orange bars on the mortality curve correspond to the 90% longevity of the population. Red bars on the age structure correspond to the mean age of the age distribution, the exact value of this mean and  $\lambda$  are also given.

[59,60]. However, although condition-dependent mortality does influence population dynamics with differential effects in relation to the life-history type (e.g., species position on the slow–fast continuum), both theoretical and empirical analyses have recently shown that early and compensatory growth are more influential than viability selection in shaping the average individual trajectory of body mass (see [58] for a theoretical analysis based on integral projection models and [61] for an empirical analysis of individual body-mass trajectories of different populations of large herbivores).

### How Does Our Current Theory of Senescence Include Condition-Dependent Mortality?

The evolution of life histories is strongly influenced by the relative vulnerability of individuals at different life stages to mortality. Empirical analyses across species have reported that a high level of random mortality of mature individuals selects for a fast life history [63]. Individuals from such species are expected to allocate resources heavily to reproduction and growth early during life, leading to reduced survival later in life [64–66]. By decreasing the force of natural selection at old age, high adult mortality could also allow mutations that have deleterious effects late in life to accumulate [67], further contributing to faster senescence. At the intraspecific level, the existence of this continuum is unclear and more complex covariation across life-history traits emerges, often in response to individual differences in personality [68,69] and in age-specific mortality risks [70]. There are occasional instances of where environmentally driven mortality may be truly condition-independent: for example in populations of *Daphnia pulex pulicaria* [71] or of the short-lived killifish *Nothobranchius furzeri* [72], which both live in seasonal pools that dry up each year, leading all animals within a drying pool to die irrespective of their phenotype. However, such unambiguous cases involving extreme and condition-independent mortality are rare in the wild.

Our review of condition dependence in juvenile mortality highlights that mortality during the juvenile stage does not often occur randomly in the wild and is usually condition-dependent. It is now acknowledged that the strength of condition dependence in mortality can have a major influence on the evolution of life histories, including senescence rates, and the strength of trade-offs between early and late-life fitness traits. The central tenet is that environmentally driven mortality in the wild is unlikely to occur randomly, but is rather expected to depend on aspects of phenotypic condition. Thus, environmentally driven mortality could select against frail individuals so that individuals with a more robust phenotype will have higher survival prospects [73] (Box 2). These robust individuals might even have a greater potential to allocate more to all competing biological functions than remaining frail individuals, including protection against senescence [74]. Models that allow environmentally driven mortality to be nonrandom can lead to different predictions compared with models of evolution of senescence assuming random mortality. For instance, Abrams [75] showed that, dependent on life stage and its

#### Box 3. Juvenile Mortality and Sex Differences in Senescence

There is an increasing number of studies that show clear sex differences in lifespan and senescence patterns across populations (e.g., [88,89]). How possible sex-specific condition-dependent effects on juvenile mortality can account for sex differences in longevity and senescence patterns has been mostly overlooked (but see [82] for an effect of condition-dependent mortality during adulthood on sex differences in *Caenorhabditis remanei* longevity using an experimental evolutionary approach). However, one recent study performed in two populations of roe deer (*Capreolus capreolus*) suggest that such effects drive the magnitude of sex differences in senescence patterns. In this deer species, sex differences in longevity are more pronounced in individuals born in poor conditions, with females being the long-lived sex [90]. This is likely explained by a sex-specific condition-dependent mortality. In poor cohorts, only robust females survive, whereas there is no such survival advantage in males based on early body condition despite an absence of sex differences in juvenile mortality. Thus, males carry the burden of their poor cohort at the adult stage. For individuals born in good cohorts, there is less of a selective sieve on female robustness and males born in good cohorts perform well for their entire lifespan, causing the sex differences in longevity to vanish.

responsiveness to density dependence, high environmentally driven mortality can lead to the evolution of shorter or longer lifespans. We note that most of the theory on this area was developed for condition dependence in adult mortality. However, because early life conditions have a high impact throughout the entire life of an individual [76], we expect juveniles to be selected for in the same way as adults (i.e., juveniles of high quality *sensu* [13] will become adults of high quality according to the concept of frailty; Box 2). Furthermore, recent evidence suggests that condition-dependent mortality at the juvenile stage can have substantial consequences in terms of sex-differences in senescence (Box 3), although these relationships remain poorly investigated.

The cause of mortality for a particular species and/or population is the major factor that controls the strength of the condition dependence in mortality (Figure 2) and will ultimately influence life-history trade-offs and senescence. As demonstrated by van Noordwijk and de Jong [77], life-history trade-offs must exist in all organisms but do not necessarily show up in the wild at the intraspecific level (i.e., among individuals within a population or among populations within a given species). In particular, these authors showed that the positive association between survival and reproduction or between current and future reproduction only occurs when the variation in resource acquisition is larger than the variation in resource allocation. Condition-dependent mortality will lead individual variation in resource acquisition to change in a complex way. When condition-dependent mortality is nonexistent or weak, large variation in resource acquisition is expected, leading life-history trade-offs to be masked. When condition-dependent mortality is strong, only robust individuals are allowed to survive, causing individual variation in resource acquisition to decrease and the detection of trade-off to become easier.

Predation is the most prominently discussed mortality cause in the literature related to condition-dependent selection pressures and senescence. It is often argued that predators selectively remove slower, poor-quality individuals from a population. In guppies, exposure to high predation in the wild was associated with longer lifespans, and this was coupled with earlier sexual maturation and higher fecundity [78]. However, as we argued previously, predators do not necessarily select individuals with low body condition. Predators can target prey of a given age class (e.g., higher predation rate for juveniles) without necessarily selecting individuals within this age class with a low body condition. While predation acts as a condition-dependent mortality factor in some predator-prey systems, with coursing predators such as wolves that prey mostly upon juveniles, yearlings, and old deer [79], predation could be condition independent in other contexts. For instance, stalking predators such as lynx (*Lynx lynx*) kill weaned roe deer (*Capreolus capreolus*) randomly in relation to age or condition [42]. By contrast, by removing only the frailest individuals of any age class, starvation consistently selects for individuals of high condition, which could lead to an increase in the average lifespan of the population (Box 2).

The implications of changing rates of mortality for the evolution of senescence depend on the age at which the mortality change occurs, on the extent to which the mortality factor is condition-dependent, and on how the viability selection generated by condition-dependent mortality influences the intensity of senescence (through the selection gradient on mortality [80]), independently or not of a higher allocation to growth or reproduction during early life that could occur to compensate the mortality increase [81]. One key laboratory experiment used temperature as a condition-dependent mortality factor, and found the evolution of both longer lifespans and greater fecundity when this type of mortality was high. Such temperature-dependent mortality may directly select for robust individuals based on the underlying physiology that promotes survival, such as heat shock protein expression [74]. Interestingly a similar outcome was found in another laboratory experiment using locomotion and chemosensory

abilities as traits driving condition dependence [82]. We highlight that mortality from predation, starvation, and disease has different relationships to body condition within a given life stage and, therefore, might each select upon physiology involved in the senescence process differently. Starvation, in particular, is strongly related to body condition and, thus, individuals from populations and/or species that are frequently exposed to periods of resource shortage are expected to evolve life histories that will favour longer lifespans and reduced senescence in body mass, thereby moving towards slower life histories. Indeed, in *Drosophila melanogaster*, artificial laboratory selection on starvation resistance led to the evolution of longer lifespans when the mortality source was removed [83,84]. However, whether such selection arises due to trade-offs with reproduction, or is a consequence of condition-dependent selection and improved individual quality, remains difficult to assess in the laboratory because such assays of early life fitness do not easily capture the diversity of components and the variable conditions that influence reproduction in the wild. Comparing situations where trade-offs do versus do not occur offers an elegant way of addressing trade-offs arising from different mortality sources. For example, Chen and Maklakov [74] found that lifetime egg production of *Caenorhabditis remanei* is impacted by the rate of random mortality exerted on a population, but is unaffected by the relative level of condition-dependent (heat shock) mortality. The use of more complex laboratory experiments would help to assess the contexts in which traits influencing early reproduction are altered by a manipulation [85,86]. Competition experiments among divergent genotypes and/or populations using variable food abundance and/or temperature have also been successful in identifying the early life-history cues involved, which might have been masked using simple assays of reproductive output [87].

### Concluding Remarks and Directions for Future Studies

Detailed longitudinal studies of mortality factors in the wild and their evolutionary consequences for population demography are now required to understand how different intensities of condition-dependent juvenile mortality might alter individual survival and reproductive trajectories, and whether this positively or negatively impacts selective pressures on other life-history traits. Laboratory or seminatural experiments that test the effect of different types of mortality at controlled rates on population demography and structure will also be helpful in understanding how the strength of condition-dependent mortality and its changes impact longevity after the condition-dependent mortality sources are removed. By combining these approaches, we hope that the full evolutionary and demographic implications of condition-dependent mortality can be revealed.

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### Supplemental Information

Supplemental information associated with this article can be found online at <http://dx.doi.org/10.1016/j.tree.2017.09.003>.

### References

- Clutton-Brock, T.H. and Harvey, P.H. (1983) The functional significance of variation in body size among mammals. In *Advances in the Study of Mammalian Behavior* (Eisenberg, J.F. and Kleiman, D.G., eds), pp. 632–663, American Society of Mammalogists
- Cook, R.C. *et al.* (2007) Validating predictive models of nutritional condition for mule deer. *J. Wildl. Manag.* 71, 1934–1943
- Schulte-Hostedde, A.I. *et al.* (2005) Restitution of mass-size residuals: validating body condition indices. *Ecology* 86, 155–163
- Rowe, L. and Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. B Biol. Sci.* 263, 1415–1421
- Clancey, E. and Byers, J.A. (2014) The definition and measurement of individual condition in evolutionary studies. *Ethology* 120, 845–854
- Pettifor, R.A. *et al.* (1988) Individual optimization of clutch size in great tits. *Nature* 336, 160–162
- Bonte, D. and De La Peña, E. (2009) Evolution of body condition-dependent dispersal in metapopulations. *J. Evol. Biol.* 22, 1242–1251
- Ronget, V. *et al.* (2017) Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals. *Biol. Rev.* Published online April 9, 2017. <http://dx.doi.org/10.1111/brv.12329>

9. Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press
10. Conner, M.M. and White, G.C. (1999) Effects of individual heterogeneity in estimating the persistence of small populations. *Nat. Resour. Model.* 12, 109–127
11. Vaupel, J.W. and Yashin, A.I. (1985) Heterogeneity ruses – some surprising effects of selection on population dynamics. *Am. Stat.* 39, 176–185
12. McNamara, J.M. and Houston, A.I. (1996) State-dependent life histories. *Nature* 380, 215–221
13. Wilson, A.J. and Nussey, D.H. (2010) What is individual quality? An evolutionary perspective. *Trends Ecol. Evol.* 25, 207–214
14. Vaupel, J.W. *et al.* (1979) The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16, 439
15. Lind, M.J. *et al.* (2017) Slow development as an evolutionary cost of long life. *Funct. Ecol.* 31, 1252–1261
16. Ozgul, A. *et al.* (2009) The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 325, 464–467
17. Chown, S.L. and Gaston, K.J. (2010) Body size variation in insects: a macroecological perspective. *Biol. Rev.* 85, 139–169
18. Wilder, S.M. *et al.* (2016) Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Funct. Ecol.* 30, 108–115
19. Barnett, C.A. *et al.* (2015) Mass-based condition measures and their relationship with fitness: in what condition is condition? *J. Zool.* 296, 1–5
20. Linnell, J.D.C. *et al.* (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildl. Biol.* 1, 209–223
21. Monteith, K.L. *et al.* (2014) Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildl. Monogr.* 186, 1–62
22. Labocha, M.K. and Hayes, J.P. (2012) Morphometric indices of body condition in birds: a review. *J. Ornithol.* 153, 1–22
23. Lack, D. (1966) *Population Studies of Birds*, Oxford University Press
24. Jones, O.R. *et al.* (2005) Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proc. R. Soc. B. Biol. Sci.* 272, 2619–2625
25. Fay, R. *et al.* (2015) Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. *J. Anim. Ecol.* 84, 1423–1433
26. Keech, M.A. *et al.* (2011) Effects of predator treatments, individual traits, and environment on moose survival in Alaska. *J. Wildl. Manag.* 75, 1361–1380
27. White, C.G. *et al.* (2010) Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *J. Wildl. Manag.* 74, 355–369
28. Singer, F.J. *et al.* (1997) Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manag.* 61, 12–25
29. Hurley, M.A. *et al.* (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in south-eastern Idaho. *Wildl. Monogr.* 178, 1–33
30. Bishop, C.J. *et al.* (2005) Mule deer survival among adjacent populations in Southwest Idaho. *J. Wildl. Manag.* 69, 311–321
31. Nelson, T.A. and Woolf, A. (1987) Mortality of white-tailed deer fawns in Southern Illinois. *J. Wildl. Manag.* 51, 326–329
32. Rödel, H.G. *et al.* (2009) Causes and predictors of nest mortality in a European rabbit population. *Mamm. Biol.* 74, 198–209
33. Norberg, H. *et al.* (2006) Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. *Wildl. Biol.* 12, 393–402
34. Horswill, C. *et al.* (2014) Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *J. Anim. Ecol.* 83, 1057–1067
35. McFadzen, M. and Marzluff, J. (1996) Mortality of Prairie Falcons during the fledging-dependence period. *Condor* 98, 791–800
36. Bouwhuis, S. *et al.* (2015) Ecological causes of multilevel covariance between size and first-year survival in a wild bird population. *J. Anim. Ecol.* 84, 208–218
37. Adriaensen, F. *et al.* (1998) Stabilizing selection on blue tit fledgling mass in the presence of sparrowhawks. *Proc. R. Soc. B Biol. Sci.* 265, 1011–1016
38. Sinclair, A.R.E. *et al.* (2003) Patterns of predation in a diverse predator–prey system. *Nature* 425, 288–290
39. Byers, J.A. (1997) *American Pronghorn. Social Adaptations and the Ghosts of Predators Past*, The University of Chicago Press
40. Jacques, C.N. *et al.* (2015) Influence of habitat and intrinsic characteristics on survival of neonatal pronghorn. *PLoS One* 10, e0144026
41. Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *J. Anim. Ecol.* 58, 275–286
42. Andersen, R. *et al.* (2007) Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in roe deer *Capreolus capreolus*. *Wildl. Biol.* 4, 467–474
43. White, C.G. *et al.* (2010) Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *J. Wildl. Manag.* 74, 355–369
44. Genovart, M. *et al.* (2010) The young, the weak and the sick: evidence of natural selection by predation. *PLoS One* 5, 1–5
45. Gosler, A.G. *et al.* (1995) Predation risk and the cost of being fat. *Nature* 377, 621–623
46. Rogers, C.M. (2015) Testing optimal body mass theory: evidence for cost of fat in wintering birds. *Ecosphere* 6, 1–12
47. Verboven, N. and Visser, M.E. (1998) Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81, 511–524
48. Covas, R. *et al.* (2002) Stabilizing selection on body mass in the sociable weaver *Philetairus socius*. *Proc. Biol. Sci.* 269, 1905–1909
49. Yapi, C.V. *et al.* (1990) Factors associated with causes of pre-weaning lamb mortality. *Prev. Vet. Med.* 10, 145–152
50. Heisey, D.M. and Patterson, B.R. (2006) A review of methods to estimate cause-specific mortality in presence of competing risks. *J. Wildl. Manag.* 70, 1544–1555
51. Lomnicki, A. (1978) Individual differences between animals and the natural regulation of their numbers. *J. Anim. Ecol.* 47, 461
52. Marzolin, G. *et al.* (2011) Frailty in state-space models: application to actuarial senescence in the dipper. *Ecology* 92, 562–567
53. van de Pol, M. and Verhulst, S. (2006) Age-dependent traits: a new statistical model to separate within- and between-individual effects. *Am. Nat.* 167, 766–773
54. van de Pol, M. and Wright, J. (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* 77, 753–758
55. Clutton-Brock, T.H. and Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* 25, 562–573
56. Tuljapurkar, S. (1990) Delayed reproduction and fitness in variable environments. *Proc. Natl. Acad. Sci. U. S. A.* 87, 1139–1143
57. Kendall, B.E. *et al.* (2011) Demographic heterogeneity, cohort selection, and population growth. *Ecology* 92, 1985–1993
58. Plard, F. *et al.* (2016) Des différences, pourquoi? Transmission, maintenance and effects of phenotypic variance. *J. Anim. Ecol.* 85, 356–370
59. Caswell, H. (2014) A matrix approach to the statistics of longevity in the gamma-Gompertz and related mortality models. *Demogr. Res.* 31, 553–592
60. Péron, G. *et al.* (2016) Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution* 70, 2909–2914
61. Hamel, S. *et al.* (2016) Cohort variation in individual body mass dissipates with age in large herbivores. *Ecol. Monogr.* 86, 517–543

62. Moorad, J.A. *et al.* (2012) A comparative assessment of univariate longevity measures using zoological animal records. *Aging Cell* 11, 940–948
63. Promislow, D.E.L. (1991) Senescence in natural populations of mammals: a comparative study. *Evolution* 45, 1869
64. Kirkwood, T.B.L. and Rose, M.R. (1991) Evolution of senescence: late survival sacrificed for reproduction. *Philos. Trans. R. Soc. B Biol. Sci.* 332, 15–24
65. Stearns, S.C. (1983) The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41, 173
66. Gaillard, J.M. *et al.* (2017) Senescence in mammalian life history traits. In *The Evolution of Senescence in the Tree of Life*, pp. 126–155, Cambridge University Press
67. Medawar, P.B. (1952) *An Unsolved Problem of Biology*, H. K. Lewis and Co.
68. Careau, V. *et al.* (2009) Exploration strategies map along fast-slow metabolic and life-history continua in muroid rodents. *Funct. Ecol.* 23, 150–156
69. Nakayama, S. *et al.* (2017) Fast-slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *J. Anim. Ecol.* 86, 192–201
70. Martin, T.E. (2015) Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* 349, 966–970
71. Dudycha, J.L. and Tessier, A.J. (1999) Natural genetic variation of life span, reproduction, and juvenile growth in *Daphnia*. *Evolution* 53, 1744
72. Terzibasi Tozzini, E. *et al.* (2013) Parallel evolution of senescence in annual fishes in response to extrinsic mortality. *BMC Evol. Biol.* 13, 77
73. Williams, P.D. and Day, T. (2003) Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution* 57, 1478
74. Chen, H.Y. and Maklakov, A.A. (2012) Longer life span evolves under high rates of condition-dependent mortality. *Curr. Biol.* 22, 2140–2143
75. Abrams, P.A. (1993) Does increased mortality favor the evolution of more rapid senescence? *Evolution* 47, 877
76. Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends Ecol. Evol.* 14, 343–348
77. van Noordwijk, A.J. and de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* 128, 137–142
78. Reznick, D.N. *et al.* (2004) Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* 431, 1095–1099
79. Wright, G.J. *et al.* (2006) Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manag.* 70, 1070–1078
80. Hamilton, W.D. (1966) The moulding of senescence by natural selection. *J. Theor. Biol.* 12, 12–45
81. Shokhirev, M.N. and Johnson, A.A. (2014) Effects of extrinsic mortality on the evolution of aging: a stochastic modeling approach. *PLoS One* 9, e86602
82. Chen, H.Y. and Maklakov, A.A. (2014) Condition dependence of male mortality drives the evolution of sex differences in longevity. *Curr. Biol.* 24, 2423–2427
83. Rose, M.R. *et al.* (1992) Selection on stress resistance increases longevity in *Drosophila melanogaster*. *Exp. Gerontol.* 27, 241–250
84. Hoffmann, A.A. and Harshman, L.G. (1999) Desiccation and starvation resistance in *Drosophila*: patterns of variation at the species, population and intrapopulation levels. *Heredity (Edinb)* 83, 637–643
85. Garratt, M. *et al.* (2014) Superoxide dismutase deficiency impairs olfactory sexual signaling and alters bioenergetic function in mice. *Proc. Natl. Acad. Sci. U. S. A.* 111, 8119–8124
86. Long, T.A.F. *et al.* (2012) The effect of sexual selection on offspring fitness depends on the nature of genetic variation. *Curr. Biol.* 22, 204–208
87. Lithgow, G.J. *et al.* (2000) Evolution of lifespan in *C. elegans*. *Nature* 405, 296–297
88. Clutton-Brock, T. and Isvaran, K. (2007) Sex differences in ageing in natural populations of vertebrates. *Proc. R. Soc. B Biol. Sci.* 274, 3097–3104
89. Tidière, M. *et al.* (2015) Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. *Evolution* 69, 3123–3140
90. Garratt, M. *et al.* (2015) High juvenile mortality is associated with sex-specific adult survival and lifespan in wild roe deer. *Curr. Biol.* 25, 759–763

## Supplemental Materials

### Appendix 1

We used the keywords “mass or weight or size” and “survival or mortality” in ISI *Web of Science* to identify the studies testing condition-dependent juvenile mortality. We found 236 studies and read all these papers to select only studies where the main cause of mortality was explicitly reported. We ended up with 47 studies testing the relationship between body condition and juvenile mortality and reporting starvation or predation as the main cause of mortality (Figure 1).

### Appendix 2

#### *Studies with starvation as main cause of juvenile mortality*

##### *Birds*

- 1 Davies, N.B. (1986) Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledging. *J. Anim. Ecol.* 55, 123–138
- 2 Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeotus*). *J. Anim. Ecol.* 58, 275–286
- 3 Overskaug, K. *et al.* (1999) Fledgling Behavior and Survival in Northern Tawny Owls. *Condor* 101, 169–174

##### *Mammals*

- 1 Keech, M.A. *et al.* (2000) Life-history consequences of maternal condition in Alaskan moose. *J. Wildl. Manage.* 64, 450

- 2 Hoffman, J.I. *et al.* (2006) No relationship between microsatellite variation and neonatal fitness in Antarctic fur seals, *Arctocephalus gazella*. *Mol. Ecol.* 15, 1995–2005
- 3 Yapi, C. V *et al.* (1990) Factors associated with causes of preweaning lamb mortality. *Prev. Vet. Med.* 10, 145–152
- 4 Mandal, A. *et al.* (2007) Factors associated with lamb mortalities in Muzaffarnagari sheep. *Small Rumin. Res.* 71, 273–279
- 5 Taillon, J. *et al.* (2006) The Effects of Decreasing Winter Diet Quality on Foraging Behavior and Life-History Traits of White-Tailed Deer Fawns. *J. Wildl. Manage.* 70, 1445–1454

### *Studies with predation as main cause of juvenile mortality*

#### *Bird*

- 1 Horswill, C. *et al.* (2014) Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *J. Anim. Ecol.* 83, 1057–1067
- 2 Vitz, A.C. and Rodewald, A.D. (2011) Influence of condition and habitat use on survival of post-fledging songbirds. *Condor* 113, 400–411
- 3 Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeotus*). *J. Anim. Ecol.* 58, 275–286
- 4 Todd, L.D. *et al.* (2003) Post-fledging survival of burrowing owls in Saskatchewan. *J. Wildl. Manage.* 67, 512–519
- 5 Suedkamp wells, K.M. *et al.* (2007) Survival of postfledging grassland birds in Missouri. *Condor* 109, 781

- 6 Naef-daenzer, B. and Nuber, M. (2001) Differential post fledging survival of great and coal tits in relation to their condition and fledging date. *J. Anim. Ecol.* 70, 730–738
- 7 Martín, C.A. *et al.* (2007) Sex-biased juvenile survival in a bird with extreme size dimorphism, the great bustard *Otis tarda*. *J. Avian Biol.* 38, 335–346
- 8 McFadzen, M. and Marzluff, J. (1996) Mortality of Prairie Falcons during the fledging-dependence period. *Condor* 98, 791–800
- 9 Keedwell, R.J. (2003) Does fledging equal success? Post-fledging mortality in the Black-fronted Tern. *J. F. Ornithol.* 74, 217–221
- 10 Robles, H. *et al.* (2007) No effect of habitat fragmentation on post-fledging, first-year and adult survival in the middle spotted woodpecker. *Ecography (Cop.)*. 30, 685–694
- 11 Yackel Adams, A.A. *et al.* (2006) Modeling Post-Fledging Survival of Lark Buntings in Response To Ecological and Biological Factors. *Ecology* 87, 178–188
- 12 Berkeley, L.I. *et al.* (2007) Postfledging survival and movement in dickcissels (*Spiza americana*): Implications for habitat management and conservation. *Auk* 124, 396–409
- 13 Anders, A.D. *et al.* (1997) Juvenile survival in a population of neotropical migrant birds. *Conserv. Biol.* 11, 698–707

### *Mammals*

- 1 Whitten, K. *et al.* (1992) Productivity and early calf survival in the Porcupine caribou herd. *J. Wildl. Manage.* 56, 201–212
- 2 Adams, L.G. (2005) Effects of maternal characteristics and climatic variation on birth masses of alaskan caribou. *J. Mammal.* 86, 506–513
- 3 Barber-Meyer, S.M. *et al.* (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildl. Monogr.* 169, 1–30

- 4 Bishop, C.J. *et al.* (2009) Effect of enhanced nutrition on mule deer population rate of change. *Wildl. Monogr.* 177, 1–28
- 5 Carstensen, M. *et al.* (2009) Survival, birth Characteristics, and cause-specific mortality of white-tailed deer neonates. *J. Wildl. Manage.* 73, 175–183
- 6 Chitwood, M.C. *et al.* (2015) Do biological and bedsite characteristics influence survival of neonatal white-tailed deer? *PLoS One* 10, 1–14
- 7 Dahle, B. *et al.* (2006) Correlates with body size and mass in yearling brown bears (*Ursus arctos*). *J. Zool.* 269, 273–283
- 8 Donadio, E. *et al.* (2012) Juvenile and adult mortality patterns in a vicuna (*Vicugna vicugna*) population. *J. Mammal.* 93, 1536–1544
- 9 Dunbar, M.R. *et al.* (1999) Health Evaluation of a Pronghorn Antelope Population in Oregon. 35, 496–510
- 10 Griffin, K.A. *et al.* (2011) Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *J. Anim. Ecol.* 80, 1246–1257
- 11 Gustafson, L.L. *et al.* (1998) Predicting early mortality of newborn guanacos by birth mass and hematological parameters: A provisional model. *J. Wildl. Manage.* 62, 24–35
- 12 Hurley, M. a. *et al.* (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildl. Monogr.* DOI: 10.1002/wmon.4
- 13 Jacques, C.N. *et al.* (2015) Influence of Habitat and Intrinsic Characteristics on Survival of Neonatal Pronghorn. *PLoS One* 10, e0144026
- 14 Jenkins, K.J. and Barten, N.L. (2005) Demography and decline of the Mentasta caribou herd in Alaska. *Can. J. Zool.* 83, 1174–1188
- 15 Keech, M.A. *et al.* (2011) Effects of predator treatments, individual traits, and environment on moose survival in Alaska. *J. Wildl. Manage.* 75, 1361–1380

- 16 Mabile, G. and Berteaux, D. (2014) Hide or die: use of cover decreases predation risk in juvenile North American porcupines. *J. Mammal.* 95, 992–1003
- 17 Monteith, K.L. *et al.* (2014) Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildl. Monogr.* 186, 1–62
- 18 Nelson, T.A. and Woolf, A. (1987) Mortality of White-Tailed Deer Fawns in Southern Illinois. *J. Wildl. Manage.* 51, 326–329
- 19 Norberg, H. *et al.* (2006) Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. *Wildlife Biol.* 12, 393–402
- 20 Reading, R.P. *et al.* (2009) Argali lamb (*Ovis ammon*) morphometric measurements and survivorship in Mongolia. *Mammalia* 73, 98–104
- 21 Singer, F.J. *et al.* (1997) Density Dependence, Compensation, and Environmental Effects on Elk Calf Mortality in Yellowstone National Park. *J. Wildl. Manage.* 61, 12–25
- 22 Tveraa, T. *et al.* (2003) An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Oecologia* 137, 370–376
- 23 Unsworth, J.W. *et al.* (1999) Mule Deer Survival in Colorado, Idaho, and Montana. *J. Wildl. Manage.* 63, 315
- 24 Warren, J.T. *et al.* (2001) Mortality of lambs in free-ranging domestic sheep (*Ovis aries*) in northern Norway. *J. Zool.* 254, 195–202
- 25 White, C.G. *et al.* (2010) Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *J. Wildl. Manage.* 74, 355–369
- 26 White, G.C. *et al.* (1987) Survival of mule deer in northwest Colorado. *J. Wildl. Manage.* 51, 852–859

## Chapter IV

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# How does female body mass influence reproduction in mammals?

**A version of this chapter is in preparation for submission:**

**Ronget, V., Lemaître, J.-F., Coulson, T. & Gaillard, J.-M.** How does female body mass variation influence reproduction in mammals?

## 1. Abstract

Reproductive success is highly variable between among females in mammalian populations and strongly influences their population dynamics. Female body mass is a key trait that has been repeatedly reported to influence the different components of reproductive success. As a general rule, heavier females have higher body reserves (in capital breeder species) or better access to high quality resources (in income breeder species) to overcome the cost of reproduction. We thus expect female body mass to influence positively reproductive success. We performed two meta-analyses of the intensity of the relationships between pregnancy rate and female body mass and between litter size and female body mass in mammals. Correcting by the confounding effect of the age of the mother, we found a clear positive effect of mother body mass on both pregnancy rate and litter size. The only factor that we found influencing the intensity was the age of the mother for the pregnancy rate with older mothers being less dependent on their body mass to reproduce than younger ones. Despite the strong assumptions from the literature, the allocation strategy to reproduction did not influence those relationships.

**Keywords:** heterogeneity, litter size, pregnancy, condition, maternal allocation

## 2. Introduction

In animal populations, individuals differ in their demographic rates. Some individuals perform better either by having a higher reproductive rate or a lower mortality risk, or both (Gaillard *et al.* 2000). Such differences in reproduction or survival can be partly explained by differences in condition among individuals because condition is a proxy for body reserves (Ronget *et al.* 2018). As expected, individuals with higher condition display higher early survival (Ronget *et al.* 2017). However, despite the accumulation of case studies that tested the relationship between condition and reproductive metrics in mammals (Cook *et al.* 2004; Simard *et al.* 2014; Borowik *et al.* 2016), no study has yet evaluated the general impact of condition on reproductive traits across mammalian species.

The fecundity rate is often defined as the number of offspring produced per female per reproductive attempt (Leslie & Ranson 1940). This fecundity rate is thus influenced by both pregnancy rate and the number of individuals produced at birth (*i.e.* litter size in mammals) by a reproductive female. Mammalian females can either produce one offspring (monotocous) or

multiple offspring (polytocous) per reproductive event. Hence, to draw the general pattern between body condition and reproductive output, we performed the meta-analyses of the relationship between the female body condition and the probability to be pregnant for all mammalian species and of the relationship between mother mass and litter size only for polytocous mammals. The relationship between body condition and pregnancy rate has been largely studied in mammals (Albon *et al.* 1983; Boyd 2000; Gaskins *et al.* 2005). A positive relationship is expected because females with higher body condition have higher body reserves (Schulte-Hostedde *et al.* 2001) and have more energy to allocate to reproduction (Gittleman & Thompson, 1988). The role of the energy reserves is especially important for female mammals because they face high energetic costs during the late gestation and early lactation stages (Sadleir 1969; Gittleman & Thompson 1988; Clutton-Brock *et al.* 1989).

As almost all mammalian species are iteroparous (i.e. have repeated reproductive events throughout their lifetime), they need to trade their energy allocation between current reproduction and survival to the next reproductive event (Clutton-Brock *et al.* 1989). It has been described that mammalian species have different strategies when it comes to reproductive allocation. We can describe two types of opposite strategies. First some species cover the cost of reproduction (pregnancy and gestation) using their own accumulated reserves, those species are called capital breeders. At the opposite some species cover the cost of reproduction using only their food intake with no uses of their individual reserves, they are called income breeders (Jönsson 1997). If body mass is a reliable proxy of the capital of a female, we thus expect the intensity of the relationship between reproduction and body mass to be weaker for income breeders. These different allocation strategies between species could explain why some studies lacked to detect any positive association between maternal mass and pregnancy rate (i.e. Boyd 2000 for the Antarctic fur seal).

The relationship between female body mass and number of offspring produced at a given reproductive event has also been intensively studied, not only in mammals but in a large range of species, notably in the context of the trade-off between offspring size and number (Lim *et al.* 2014). Although, the number of offspring produced at a given reproductive event should increase with female mass because heavier females store higher energetic reserves (in capital breeders) or have access to higher quality resources (in income breeders) (Andersen *et al.* 2000), which leads them to allocate a higher absolute amount of energy to reproduction and thereby to raise successfully more offspring (Fokidis *et al.* 2007; MacLeod *et al.* 2015). As well as the previous relationship we expect the allocation strategy to be a major driver

shaping the relationship linking litter size and mother body mass which could explain why some studies did not report any effect of body mass on litter size (Gonzalez *et al.* 2012; Paronis *et al.* 2015).

All studies seeking to evaluate the effect of female body mass on pregnancy rate and body condition face a major issue. Individual differences in female body mass do not only reflect differences in body reserves but also come from differences in age. Mammalian females typically start reproducing prior to the end of their growth period (*e.g.* when about 80% of asymptotic adult mass is reached in most large herbivores (Servanty *et al.* 2007)) and lighter reproductive females are most likely primiparous. Thus, young primiparous females are expected to have lower pregnancy rates than older multiparous females (Côté & Festa-Bianchet 2001). We should then expect a positive relationship between pregnancy rate and maternal mass even when variation in maternal body mass is less related to the amount of energy reserves, like in income breeders. In such a situation, body mass rather corresponds to an index of maturity. The same confounding effect is expected to arise for the relationship between litter size and mother body mass. As a general rule, primiparous females of mammals are younger and lighter than multiparous ones, and generally also have lower litter size than older heavier multiparous females (Dobson & Michener 1995; Packer *et al.*, 1998; Sherman & Runge 2002). Consequently, we expected a positive effect of body mass on litter size to occur. However, only reproductive females, that are more likely to be old, are considered when measuring litter size which are more likely to be old, so that age should be less influential on litter size than on pregnancy rates. The simplest way to account for this confounding effect is to describe the relationships only for some age class for instance for primiparous individuals or multiparous individuals (Reimers 1983; Gedir & Michener 2014). One other way is to add also age as a covariate of the relationship (Hamel *et al.* 2012). With those age corrected relationships, we can thus decipher if the body mass influences reproduction independently of age or if only age influences reproduction.

Although body mass should positively influence reproductive traits, empirical studies performed so far have reported contrasting patterns and there is to date no clear consensus on how maternal body mass influences female reproductive success. To fill this knowledge gap, we performed four phylogenetically-corrected meta-analyses of the relationships between female body mass and the probability to be pregnant corrected or not by age and between female body mass and litter size corrected or not by age. We aimed to get the average effect of female body mass on each of these two major reproductive traits and to decipher whether

this effect is independent of age or not. Moreover, we looked for testing whether the large variation observed in reproductive traits among females both within and across mammalian species can be related to some explanatory factors such as species-specific traits such as the reproductive strategy or the impact of environmental conditions.

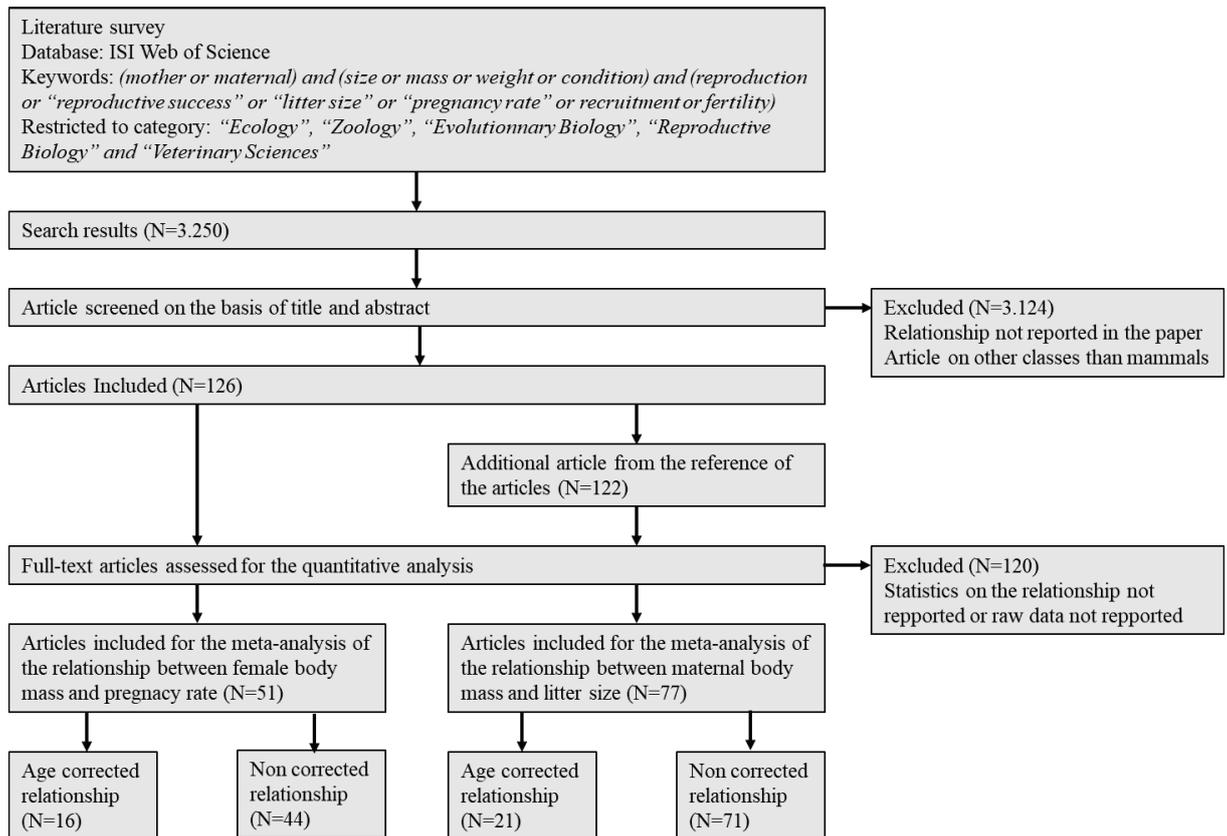
### 3. Material and Methods

#### *Literature search*

We first collected published papers for the meta-analysis by performing a bibliographic research in ISI Web of Science. We used the following keywords: "(mother or maternal) and (size or mass or weight or condition) and (reproduction or “reproductive success” or “litter size” or “pregnancy rate” or recruitment or fertility)" and restricted the results to the category “*Ecology*”, “*Zoology*”, “*Evolutionary Biology*”, “*Reproductive Biology*” and “*Veterinary Sciences*”. The search was performed in April 2018 and we ended up with 3,250 articles. The results were screened based on the title and on the abstract of each retrieved paper, and papers were excluded when the relationship between pregnancy rate or litter size and maternal mass was not reported or when the species was not a mammal. Using this procedure, we ended with 126 papers. As old papers and reports were poorly referenced in this database, we screened all references in the selected papers to identify more studies with the required information. Using this procedure, we added 122 papers to the previous search (Fig. 4.1.).

We then screened all the papers to get the information needed for the analysis. For the relationship between pregnancy rate and maternal mass we looked for a relationship including the probability to be pregnant, or when not reported, the probability to give birth or the probability to recruit at least one offspring at a given reproductive attempt. To assess female mass, we gave priority to the relationships for which the absolute total body mass of females was reported. When this information was not available, any measurement of body condition was retrieved. For the relationship between litter size and female mass, we looked for any relationship involving the litter size at birth. When this was not possible, we considered the number of embryos or the number of offspring at weaning as a measure of litter size. Some studies reported the relationship for females at different age (e.g. young vs. old mothers,

(Skibieli *et al.*, 2009; Price-Rees *et al.*, 2012)) or added the age of the female as covariate (Hamel *et al.*, 2012). In that case, all those relationships were compiled in different age-corrected dataset. When data were available the relationship corrected by age as well as the relationship non-corrected were added in the two different datasets.



**Figure 4.1.** PRISMA flow diagram (search procedure according to the PRISMA statement, (Liberati *et al.* 2009) for the meta-analysis of the relationship between female body mass and pregnancy rate and for the meta-analysis of the relationship between female body mass and litter size.

### Data extraction

The relationship between pregnancy rate and female mass was mostly reported as a logistic regression because of the binomial distribution of the probability to be pregnant. We recorded the slope of the logistic relationship and the associated standard error (SE). Sometimes, this information was not reported explicitly in the paper, and only a figure was provided. We then used WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>) to extract

the data from the figure and ran a logistic regression on the data using the R package "betareg" (Cribari-Neto & Zeileis 2010) to estimate the slope and the SE. Several studies only reported the body mass mean and SE for pregnant vs. non-pregnant females. In that case, we used the same procedure as described in (Ronget *et al.* 2017). We assumed that body mass was normally distributed for both pregnant and non-pregnant females and we performed 1,000 simulations of these mass distributions. We then fitted a logistic regression to each of these 1,000 datasets and averaged the slope and calculated the SE. To compare the female mass-pregnancy rate relationship across mammalian species, we standardized each slope and SE to make studies comparable (Nakagawa & Santos 2012). We then standardized each slope by the SE of the female mass distribution because populations displayed markedly different mass distributions, we did that by multiplying the slope and the SE by the female mass SE, and then got a semi-standardized logistic slope (Menard 2011). When the female mass SE was not reported in the paper, we used the mass range to infer the SE. Assuming that female mass was normally distributed, 95% of the individual masses should rank between  $-1.96*SE$  and  $1.96*SE$ . We thus assumed that the range of female mass in the focal population was equal to the 95% interval for the distribution of mass for the population. The slopes were converted to odd ratio to facilitate the interpretation (Lipsey & Wilson 2001). We did that conversion by taking the exponential of the slope. Hence, an odd ratio of 1 corresponded to a null effect and an odd ratio higher than 1 corresponded to a positive effect. The odd ratio (i.e. the ratio between the probability to be pregnant and the probability to not be pregnant) measures the factor by which the probability to be pregnant would increase in response to an increase by one SE of female body mass.

The relationship between litter size and female body mass was mostly reported as a linear relationship associated with a Pearson correlation coefficient. We thus recorded this correlation coefficient. When the correlation coefficient was not reported in the paper, but raw data were displayed in a figure, we used WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>) to extract the data and ran the function `cor.test` of R (version R.3.4.3, R Development Core Team 2017) on these data. We also used  $\chi^2$ , t and F statistics to estimate correlation coefficients using the formula in (Lipsey & Wilson 2001). In some studies, the distribution of female mass was reported for each litter size. In that case, we considered each distribution as being normally distributed and we performed 1,000 simulations of the mass distributions. We then calculated the average correlation coefficient. The correlation coefficients were converted to a Fisher  $Z_r$  coefficient, which is an unbounded

measure of the effect size for correlation coefficients (Lipsey Wilson 2001). Zr coefficient of 0.1, 0.3 and 0.5 correspond to low, moderate and strong effects, respectively (Cohen 1988).

### *Statistical analysis*

We performed a multi-level meta-analysis because of the non-independence among the different effect sizes. Spurious correlation can arise between effect sizes simply because the effect sizes are estimated from the same species, from closely related species, or from the same population and are analyzed by the same author. We performed a Bayesian linear mixed model for these meta-analyses, which is recommended to handle phylogenetic meta-analysis (Nakagawa & Santos 2012). We used the function MCMCglmm of the package MCMCglmm (Hadfield 2010; Hadfield & Nakagawa 2010) for the analysis.

For each meta-analysis, we fitted a first meta-analysis model with each effect size entered as the dependent variable and no fixed effect to get the overall mean. For each model, the variance of each effect size was implemented using the mev argument in MCMCglmm. We included as random effects the phylogeny and the species name independently of the phylogeny because females from the same species can share characteristics that are independent of the phylogenetic history, the name of the author. To correct for phylogenetic relatedness (Harvey & Pagel 1991), we used a phylogenetic tree for mammals (Bininda-Emonds *et al.*, 2007). From this tree, we extracted the covariance matrix among species, which was used as a random factor. For the age-corrected relationship linking pregnancy rate to mother mass the correction of the phylogeny was not included because of the too low number of species represented (N=9). There was no a priori information, so we used a non-informative prior in our model (Inverse Wishart prior with  $v=0.02$  and  $V=1$ ). Each model was run for 2,000,000 iterations. We assessed the convergence of the model by using the Gelman.diag function in R and we also checked the sensibility of our results to the prior choice by rerunning the models with a parameter expanded prior ( $v=1$ ,  $V=1$ ,  $\alpha.\mu=0$ ,  $\alpha.V=1,000$ ). This analysis did not point out any effect of the prior choice.

For each model, we presented the mean of the posterior distribution associated with the 95% credibility interval of the highest posterior density distribution (HPDI). The  $I^2$  statistics were calculated to quantify the percentage of the total variance explained by each random effect. For each  $I^2$  statistic, 95% credibility intervals were provided.

Meta-analyses are subjected to publication bias because studies with no detectable effect are less likely to be published. This could result in an over-representation of studies with a detectable effect, which could lead to an overestimation of the meta-analysis mean. (Nakagawa & Santos 2012) recommended the use of a funnel plot to diagnose this bias. The funnel plots recommended for meta-analysis with random effects plot the precision of the study (measured as the inverse of the SE) against the residuals of the meta-analysis. In absence of any publication bias residuals should be equally distributed around 0, leading to a symmetric funnel plot. To test the symmetry of the diagram we performed an Egger regression (Egger *et al.* 1997) involving the regression of residuals of the meta-analysis against the precision. When the intercept does not differ from 0 the funnel plot is considered to be symmetrical and there is no publication bias. Otherwise, there is a publication bias. We assessed the importance of this publication bias using the trim and fill method of the package metafor (Viechtbauer 2010). This method allows estimating the strength of the publication bias and provides an estimate of the number of studies lacking in the funnel as well as a correction for the overall mean of the meta-analysis.

As a second step, we fitted the same meta-analysis models by adding moderators as fixed factors to explain the variation observed in the intensity of the relationships. We implemented the following moderators:

- *Capital vs. Income breeder*- As the strategy of allocation is expected to influence the intensities of these relationships we categorized species as Capital or Income breeder (Jönsson 1997). Species were classified as income breeder if there is data in the literature proving that the food intake increase during the pregnancy or lactation and if there is no evidence of decrease in body reserve. Species were classified as capital breeder if there is any evidence that the amount of reserves decrease during gestation or lactation.
- *wild vs. captive population*- As captive females benefit from a safer environment with less resource limitations than their wild counterparts (Tidière *et al.* 2016) they are expected to be less dependent of their body reserves for successful reproduction.
- *body mass measure*- Female body mass could include or not the fetal or litter mass (Boyd 2000). In some studies (N = 37), the period of measurement for female body mass included the gestation time, which leads mother body mass to be overestimated.
- *monotocous vs. polytocous*- As polytocous mammals, but not monotocous ones, can adjust their reproductive output at a given attempt by producing more or less offspring within a

litter; we distinguished between the two groups of mammals in the analysis of pregnancy rate in relation to female body mass.

- *age*- This moderator was only use for the age-corrected relationships. We made three categories ‘All ages’, ‘Young’, and ‘Old’ that corresponded to relationships in which females from all ages were included, only young females were included, or only old females were included, respectively,

## 4. Results

### *Dataset*

A description of the dataset is reported in the table 4.1. There were markedly less studies included and a lower diversity of species for the relationships corrected by age in comparison to the non-corrected relationship.

**Table 4.1.** Number of studies, effect sizes and species included the 4 different meta-analyses. The composition of the different datasets for the three main orders reported in the literature (Artiodactyles, Rodents and Carnivores) is also reported. Phylogenetic trees used in the analysis are presented in the supplementary materials (Fig. S4.1. for the pregnancy rate and maternal mass non-corrected by age relationship, Fig. S4.3. for the litter size and maternal mass non-corrected by age relationship, Fig. S4.4. for the litter size and maternal mass corrected by age relationship)

	Studies included	Effect sizes extracted	Species included	Species of Artiodactyles	Species of Rodents	Species of Carnivores
Pregnancy rate and maternal mass non-corrected by age	44	57	29	10	8	7
Pregnancy rate and maternal mass corrected by age	16	24	9	6	2	0
Litter size and maternal mass non-corrected by age	71	77	51	6	30	7
Litter size and maternal mass corrected by age	21	35	17	2	11	0

### *Relationship between pregnancy rate and maternal mass non-corrected by age*

Pregnancy rates were positively related to maternal mass (mean<sub>meta-analysis</sub> = 2.58, [HPDI= (1.47; 4.37)]). The heterogeneity analysis revealed that the effect of the species independently of the phylogeny did account for a substantial proportion of the total variance compared to the other random effects (close to 40 % for the species effect, Tab. 4.2.). This means that distinct populations from the same species are likely to have similar slope independently of the phylogenetic relatedness. There was no detectable publication bias (Egger regression: intercept=0.18 HPDI= (-0.21;0.58)). The funnel plot was symmetrical (Figure S4.2.A), which indicates that there is no publication bias was. There was no detectable difference in the intensity of the relationship between capital and income breeder, wild and captive populations, between populations where fetal or litter mass was included in or excluded from female mass estimate, or between monotocous and polytocous species (Fig. 4.2.A).

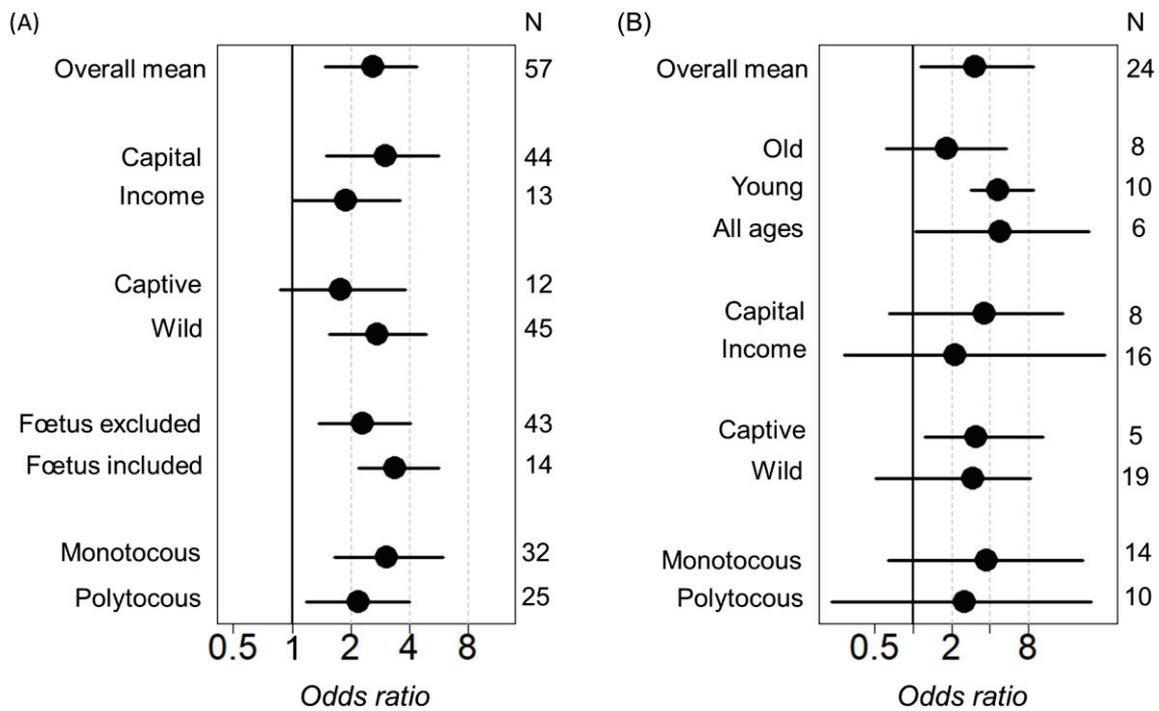
**Table 4.2.**  $I^2$  values associated with each random effect for the relationship between female body mass and pregnancy rate non-corrected by age. For each value (Mean) the lower and the upper high posterior density interval limits of the credibility intervals are reported.

	<b>Mean</b>	<b>Lower HPDI</b>	<b>Upper HPDI</b>
$I^2$ Phylogeny	20.8	0.1	57.0
$I^2$ Species	40.8	0.1	71.7
$I^2$ Author	12.9	0.1	12.9
$I^2$ Residuals	23.6	3.8	52.6

### *Relationship between pregnancy rate and maternal mass corrected by age*

Pregnancy rates were positively related to maternal mass even when the relationship was age-corrected (mean<sub>meta-analysis</sub> = 3.06, [HPDI= (1.14; 8.93)]). We did not present the heterogeneity analysis here as there was not species to interpret these values. There was a detectable publication bias (Egger regression: intercept=0.54 [HPDI=(0.10;0.96)]). The funnel plot was not symmetrical (Fig. S4.2.B), which indicates that there is publication bias was towards positive results. The trim and fill method indicated that 7 studies were lacking on the left side of the funnel plot. The adjusted mean effect size (obtained by removing 0.77 to the estimated value) was 2.29. There was a difference in the intensity of the relationship between

young females and old females with pregnancy rate of older females being little to not influenced by their body mass (mean-difference<sub>old vs young</sub> = 0.9326 [HPDI=(0.43;1.58)]. Aside from this effect, there was no detectable difference in the intensity of the relationship between capital and income breeder, wild and captive populations or between monotocous and polytocous species (Fig. 4.2.B).



**Figure 4.2.** Meta-analysis means for each moderator for the relationship between female body mass and pregnancy rate (A) non-corrected by age or (B) age-corrected. For each group, the means are reported along with their 95% credibility interval.

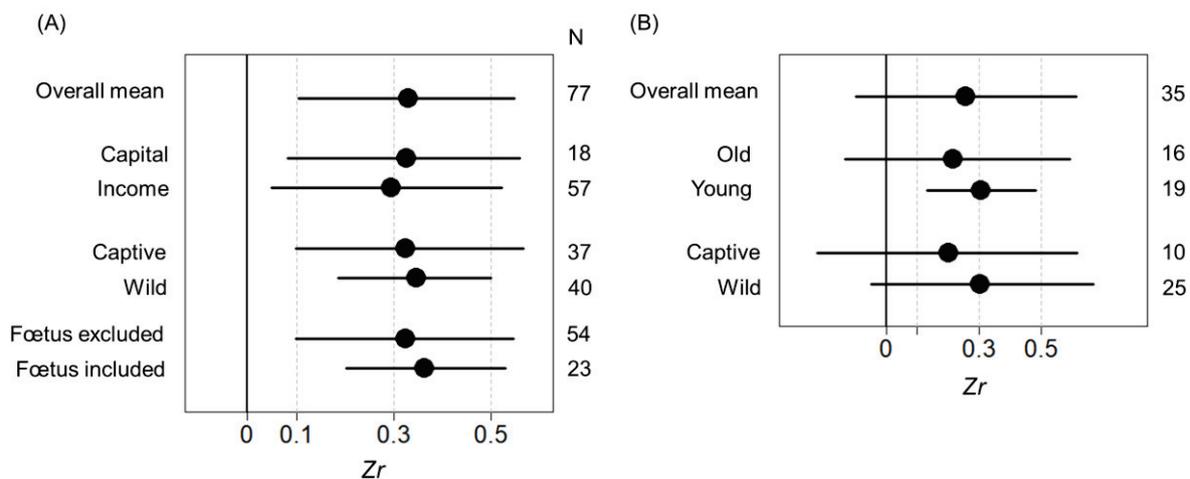
### *Relationship between litter size and maternal mass non-corrected by age*

A positive relationship occurred between litter size and female mass (mean<sub>meta-analysis</sub> = 0.33, HPDI= (0.10; 0.55)). None of the random factors explained a substantial proportion of the total variance (All  $I^2$  close to 25%, Table 4.3.). The funnel plot was symmetrical, which indicated the absence of any publication bias (Fig. S4.5.A) (Egger regression intercept= -0.01 HPDI=(-0.08;0.04)). There was no detectable effect of the allocation strategy on the intensity of the relationship between litter size and female mass (Figure 3B). Likewise, the intensity of

this relationship did not differ between wild and captive populations, nor between studies including or excluding litter mass from the female mass measurement (Fig. 4.3.A).

### *Relationship between litter size and maternal mass corrected by age*

As well as the previous relationship there was markedly less studies included in this dataset. 35 odd ratios were collected from 21 studies. Data were collected for 17 species mostly including the orders of Rodents (11 species) (Fig. S4.4.). When the relationship is corrected by age there was still a positive effect of female body mass on litter size ( $\text{mean}_{\text{meta-analysis}} = 0.26$ ,  $\text{HPDI} = (-0.09; 0.55)$ ) However the 95% credibility interval did overlap the null effect highlighting either a weaker relationship or most likely a weak power of the analysis due to the low sample size. We did not present the heterogeneity analysis because of the low sample size which prevent any valuable interpretation. There was no publication bias detected (Fig. S4.5.B) (Egger regression intercept= 0.02  $\text{HPDI} = (-0.10; 0.14)$ ). There was no effect of the age of the mother on the intensity of the age-corrected relationship and there was no difference between wild and captive populations. Most of the species used in this dataset were considered as income breeders (15 out of 17 species) and foetus mass was excluded for most of the populations (33 out of 35 populations) we thus could not compare the effect of the allocation strategy on this relationship and the effect of including foetus mass. (Fig. 4.3.B).



**Figure 4.3.** Meta-analysis means for each moderator for the relationship between female body mass and litter size (A) non-corrected by age or (B) age-corrected. For each group, the means are reported along with their 95% credibility interval.

**Table 4.3.**  $I^2$  values associated with each random effect for the relationship between female body mass and litter size rate non-corrected by age. For each value (Mean) the lower and the upper high posterior density interval limits of the credibility intervals are reported.

	Mean	Lower HPDI	Upper HPDI
$I^2$ Phylogeny	22.7	2.1	48.1
$I^2$ Species	20.7	2.0	43.5
$I^2$ Author	29.9	2.5	60.0
$I^2$ Residuals	23.6	0.2	54.0

## 5. Discussion

As predicted, the four meta-analyses provided a quite strong support towards a positive effect of female body mass on both studied reproductive traits. However, our analyses highlighted some unexpected variations, which shed new light on the role of female body mass on reproductive output across mammalian populations.

We demonstrated a clear positive effect of female body mass on pregnancy rate. Because we even found a positive effect of body mass when correcting by the confounding effect of mass, we can confirm the intrinsic positive effect of body mass on reproduction. We found that body mass was a major driver of pregnancy rate with both effect size close to 3 for the corrected and non-age corrected relationship meaning that for an increase of 1 standard deviation of female body mass the probability of being pregnant is multiplied by 3. We found that populations from the same species were likely to have similar intensity on the relationship, but we found that those species were not necessarily closely phylogenetically related. For instance, for *Cervus elaphus* we found a mean effect size of 7.21 for 9 populations and for *Ovis aries* we found a mean effect size of 1.40 for 7 populations. To explain these variations, we tried to find some species related characteristics that were not related to the phylogeny.

We predicted that the allocation strategy of the species could explain the variability of the intensity of the relationship between species with for instance capital breeders being really dependent on their reserves which is related to their body mass (Jönsson 1997). However, we did not find any difference between capital and income breeder species in the intensity of the

relationship. This finding highlights the fact that body mass is not only a proxy of individual reserves. For instance, some species because they did not store fat reserves rely heavily on the amount of food intake to make a successful reproduction. However, to increase their food intakes those females need to have access to high quality food (McDonald *et al.*, 2012). However, there is a high competition between individuals for gaining access to high-quality resources and bigger and heavier individuals are thus likely to be favored in the competition for resources (Andersen *et al.*, 2000). Therefore, we can thus consider that body mass is not strictly a proxy of reserves in mammalian females but also a proxy of individual quality in the broader sense (Wilson & Nussey 2010). One other reason that can explain the absence of effect of the strategy allocation is that opposing capital to income breeder is an oversimplification of the reality. The classification of the allocation strategies is more a continuum from capital to income breeder with for instance some intermediate species relying on both reserves and food intake (i.e. *Sus scrofa* (Servanty *et al.* 2007)). As it is difficult to tease apart the amount of energy used for reproduction coming from the reserves or from the food intake (Stephens *et al.* 2009) only two categories are generally considered. Nonetheless classified allocation strategies into two dichotomous categories could be inaccurate to perform a precise comparison of the difference in the relationship between reproduction and body mass for species with different allocation strategies.

When individuals were split by age-classes (i.e. the age effect on body mass was removed), the intensity of the relationship was higher for the young individuals class compared to the adult ones. The reproduction of young individuals is likely to be mostly influenced by resource abundance and quality, which are related to environmental conditions shaped by density population and climatic conditions (Clutton-Brock *et al.*, 1987; Gaillard *et al.*, 2000). Frail young females have much less energy to allocate to reproduction because they still allocate resources to the growth process, which might reinforce the relationship between body mass and pregnancy rate for these females (Borowik *et al.*, 2016). On the contrary prime-aged and old individuals should be less dependent of the quantity of reserve or the quality of their food intake which ultimately results in a weaker relationship. The intensity relationship for older individuals even overlapped the null effect which demonstrate the very weak importance of body mass on the pregnancy rate here. However, we should also be cautious to not generalize to much this result as it based on only 8 populations for old individuals. Contrary to our expectation, there was no difference in the intensity of the female mass-pregnancy rate relationship between wild and captive populations.

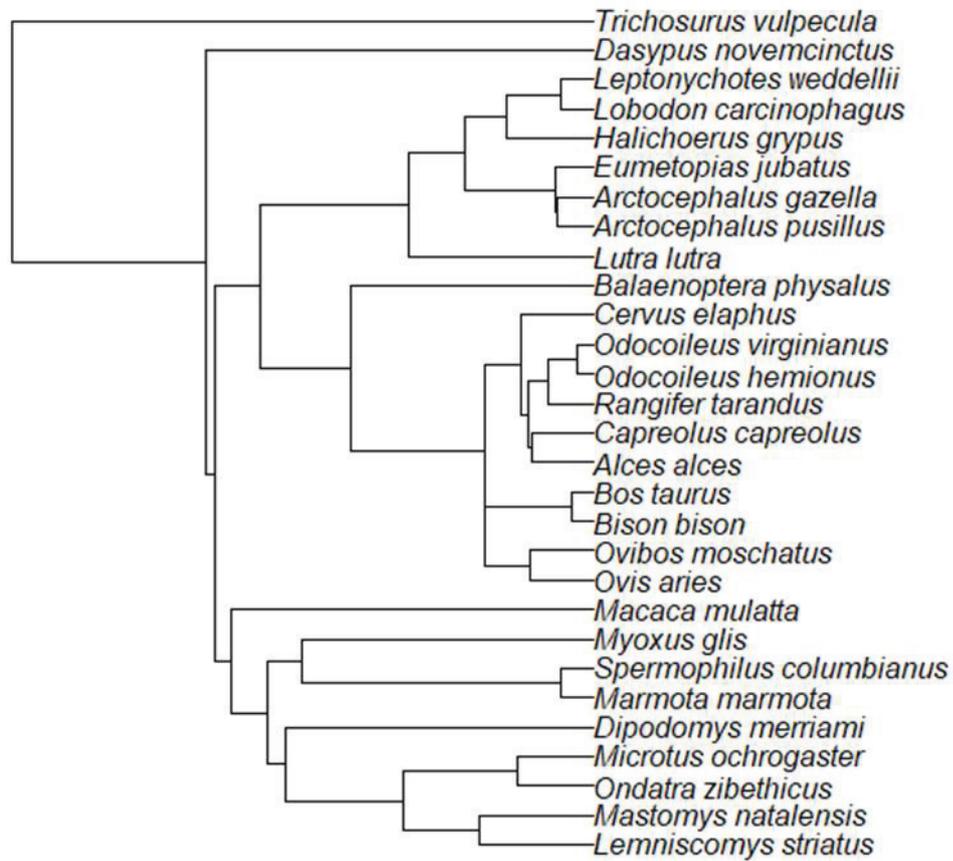
Female body mass was positively correlated to litter size. The effect was only moderate for non-age-corrected relationship and even overlap the null effect for the age-corrected relationship contrary to the very high effect found for the pregnancy rate. This highlights the possibly weaker relationship between litter size and female body mass compared to the mass-pregnancy rate relationship. One of the major differences between these relationships is the restriction to mass distribution of females that reproduced when studying litter size. As heavier females are more likely to reproduce, we expect less variation in body mass among females producing a litter than among all sexually mature females. However, we still found a consistent positive effect of female body mass on litter size, possibly be due to the fact that individuals with higher reserves or better access to resources can afford to produce more offspring (Michener 1989). They are mainly two pathways for a female to enhance their reproductive success. To increase the number of recruits, females can either produce more offspring or produce heavier offspring to increase offspring survival. This leads to the well-established trade-off between size and number of offspring produced (Lack 1947; Charnov & Ernest 2006), which can also decrease the intensity of the relationship between female mass and litter size.

We found no effect of the allocation strategy to reproduction on the intensity of this relationship between litter size and mother body mass. As explained earlier mass is a proxy of the overall quality of the female and can therefor affect the litter size of capital breeder as well as income breeder. Contrary to the previous relationship we found no effect of age on the intensity of the relationship, this could be explained because young individuals included in this relationship already reproduced and therefor have a high body mass close to the distribution of body mass of older individuals (Dobson 1992; Skibieli *et al.* 2009). We also found no effect of captivity on the relationship.

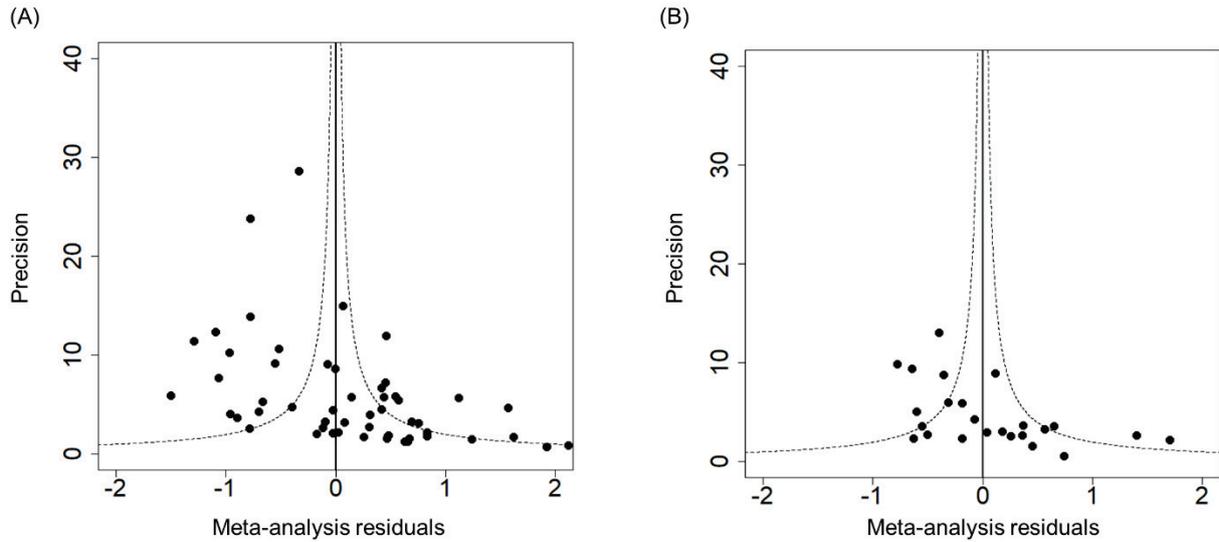
To conclude, we demonstrated that female body mass impacts positively the pregnancy rate as well as the litter size, but we found marked differences in intensity between those two relationships. This finding highlights a low repeatability of litter size for a given mass, which might be caused by variation in adaptive reproductive tactics involving the offspring number-size trade-off and by changes in environmental conditions. We highlight here because there is no effect of the allocation strategy to reproduction on the intensity of the relationship that body mass is not only related to reproduction because it is a proxy of the different reserves but because it is an overall indicator of individual quality which confirms

what was already found for other vital rates than reproduction (Ronget *et al.* 2018) in mammals.

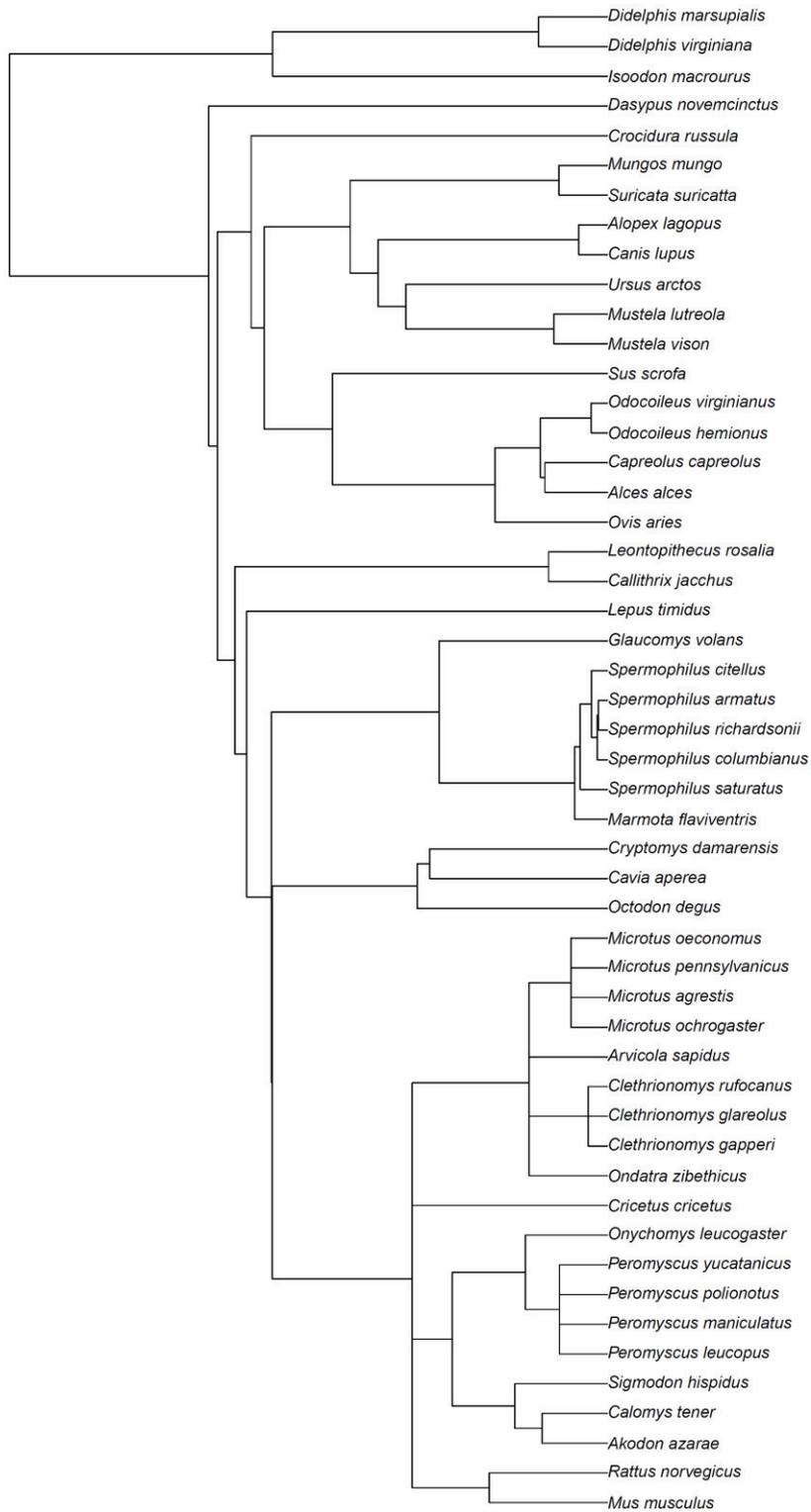
## 6. Supplemental materials



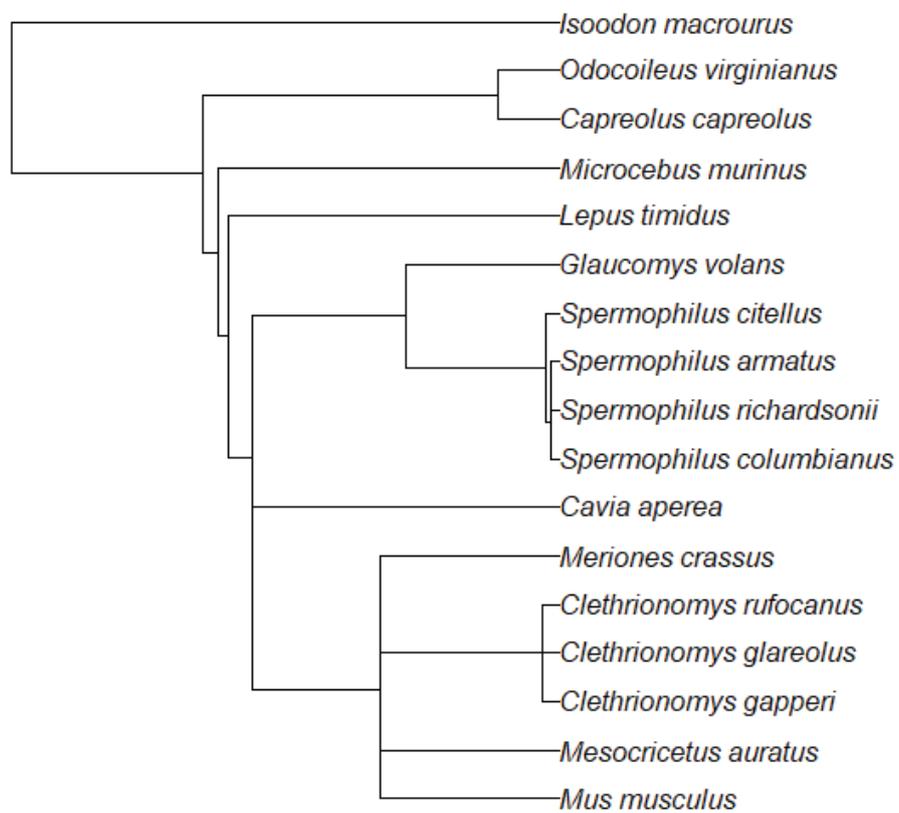
**Figure S4.1.** Phylogeny of mammal species (from Bininda-Emonds et al., 2007) included in the meta-analysis between pregnancy rate and female body mass non-corrected by age



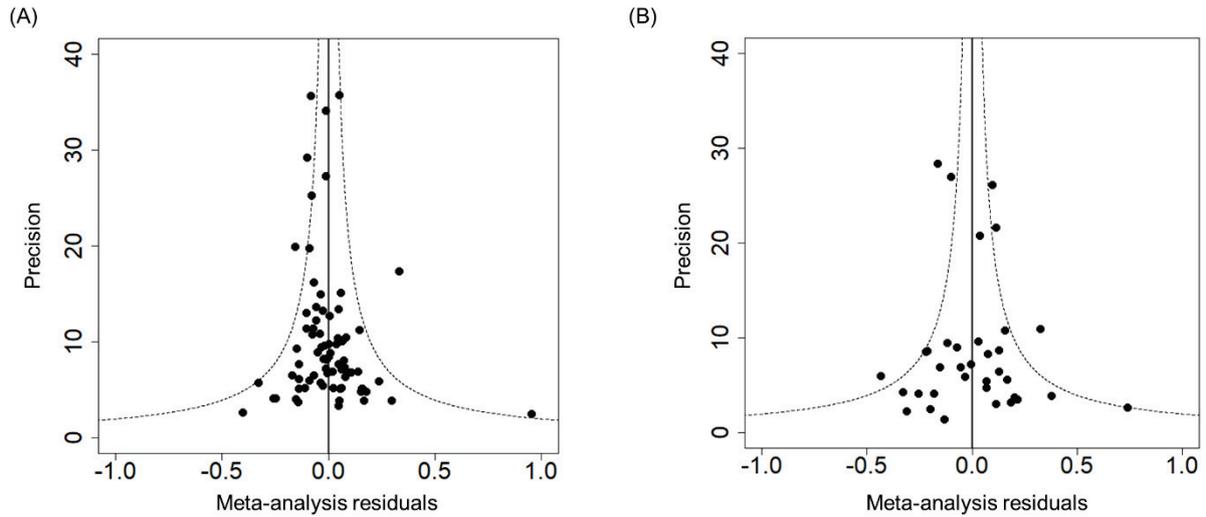
**Figure S4.2.** Funnel plot of the different effect sizes for the relationship between female body mass and pregnancy rate (A) for non-corrected by age relationships (B) for age-corrected relationship. The means are reported along with their 95% credibility interval. As recommended by Nakagawa & Santos (2012) the precision is plotted against the residuals of the meta-analysis.



**Figure S4.3.** Phylogeny of mammal species (from Bininda-Emonds et al., 2007) included in the meta-analysis between litter size and female body mass non-corrected by age



**Figure S4.4.** Phylogeny of mammal species (from Bininda-Emonds et al., 2007) included in the meta-analysis between litter size and female body mass corrected by age.



**Figure S4.5.** Funnel plot of the different effect sizes for the relationship between female body mass and litter size (A) for non-corrected by age relationships (B) for age-corrected relationship. The means are reported along with their 95% credibility interval. As recommended by Nakagawa & Santos (2012) the precision is plotted against the residuals of the meta-analysis.

## Part II

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# Identifying senescence patterns for populations of mammals in the wild

### Overview

In this part, I will focus on assessing the relationship between age and vital rates for wild populations of mammals. Most studies assessing general patterns of senescence have been done in captive conditions, which cannot be applied directly to wild environments. Thus, to assess the general patterns of senescence, a compilation of the demographic datasets available for wild mammals is needed. In the first chapter I present the Malddaba database my supervisors and I built during my thesis. This database compiled relationships linking age to reproduction or survival from published studies in the literature. In the second chapter, I perform a comparative analysis of the sex differences in actuarial senescence patterns for wild populations of mammals using the data compiled in Malddaba. In the third chapter I review the different metrics commonly used in comparative analyses and provide guidelines for authors to assess adequately the actuarial senescence patterns using the distribution of ages at death.

## Chapter V

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# The MAMmaLian Demographic DATABase



This work was made in collaboration with Jean-Michel Gaillard, Jean-François Lemaître, Morgane Tidière, Vérane Berger, Frederic Douhard, Lionel Humblot and Bruno Spataro.

## 1. Aim of the database

Studying the effect of age on the different vital rates have received much attention (Monaghan *et al.*, 2008). One major axis of research in demography is the comparison of senescence patterns across species and the identification of factors that explain this observed diversity (Jones *et al.*, 2014). To perform comparative analyses of senescence across mammals, we need first to assess the relationships between age and vital rates in each of the species. For such computation, an extended amount of age-specific demographic data is required. For long-lived species such as mammal long-term datasets are needed. These datasets are very resource-demanding for the research groups that collect the data and therefore they are only available for a relatively small number of species (Mills *et al.*, 2015). For this reason, most studies comparing the patterns of senescence across mammalian species used zoo data (Ricklefs & Scheuerlein, 2001; Ricklefs, 2010). Most demographic data available for captive populations are extracted from the Species360 database (<https://www.species360.org/>) compiling life-tables from more than 1000 zoos and aquariums (e.g. Tidière *et al.*, 2015). However, patterns of senescence markedly differ between wild and captive conditions, mostly because wild and captive populations do not suffer from the same causes of mortality (Tidière *et al.*, 2016a). Wild populations typically suffer more from environmentally-driven mortality such as starvation or predation, which can change differently with age, than from mortality related to individual attributes (Lemaître *et al.*, 2013). Those studies are thus not fully transposable into the wild, especially if we try to assess the effect of environmental conditions on the population.

Compiling demographic data for wild populations of animals have recently received more and more attention with the creation of the COMPADRE database (<https://www.compadre-db.org/>, Salguero-Gómez *et al.*, 2015). To date, this database is the only open database making available demographic data for animals in the wild. The COMPADRE database reports projection matrices from (st)age-structured populations. Some studies extracted demographic information from this database to conduct comparative analyses on demographic outputs in a wide range of species from plants to animals (e.g. Paniw, Ozgul, & Salguero-Gómez, 2018). However, those matrices are not suited to perform any comparative analysis of aging because most of those matrices are not fully age-dependent. The most appropriate way to get the full age-dependence in demographic traits is to use life tables (Caughley, 1966). There are two major advantages to use those tables for comparative analyses. First, there is a long tradition of reporting life tables in every study

measuring the effect of age on mortality or on reproduction in wild populations of mammals (e.g. Spinage, 1972; Millar & Zammuto, 1983). Thus, these age-specific demographic data are available for a relatively large number of species. Second, the presentation of life tables is generally standardized and we can thus easily extract and use comparable data across species. For instance, mortality rates hold the same definition whatever the species studied.

In the Mammalian demographic database (Malddaba) we chose to compile mortality rates as well as reproductive rates in function of age coming mostly from published life tables for wild mammalian populations. As the main focus of this database is to provide resources to perform comparative analyses for evolutionary ecologists, we aim to compile these data for the maximum number of species. Since there are sometimes marked differences in age-dependent relationships between different populations from the same species (i.e. Loison *et al.*, 1999; Garrott *et al.*, 2002; Clutton-Brock & Isvaran, 2007), taking only one population can sometimes lead to spurious conclusions in interspecific comparative analyses (Freckleton, 2009). We thus compiled data at the population level by extracting age-specific demographic data from several populations of the same species and in both males and females, when such data were available.

## **2. Data collection**

### *2.1. Literature review*

In the database we only included demographic data from published studies. The studies compiled in the database come from an intensive research of the life tables available in the literature. The compilation of studies reporting life tables for mammals started before the beginning of my thesis by Jean-Michel Gaillard and Jean-François Lemaître but from then I actively contribute to update the literature search. We then identified new papers by looking for the references of each paper providing life tables. With this literature search protocol, we were able to find studies that were not detected through more classical literature search using ISI Web of Knowledge (e.g. old research papers or reports such as Kasuya & Marsh, 1984). We did include all studies reporting any measurement of survival in function of age or any measurement of reproductive rate in function of age. Consequently, the data did not only come from life tables but survival or reproduction in relation to age was presented graphically

instead of being reported in the standard life table format. We also extracted information from those studies by using WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>). To date there are data from 244 papers included in the database. However, because of the large diversity of mammalian species coming from the different papers, methodology used to compute demographic rates are likely to be very heterogeneous (Lebreton *et al.*, 2012). Species are likely to have different environments and biological cycles, leading to very different methodologies used to compute demographic rates. Moreover, depending on the time investment from the research team, we are also likely to see different methodologies. We emphasize in the database the recordings of the method used as it can have critical impact on the results (Freckleton, 2009).

## *2.2. Extracting life tables data from datasets of different qualities*

### 2.2.a. Reporting mortality rates

There are two types of dataset used to build life tables. The first type of data comes from longitudinal monitoring that is considered to provide the highest quality datasets. In longitudinal datasets, individuals are marked at birth (or at least very early in life when age can be easily determined) and then recaptured regularly through their lifetime. From those datasets, lifespan of each individual is known, which allows an easy computation of the mortality rates. We can describe two types of longitudinal data for mortality:

- Cohort data: in this type of demographic data individuals are all born the same year and they thus belong to the same cohort. Because all individuals are subjected to the same environmental hazards at the same time of their life, those data are considered as the highest quality data. However, those are rarely reported because a high number of individuals marked at birth for one year is needed to be able to obtain the whole range of age-specific mortality rates, which is most often not technically feasible in wild populations of mammals. However, those data are massively available for human populations. In lots of countries, individuals are censused at birth and the history of each individual is easily tracked, which allows building high quality life tables. Such data are reported for more than 40 countries in the human mortality database (<https://www.mortality.org/>).

- Period data: the demographic monitoring is made over a period regardless of the year of birth. One of the major advantages of these types of data is that it merges individuals from

different cohorts and thus increases the sample size for each of the mortality rates. This will also provide more accurate estimates of mortality at old ages, which constitutes one of the major issues when studying the demography of wild populations and especially when studying the senescence patterns (Nichols *et al.*, 1997). However, as those data merge different cohorts, they also mix individuals with different history that could have experienced extreme environmental hazards at different periods of their life, which are likely to bias mortality rate estimates. Nevertheless, we can reasonably assume that extreme hazards are likely to be buffered if the monitoring is made over a sufficient period of time, which itself directly depends of the species life history. Those longitudinal periods provide the most high-quality datasets available in the wild but are also the most resource-demanding (Mills *et al.*, 2015), explaining why those datasets are not available for a large number of species.

As they are considered as the most accurate data reported in the wild, we directly report the survival rates per age presented in those longitudinal studies as well as the sample size associated at each age.

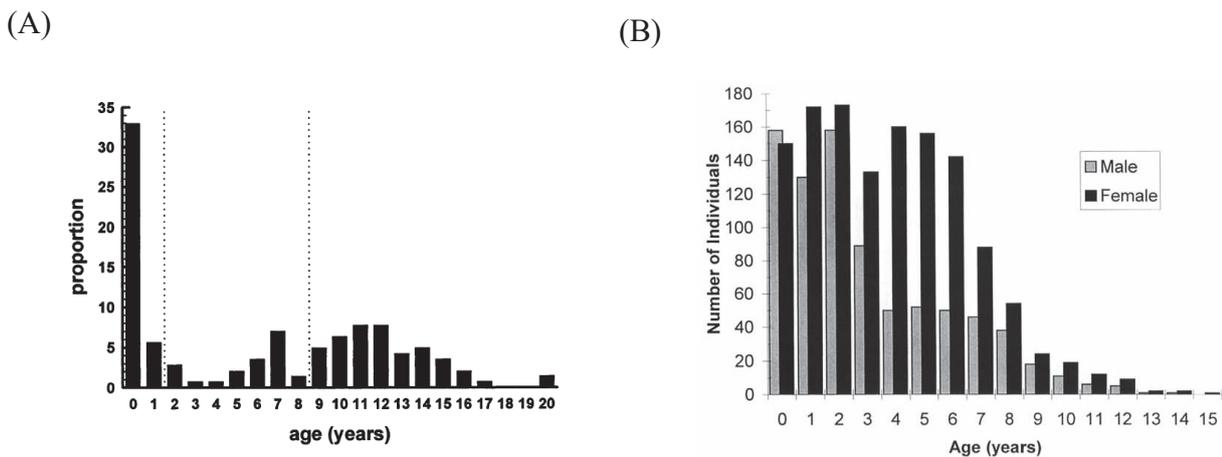
The second type of data come from transversal data collected in a population and are usually considered as low quality datasets (at least compared to longitudinal datasets). In such transversal studies, individuals are not monitored through time and demographic estimates are based on the sampling of individuals of different ages at the same time. Therefore, the calculation of the mortality rates is based on the fact that sampled individuals can be aged without following them through their lifetime by using indirect methods (i.e. using tooth size or tooth wear Willey, 1974; Munro, Bar-Oz, & Stutz, 2009)). We can then distinguish two types of transversal data:

- Transversal data on the age distribution of dead individuals (called transversal dx): in these studies, carcasses of individuals are collected (Fig 5.1.A for an example). The distribution of age of the individuals sampled can be considered as an analogous of the distribution of ages at death in the population. With such distribution, it is possible to compute mortality rates. The major issue with this approach is that, to really represent the distribution of ages at death, the size of the population should be constant with time (Caughley, 1966). If we take the example of a population that recently increased in size, this population will display an over-representation of young individuals, which would lead to a mis-representation of the distribution of ages at death. The second problem is that those transversal data rely heavily on

the methods used to assess the ages of the dead individuals, which has been proven to be inaccurate most of the time (Hamlin *et al.*, 2000).

- Transversal data on the age distribution of individuals alive (called transversal lx): in this type of study individuals are sampled alive and aged, but they are not monitored throughout their lifetime (Fig 5.1.B for an example). The distribution of age of those individuals alive can be then considered as an analogous of the cumulative survival function. For the same reasons as the transversal dx data, transversal lx data are considered as low-quality data. The distribution of individuals alive is thus comparable to the cumulative survival function but only if the size of the population did not change over time and if the estimation depends also on the accuracy of method used to assign an age to individuals.

As the computation of mortality rates for transversal data relies on strong assumptions, we chose to report only the distribution of ages at death in Malddaba.



**Figure 5.1.** Two examples of transversal life tables (A) distribution of dead females of sea otter (*Enhydra lutris*) extracted from (Monson *et al.*, 2000) (B) distribution of alive males and females Dall's porpoise (*Phocoenoides dalli*) extracted from (Ferrero & Walker, 1999)

### 2.2.b. Reporting reproductive rates

In life tables including reproductive performance as a function of age,  $m(x)$  values are the standard statistics (Leslie, 1945, see definition below). However, most studies did not monitor the individuals through all their reproductive cycle and only components of the age-

specific reproductive success are provided for females. In Malddaba, all relationships linking any reproductive component to the age of the mother were reported. For the reproductive data, we thus reported the following measurements:

- $m(x)$  is the average number of females produced by females of age  $x$  (i.e. Packer *et al.*, 1998; Moss, 2001)
- juvenile survival is the average survival rate of newborns born from mothers of age  $x$  (i.e. Festa-Bianchet & Côté, 2012)
- pregnancy rate is the average pregnancy rate of mothers of age  $x$  (i.e. Sacks, 2005; Gogan *et al.*, 2013)
- litter size is the average litter size produced by females of age  $x$  (Saunders *et al.*, 2002)

Most data linking age to reproduction are available only for females. However, for some species data were also available for males. We also reported them in that case.

### 2.2.c. Other information reported

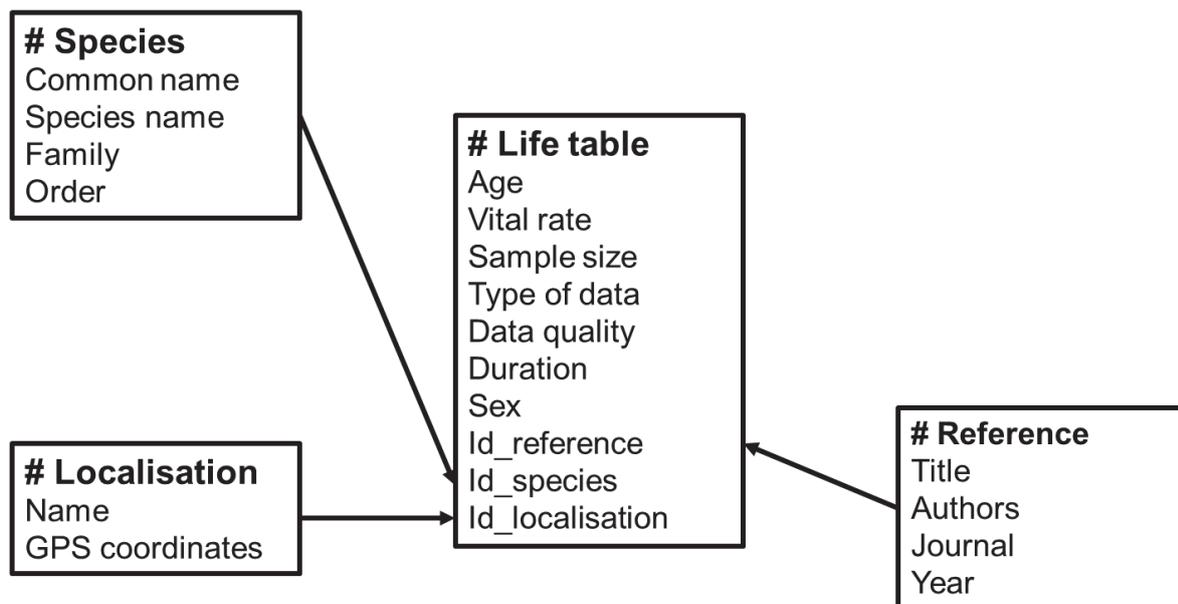
We reported also any information on the methodology of the focal study, which could impact the mortality rates as well as any information needed to recover to the original paper associated with the life table. We thus reported for each life table:

- The full reference of the original paper
- the sex of the individuals monitored if the life table was sex-specific
- The GPS coordinate for the localization of the individuals sampled
- the full taxonomic information of the species studied (Species, Genus, Family)
- the duration of the study
- whether all ages were included in the life table, and if not, at which age does it begins and ends

### 3. Building the database

#### 3.1. The structure of the database

Malddaba is built as a relational database coded in SQL language. The basis of this type of database is that the different information of the database is compiled into different tables composed of different fields. Those different tables are identified by keys and logical relationships are made between the different tables using these different keys. For instance, the information about the life table is reported in one table (See Fig 5.2) and this table is always associated with one reference, one species and one location. The major advantage for using this type of database is that it makes extraction of data easy by request. We can basically request anything based on the fields of the tables. For example, we can request using this structure any survival data from longitudinal monitoring of carnivores.



**Figure 5.2.** Schema of the structure of the database, each rectangle represents a table in the database, the arrows represent the logical relationships between the different tables. The demographic information of the life table is stored in vectors for the fields “Age”, “Vital rate” and “Sample size” and the field type of data corresponding to whether it is a reproduction or a survival life table.

### *3.2. Some statistics about Malddaba*

As it stands, Malddaba is a database including:

- 666 life tables from 244 studies
- 496 life tables on survival with 208 coming from longitudinal monitoring and 288 coming from transversal monitoring
- 170 life tables on reproduction with 111 tables reporting directly  $m(x)$
- 171 species of mammals from 15 different orders (Artiodactyla, Carnivora, Cetacea, Chiroptera, Didelphimorphia, Diprotodontia, Erinaceomorpha, Eulipotyphla, Hyracoidea, Lagomorpha, Perissodactyla, Primate, Proboscidea, Rodent, and Scandentia)
- 80 species with full demographic data including survival and reproduction rates for the same population
- Data compiled from 244 papers
- 2 papers submitted so far, one describing the difference between sexes in senescence pattern for wild mammals (See Chapter V) and one assessing the accuracy of the generation time compiled by the IUCN red list (See Appendices).

## **4. The Future of the database**

We are now in the era of the open-access data for research (Whitlock, 2011). We thus aimed to build Malddaba as an open access database that could be used by any biologist or demographer interested by age-dependent demographic patterns. There are multiple ways to present databases. Some databases can just provide the raw data from a request while others can display a more integrative interface. I will show next how these two presentations that are not mutually exclusive can be applied to Malddaba and then I will present some extension of the dataset that will be done to provide new perspectives for comparative analyses.

#### *4.1. Using the database to perform demographic comparative analyses*

The first aim of development for this database was to provide detailed demographic data of mammalian populations in the wild to demographers and evolutionary biologists. We highlighted two major axes of research for which those data can be used. First, those data can be used in aging research to compare patterns of aging among mammalian species (or populations). For instance, our first intention by building that database was to compare aging patterns between male and females in the wild (See Chapter VI). Those data could be also used to improve the methods to model reproduction rate as it receives much less attention than the modelling of mortality rates (Emlen, 1970). The second axis of research that could benefit from this database is the study of population dynamics of mammals in the wild. For species in which survival and reproduction are available, demographic models can be built and used to produce outputs on the state of the population. Those outputs can be critical to help managing populations and thus are also very important for the field of conservation biology. We did this for instance for generation times (See Appendices). IUCN status ([www.iucnredlist.org](http://www.iucnredlist.org)) is based on generation times calculated by the IUCN and therefore the methods to assess the generation time is crucial to determine if the species is endangered or not. By using demographic data of mammals in the wild, we were able to point out the inaccuracy of the methods used by the IUCN. Researchers working on all those research questions have always a good demographic knowledge and thus are familiarized with those life table data. In that case, raw data are preferred because they will be able to choose the appropriate models for the scientific question asked. Those users thus need only an effective request system to extract easily the raw data they required.

#### *4.2. Provide accurate description of age-related patterns*

Malddaba was firstly devised for demographers. However, comparative analyses of aging are not restricted strictly to demographers (Gomes *et al.*, 2011; Aledo *et al.*, 2012). As demographers have tried to assess the diversity of aging patterns, some researchers are more interested by the mechanism of aging and try to link the differences of aging patterns to physiological differences (Gomes *et al.*, 2011; Aledo *et al.*, 2012). Those researchers are not focused on the demographic approach and thus use available databases on aging to assess the difference in aging patterns. Longevity is by far the most commonly used metrics in comparative analyses of aging, most of those longevities are maximal longevities coming

from AnAge database (Magalhães & Costa, 2009) or from Pantheria database (Jones *et al.*, 2009). However, those measurements have proven to be inaccurate to assess patterns of aging (Moorad *et al.*, 2012) (See Chapter 6 for a critical review of longevity measurements). Because of the high quality of the life table datasets, we can compute more accurate metrics such as longevity 90% or life expectancy for all the species in the database. The second goal of this database is thus to present accurate metrics for assessing the senescence patterns. As requests of raw data are easily feasible from our database, the building of an interface to present senescence patterns for each species will be much more resource-demanding but will appeal a much larger audience of researchers. Moreover, we could also link Malddaba to other databases already available such as Anage to provide more robust longevity metrics than maximal longevity.

#### *4.3. Integrating morphological measurements in function of age*

Demographic rates are not the only quantities that are reported in function of age in the literature. Morphological measurements and more specifically mass and size are reported in function of age. Those growth curves can provide information on how much an individual allocate to growth. As there is a trade off between early allocation to growth and late survival (Lemaître *et al.*, 2015) we expect that growth patterns could influence the senescence patterns and thus the description of those growth patterns could help us understand the diversity of the senescence patterns (Douhard *et al.*, 2017). As those growth data are close to reproduction patterns in terms of presentation (i.e. with one value and a sample size associated to an age) we can easily add them to the initial structure of Malddaba.

## Chapter VI

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# Sex differences in longevity and aging rates across wild mammals

A version of this chapter was submitted to Science:

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\*equal contribution

## 1. Abstract

In human populations, women consistently benefit from longer lifespan than men, which suggests profound biological foundations for sex differences in survival. Quantifying whether such sex differences are also pervasive in wild mammals is a crucial challenge in both evolutionary biology and biogerontology. Here we use demographic data from 135 mammal populations, encompassing 102 species, to show that female mammals live on average 18.4% longer than conspecific males, whereas in humans the female advantage is 4-9%. Sex differences in longevity and aging rates are both highly variable across species but sex differences in aging rates are not consistent across species. Our analyses reveal that local environmental conditions, rather than sex-specific reproductive strategies, predominantly shape the magnitude of sex differences in mammalian mortality patterns.

## 2. Main Text

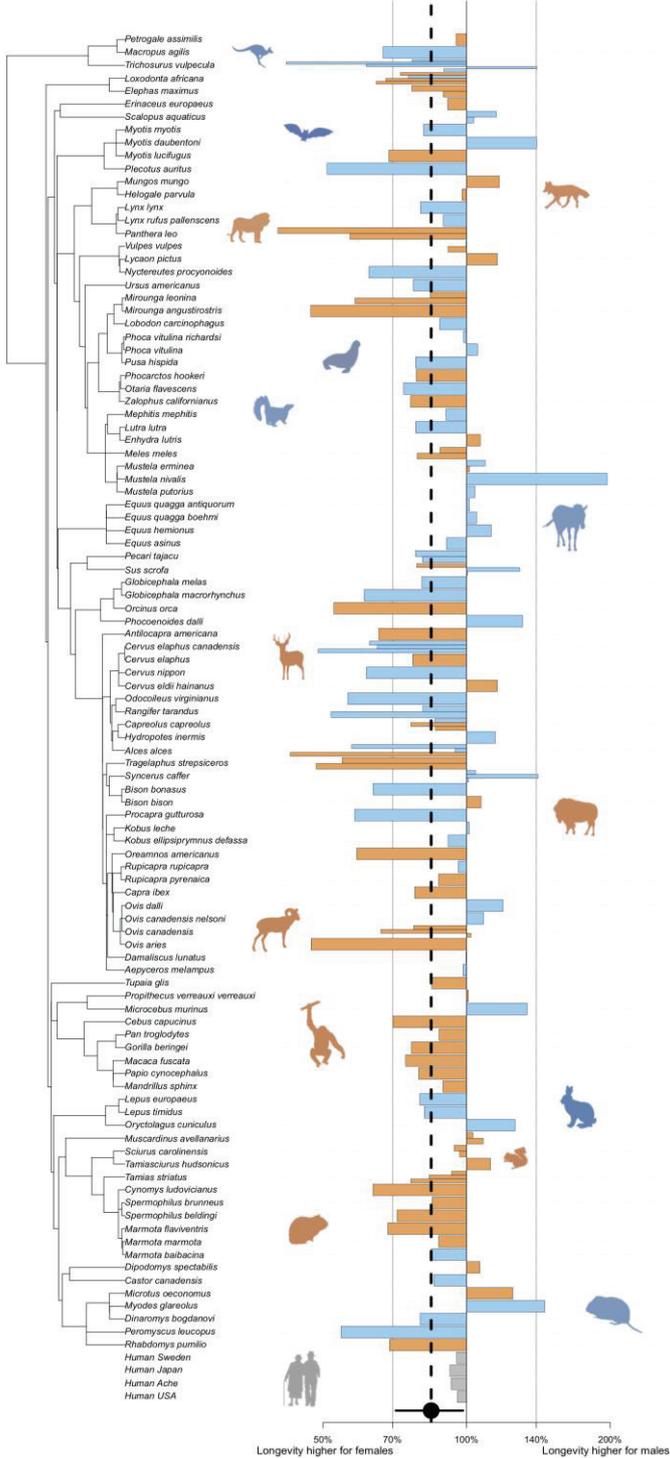
In all countries worldwide, women enjoy a longer life expectancy at birth than men (Masoro & Austad, 2010; Rochelle *et al.*, 2015; Zarulli *et al.*, 2018). This pattern of longer-lived women is consistent from the mid-18th century (when the first accurate birth records became available) till now (Austad, 2006; Masoro & Austad, 2010), and explains why about 90% of supercentenarians (i.e. people reaching 110 years old or more) are women<sup>1</sup>. While social factors reinforce the gender gap in longevity (Rochelle *et al.*, 2015), the greater survival prospects of women over men are observed even when both sexes share the same social habits (Luy, 2003). The female advantage in lifespan has thus been labelled as one of the most robust features of human biology (Masoro & Austad, 2010). How much sexes differ in aging trajectories is a question of paramount importance associated with severe economical and biomedical implications (George, 2010; Austad & Fischer, 2016). Indeed, men and women show differences in the dynamics of virtually all age-associated diseases, which are currently increasing in prevalence due to a growing aging population (Kennedy *et al.*, 2014). In line with human populations, it is usually assumed that female mammals generally live longer than males (Promislow, 1992; Clutton-Brock & Isvaran, 2007), although this belief relies either on a few detailed case studies or from longevity records in captivity (Carey & Judge, 2000), where lifespan and aging rates are often not representative of conspecifics in the wild (Tidière *et al.*, 2016b). However, identifying the evolutionary mechanisms underlying sex-

specific survival requires a thorough overview of the sex differences in longevity across mammals in the wild.

We show that mammalian females live 18.4 % (mean value of four longevity metrics, see Tab. 6.1) longer than males in wild mammals from the most complete compilation of sex-specific life tables ever done, which includes 135 mammalian populations of 102 species spanning the wide diversity of mammal orders (Fig. 6.1). This magnitude of sex differences in longevity is robust with respect to four metrics of longevity commonly used (Coefficient of variation: 9.0%, Tab. 6.1) and we thus choose to present results obtained with the most reliable longevity metric (i.e. the longevity 80% that corresponds to the age at which 20% of the adult population remains alive, see Material and Methods). We find that sex differences in longevity are also larger in longitudinal than in transversal studies (Fig. S6.1). As individuals are followed from birth to death in longitudinal studies, these latter provide the most accurate demographic estimates (Nussey *et al.*, 2008), revealing that females live 20.0% more than males (65 populations encompassing 51 species). Although sex differences in longevity from culturally and geographically distinct human populations (Americans: 4.9%, Japanese: 7.7%, Swedish: 4.5%, Aché: 8.3%) are consistent with our estimates from non-human mammals, mammalian females display a survival advantage greater than women in 64.4% of the sampled populations (Fig. 6.1).

In his pioneering contribution to the evolution of aging, Georges C. Williams predicted that the sex exposed to the highest level of environmentally-driven mortality should undergo a faster rate of aging (Williams, 1957), and consequently that male sexual competition should result in higher mortality and lead to faster aging rates in males (Williams, 1957; Gaillard & Lemaître, 2017). To investigate whether sex differences in aging rate matched sex differences in longevity, we estimated the rate of aging (as the rate of change of mortality with age during adulthood, see Methods) in populations where information on the distribution of ages at death was available (83 populations representing 66 species). We find no consistent differences in aging rate between males and females (Table S6.1, Fig. 6.2), which reveal that consistently longer female longevities do not involve a lower aging rate. It thus appears that the overall sex bias in longevity we report across mammalian populations can be shaped by a diversity of sex-specific demographic features that characterize a species or a population, but does not systematically involve a higher aging rate in males. Such a decoupling between longevity and aging rate matches the human mortality pattern since age-

specific mortality in human populations studied to date increase at the same rate in both sexes even if women live longer (Masoro & Austad, 2010).



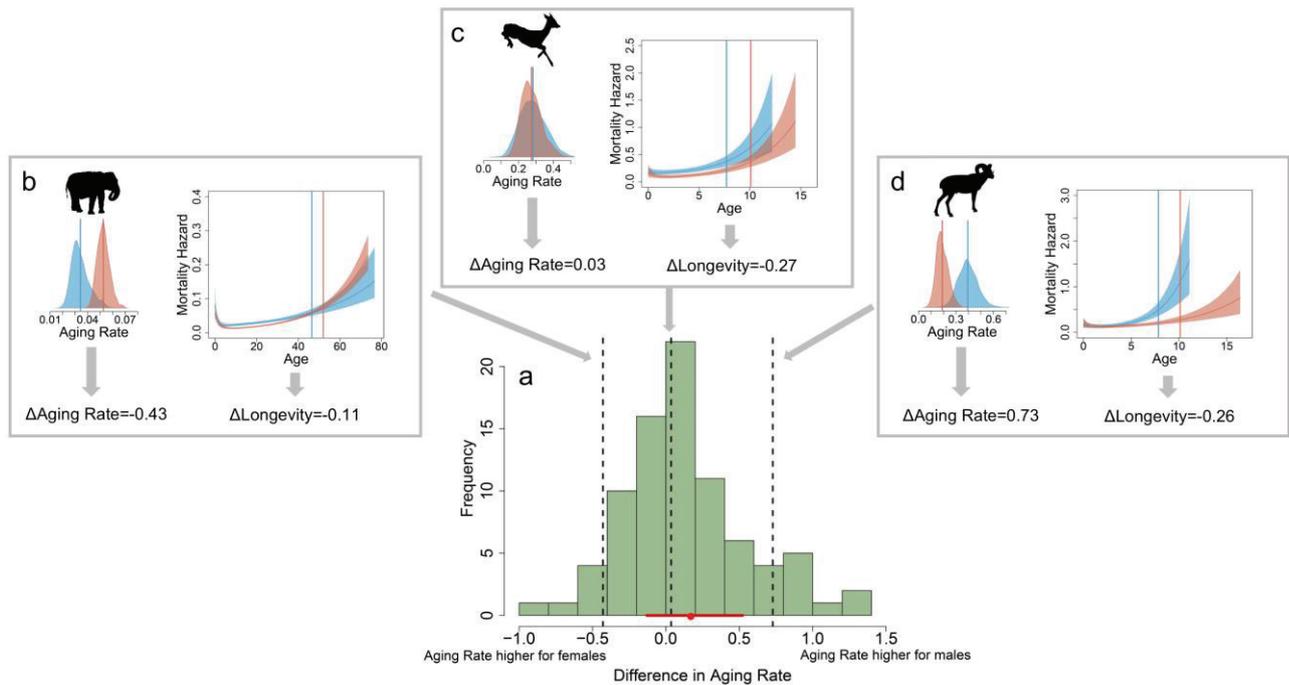
**Figure 6.1.** Sex differences in longevity across mammals. For a given population, the sex difference is measured as the ratio  $\log[(\text{Male longevity})/(\text{Female longevity})]$ . Multiple bars for a given species represent estimates gathered from different populations. Orange bars correspond to longitudinal data, blue bars correspond to transversal data, and grey bars

correspond to the human populations. The black dot corresponds to the overall effect for non-human mammals and is associated with its 95 % credibility interval.

Sex differences in longevity and aging rate are both highly variable across species (coefficient of variation of 157% and 291% for longevity and aging rate, respectively, Fig. 6.1, Fig. 6.2). Dissimilarities in sex-chromosome content is an influential explanation for sex differences in mortality (Trivers, 1985), which suggests that within species, the heterogametic sex (i.e. XY males in mammals) should suffer from impaired survival compared to the homogametic sex. While the exact biological mechanisms linking sex chromosomes and longevity remain unclear (Trivers, 1985), this hypothesis successfully explains the direction of sex differences in mortality across tetrapods (Marais *et al.*, 2018). However, our findings demonstrate that even within mammalian species that all share the same sex determination system, variation in the magnitude of sex differences in longevity and aging is particularly large.

**Table 6.1.** Mean percentage differences and mean log longevity differences (with 95% credibility intervals (CI)) between mammalian males and females for four longevity metrics. N corresponds to the number of populations included in the analyses.

Metrics	Mean percentage	Mean log	Lower CI	Upper CI	<i>N</i>
Longevity 80%	18.6	-0.171	-0.329	-0.007	135
Median Longevity	18.1	-0.166	-0.372	0.044	135
Life expectancy	16.4	-0.152	-0.394	0.107	60
Maximum Longevity	20.4	-0.186	-0.365	-0.013	60



**Figure 6.2.** Frequency distribution of the magnitude of sex differences in aging rates across mammals in the wild (a). The red dot corresponds to the overall effect for non-human mammals and is associated with its 95 % credibility interval. Aging patterns for three mammalian populations are displayed. For each population the mortality curve with the line representing the longevity 80% and the posterior distribution of the aging rate  $b_1$  are given in red for females and in blue for males. In the three populations, females live longer than males. However, in (b) Asian elephant (Myanmar population), females have a higher aging rate, in (c) roe deer (Chizé, France) no difference in aging rates is observed while in (d) bighorn sheep (Sheep River, Canada) males show a higher rate of aging than females.

We investigated ecological and behavioral predictors of sex-specific survival in a phylogenetic framework. First, phylogenetic closeness is the key driver of the variation in longevity and aging rates across species when considering each sex separately ( $H^2 = 91\%$  and  $H^2 = 90\%$  for female and male longevity;  $H^2 = 87\%$  and  $H^2 = 88.0\%$  for female and male aging rates), whereas it accounts only for a low percentage of variation in sex differences in both longevity ( $H^2 = 20\%$ ) and aging rates ( $H^2 = 27\%$ ) across species. These findings indicate that allometry (through the species-specific body size (Calder, 1996)) and pace of life (through the species-specific position along the slow-fast continuum (Kliman, 2016)), which

both closely track phylogenetic closeness (Blomberg, Garland, & Ives, 2003), mostly determine the mortality pattern of a given mammalian species (Healy *et al.*, 2014) but have little influence on sex differences in longevity and aging. Overall the extant sexual dimorphism in survival metrics is fine-tuned by variation in environmental conditions, which varies strongly among populations within a given species. Second, in support of the potential influence of environmental variation in shaping sex differences in mortality patterns, females from hunted populations (N = 23) live longer relative to males than females from non-hunted populations (29.7% vs. 17.1%, respectively, Fig. S6.1). Trophy hunting thus reinforces the male penalty in longevity (Milner, Nilsen, & Andreassen, 2007) and likely shapes the magnitude of sex differences in mortality patterns across wild populations of mammals where such anthropogenic interactions occur. Third, sexual selection commonly assumed to shape sexual dimorphism in mortality patterns has no detectable effects on sex differences in longevity and aging rates in the wild (Tab. S6.2 and S6.3). Although males are expected to pay survival costs of substantial allocation to sexual competition (e.g. through the growth and maintenance of conspicuous sexual traits) (Clutton-Brock & Isvaran, 2007; Tidière *et al.*, 2015), evidence reported so far is equivocal at best (Tidière *et al.*, 2015; Marais *et al.*, 2018) and relies on small datasets (Promislow, 1992; Clutton-Brock & Isvaran, 2007; Lemaître & Gaillard, 2013) or on captive populations (Tidière *et al.*, 2015). Our broad scale analysis on mammals in the wild reveals that neither sexual size dimorphism nor mating system reliably predict the direction and magnitude of sex differences in longevity and aging rate (Tab. S6.2 and S6.3), challenging the current thinking in evolutionary biology of aging (Clutton-Brock & Isvaran, 2007; Maklakov & Lummaa, 2013; Regan & Partridge, 2013; Brooks & Garratt, 2017). Physiological adaptations to male sexual competition (e.g. higher production of testosterone (Brooks & Garratt, 2017)) might explain sex differences in longevity observed in captive populations when individuals are protected from environmental severity. However, we argue that local environmental conditions (e.g. climate harshness, anthropogenic activities) predominantly shape sex differences in longevity and aging rate in the wild. A better understanding of the sex-specific role played by environmental conditions on mortality patterns would undeniably be beneficial in terms of conservation strategies.

In humans and laboratory animals sex differences in aging extend to sex differences in frailty, neurological decline and comorbidity (Austad, 2006). In laboratory rodents, the survival benefits associated with anti-aging interventions (genetic or pharmacological) are also frequently sex-specific (Austad & Bartke, 2016; Austad & Fischer, 2016). These effects

are often associated with sex differences in physiological systems (e.g. hormonal profiles) that modulate longevity and aging (Garratt *et al.*, 2017). From an evolutionary perspective, such sex-specific physiological systems are the direct consequences of both natural and sexual selection pressures that have been exerted independently on males and females (Regan & Partridge, 2013) and that differentially sensitize either sex to specific environmental conditions. Therefore, we propose that variation in the magnitude of sex differences in both longevity and aging rate is likely a response to interactions between sex-specific physiological pathways and the diversity of environmental conditions met by mammals across the world. Albeit challenging, research programs that will solve this complex network will undoubtedly provide innovative insights into the evolutionary roots and physiology underlying aging in both sexes.

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### **3. Materials and Methods**

#### *3.1. Data collection*

Age- and sex-specific mortality data were extracted from published life tables or graphs using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). We limited our literature search to mortality or survival estimates published for both sexes for wild populations of mammals, for a total of 184 populations encompassing 128 species. Based on

the methods used to estimate age-specific mortality in the initial source, we distinguished three main categories of studies. The first type of studies corresponds to age-specific mortality estimates obtained from the long-term monitoring of individuals marked at birth (i.e. longitudinal data). The second type of studies corresponds to age-specific mortality estimates obtained from dead animals collected in the field (i.e. transversal data using the standard dx series procedure (Caughley, 1966)). Finally, the third type of studies corresponds to age-specific mortality estimates computed from the sampling of individuals alive in the population (i.e. transversal data using the standard lx series procedure (Caughley, 1966)). For transversal data, population size has to be considered as constant and the distribution of ages of dead or alive individuals in the population as stable (Caughley, 1966). Mortality estimates extracted from transversal data also depend on the precision of the methods used to assess the age of the individuals. Longitudinal data provide much more accurate estimates of age-specific mortality than transversal data (Hamlin *et al.*, 2000). Sampled populations were also classified as hunted vs. non-hunted according to the information reported in the original publication.

To compare results obtained from wild populations to humans, we recovered age- and sex-specific mortality data from four human populations (all longitudinal). These data were extracted for three contemporary countries (Japan, Sweden and USA (Human mortality database)) and for one ancestral population (Aché (Hill & Hurtado, 1996)). We used a similar procedure (see section ‘Estimation of longevity and rate of aging’ below) to compute longevity and aging rate in wild mammals and humans. However, human estimates were only used in comparison with wild populations of mammals and were not included in the analysis.

For each species, we collected data on life history traits that could explain sex differences in longevity and aging rates. As both sexual selection and sociality have been suggested to influence sex-specific survival (Bonduriansky *et al.*, 2008; Tidière *et al.*, 2015; Berger *et al.*, 2018), we collected data on mating system, social system and sex-specific body mass (to measure sexual size dimorphism). Following previous comparative studies in mammals (Lukas & Clutton-Brock, 2012; Tidière *et al.*, 2015), we classified the species in terms of mating (i.e. monogamous, polygynous, or promiscuous) and social (i.e. cooperative breeders vs. non-cooperative breeders) systems. The intensity of sexual selection is expected to be smaller in monogamous species compared to polygynous and polyandrous species, which might reduce sex differences in mortality patterns (Clutton-Brock & Isvaran, 2007). In cooperative breeders, costs of reproduction are shared among females (Bourke, 2007), which

might also increase sex differences in mortality patterns through a reduced female mortality. For each life-history trait, we prioritized data recovered from the same population.

### 3.2. Estimation of longevity and rate of aging

To estimate sex-specific longevity (in years) for each population we computed the age when 80% of the individuals alive at the age of first reproduction were dead (i.e. when cumulative survivorship is 0.2 starting at female age at maturity). We excluded juvenile mortality since, in mammals, juvenile mortality is generally higher than adult mortality and can vary considerably among species and populations and even among years within a same population (Gaillard *et al.*, 1998). Moreover, in the wild, juveniles are not easily detected (in lx series) or recovered (in dx series), which can lead to inaccurate juvenile mortality estimates in life tables built from transversal data. We thus excluded the juvenile stage from our analyses and focused on adult data only (i.e. analyses were done on age-specific data starting from the female age at first reproduction). Although this is the most often studied survival metric in comparative studies of aging, we did not focus on maximum longevity because it is highly sensitive to sample size (Krementz, Sauer, & Nichols, 1989). However, we still computed the amount of sex differences in maximum longevity and reported it in Table 6.1.

For each population, we fitted parametric mortality models for males and females separately and assessed the age when 80% of the individuals alive at the age of first reproduction were dead. For the ‘longitudinal’ and ‘transversal-dx’ data, the exact age at death of each individual was reported. We then used the R package BaSTA (Colchero, Jones, & Rebke, 2012) to fit a Siler model on age-specific survival data (Siler, 1979) for each population to obtain comparable metrics. The five-parameter Siler model is given by

$$\mu(x) = a_0 \exp(-a_1 x) + c + b_0 \exp(b_1 x) \quad (1)$$

where  $a_0, a_1, b_0, b_1, c \geq 0$  are the parameters of the mortality function and  $x$  the age in years. The first exponential function on the right-hand side of Eq. (1) corresponds to the decline in early mortality (e.g. juvenile mortality), the  $c$  parameter provides the lower limit of mortality during the adult stage, and the second exponential function corresponds to the mortality increase during the senescent stage. The hazard rate ( $\mu(x)$ ) in Eq. (1) allows a more flexible shape than the standard Gompertz mortality model, given by

$$\mu(x) = a \exp(b x) \quad (2)$$

where  $a > 0$  and  $b \geq 0$  are the Gompertz parameters (43), with  $a$  representing the baseline mortality at the starting age and  $b$  the exponential rate of increase in mortality with age, often used to measure aging rates.

For longitudinal and transversal-dx data, we restricted the analyses to populations that included at least 30 males and 30 females at the female age at first reproduction. For transversal-lx data, we only had access to the frequency of age for individuals alive. As the range of ages covered was quite low for some species, it was not possible to fit the Siler model (see (Bronson, 1979; McDonald & Harris, 2002) for some examples in Golden-Mantled Ground Squirrel, *Spermophilus lateralis* or weasels, *Mustela nivalis*). In such cases, we fitted a Gompertz model (with two parameters, see Eq. (2)) on the observed distribution of ages among individuals alive. As individuals for transversal-lx data are all sampled only once and are thus not monitored through their entire life, we took a larger sample size threshold for our selection procedure. Therefore, for transversal-lx data, we excluded populations when the sample size was below 50 individuals for at least one of the two sexes. To assess the accuracy of the longevity estimate based on a Gompertz model fitted to the distribution of animals alive (transversal-lx data), we also used this method to estimate longevity from longitudinal and transversal-dx data. The correlation between estimates obtained with the two methods (for longitudinal and transversal-dx data only) was extremely high ( $R^2 = 0.998$ , Fig. S6.2), which indicates that the discrepancy in the computation procedure did not influence the outcome of our analyses. To verify the robustness of our results, we analysed sex differences in longevity using different longevity metrics. We thus calculated the median longevity (i.e. age at which half of the individuals in the population are dead) using the same dataset as for the longevity 80%. We also extracted maximum longevity (see above) and life expectancy (i.e. mean of ages at death) from the distribution of ages at death (using longitudinal and transversal-dx data with no censoring at old age). Results obtained with the four longevity metrics are displayed in Table 1.

Aging rates were estimated from the parameters of the Siler model fitted for each sex. We therefore only used populations in which the Siler model was fitted (i.e. longitudinal and transversal-dx data). Contrary to the Gompertz model, the Siler model allows mortality to increase at any age after the age at first reproduction. As a metric of aging rate, we used the  $b_1$  parameter of the Siler model (see Eq. (1)) that measures the exponential increase in mortality rate with age during the senescence stage.

### 3.3. Statistical analyses

For each population, we quantified sex differences in longevity as the ratio between male longevity and female longevity on a log scale (difference longevity =  $\log\left[\frac{\text{longevity male}}{\text{longevity female}}\right]$ ). For the analysis of sex differences in longevity, we ran a Bayesian hierarchical model using the package MCMCglmm (Hadfield, 2010) with the value of the longevity difference as the response variable. As species from our dataset were not independent because they share phylogenetic relatedness, we corrected all our analyses for phylogeny using the phylogenetic variance-covariance matrix extracted from a mammalian phylogenetic tree (Bininda-Emonds, Gittleman, & Purvis, 1999). Moreover, in some species (N = 21), estimates from several populations were available and the data from these populations were thus not independent. Thus, we fitted the species independently of the phylogeny as a random effect because individuals from the same species can share different ecological characteristics, which are not necessarily linked to the phylogenetic relatedness. To test the sensitivity of the results to the priors, we used two sets of priors for the random effects in the model (uninformative inverse Wishart prior with  $\nu=0.02$  and  $V=1$  and expanded prior with  $\nu=1$   $V=1$   $\alpha.\nu=0$   $\alpha.V=1000$ ). Models with different priors did not show any detectable difference (Gelman and Rubin's convergence diagnostic very close to 1 for each MCMC chain (Gelman & Rubin, 1992)). From this model we were able to extract the percentage of the total variance explained by the phylogenetic effect (named phylogenetic heritability  $H^2$ ) (Hadfield & Nakagawa, 2010). The value of  $H^2$  can be interpreted as a direct equivalent to the phylogenetic signal ( $\lambda$ ) of Pagel (Harvey & Pagel, 1991), a value close to 1 means that there is a strong phylogenetic signal and a value close to 0 means that there is no phylogenetic signal. For each parameter, the mean of highest posterior density distribution, the lower and upper limits of the 95 % credibility interval and the p-values are reported.

The first aim of our analyses was to estimate the average sex difference in longevity across the whole set of mammals. We thus ran the model of sex difference in longevity without any independent covariate or factor and found a longer longevity for females in the dataset with an overall negative effect (see Tab. S6.4a for all coefficients). There was no detectable phylogenetic effect for the sex difference in longevity ( $H^2 = 20\%$ ). When running the same model using longevity as the dependent variable, a high phylogenetic effect occurred in both females ( $H^2 = 91\%$ ) and males ( $H^2 = 90\%$ ).

In a second step, we aimed to test whether some species-specific traits (sexual size dimorphism, mating system, social system) or population characteristics (hunting status, data quality) explained sex differences in longevity observed across mammals. We included sexual size dimorphism (SSD, computed as the ratio between male and female body mass on a log scale), the hunting status of the population (i.e. hunted vs. non-hunted), the data quality (longitudinal vs. transversal data) and all the two-way interactions among these factors. To identify the model of sex differences in longevity with highest support, we fitted different models with all the possible combinations of variables from the full model (N = 18 models). These models were then ranked by the Deviance Information Criterion (Spiegelhalter *et al.*, 2002) (Table S6.2). The selected model included additive effects of hunting (i.e. sex differences in longevity were highest in hunted populations) and data quality (i.e. higher sex differences occurred in longevity with high quality data, Tab. S6.4.B and Fig. S6.1).

The social system was highly correlated to the mating system. Indeed, except for the four-striped grass mouse (*Rhabdomys pumilio*) (Schradin, Kinahan, & Pillay, 2009) all cooperative breeders (N = 6) in our dataset were monogamous. We thus tested separately the influence of the mating and social systems. The independent model including only mating system as a covariate did not reveal any effect on sex differences in longevity (mean difference monogamous vs. polygynous = -0.02 [-0.27 ; 0.23], mean difference monogamous vs. promiscuous = -0.03 [-0.29 ; 0.23]). Similarly, the model including only social system did not reveal any detectable effect (mean difference cooperative vs. non-cooperative breeder = 0.01 [-0.23 ; 0.25]).

For each population, we computed sex differences in aging rates as the ratio between male and female aging rates on a log scale (difference aging rate =  $\log\left(\frac{\text{aging rate male}}{\text{aging rate female}}\right)$ ). We then followed the same procedure as used for sex differences in longevity. We found no statistical support for consistent sex differences in aging rates across species (Tab. S6.1). The phylogenetic relatedness only accounted for a low proportion of variance ( $H^2 = 27\%$ ). When running the same model using only aging rate as the dependent variable, a high phylogenetic effect occurred in both females ( $H^2 = 87\%$ ) and males ( $H^2 = 88\%$ ).

We performed a second set of analyses to test whether some life history traits can explain possible sex differences observed in aging rates across mammals. Similar to the analyses performed for sex differences in longevity, we included SSD, hunting status and data quality (Tab. S6.2) and all the two-way interactions between these variables. We also tested

all combinations of the full model and ranked them based on their DIC score to identify the variables influencing the difference in aging rates. The Null model was ranked first, revealing that none of these variables influenced the magnitude and the direction of sex differences in aging rates (Tab. S6.3). Moreover, additional analyses did not reveal any effect of either mating or social system (mean difference monogamous vs. polygynous = -0.05 [-0.58 ; 0.46], mean difference monogamous vs. promiscuous = 0.02 [-0.52 ; 0.54] - (mean difference cooperative vs. non-cooperative breeder = -0.19 [-0.59 ; 0.21]).

## 4. Supplementary Text

### 4.1. Aging rate relative to longevity

Longevity and aging rates were closely associated across mammals (phylogenetic regression: slope =  $-0.72 \pm 0.06$ ,  $p < 0.001$ ,  $R^2 = 0.64$ , see statistical analyses for method and models used for all the regressions and the Fig. S6.3). Short-lived species age thus faster than long-lived species, as well established in the aging literature (25, 26). To obtain measures of aging rates independent of longevity (hereafter called relative aging rate), we also computed the aging rate relative to longevity as the residuals of the phylogenetically corrected relationship between the parameter  $b_1$  (see methods, Eq. (1)) and longevity (both log-transformed) as follows

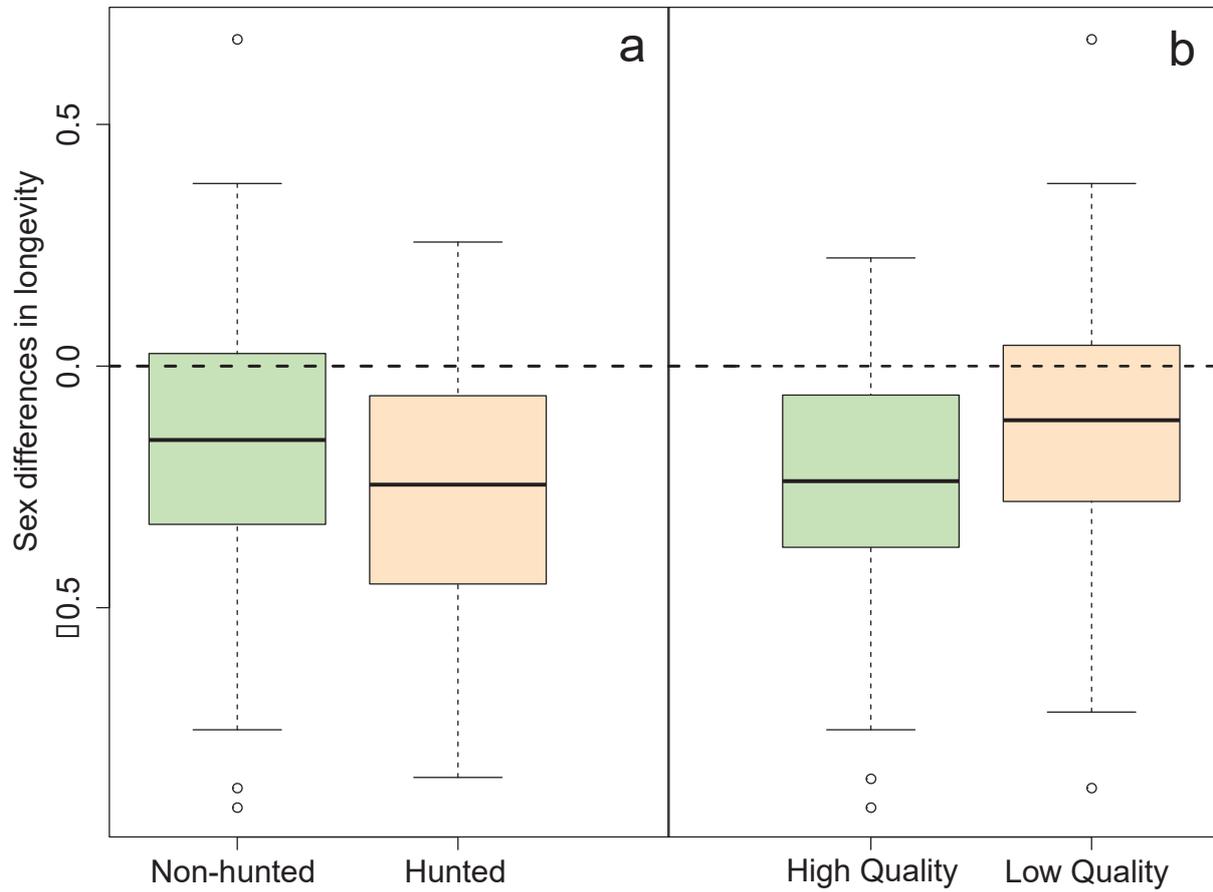
$$\text{relative aging rate} = \log(\text{aging rate}) - (-0.72) \times \log(\text{longevity}) - 0.29 \quad (3)$$

To account for the negative association between longevity and aging rate, we performed a similar analysis to absolute aging rate (see Methods) using the relative aging rate and we found similar results. There were no consistent differences between males and females in relative aging rates (Tab. S6.5). The Null model was ranked first (Tab. S6.6), revealing that none of the sexual size dimorphism, hunting status and data quality influenced the magnitude of sex differences in relative aging rates. There was also no effect of mating or social system (mean difference monogamous vs. polygynous = -0.19 [-0.69; 0.34], mean difference monogamous vs. promiscuous = -0.12 [-0.63; 0.41] - (mean difference cooperative vs. non-cooperative breeder = -0.19 [-0.60; 0.21]).

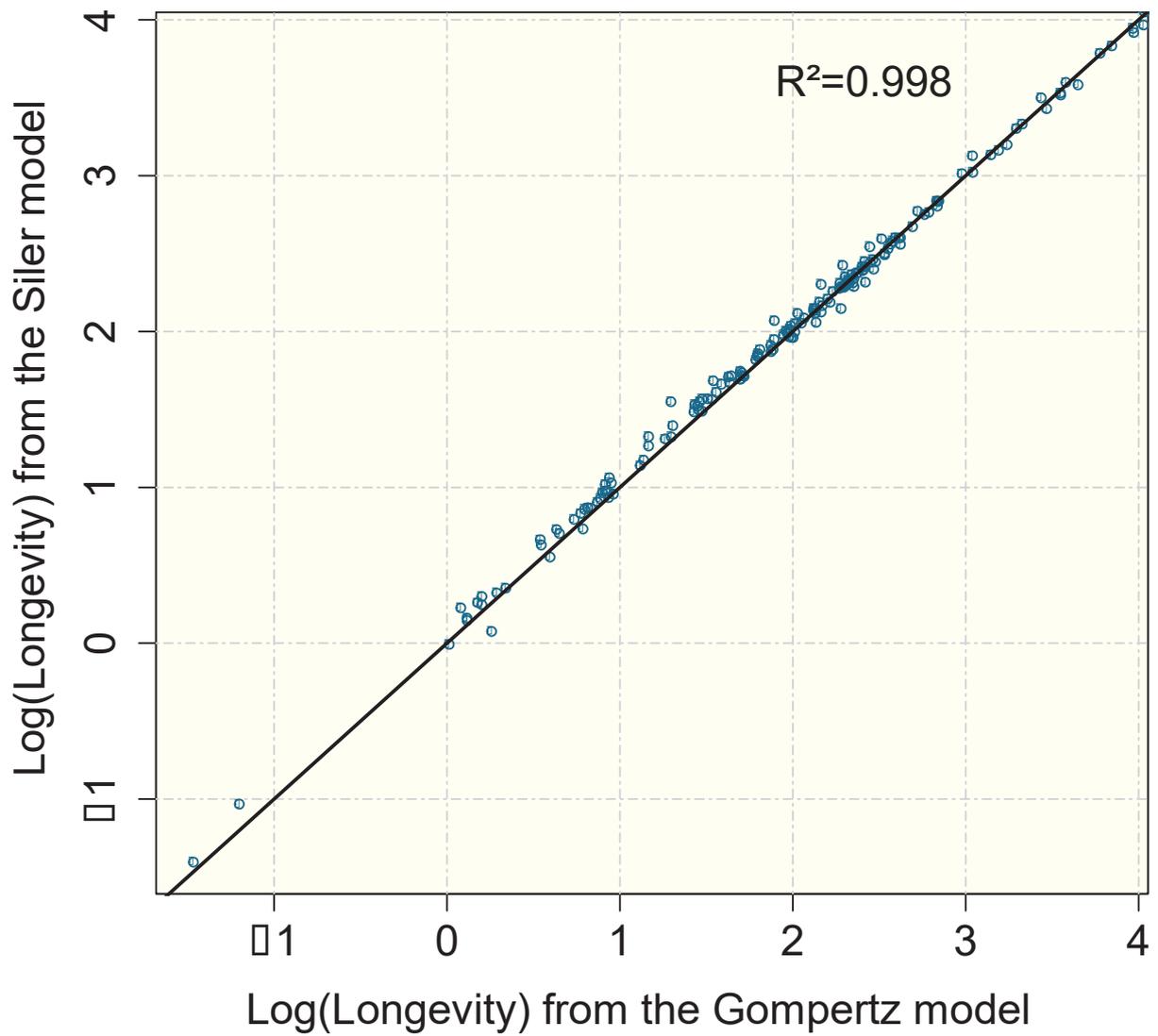
#### *4.2. Relationship between male and female longevity*

To assess whether sex differences in longevity were the same in fast or slow life histories, we first ran a Bayesian hierarchical analysis (see Material and Methods) for all species by regressing male longevity against female longevity. Same sex differences in longevity between slow and fast life histories should lead to a slope close to 1. However, the estimated slope was lower than 1 (slope =  $0.90 \pm 0.03$ , Fig S6.4), showing that sex differences in longevity increase with female longevity (i.e. longer-lived species).

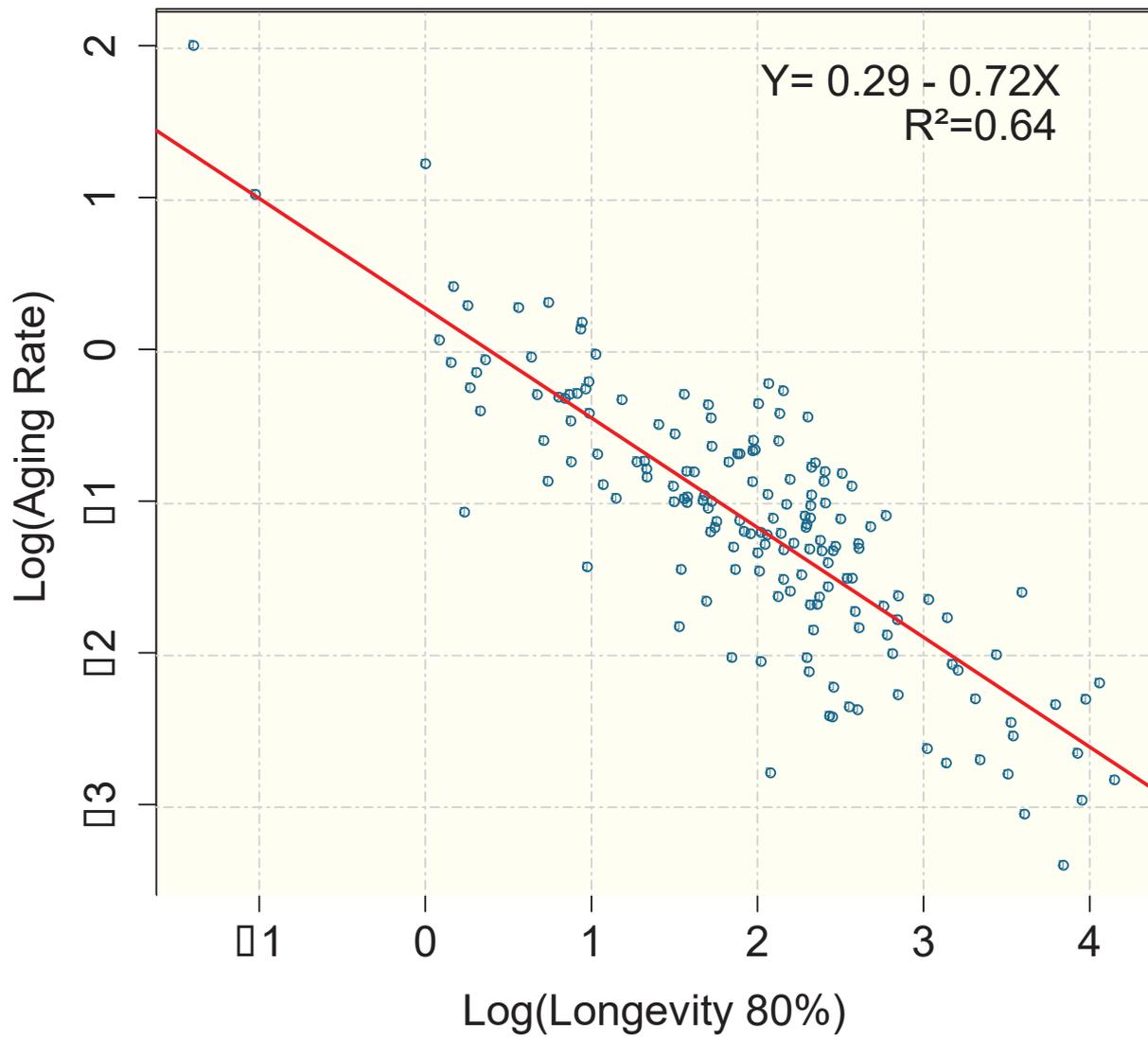
## 5. Supplemental Figures



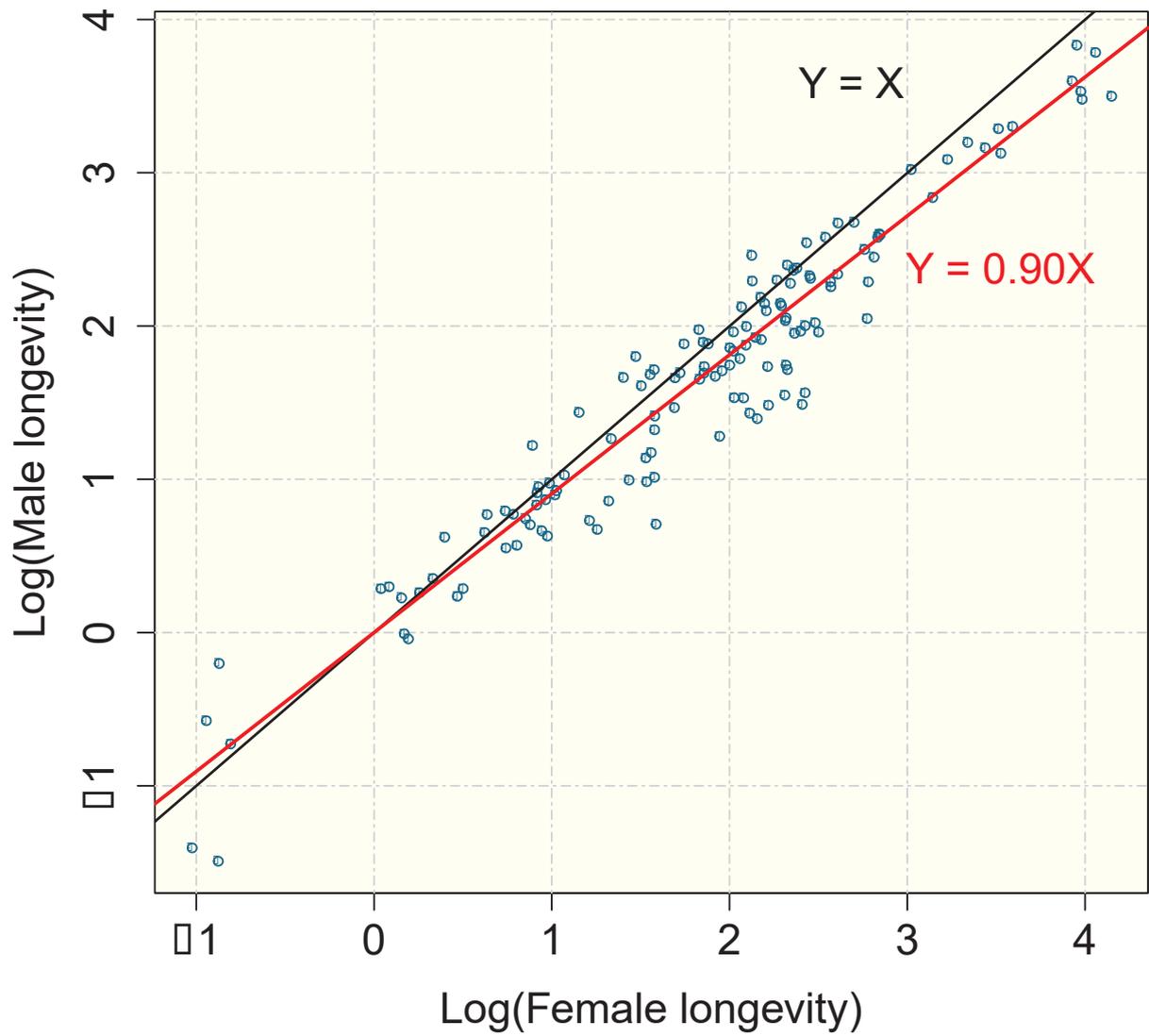
**Figure S6.1.** Effect of hunting (hunted vs. non-hunted populations, (a)) and data quality (longitudinal-high quality vs. transversal-low quality (b)) on sex differences in longevity across mammals.



**Figure S6.2.** Relationship between longevity estimated using a Gompertz model and longevity estimated using a Siler model (only ‘longitudinal’ and ‘transversal-dx’ data were included in this analysis).



**Figure S6.3.** Relationship between aging rate and longevity on a log-log scale.



**Fig. S6.4.** Allometric relationship between male and female longevity. The best regression line is in red. The black line represents isometry (i.e. slope of 1).

**Table S6.1.** Mean of the posterior distribution of the difference between sexes in aging rate (null model selected). The mean sex difference is associated with the 95% credibility interval and with the p-value.

Parameter	Mean	Lower CI	Upper CI	<i>P</i>
Sex difference (Intercept)	0.180	-0.131	0.522	0.207

**Table S6.2.** Ranking of the different models for the analysis of sex differences in longevity using Deviance Information Criterion. The selected model is in bold (SSD: sexual size dimorphism). Only the five models with the highest support and the null model are presented.

Models	DIC	$\Delta$ DIC
<b>Hunted+Quality</b>	<b>18.8</b>	<b>0</b>
Hunted+Quality+SSD	19.18	0.38
Hunted+Quality+SSD+Quality*SSD	19.38	0.58
Hunted+Quality+SSD+Hunted*SSD+Quality*SSD	20.11	1.31
Hunted+Quality+Hunted*Quality	20.79	1.99
...	.	.
Null	27.65	8.85
...	.	.

**Table S6.3.** Ranking of the different models for the analysis of the sex differences in aging rate using Deviance Information Criterion. Selected model is in bold (SSD: sexual size dimorphism). Only the five models with the highest support (including the null model) are presented.

Models	DIC	$\Delta$ DIC
<b>Null</b>	<b>89.1</b>	<b>0</b>
Quality	89.43	0.33
SSD	90.36	1.26
Quality + SSD	90.66	1.56
Hunted	90.69	1.59
...	.	.

**Table S6.4.** Mean of the posterior distribution of sex differences in longevity from the null model (a) and the model with the highest support (b). Each parameter is associated with the lower and upper limits of 95% credibility interval and also with the Bayesian p-value.

a: Null Model

Parameter	Mean	Lower CI	Upper CI	<i>P</i>
Sex difference (Intercept)	-0.171	-0.329	-0.007	0.038

b: Model with highest support based on DIC

Parameters	Mean	Lower CI	Upper CI	<i>P</i>
Intercept	-0.227	-0.395	-0.045	0.015
Hunted (Yes)	-0.128	-0.259	0.005	0.058
Data quality (transversal)	0.140	0.042	0.249	0.010

**Table S6.5.** Mean of the posterior distribution of sex differences in *relative* aging rate from the null model. The mean sex difference is associated with the lower and upper limits of 95% credibility interval and with the p-value.

Parameter	Mean	Lower CI	Upper CI	<i>P</i>
Sex difference (intercept)	0.061	-0.291	0.382	0.690

**Table S6.6.** Ranking of the different models of the sex difference in *relative* aging rate using Deviance Information Criterion. The selected model is in bold (SSD: sexual size dimorphism). Only the five models with the highest support (including the null model) are presented.

Models	DIC	$\Delta$ DIC
<b>Null</b>	<b>88.7</b>	<b>0</b>
SSD	89.49	0.79
Quality	90.27	1.57
Hunted	90.48	1.78
Quality + SSD	91.18	2.48
...	.	.

## Chapter VII

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# **Analysing the distribution of ages at death: a new way to assess the diversity of senescence patterns in the wild**

**A version of this chapter is in preparation for submission to a special feature of Functional Ecology:**

**Victor Ronget & Jean-Michel Gaillard.** Analysing the distribution of ages at death: a new way to assess the diversity of senescence patterns in the wild

## 1. Abstract

An increasing number of studies has investigated the diversity of actuarial senescence patterns in the wild. Most of these studies used maximum longevity as a metric and only some of them were based on the analysis of mortality or survival curves. We first review why maximum longevity should not be used in comparative analyses of senescence as commonly done in some fields such as genomics of aging. However, age-specific mortality curves that allow estimating relevant metrics such as the rate and the onset of actuarial senescence display markedly different shape across species and even among populations within a given species, leading comparative analyses difficult to perform in absence of standardized metrics. We propose to solve this problem by analysing the distribution of the ages at death as an alternative to mortality or survival curves. The distribution of the ages at death along with its probability density function is commonly used to study actuarial senescence in human demography. We review the different metrics that allow assessing the age at death distribution, including the mean, the variance and the mode. We then show how those metrics are associated with different patterns of mortality increase and we provide guidelines on how to use mean of the age at death distribution in a comparative framework by rescaling the distribution of ages at death by the longevity. We illustrate our approach by performing, using a simple metrics, a comparative analysis of actuarial senescence across 30 species of mammals. The results strongly support the relevance of using metrics based on the distribution of the ages at death to assess reliably patterns of actuarial senescence. In particular, we found that life expectancy rescaled is closely related to the generation time. We conclude that the metrics defined from the distribution of ages at death provide a complementary approach to mortality or survival curve analysis and, by offering straightforward standardization, provide promising tools for future comparative analyses of actuarial senescence across the tree of life.

## 2. Introduction

The actuarial senescence is described as the increase of mortality with age (Monaghan *et al.*, 2008). Those patterns of senescence are widespread through the animal kingdom (Jones *et al.*, 2008) and they are also very variable between species and even between populations (Jones *et al.*, 2014). One of the major questions in aging research now is to understand the factors explaining the differences between those patterns. This has led to large number of

studies trying to understand the mechanisms influencing senescence using a comparative approach (Austad & Fischer, 1991; Gomes *et al.*, 2011; Aledo *et al.*, 2012). However, to explain those variations between species an accurate description of the patterns of actuarial senescence is first needed. There has been many metrics developed by demographers to describe actuarial senescence such as longevity, rate of senescence or onset of senescence, with most of the comparative analyses in aging research being based on longevity.

In this review, we want to present different ways to extract metrics for comparative analysis from patterns of senescence. We thus review the uses of longevity in comparative analyses of actuarial senescence by presenting the advantage and disadvantage of the three metrics of longevity, the maximal longevity, the life expectancy and the 90% longevity. In a second part we will focus on applying new metrics first developed for human demography to describe the distribution of ages at death.

### **3. The uses and misuses of longevity**

#### *3.1. Describing the patterns using mortality curves*

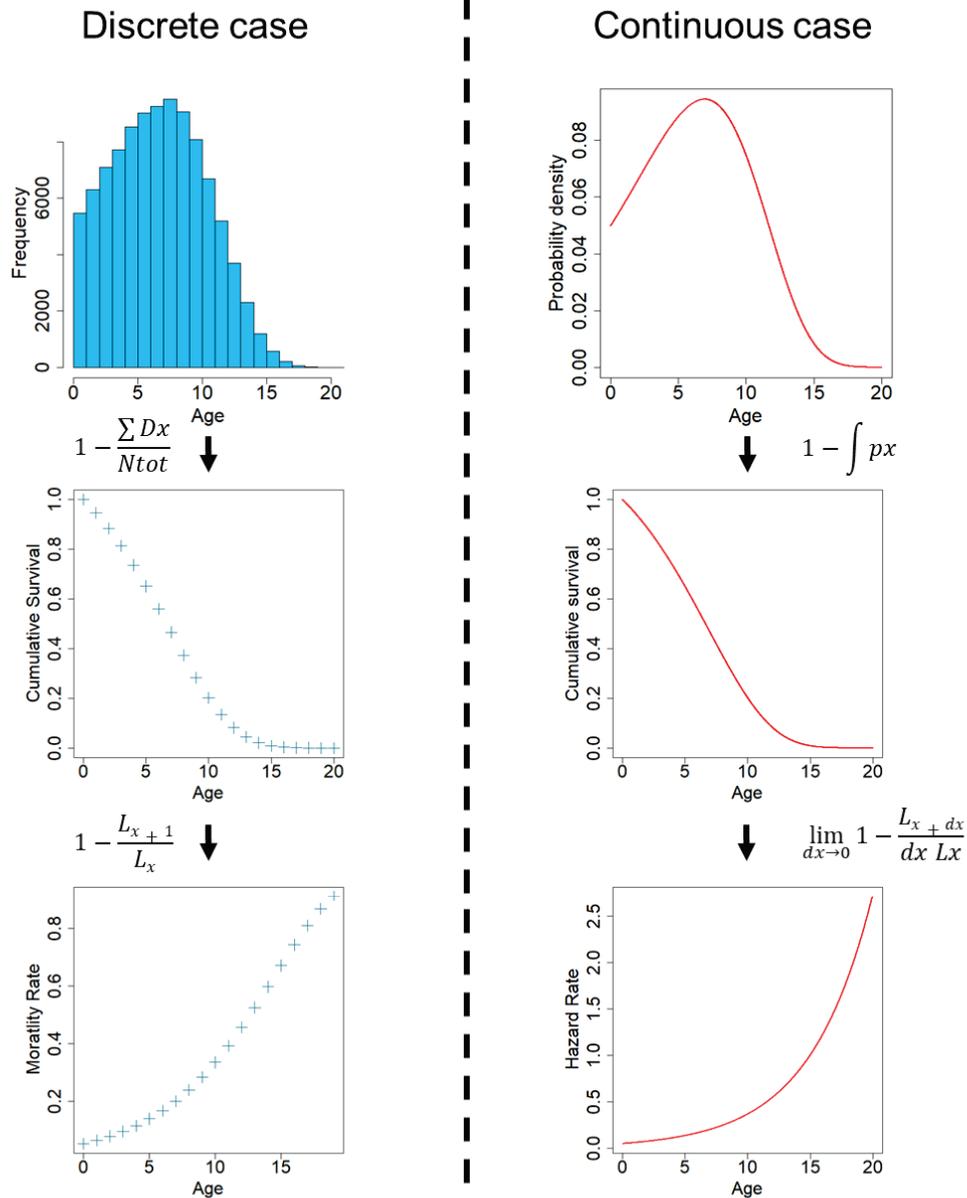
Every aged-structured demographic dataset can be describe using their rawest form. For each individual in the population his lifespan is recorded. We can thus present the distribution of the lifespan in the focal population which is also called distribution of ages at death of a population. From this distribution, other quantities such as the mortality rates per age as well as the cumulative survival can be calculated (See Fig. 7.1). Most of the demographic studies have focused on the modelization of the mortality rate or of the force of mortality to describe the variation of the actuarial senescence between species (Ricklefs, 2010). The main practice is to model the mortality rates using continuous model such as the Gompertz model or the Weibull model (Promislow & Harvey, 1990; Ricklefs & Scheuerlein, 2001). Thus, by extracting metrics for these curves we can describe the actuarial senescence pattern with for instance the basal mortality rate and the rate of senescence for the Gompertz model (Tidière *et al.*, 2015). There are two types of metrics used to describe the patterns of senescence, metrics describing the pace or metrics describing the shape of the patterns of senescence (Baudisch, 2011). Pace metrics are associated with the duration of the pattern of senescence whereas shape metrics are associated with the form of the pattern of senescence

(i.e. how does the mortality increase). There has been lot of methodological advance in demography to devise such metrics which were highly used in comparative analysis in evolutionary demography. However, one of the major drawbacks is that to model those patterns demographic datasets with high sample sizes are needed. To get accurate mortality rate for old ages we need a sufficiently high number of individuals to survive to old ages. This is not an issue for some species well monitored such as human with for instance life tables easily accessible from the Human Mortality Database (<https://www.mortality.org/>). Nonetheless for comparative analysis metrics describing the actuarial senescence are needed for multiple species which are not necessarily well monitored, or in which data are not easily accessible.

### *3.2. The different metrics of longevity*

Instead of using metrics from mortality curves most of the comparative analysis used species longevity. We first need to define the notion of longevity. Through the manuscript we refer to longevity as the notion answering the question of how far individuals of a population can survive. In the rest of this paper we thus describe longevity as any scale metric describing the duration of the pattern of actuarial senescence. There are three metrics mainly used when referring to longevity, the maximal longevity, the life expectancy at birth and the 90% longevity. All those metrics are position indices for the distribution of ages at death. We will next define those metrics and review their uses in comparative analyses:

- The maximal longevity or maximum recorded lifespan is defined as the oldest age at death for a population. The simplicity of this metrics explains most of his success in the literature of aging (Finch, Pike, & Witten, 1990; Austad & Fischer, 1991; Clutton-Brock & Isvaran, 2007). Full knowledge of the age at distribution are not even needed to compute this metrics, just some records of the age at death for old individuals are needed to get the maximum longevity making it easy to get maximum longevity records for most of the species. Those maximum longevity are now compiled in several aging database such as Anage (Magalhães & Costa, 2009) or Pantheria (Jones *et al.*, 2009) making it easy to include it into analysis of actuarial senescence. Because of the accessibility of these data most of the comparative analyses on aging non-focused on demographic aspects used maximum longevity and thus tried to find the traits that explain the difference in maximal longevity between species (Aledo *et al.*, 2012).



**Figure 7.1.** Going through the different presentation of age-structured datasets from discrete to continuous timestep. Every age structured population can be described using discrete time step. Here we take an example of a population following a Gompertz law of mortality. On the left, the population is described using a yearly timestep, we can thus describe the distribution of ages at death and its probability density associated for the continuous case in the right. From those distributions we can compute the cumulative survival function which represents the proportion of individuals still alive. From this function we can compute the mortality rate  $q_x$  which is the probability for an individual to die between the age  $x$  and  $x+1$  and we can also compute its continuous analogous the hazard rate which consider a timestep tending to zero.

- The life expectancy at birth is defined as the average lifespan of the individuals in a population (or the mean of the distribution of the ages at death). This definition is also simple to grasp and explain his success notably in describing the difference in longevity between human populations. Instead of basing the measurement of longevity on only one individual, the measurement of longevity here is based on all the individuals of the population. However, one the greatest disadvantage of such metrics is that we need to know the entirety of the distribution of age at death which is easily accessible for most of human population explaining its success in human demography (Olshansky, Carnes, & Désesquelles, 2001; Oeppen & Vaupel, 2002). Moreover, the life expectancy is dependent on all the individuals in the population thus if most of the individuals died in early age this is likely to drag the value toward younger ages, in that case life expectancy did not fit well with the definition of longevity because it does not inform us on the duration of the pattern of life. In human young and adult mortality are typically very low (Rosano *et al.*, 2000) thus life expectancy is mostly dependent on the old individuals which grasp more the notion of longevity however in most of animals most of the individuals still die mostly at young ages because of extrinsic mortality such as predation (Linnell *et al.*, 1995). We thus conclude that for most of the species life expectancy could be inadequate to integrate longevity in comparative analyses.

- 90% longevity or 90<sup>th</sup> quantile of longevity is described as the age where at least 90 % of the individuals of a population died (or the 90<sup>th</sup> quantile of the ages at death distribution), this last metric was developed recently by demographers (Moorad *et al.*, 2012). The basic idea is to not base the measurement of longevity on only one individual as for the maximal longevity but on the 10% of older individuals. By doing this we can get an accurate measurement of longevity which is not so dependent on the early mortality. However, as well as the life expectancy the full knowledge of the distribution of ages at death is needed which explains why it was less used than maximal longevity in comparative analysis. In fact, it was mostly used in demographic comparative analysis by research groups having the highest quality datasets (Tidière *et al.*, 2015, 2016a).

### 334. *The impact of sample size on the three-longevity metrics*

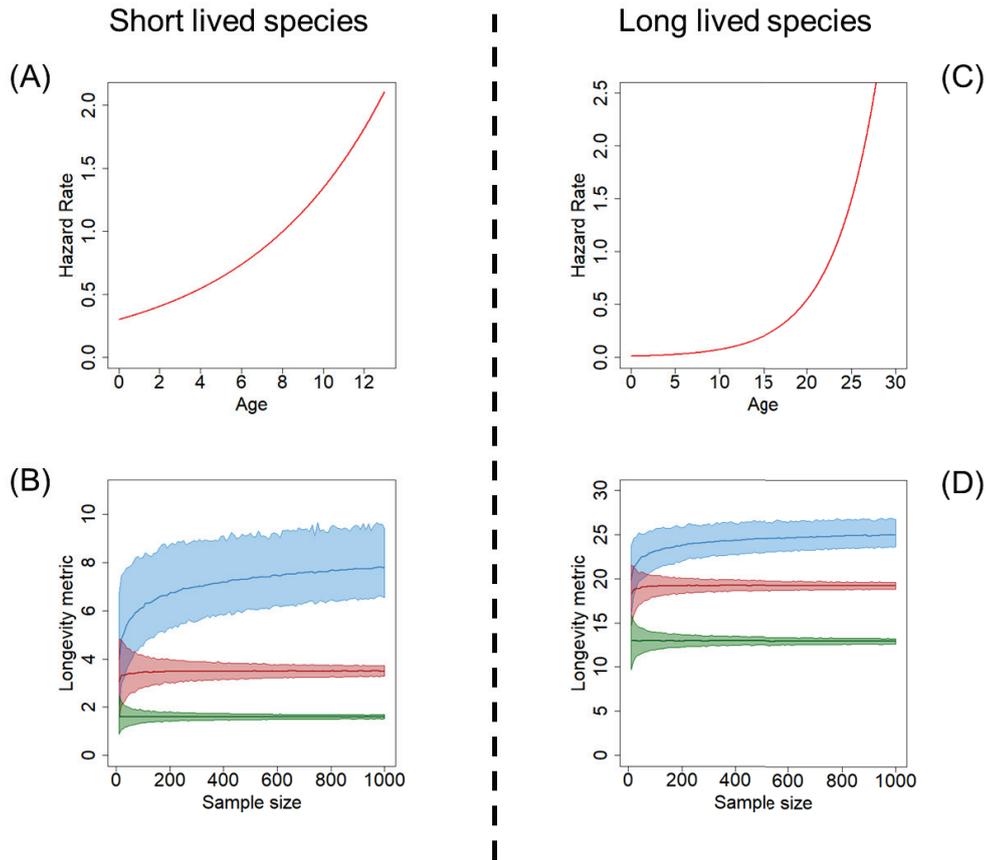
It clearly appears that most of the comparative study used the maximum longevity as a measurement of longevity. It is understandable why this metric is so much used, databases are well developed and well referenced in the literature. 90% longevity was developed as an alternative to maximal longevity. Some authors already warn about the uses of maximum longevity and particularly the fact that maximum longevity is dependent on the sample size (Moorad *et al.*, 2012). In the new part we will comparatively assess how does the three different metrics respond to the sample size of the demographic dataset.

We can assess by simulation how the three metrics respond to sample size for a population in which we know the exact force of mortality. We define two different population with a force of mortality following a Gompertz law (Gompertz, 1825).

$$\mu(x) = ae^{bx}$$

With  $a$  the initial hazard of mortality and  $b$  the rate of mortality increase.

We simulate one population corresponding to a long lived species with  $a=0.01$  and  $b=0.2$  and one other population corresponding to a short lived species with  $a=0.5$  and  $b=0.15$ . We thus simulate the sampling of individuals when monitoring populations by randomly sampling lifespan of individuals on the continuous probability density distribution of ages at death. For each sample size, 10000 distributions of age at death were sampled, for each distributions the three metrics of longevity were calculated. We thus can calculate for each sample sizes, the average as well as the 95 % interval (sampling variance) of each of the three metrics. Results are presented in the figure 7.2.



**Figure 7.2.** The effect of sample size on three longevity metrics. Hazard of mortality in function of age for (A) short lived species and (B) long lived species. Longevity metrics in function of sample size for (B) short lived species and (D) long lived species with in blue maximal longevity, in red life longevity 90% and in green life expectancy at birth. For each sample size and each metrics, the average value as well as the 95% quantiles are presented.

As previously demonstrated in the literature, maximal longevity average value increase with sample but life expectancy and 90 % longevity did not (Moorad *et al.*, 2012). The probability to find a very old individual in the population increase with the sample size thus results of comparative analyses are likely to depend on the sample size of the demographic record used for each species included in the analysis. On the contrary the average value does not change with sample size for the life expectancy and the 90% longevity in the short lived and long lived cases. Moreover, we found that the 95% quantiles representing the sampling variance of the metrics stays high regardless of the sample size for the maximum longevity. This highlights the fact that whatever the sample size the value of the maximal longevity is always based on one individual and thus could be very variable

depending on the individual sampled. On the contrary, for the longevity 90% and the life expectancy the sampling variance decrease with an increasing sample size. Longevity 90% and life expectancy are based on all the individuals and thus as the sample size increases, we expect those metrics to be less variable.

### *3.4. Which longevity metrics use in comparative analysis*

We described the advantages and the disadvantages of each of the longevity metrics (Tab. 7.1.) and from our conclusion the 90% longevity is the most adapted one for comparative analysis using animal datasets. The statistical issue associated with the maximal longevity are too important to be neglected and we even argue that they can have a major impact on the final results of the study. However, to use widely these 90% longevity metrics there is still a major drawback associated with the demographic data needed to compute this metrics. We argue here that comparative analysis reporting 90% are more and more common and thus instead of using maximal longevity researcher should use when possible the longevity from those comparative analysis (i.e. Tidière *et al.*, 2016).

## **4. Other metrics to describe the age at death distribution**

### *4.1. Describing the distribution of ages at death*

When describing the patterns of actuarial senescence most of the study in the wild focus on the mortality curve and thus describe standard metrics such as the rate of senescence (slope of the relationship) or the onset of senescence (Jones *et al.*, 2008) (when the senescence pattern begins). The distribution of age at death received much less attention in comparative studies despite the works in human demography describing this distribution (Wilmoth, 2000). The longevity metrics can in fact be considered more as descriptors of the distribution of age at death because they are position indices for this distribution. There are other metrics than position indices that are typically used when describing distributions.

**Table 7.1** The advantages and disadvantages of each longevity metrics

	<b>Advantages</b>	<b>Disadvantages</b>
<b>Maximal longevity</b>	<ul style="list-style-type: none"> <li>- Full distribution of the ages at death not necessarily needed for calculation</li> <li>- Reported for most of the species</li> </ul>	<ul style="list-style-type: none"> <li>- Increases with sample size</li> <li>- High sampling variance independent of sample size</li> </ul>
<b>Life expectancy</b>	<ul style="list-style-type: none"> <li>- Sampling variance decreases with sample size</li> <li>- Average value consistent with the sample size</li> </ul>	<ul style="list-style-type: none"> <li>- Full distribution of the ages at death needed for calculation</li> <li>- Based on the ages at death of all individuals (not only the oldest ones)</li> </ul>
<b>90% Longevity</b>	<ul style="list-style-type: none"> <li>- Sampling variance decrease with sample size</li> <li>- Average value consistent with the sample size</li> <li>- Based on the 10% oldest individuals</li> </ul>	<ul style="list-style-type: none"> <li>- Full distribution of the ages at death needed for calculation</li> </ul>

The most common metric to describe a distribution in statistics after the mean is the variance. There has been lot of work in human demography focusing on the variance of the distribution (Tuljapurkar, 2010). In most of human populations, individuals tend to die more and more at old age and less and less at young age (Edwards & Tuljapurkar, 2005). One graphical way to see this phenomenon is to look at the cumulative survival function which tend to be more and more rectangular with no individuals dying young and most of the individuals dying old resulting in a net decrease of the cumulative for these ages. This phenomenon is called the rectangularization of the survival curve (Manton & Tolley, 1991; Nusselder & Mackenbach, 1996). One of the most efficient way to measure this rectangularization of the curve is to measure the variance of the age at death distribution. As most of the individuals are now dying approximatively at the same old ages, the variance is decreasing with the rectangularization of the survival function. Moreover, variance was also

linked to key patterns of the mortality curve. For instance, it was demonstrated that the rate of senescence from a Gompertz model is inversely related with the variance of the distribution of age at death (Tuljapurkar & Edwards, 2011).

Closely related to the study of variance for human populations, the description of the topology of the distribution of age at death has also received much attention. One of the key topological features of the distribution of age at death in human is the mode of mortality associated with all the individuals dying at old ages. In most of human populations we can describe a mode of mortality at old ages and thus the age at which the mode occurs called modal age at death has been used to describe the evolution of mortality within the history of humanity (Horiuchi *et al.*, 2013). For instance there is an increase of the modal age at death in most of the population of humans associated with the rectangularization of the survival curve (Canudas-Romo, 2008). Like the variance, the modal age at death has been linked to parameters of the mortality curve. With for instance a positive correlation between the Gompertz rate of aging and the modal age at death (Missov *et al.*, 2015).

To date there is no comparative analysis to our knowledge that tried to investigate the patterns of variance or the modal age at death for animals. As we saw those two metrics are closely linked to the Gompertz rate of senescence which can inform us on the shape of the mortality curve without modelling the force of mortality. However, the interpretations of those metrics should be more difficult because of the large diversity of actuarial senescence patterns in animal populations and for instance a mode of mortality is not necessarily expected in all species depending on the topology of the age at death distribution.

#### *4.2. Rescaling ages at death by longevity*

Longevity measurement are considered as pace metrics but some metrics especially the variance can inform us more on the shape of the actuarial senescence patterns. The major issue with the variance is that it is highly correlated with longevity when comparing species with very different patterns of aging. The value of variance should increase as the range of ages increases. Thus, long lived species have mathematically a higher variance than short lived species. In humans, variance was used to define if there is any area in the distribution of age at death where the mortality is concentrated. We can get a similar metrics by rescaling all ages at death by the 90% longevity of the population. Using this scaling, we can remove the

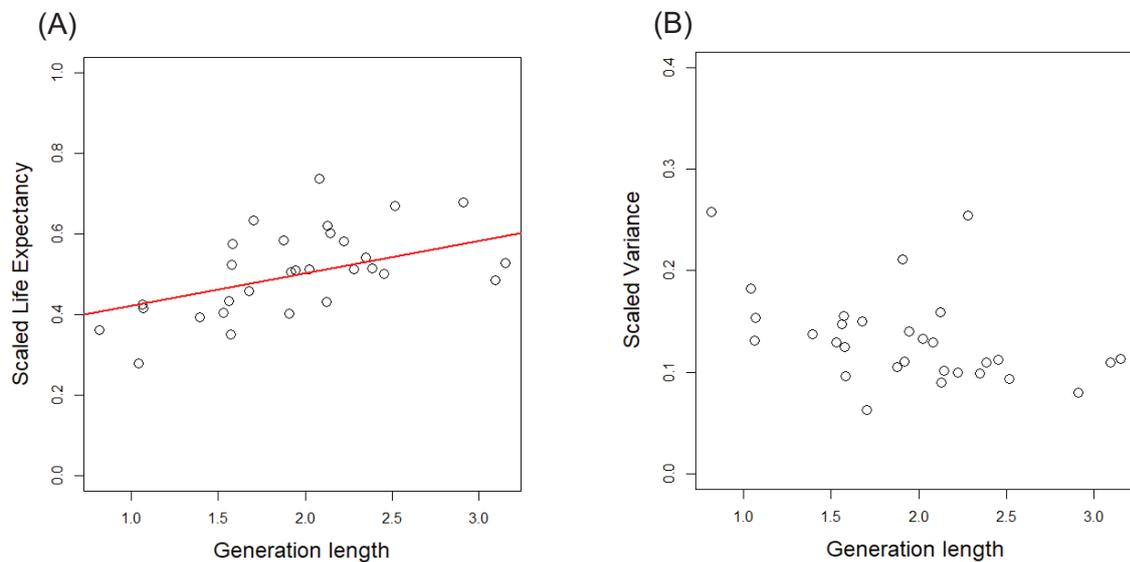
correlation between the longevity and the variance and compute a measurement of shape of aging to see if the mortality is concentrated at certain age or is scattered through all ages.

The modal age at death inform us on which age does most of the individuals dies in the population. It is difficult to apply directly this method to animal distribution of age at death because the presence of a clear mode is not expected as a large proportion of adult individuals can die relatively young. However, the mean of the distribution (i.e. the life expectancy) can inform us on the average age at death at thus by rescaling by the longevity as previously we can assess if the individuals are likely to die at old age comparatively to the 90% longevity of the population.

To assess the performance of those two new metrics, we compiled the distributions of ages at death for 30 species of mammals (See Tab. S7.1. for species included and references). To limit the impact of the high juvenile mortality observed in mammals, we chose to begin the distribution of ages at death at the age of first reproduction. All ages were rescaled by the 90% longevity of each populations and mean and variance of the distribution of ages at death were calculated based on those rescaled ages at death. To assess the how much those metrics are appropriate to describe the diversity of actuarial senescence pattern we compute the generation length for each of the species as a proxy of the slow-fast continuum of species (See Appendices for details on the calculation of generation length). We then compute the relationship between scaled mean and generation length in logarithm scale and between scaled variance and generation length in logarithm scale using the package *MCMCglmm* (Hadfield, 2010) and correcting by the phylogenetic relatedness (Bininda-Emonds *et al.*, 2007).

We found only a positive relationship for the relationship between scaled life expectancy and generation length (slope=0.082; 95%CI= [-0.009;0.168]). This demonstrates that individuals from long lived species are more likely to die at old age comparatively to their longevity and short-lived species on the contrary die relatively young compared to their longevity. Interestingly we found no relationship between scaled variance and generation length. All scaled variances appear to be very closed which could potentially indicate that the ages at death are evenly dispersed. This also makes sense when looking at the range of scaled life expectancy which are between 0.2 and 0.8. There are no populations like humans in which distribution is heavily biased towards very old individuals and thus are likely to have a very compressed mode associated with a low variance. This primary attempt to used scaled metrics to describe the age at death provide promising results however we still need to

calculate variances on a much greater dataset to understand better the diversity of the distribution of ages at death.



**Figure 7.3.** Relationship between scaled descriptors of the distribution of ages at death and the generation time for 30 species of mammals. (A) relationship between scaled life expectancy and generation length (B) relationship between scaled variance and generation length

## 5. Conclusion

In this study we reviewed different approaches to describe actuarial senescence patterns using the distribution of ages at death. We demonstrated the importance of using 90% longevity instead of maximal longevity. Despite the wide use of the maximum lifespan in the literature we warn about the statistical issue arising from the use of an extreme value of a distribution which could have critical impact on the results of comparative analysis. We believe that the description of the distribution of age at death using variance and modal age at death could provide promising tools to understand the diversity of actuarial senescence patterns. We provide some perspective using rescaled metrics that could permit to apply metrics typically used for human demography to comparative analysis of animals. We thus urge researchers in aging to not only use only mortality curves or longevity to understand senescence patterns but to uses also other metrics described in the literature to get a complementary vision on those patterns.

## 6. Supplemental materials

**Table S7.1.** References for survival and reproduction used to calculate mean and variance of the ages at death and the generation time for each mammalian species.

<b>Species</b>	<b>Reference Survival</b>	<b>Reference Reproduction</b>
<i>Alces alces</i>	(Ericsson <i>et al.</i> , 2001)	(Ericsson <i>et al.</i> , 2001)
<i>Bison bison</i>	(Millsbaugh <i>et al.</i> , 2008)	(Millsbaugh <i>et al.</i> , 2008)
<i>Capreolus capreolus</i>	(Gaillard <i>et al.</i> 2017 Unpublished)	(Gaillard <i>et al.</i> 2017 Unpublished)
<i>Cebus capucinus</i>	(Bronikowski <i>et al.</i> , 2016)	(Bronikowski <i>et al.</i> , 2016)
<i>Cercopithecus mitis</i>	(Bronikowski <i>et al.</i> , 2016)	(Bronikowski <i>et al.</i> , 2016)
<i>Cervus elaphus</i>	(Benton, Grant, & Clutton- Brock, 1995)	(Benton <i>et al.</i> , 1995)
<i>Cervus nippon</i>	(Minami, Ohnishi, & Takatsu 2009b)	(Minami <i>et al.</i> , 2009a)
<i>Cynomys ludovicianus</i>	(Hoogland, 1995)	(Hoogland, 1995)
<i>Gorilla beringei</i>	(Bronikowski <i>et al.</i> , 2016)	(Bronikowski <i>et al.</i> , 2016)
<i>Kobus leche</i>	(Sayer & Lavieren, 1975)	(Rees, 1978)
<i>Loxodonta africana</i>	(Moss, 2001)	(Moss, 2001)
<i>Lycaon pictus</i>	(Creel & Creel, 2002)	(Creel & Creel, 2002)
<i>Marmota flaviventris</i>	(Schwartz, Armitage, & Van Vuren, 1998)	(Schwartz <i>et al.</i> , 1998)
<i>Marmota marmota</i>	(Berger <i>et al.</i> , 2016)	(Berger <i>et al.</i> , 2015)
<i>Meles meles</i>	(Dugdale <i>et al.</i> , 2011b)	(Dugdale <i>et al.</i> , 2011b)
<i>Mirounga angustirostris</i>	(Le Boeuf & Laws, 1994)	(Le Boeuf & Laws, 1994)
<i>Mirounga leonina</i>	(Le Boeuf & Laws, 1994)	(Le Boeuf & Laws, 1994)
<i>Odocoileus virginianus</i>	(Delgiudice <i>et al.</i> , 2006)	(DelGiudice, Lenarz, & Powell, 2007)
<i>Otaria flavescens</i>	(Grandi, Dans, & Crespo, 2011)	(Grandi <i>et al.</i> , 2016)
<i>Ovis canadensis</i>	(Festa-Bianchet <i>et al.</i> , 2006)	(Bérubé, Festa-Bianchet, & Jorgenson, 1999)
<i>Pan troglodytes</i>	(Bronikowski <i>et al.</i> , 2016)	(Bronikowski <i>et al.</i> , 2016)
<i>Panthera leo</i>	(Packer <i>et al.</i> , 1998)	(Packer <i>et al.</i> , 1998)
<i>Panthera pardus</i>	(Balme <i>et al.</i> , 2013)	(Balme <i>et al.</i> , 2013)
<i>Papio cynocephalus</i>	(Bronikowski <i>et al.</i> , 2016)	(Bronikowski <i>et al.</i> , 2016)
<i>Propithecus diadema</i>	(Pochron, Tucker, & Wright, 2004)	(Pochron <i>et al.</i> , 2004)
<i>Rucervus eldii</i>	(Nie <i>et al.</i> , 2011)	(Nie <i>et al.</i> , 2011)
<i>Tamasciurus hudsonius</i>	(McAdam <i>et al.</i> , 2007)	(McAdam <i>et al.</i> , 2007)
<i>Urocitellus beldingi</i>	(Sherman & Morton, 1984)	(Sherman & Morton, 1984)
<i>Urocitellus brunneus</i>	(Sherman & Runge, 2002b)	(Sherman & Runge, 2002b)
<i>Ursus arctos</i>	(Zedrosser <i>et al.</i> , 2013)	(Zedrosser <i>et al.</i> , 2013)



## **Chapter VIII**

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### **General discussion and perspectives**

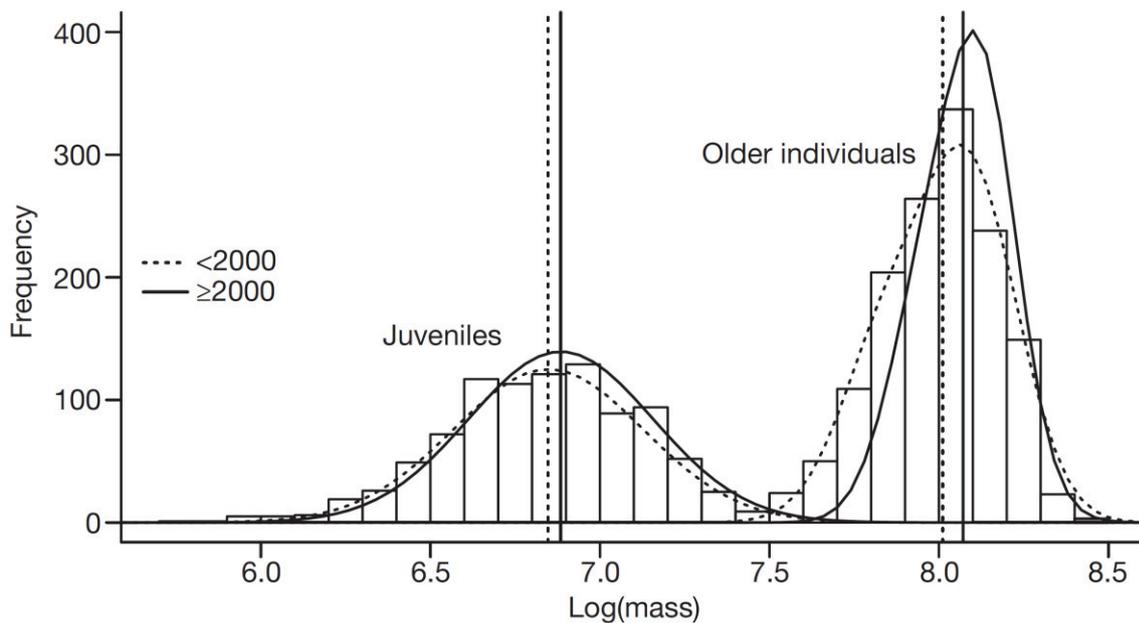
# 1. Building general IPMs to manage vertebrate populations in the wild

With these series of meta-analyses, I demonstrated that a positive link does exist between body mass and vital rates. The first finding I want to highlight is that those relationships are widespread in birds and mammals and thus it is critical to account for these differences in body mass to make reliable prediction on populations dynamics because heterogeneity can affect all demographic outputs such as the growth rate of a population (Hamel *et al.*, 2018, p. 218). I believe that the empirical demonstration of the ubiquity of those links will help generalize the use of integral projection models to assess population dynamics and will provide data to help building IPMs for populations with incomplete datasets.

In the first part of my thesis, I assessed the intensity of the relationships linking body mass to vital rates and identified key factors influencing the variation in intensity between the relationships of different populations. For instance, I showed a negative impact of predation on the intensity of the relationship linking juvenile body mass to juvenile survival. However, each relationship was assessed independently of each other and thus I could not make any prediction on how the change in intensity of those relationships will impact population dynamics. To do this we need to combine the different relationships into an integral projection model (Coulson, 2012). There has been some studies trying to assess the relative importance of each of the relationships on the general outputs of demographic models by building a general IPM (Plard *et al.*, 2016). It was then demonstrated that the inheritance function has a high impact on the population growth rate. Using the same kind of approach can be one way to assess the importance of the observed variation in the intensity of the key relationships on population dynamics. Then, for a future study we could build integral projection models for key species with different environments (i.e. short- vs fast-living species in presence vs. absence of predators). By building those IPMS we could measure the elasticities (i.e. the sensibility of the population growth rate to a given proportional change of a demographic parameter) associated with each relationship. Finding the key relationships impacting population growth rate can have a critical importance when managing populations because it can help to choose which individuals in a population should be particularly protected (Kroon *et al.*, 1986).

Aside from the kernel function, there is one key parameter that is required to build an IPM. The primary goal of an IPM is to follow the distribution of a given trait over time (Ellner & Rees, 2006). In my analyses the focal trait was body mass. We thus need to know the initial distribution of body mass among individuals to build IPMs (Ozgul *et al.*, 2010). Trait distribution is rarely reported for all individuals unless we have access to the complete monitoring of individuals. Most often, the only distributions recorded concern one age only (Adams & Dale, 1998; Milner *et al.*, 2013). However, two relationships are reported in most cases, which can be used to obtain this distribution. For most species the age distribution of the population is known at least roughly because it can be reconstructed from the mortality curves that are all compiled in Malddaba. Moreover, the relationship linking age to body mass (i.e. growth process) is available for most species included in Malddaba. Thus, we can associate a body mass to each individual using the age distribution. One interesting perspective would be to compare those distributions among species in the same manner as we compared age distributions across species. Thus, by comparing the mean, the variance and the mode of the distribution (See Fig.8.1. for an example of a body mass distribution) we will be able to extract species-specific patterns of body mass distributions and also to highlight if there are differences among populations and what are the factors shaping those differences.

My analyses clearly indicate that heavier individuals outperform lighter ones in terms of survival rates and in terms of reproduction rates. If among-individual variation in body mass is heritable, then we can make the basic prediction that individual body mass will increase over time for all populations of mammals. However, mammals are not all gigantic so how can we explain this apparent contradiction? There are also marked disadvantages to have a very high body mass. The disadvantages of obesity have been convincingly demonstrated in humans but also in captive animals, in which obesity leads both survival (Manson *et al.*, 1987) and fertility (Edwards *et al.*, 1996) rates to decrease. Thus, there is a structural limit to which individuals of a given species can grow. This limit is rarely attained by individuals because the amount of resources available to them is limited in the wild. Also, to increase the mean size of the individuals, the functions of the IPM should all be positive. We cannot check that it was the case because in most studies we compiled only one relationship was investigated.



**Figure 8.1.** An example of a mass distribution for a population of yellow-bellied marmots *Marmota flaviventris* extracted from (Ozgul *et al.*, 2010). This is a bimodal distribution with one mode associated with juvenile individuals and one mode associated with older (i.e. adult) individuals. The IPM constructed for this population predicts that the modes of the mass distributions of mass will increase over time.

One of the key questions in conservation biology is to assess the impact of global change on population dynamics (Thomas *et al.*, 2004). Global change is characterized by a change in average climatic values, but also by an increase in the frequencies of extreme climatic events (Katz & Brown, 1992). These changes are likely to affect the amount of resources available and thus change the trait distributions in wild population (Walther *et al.*, 2002). In the chapter IV I provided new insights on the negative link between the amount of resources and the intensity of the relationship between juvenile condition and juvenile survival. However, in all the meta-analyses performed in my thesis, I was just able to assess how the intensity of the relationships change across species and to a lesser extent among populations. I could not really assess whether any variation occurred among years within the

same population in the different meta-analyses I performed because in most studies the relationships I gathered corresponded to average across different years. Populations monitored over a long period of time are needed to be able to assess the between-year variation in those relationships. We will then predict, for instance, that extreme climatic events should diminish the amount of resources available in a given year for herbivores, and thereby should increase the intensity of the relationship linking juvenile body mass to juvenile survival. Most of the IPM kernel functions are based on average relationships (Rees *et al.*, 2014). Thus, the next step will be to include yearly variation into demographic models to assess how populations will respond to global change.

## 2. Future comparative analyses using Malddaba

Using the data compiled in Malddaba I confirmed the expectation that actuarial senescence is widespread in populations of mammals in the wild (Jones *et al.*, 2008). Most studies have focused on among-species differences and assumed that between-population variation in senescence patterns are negligible compared to variation observed across species (Promislow & Harvey, 1990; Ricklefs & Scheuerlein, 2001). However, it has been demonstrated that there is substantial variation in longevity among populations within the same species (Garnett, 1981; Tidière *et al.*, 2016a). We have yet to quantify the variability of actuarial senescence at the intra-specific level (But see chapter VI for a preliminary analysis on the variation in longevity across populations).

I found that female longevity is on average higher than male longevity in mammals in the wild. Differences between sexes in survival have been also highlighted for juvenile individuals {Formatting Citation}. Thus, we could argue that the sex of the individuals should be included as another axis of heterogeneity among animal populations and thus be included when studying the dynamics of population in the wild (Schindler *et al.*, 2015). Most of the demographic models are female-centered, those models only include the fate of females and disregard the impact of males on population dynamics (Caswell, 2001). However, the importance of incorporating males into demographic models has been already highlighted (Mysterud, Coulson, & Stenseth, 2002). One of the major issues is the difficulty to get access

to the reproductive rates of males by just monitoring a population. As it is straightforward to monitor the pregnancy status of mammalian females to assess their reproductive rate, it is not possible for males and therefore there are little data on reproduction available for males (but see (Clinton & Le Boeuf, 1993; Dugdale *et al.*, 2011a)). However, with the increasing use of genetic tools to determine paternity the reproductive rate of male mammals should be increasingly available in the future (Coltman *et al.*, 1999), which could provide more data to model accurately population dynamics.

In the last part of my thesis I focused on actuarial senescence by providing new data from Malddaba to perform comparative analyses. Moreover, we also compiled data on age-specific female reproduction. As I explained earlier those data are less studied in comparative analyses than survival data (Lemaître & Gaillard, 2017). Then the first step to use them into a comparative analysis is to provide a mathematical framework to assess the pattern of reproductive senescence, so to provide similar metrics as those used for actuarial senescence. Thus, I looked for both an onset and a rate of reproductive senescence. One possible approach is to use the work already existing to model the relationship between sport performance and age (Moore, 1975). Sport performance and reproduction rate indeed display similar shape of age-dependence with first an increase with age during early adulthood, then a plateau during the prime-aged stage, and then a decrease with increasing age during the senescence stage. Once we will be able to model accurately this pattern, we could perform some new comparative analyses. No study to date tried to compile the onsets of reproductive senescence and use them into a comparative framework. One interesting question is to compare whether those onsets of reproductive senescence are similar to the onsets of actuarial senescence because it is expected that those two patterns of senescence begin at the age at first reproduction (Williams, 1957). The data from Malddaba could help do this as we have demographic data on survival and reproduction in the same population for about 80 species.

The latest data we are adding to Malddaba are the growth relationships linking the mass or size of the individuals to their age. As explained earlier those data are first needed to build IPMs (Coulson, 2012). From those growth curves we can derive the growth function of the IPMs kernel, which is the relationship linking the mass of the individual at age  $i$  to the mass at age  $i+1$ . Our second goal is to analyse these growth curves in the context of a tradeoff between early and late life performance (Lemaître *et al.*, 2015). We aim to assess how

allocation to growth in young mammals could affect actuarial senescence. The basic prediction is that a high allocation to growth early in life should lead to less allocation to maintenance later in life and therefore increase the rate of aging. However, one of the big issues is to quantify the amount of allocation in growth from these growth curves. Many different forms of growth curves has been reported to exist and a high diversity of growth curves occur in mammals (Gaillard *et al.*, 1997). This diversity requires obtaining new standard metrics to assess the different growth curves existing in mammals.

### **3. Personal notes**

During my work, I highlighted the general patterns of the relationships linking body mass and age to vital rates. Most of my results come from meta-analyses or comparative analyses. In addition to provide relevant tools to compare the different relationships, this type of research was a great way to enter the field of evolutionary demography for me. I will therefore conclude my thesis by showing the educative value of performing such comparative procedures for researchers. Any meta-analysis or comparative analysis can be decomposed into three main steps: the compilation, the extraction and the analysis of data. First, as an intensive compilation of studies is needed, most people consider this part as the most tedious one. We require reading hundreds of papers that have most often a very narrow focus. However, when I first began the compilation procedure for my thesis back in 2015 I just had very little knowledge about population dynamics and I argue that this part was highly educative for me. By reading all those papers I was able to grasp the different concepts and the state of art in this discipline. On a second time, the extraction procedure requires a more advanced knowledge of the papers because a complete understanding of the analysis done in the focal paper is needed. As well, a clear view of the diversity of papers in the literature to devise standardized metrics applicable to different studies is needed. The last step, which is common to all scientific studies is to analyze the data extracted and therefore to provide new insights on the research field. I thus believe that the sequence of those three steps provides one of the best ways for a researcher to enter a new field efficiently.

# REFERENCES

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- Adams, L.G. & Dale, B.W. (1998) Reproductive Performance of Female Alaskan Caribou. *The Journal of Wildlife Management* 62, 1184.
- Albon, S.D., Mitchell, B. & Staines, B.W. (1983) Fertility and Body Weight in Female Red Deer: A Density-Dependent Relationship. *The Journal of Animal Ecology* 52, 969.
- Aledo, J.C., Valverde, H. & de Magalhães, J.P. (2012) Mutational Bias Plays an Important Role in Shaping Longevity-Related Amino Acid Content in Mammalian mtDNA-Encoded Proteins. *Journal of Molecular Evolution* 74, 332–341.
- Andersen, R., Gaillard, J., John, D., Linnell, C. & Duncan, P. (2000) Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology* 69, 672–682.
- Austad, S.N. & Bartke, A. (2016) Sex Differences in Longevity and in Responses to Anti-Aging Interventions: A Mini-Review. *Gerontology* 62, 40–46.
- Austad, S.N. & Fischer, K.E. (1991) Mammalian Aging, Metabolism, and Ecology: Evidence From the Bats and Marsupials. *Journal of Gerontology* 46, B47–B53.
- Austad, S.N. & Fischer, K.E. (2016) Sex Differences in Lifespan. *Cell metabolism* 23, 1022–1033.
- Austad, S.N. (2006) Why women live longer than men: sex differences in longevity. *Gender Medicine* 3, 79–92.
- Bacaër, N. (2011) Halley's life table (1693). In *A Short History of Mathematical Population Dynamics* (ed N. Bacaër), pp. 5–10. Springer London, London.
- Balme, G.A., Batchelor, A., de Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W. & Hunter, L.T.B. (2013) Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* 43, 221–237.
- Baudisch, A. (2011) The pace and shape of ageing. *Methods in Ecology and Evolution* 2, 375–382.
- Beissinger, S.R. & Westphal, M.I. (1998) On the Use of Demographic Models of Population Viability in Endangered Species Management. *The Journal of Wildlife Management* 62, 821–841.
- Benton, T.G., Grant, A. & Clutton-Brock, T.H. (1995) Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. *Evolutionary Ecology* 9, 559–574.

- Berger, V., Lemaître, J.-F., Allainé, D., Gaillard, J.-M. & Cohas, A. (2018) Early and Adult Social Environments Shape Sex-Specific Actuarial Senescence Patterns in a Cooperative Breeder. *The American Naturalist* 192, 525–536.
- Berger, V., Lemaître, J.-F., Dupont, P., Allainé, D., 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.
- 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.
- Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80, 2555–2565.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature* 446, 507–512.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for Phylogenetic Signal in Comparative Data: Behavioral Traits Are More Labile. *Evolution* 57, 717–745.
- Bonduriansky, R., Maklakov, A., Zajitschek, F. & Brooks, R. (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology* 22, 443–453.
- Borowik, T., Wawrzyniak, P. & Jędrzejewska, B. (2016) Red deer (*Cervus elaphus*) fertility and survival of young in a low-density population subject to predation and hunting. *Journal of Mammalogy* 97, 1671–1681.
- Bourke, A.F.G. (2007) Kin Selection and the Evolutionary Theory of Aging. *Annual Review of Ecology, Evolution, and Systematics* 38, 103–128.
- Boyd, I.L. (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Functional Ecology* 14, 623–630.
- Bronikowski, A.M., Cords, M., Alberts, S.C., Altmann, J., Brockman, D.K., Fedigan, L.M., Pusey, A., Stoinski, T., Strier, K.B. & Morris, W.F. (2016) Female and male life tables for seven wild primate species. *Scientific Data* 3, 160006.

- Bronson, M.T. (1979) Altitudinal Variation in the Life History of the Golden-Mantled Ground Squirrel (*Spermophilus Lateralis*). *Ecology* 60, 272–279.
- Brooks, R.C. & Garratt, M.G. (2017) Life history evolution, reproduction, and the origins of sex-dependent aging and longevity. *Annals of the New York Academy of Sciences* 1389, 92–107.
- Calder, W.A. (1996) *Size, function, and life history*. Courier Corporation.
- Canudas-Romo, V. (2008) The modal age at death and the shifting mortality hypothesis. *Demographic Research* 19, 1179–1204.
- Carey, J.R. & Judge, D.S. (2000) Longevity records: life spans of mammals, birds, reptiles, amphibians and fish. *Odense Monographs on Population Aging* (ed. B. Jeune and JW Vaupel). Odense: Odense University Press.
- Caswell, H. (2001) *Matrix populations models*. Sunderland, MA: Sinauer Associates Inc.
- Caughley, G. (1966) Mortality Patterns in Mammals. *Ecology* 47, 906–918.
- Charnov, E.L. & Ernest, S.K.M. (2006) The Offspring-Size/Clutch-Size Trade-Off in Mammals. *the American Naturalist* 167, 578–582.
- Charnov, E.L. (1993) *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford University Press, USA.
- Choquet, R., Reboulet, A.-M., Pradel, R., Giménez, O. & Lebreton, J.-D. (2004) M-SURGE: new software specifically designed for multistate capture–recapture models. *Animal Biodiversity and Conservation* 27, 207-215–215.
- Clinton, W.L. & Le Boeuf, B.J. (1993) Sexual Selection’s Effects on Male Life History and the Pattern of Male Mortality. *Ecology* 74, 1884–1892.
- Clutton-Brock, T. & 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 & Evolution* 25, 562–573.
- Clutton-Brock, T.H. & Isvaran, K. (2007) Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society of London B: Biological Sciences* 274, 3097–3104.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989) Fitness costs gestation and lactation in wild mammals. *Nature* 337, 260–262.

- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313, 131–133.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1987) Interactions Between Population Density and Maternal Characteristics Affecting Fecundity and Juvenile Survival in Red Deer. *The Journal of Animal Ecology* 56, 857.
- Cohen, J. (1988) *Statistical power analysis for the behavioral studies*. Academic press, New york.
- 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, 466–470.
- Coltman, D.W., Bancroft, D.R., Robertson, A., Smith, J.A., Clutton-brock, T.H. & Pemberton, J.M. (1999) Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology* 8, 1199–1209.
- Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T.I.M., Bryant, L.D. & Irwin, L.L. (2004) Effects of Summer-Autumn Nutrition and Parturition Date on Reproduction and Survival of Elk. *Wildlife Monographs* 155, 1–61.
- Côté, S.D. & Festa-Bianchet, M. (2001) Reproductive success in female mountain goats: the influence of age and social rank. *Animal Behaviour* 62, 173–181.
- Coulson, T. (2012) Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos* 121, 1337–1350.
- Creel, S. & Creel, N.M. (2002) *The African wild dog: behavior, ecology, and conservation*. Princeton University Press.
- Cribari-Neto, F. & Zeileis, A. (2010) Beta Regression in R. *Journal of Statistical Software* 34.
- Darwin, C. (1859) *On the origin of species*.
- Delgiudice, G.D., Fieberg, J., Riggs, M.R., Powell, M.C. & Pan, W. (2006) A Long-Term Age-Specific Survival Analysis of Female White-Tailed Deer. *Journal of Wildlife Management* 70, 1556–1568.
- 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, 427–435.

- Derocherand, A.E. & Stirling, I. (1994) Age-specific reproductive performance of female polar bears (*Ursus maritimus*). *Journal of Zoology* 234, 527–536.
- Dobson, F.S. & Michener, G.R. (1995) Maternal traits and reproduction in Richardson's ground squirrels. *Ecology* 76, 851–862.
- Dobson, F.S. (1992) Body mass, structural size, and life-history patterns of the Columbian ground squirrel. *American naturalist*, 109–125.
- Douhard, F., Gaillard, J.-M., Pellerin, M., Jacob, L. & Lemaître, J.-F. (2017) The cost of growing large: costs of post-weaning growth on body mass senescence in a wild mammal. *Oikos* 126, 1329–1338.
- Dugdale, H.L., Pope, L.C., Newman, C., Macdonald, D.W. & Burke, T. (2011a) Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology* 20, 3261–3274.
- Dugdale, H.L., Pope, L.C., Newman, C., Macdonald, D.W. & Burke, T. (2011b) Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology* 20, 3261–3274.
- Durham, M.F., Magwire, M.M., Stone, E.A. & Leips, J. (2014) Genome-wide analysis in *Drosophila* reveals age-specific effects of SNPs on fitness traits. *Nature Communications* 5, 4338.
- Edwards, L.E., Hellerstedt, W.L., Alton, I.R., Story, M. & Himes, J.H. (1996) Pregnancy complications and birth outcomes in obese and normal-weight women: Effects of gestational weight change. *Obstetrics & Gynecology* 87, 389–394.
- Edwards, R.D. & Tuljapurkar, S. (2005) Inequality in Life Spans and a New Perspective on Mortality Convergence Across Industrialized Countries. *Population and Development Review* 31, 645–674.
- Egger, M., Davey Smith, G., Schneider, M. & Minder, C. (1997) Bias in meta-analysis detected by a simple, graphical test. *BMJ : British Medical Journal* 315, 629–634.
- Ellner, S.P. & Rees, M. (2006) Integral Projection Models for Species with Complex Demography. *The American Naturalist* 167, 410–428.
- Emlen, J.M. (1970) Age Specificity and Ecological Theory. *Ecology* 51, 588–601.

- Ergon, T., Borgan, Ø., Nater, C.R. & Vindenes, Y. (2017) Study mortality with hazard rates, not probabilities. *bioRxiv*, 216739.
- Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. (2001) Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82, 1613–1620.
- Ferrero, R.C. & Walker, W.A. (1999) Age, Growth, and Reproductive Patterns of Dall's Porpoise (*Phocoenoides Dalli*) in the Central North Pacific Ocean. *Marine Mammal Science* 15, 273–313.
- Festa-Bianchet, M. & Côté, S.D. (2012) *Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate*. Island Press.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T. & Pelletier, F. (2006) Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* 273, 1537–1543.
- Finch, C.E., Pike, M.C. & Witten, M. (1990) Slow mortality rate accelerations during aging in some animals approximate that of humans. *Science* 249, 902–905.
- Fokidis, H.B., Risch, T.S. & Glenn, T.C. (2007) Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour* 73, 479–488.
- Freckleton, R.P. (2009) The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology* 22, 1367–1375.
- Fu, C., Cao, Z.-D. & Fu, S.-J. (2019) Predation experience underlies the relationship between locomotion capability and survival. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 227, 32–38.
- Gaillard, J.-M. & Lemaître, J.-F. (2017) The Williams' legacy: A critical reappraisal of his nine predictions about the evolution of senescence. *Evolution* 71, 2768–2785.
- Gaillard, J. -M., Yoccoz, N.G., Lebreton, J. -D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D. & Allaine, D. (2005) Generation Time: A Reliable Metric to Measure Life-History Variation among Mammalian Populations. *The American Naturalist* 166, 119–123.
- Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal Variation in Survival of Mammals: A Case of Environmental Canalization? *Ecology* 84, 3294–3306.

- Gaillard, J.-M., Duncan, P., Delorme, D., Van Laere, G., Pettorelli, N., Maillard, D. & Renaud, G. (2003) Effects of Hurricane Lothar on the Population Dynamics of European Roe Deer. *The Journal of Wildlife Management* 67, 767–773.
- Gaillard, J., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology, Evolution, and Systematics* 31, 367–393.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13, 58–63.
- Gaillard, J.-M., Pontier, D., Allaine, D., Loison, A., Herve, J.-C. & Heizman, A. (1997) Variation in growth form and precocity at birth in eutherian mammals. *Proceedings of the Royal Society of London B: Biological Sciences* 264, 859–868.
- Garnett, M.C. (1981) Body Size, Its Heritability and Influence on Juvenile Survival Among Great Tits, *Parus Major*. *Ibis* 123, 31–41.
- Garratt, M., Bower, B., Garcia, G.G. & Miller, R.A. (2017) Sex differences in lifespan extension with acarbose and 17- $\alpha$  estradiol: gonadal hormones underlie male-specific improvements in glucose tolerance and mTORC2 signaling. *Aging Cell* 16, 1256–1266.
- Garrott, R.A., Eberhardt, L.L., Otton, J.K., White, P.J. & Chaffee, M.A. (2002) A Geochemical Trophic Cascade in Yellowstone's Geothermal Environments. *Ecosystems* 5, 0659–0666.
- Gaskins, C.T., Snowder, G.D., Westman, M.K. & Evans, M. (2005) Influence of body weight, age, and weight gain on fertility and prolificacy in four breeds of ewe lambs. *Journal of Animal Science* 83, 1680.
- Gedir, J. V. & Michener, G.R. (2014) Litter sex ratios in Richardson's ground squirrels: Long-term data support random sex allocation and homeostasis. *Oecologia* 174, 1225–1239.
- Gelman, A. & Rubin, D.B. (1992) Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science* 7, 457–472.
- George, L. (2010) *Handbook of aging and the social sciences*. Academic Press.
- Gittleman, J.L. & Thompson, S.D. (1988) Energy Allocation in Mammalian Reproduction. *Integrative and Comparative Biology* 28, 863–875.

- Gogan, P.J.P., Russell, R.E., Olexa, E.M. & Podruzny, K.M. (2013) Pregnancy rates in central Yellowstone bison. *The Journal of Wildlife Management* 77, 1271–1279.
- Gomes, N.M.V., Ryder, O.A., Houck, M.L., Charter, S.J., Walker, W., Forsyth, N.R., Austad, S.N., Venditti, C., Pagel, M., Shay, J.W. & Wright, W.E. (2011) Comparative biology of mammalian telomeres: hypotheses on ancestral states and the roles of telomeres in longevity determination. *Aging Cell* 10, 761–768.
- Gompertz, B. (1825) XXIV. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. In a letter to Francis Baily, Esq. *F. R. S. &c. Philosophical Transactions of the Royal Society of London* 115, 513–583.
- Gonzalez, O., Zedrosser, A., Pelletier, F., Swenson, J.E. & Festa-Bianchet, M. (2012) Litter reductions reveal a trade-off between offspring size and number in brown bears. *Behavioral Ecology and Sociobiology* 66, 1025–1032.
- Grandi, M.F., Dans, S.L. & Crespo, E.A. (2016) Improvement in Survivorship: The Key for Population Recovery? *Zoological Studies* 55.
- Hadfield, J.D. & Nakagawa, S. (2010) General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* 23, 494–508.
- Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33, 1–22.
- 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, 1628–1639.
- Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Bassar, R.D., Bouwhuis, S., Caswell, H., Douhard, M., Gangloff, E.J., Gimenez, O., Lee, P.C., Smallegange, I.M., Steiner, U.K., Vedder, O. & Vindenes, Y. (2018) General conclusion to the special issue Moving forward on individual heterogeneity. *Oikos* 127, 750–756.
- Hamilton, W.D. (1966) The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12, 12–45.

- Hamlin, K.L., Pac, D.F., Sime, C.A., DeSimone, R.M. & Dusek, G.L. (2000) Evaluating the Accuracy of Ages Obtained by Two Methods for Montana Ungulates. *The Journal of Wildlife Management* 64, 441–449.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press.
- Healy, K., Guillerme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D., Kelly, D.J., Donohue, I., Jackson, A.L. & Cooper, N. (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society of London B: Biological Sciences* 281, 20140298.
- Hill, K. & Hurtado, A.M. (1996) *The ecology and demography of a foraging people*. New York: Aldine de Gruyter.
- Hoogland, J.L. (1995) *The black-tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press.
- Horiuchi, S., Ouellette, N., Cheung, S.L.K. & Robine, J.-M. (2013) Modal age at death: lifespan indicator in the era of longevity extension. *Vienna Yearbook of Population Research* 11, 37–69.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O’Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648–2648.
- Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T., Dobson, F.S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., et al. (2008) Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecology Letters* 11, 664–673.
- Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren, J.P., Ehrlén, J., García, M.B., Menges, E.S., Quintana-Ascencio, P.F., Caswell, H., Baudisch, A. & Vaupel, J.W. (2014) Diversity of ageing across the tree of life. *Nature* 505, 169–173.
- Jönsson, K.I. (1997) Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. *Oikos* 78, 57.

- Kasuya, T. & Marsh, H. (1984) Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. Report of the International Whaling Commission, Special 6, 259–310.
- Katz, R.W. & Brown, B.G. (1992) Extreme events in a changing climate: Variability is more important than averages. *Climatic Change* 21, 289–302.
- Keane, B., Bryant, L., Goyal, U., Williams, S., Kortering, S.L., Lucia, K.E., Richmond, A.R. & Solomon, N.G. (2007) No effect of body condition at weaning on survival and reproduction in prairie voles. *Canadian Journal of Zoology* 85, 718–727.
- Kennedy, B.K., Berger, S.L., Brunet, A., Campisi, J., Cuervo, A.M., Epel, E.S., Franceschi, C., Lithgow, G.J., Morimoto, R.I., Pessin, J.E., Rando, T.A., Richardson, A., Schadt, E.E., Wyss-Coray, T. & Sierra, F. (2014) Geroscience: Linking Aging to Chronic Disease. *Cell* 159, 709–713.
- Kirkwood, T.B.L. (1977) Evolution of ageing. *Nature* 270, 301–304.
- Kliman, R.M. (2016) *Encyclopedia of Evolutionary Biology*. Academic Press.
- Krementz, D.G., Sauer, J.R. & Nichols, J.D. (1989) Model-Based Estimates of Annual Survival Rate Are Preferable to Observed Maximum Lifespan Statistics for Use in Comparative Life-History Studies. *Oikos* 56, 203–208.
- Kroon, H. de, Plaisier, A., Groenendael, J. van & Caswell, H. (1986) Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. *Ecology* 67, 1427–1431.
- Lack, D. (1947) The Significance of Clutch-size. *Ibis* 89, 302–352.
- Lack, D.L. (1966) *Population studies of birds*. Clarendon P.
- Le Boeuf, B. & Laws, R. (1994) *Elephant seals population ecology behavior and physiology*. Univ of California Press.
- Lebreton, J.-D., Devillard, S., Popy, S., Desprez, M., Besnard, A. & Gaillard, J.-M. (2012) Towards a vertebrate demographic data bank. *Journal of Ornithology* 152, 617–624.
- Lemaître, J.-F. & Gaillard, J.-M. (2013) Male survival patterns do not depend on male allocation to sexual competition in large herbivores. *Behavioral Ecology* 24, 421–428.

- Lemaître, J.-F. & Gaillard, J.-M. (2017) Reproductive senescence: new perspectives in the wild. *Biological Reviews* 92, 2182–2199.
- Lemaître, J.-F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F. & Gaillard, J.-M. (2015) Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R. Soc. B* 282, 20150209.
- Lemaître, J.-F., Gaillard, J.-M., Lackey, L.B., Clauss, M. & Müller, D.W.H. (2013) Comparing free-ranging and captive populations reveals intra-specific variation in aging rates in large herbivores. *Experimental Gerontology* 48, 162–167.
- Leslie, P.H. & Ranson, R.M. (1940) The Mortality, Fertility and Rate of Natural Increase of the Vole (*Microtus agrestis*) as Observed in the Laboratory. *The Journal of Animal Ecology* 9, 27.
- Leslie, P.H. (1945) On the Use of Matrices in Certain Population Mathematics. *Biometrika* 33, 183–212.
- Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gotzsche, P.C., Ioannidis, J.P.A., Clarke, M., Devereaux, P.J., Kleijnen, J. & Moher, D. (2009) The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate healthcare interventions: explanation and elaboration. *BMJ* 339, b2700–b2700.
- Lim, J.N., Senior, A.M. & Nakagawa, S. (2014) Heterogeneity in individual quality and reproductive trade-offs within species. *Evolution* 68, 2306–2318.
- Linnell, J.D.C., Aanes, R. & Andersen, R. (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1, 209–223.
- Lipsey, M.W. & Wilson, D.B. (2001) *Practical meta-analysis*. Thousand Oaks, CA : Sage publications.
- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Jullien, J.-M. (1999) Age-Specific Survival in Five Populations of Ungulates: Evidence of Senescence. *Ecology* 80, 2539–2554.
- Lukas, D. & Clutton-Brock, T. (2012) Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society of London B: Biological Sciences*, 2151–2156.

- 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, 827–840.
- Luy, M. (2003) Causes of Male Excess Mortality: Insights from Cloistered Populations. *Population and Development Review* 29, 647–676.
- Lynsdale, C.L., Mumby, H.S., Hayward, A.D., Mar, K.U. & Lummaa, V. (2017) Parasite-associated mortality in a long-lived mammal: Variation with host age, sex, and reproduction. *Ecology and Evolution* 7, 10904–10915.
- MacLeod, K.J., McGhee, K.E. & Clutton-Brock, T.H. (2015) No apparent benefits of allonursing for recipient offspring and mothers in the cooperatively breeding meerkat. *Journal of Animal Ecology* 84, 1050–1058.
- Magalhães, J.P.D. & Costa, J. (2009) A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology* 22, 1770–1774.
- Magrath, R.D. (1991) Nestling Weight and Juvenile Survival in the Blackbird, *Turdus merula*. *Journal of Animal Ecology* 60, 335–351.
- Makeham, W.M. (1867) On the Law of Mortality. *Journal of the Institute of Actuaries (1866-1867)* 13, 325–358.
- Maklakov, A.A. & Lummaa, V. (2013) Evolution of sex differences in lifespan and aging: Causes and constraints. *BioEssays* 35, 717–724.
- Maness, T.J. & Anderson, D.J. (2013) Predictors of juvenile survival in birds. *Ornithological Monographs* 78, 1–55.
- Manson, J.E., Stampfer, M.J., Hennekens, C.H. & Willett, W.C. (1987) Body Weight and Longevity: A Reassessment. *JAMA* 257, 353–358.
- Manton, K.G. & Tolley, H.D. (1991) Rectangularization of the Survival Curve: Implications of an Ill-Posed Question. *Journal of Aging and Health* 3, 172–193.
- Marais, G.A.B., Gaillard, J.-M., Vieira, C., Plotton, I., Sanlaville, D., Gueyffier, F. & Lemaitre, J.-F. (2018) Sex gap in aging and longevity: can sex chromosomes play a role? *Biology of Sex Differences* 9.

- Martin, T.E. (1995) Avian Life History Evolution in Relation to Nest Sites, Nest Predation, and Food. *Ecological Monographs* 65, 101–127.
- Martin, T.E., Tobalske, B., Riordan, M.M., Case, S.B. & Dial, K.P. (2018) Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Advances* 4, eaar1988.
- Masoro, E.J. & Austad, S.N. (2010) *Handbook of the Biology of Aging*. Elsevier.
- 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.
- McDonald, B.I., Goebel, M.E., Crocker, D.E. & Costa, D.P. (2012) Dynamic influence of maternal and pup traits on maternal care during lactation in an income breeder, the antarctic fur seal. *Physiological and Biochemical Zoology* 85, 243–254.
- McDonald, R.A. & Harris, S. (2002) Population biology of stoats *Mustela erminea* and weasels *Mustela nivalis* on game estates in Great Britain. *Journal of Applied Ecology* 39, 793–805.
- Medawar, P.B. (1952) *An unsolved problem of biology*. H. K. Lewis, London.
- Menard, S. (2011) Standards for standardized logistic regression coefficients. *Social Forces* 89, 1409–1428.
- Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E.K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R. & McMahon, S.M. (2014) Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution* 5, 99–110.
- Metcalf, C.J.E., McMahon, S.M., Salguero-Gómez, R. & Jongejans, E. (2013) IPMPack: an R package for integral projection models. *Methods in Ecology and Evolution* 4, 195–200.
- Michener, G.R. (1989) Reproductive effort during gestation and lactation by Richardson's ground squirrels. *Oecologia* 78, 77–86.
- Millar, J.S. & Zammuto, R.M. (1983) Life Histories of Mammals: An Analysis of Life Tables. *Ecology* 64, 631–635.
- Mills, J.A., Teplitsky, C., Arroyo, B., Charmantier, A., Becker, P.H., Birkhead, T.R., Bize, P., Blumstein, D.T., Bonenfant, C., Boutin, S., Bushuev, A., Cam, E., Cockburn, A., Côté, S.D., Coulson, J.C., et al. (2015) Archiving Primary Data: Solutions for Long-Term Studies. *Trends in Ecology & Evolution* 30, 581–589.

- Millspaugh, J.J., Gitzen, R.A., Licht, D.S., Amelon, S., Bonnot, T.W., Jachowski, D.S., Jones-Farrand, D.T., Keller, B.J., McGowan, C.P., Pruett, M.S., Rittenhouse, C.D. & Suedkamp Wells, K.M. (2008) Effects of Culling on Bison Demographics in Wind Cave National Park, South Dakota. *Natural Areas Journal* 28, 240–250.
- Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic Side Effects of Selective Hunting in Ungulates and Carnivores. *Conservation Biology* 21, 36–47.
- Milner, J.M., van Beest, F.M., Solberg, E.J. & Storaas, T. (2013) Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. *Oecologia* 172, 995–1005.
- Minami, M., Ohnishi, N. & Takatsuki, S. (2009b) Survival Patterns of Male and Female Sika Deer on Kinkazan Island, Northern Japan. In *Sika Deer* pp. 375–384. Springer Japan, Tokyo.
- Minami, M., Ohnishi, N., Higuchi, N., Okada, A. & Takatsuki, S. (2009a) Life-Time Reproductive Success of Female Sika Deer on Kinkazan Island, Northern Japan. In *Sika Deer* pp. 319–326. Springer Japan, Tokyo.
- Missov, T.I., Lenart, A., Nemeth, L., Canudas-Romo, V. & Vaupel, J.W. (2015) The Gompertz force of mortality in terms of the modal age at death. *Demographic Research* 32, 1031–1048.
- Monaghan, P., Charmantier, A., Nussey, D.H. & Ricklefs, R.E. (2008) The evolutionary ecology of senescence. *Functional Ecology* 22, 371–378.
- Monson, D.H., Estes, J.A., Bodkin, J.L. & Siniff, D.B. (2000) Life history plasticity and population regulation in sea otters. *Oikos* 90, 457–468.
- Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Kie, J.G. & Bowyer, R.T. (2014) Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs* 186, 1–62.
- Moorad, J.A., Promislow, D.E.L., Flesness, N. & Miller, R.A. (2012) A comparative assessment of univariate longevity measures using zoological animal records. *Aging Cell* 11, 940–948.
- Moore Ii, D.H. (1975) A study of age group track and field records to relate age and running speed. *Nature* 253, 264–265.
- Moss, C.J. (2001a) The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* 255, 145–156.

- Munro, N.D., Bar-Oz, G. & Stutz, A.J. (2009) Aging mountain gazelle (*Gazella gazella*): refining methods of tooth eruption and wear and bone fusion. *Journal of Archaeological Science* 36, 752–763.
- Mysterud, A., Coulson, T. & Stenseth, N.C. (2002) The role of males in the dynamics of ungulate populations. *Journal of Animal Ecology* 71, 907–915.
- Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70, 730–738.
- Nakagawa, S. & Santos, E.S. a (2012) Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* 26, 1253–1274.
- Neuhaus, P., Broussard, D.R., Murie, J.O. & Dobson, F.S. (2004) Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. *Journal of Animal Ecology* 73, 36–43.
- Nichols, J.D., Hines, J.E. & Blums, P. (1997) Tests for Senescent Decline in Annual Survival Probabilities of Common Pochards, *Aythya Ferina*. *Ecology* 78, 1009–1018.
- Nie, H., Song, Y., Zeng, Z. & Zhang, Q. (2011) Life history pattern and fitness of an endangered Hainan Eld's deer population. *Integrative Zoology* 6, 63–70.
- Nusselder, W.J. & Mackenbach, J.P. (1996) Rectangularization of the Survival Curve in the Netherlands, 1950-1992. *The Gerontologist* 36, 773–782.
- Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J.-M. (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology* 22, 393–406.
- Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M. & Austad, S.N. (2013) Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews* 12, 214–225.
- Oeppen, J. & Vaupel, J.W. (2002) Broken Limits to Life Expectancy. *Science* 296, 1029–1031.
- Olesiuk, P., Bigg, M.A. & M. Ellis, G. (1990) Life History and Population Dynamics of Resident Killer Whales (*Orcinus orca*) in the Coastal Waters of British Columbia and Washington State. Report - International Whaling Commission, Special Issue 12, 209–243.

- Olshansky, S.J., Carnes, B.A. & Désesquelles, A. (2001) Prospects for Human Longevity. *Science* 291, 1491–1492.
- Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S. & Coulson, T. (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466, 482–485.
- Packer, C., Tatar, M. & Collins, A. (1998) Reproductive cessation in female mammals. *Nature* 392, 807–811.
- Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. Lond. B* 255, 37–45.
- Paniw, M., Ozgul, A. & Salguero-Gómez, R. (2018) Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. *Ecology Letters* 21, 275–286.
- Paronis, E., Samara, A., Polyzos, A., Spyropoulos, C. & Kostomitsopoulos, N.G. (2015) Maternal weight as an alternative determinant of the gestational day of Wistar rats housed in individually-ventilated cages. *Laboratory Animals* 49, 188–195.
- Péron, G., Gimenez, O., Charmantier, A., Gaillard, J.-M. & Crochet, P.-A. (2010) Age at the onset of senescence in birds and mammals is predicted by early-life performance. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20100530.
- Plard, F., Gaillard, J.-M., Coulson, T. & Tuljapurkar, S. (2016) Des différences, pourquoi? Transmission, maintenance and effects of phenotypic variance. *Journal of Animal Ecology* 85, 356–370.
- Plard, F., Gaillard, J.-M., Coulson, T., Hewison, A.J.M., Douhard, M., Klein, F., Delorme, D., Warnant, C. & Bonenfant, C. (2015) The influence of birth date via body mass on individual fitness in a long-lived mammal. *Ecology* 96, 1516–1528.
- Pletcher, S.D. & Curtsinger, J.W. (1998) Mortality Plateaus and the Evolution of Senescence: Why Are Old-Age Mortality Rates so Low? *Evolution* 52, 454–464.
- Pochron, S.T., Tucker, W.T. & Wright, P.C. (2004) Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 125, 61–72.

- Price-Rees, S.J., Congdon, B.C. & Krockenberger, A.K. (2012) Size delays female senescence in a medium sized marsupial: The effects of maternal traits on annual fecundity in the northern brown bandicoot (*Isodon macrourus*). *Austral Ecology* 37, 313–322.
- 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, 417–437.
- Promislow, D.E.L. (1992) Costs of sexual selection in natural populations of mammals. *Proc. R. Soc. Lond. B* 247, 203–210.
- Rees, M., Childs, D.Z. & Ellner, S.P. (2014) Building integral projection models: a user’s guide. *Journal of Animal Ecology* 83, 528–545.
- Rees, W.A. (1978) The Ecology of the Kafue Lechwe: As Affected by the Kafue Gorge Hydroelectric Scheme. *The Journal of Applied Ecology* 15, 205.
- Regan, J.C. & Partridge, L. (2013) Gender and longevity: Why do men die earlier than women? Comparative and experimental evidence. *Best Practice & Research Clinical Endocrinology & Metabolism* 27, 467–479.
- Reimers, E. (1983) Reproduction in wild reindeer in Norway. *Canadian Journal of Zoology* 61, 211–217.
- Ricklefs, R.E. & Scheuerlein, A. (2001) Comparison of aging-related mortality among birds and mammals. *Experimental Gerontology* 36, 845–857.
- Ricklefs, R.E. (2010) Life-history connections to rates of aging in terrestrial vertebrates. *Proceedings of the National Academy of Sciences* 107, 10314–10319.
- Rochelle, T.L., Yeung, D.K.Y., Bond, M.H. & Li, L.M.W. (2015) Predictors of the gender gap in life expectancy across 54 nations. *Psychology, Health & Medicine* 20, 129–138.
- Ronget, V., Gaillard, J.M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J.C. & Lemaître, J.F. (2018) Causes and consequences of variation in offspring body mass: Meta-analyses in birds and mammals. *Biological Reviews* 93, 1–27.
- Ronget, V., Garratt, M., Lemaître, J.-F. & Gaillard, J.-M. (2017) The ‘Evo-Demo’ Implications of Condition-Dependent Mortality. *Trends in Ecology & Evolution* 32, 909–921.

- Rosano, A., Botto, L.D., Botting, B. & Mastroiacovo, P. (2000) Infant mortality and congenital anomalies from 1950 to 1994: an international perspective. *Journal of Epidemiology & Community Health* 54, 660–666.
- Sacks, B.N. (2005) Reproduction and Body Condition of California Coyotes (*Canis latrans*). *Journal of Mammalogy* 86, 1036–1041.
- Sadleir, M.F.S. (1969) The ecology of reproduction in wild and domestic mammals. London: Methuen & Co. Ltd.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., Buhr, H. de, Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., et al. (2016) COMADRE: a global data base of animal demography. *Journal of Animal Ecology* 85, 371–384.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D.A., Brinks, E., Buhr, H. de, Farack, C., Gottschalk, F., Hartmann, A., Henning, A., et al. (2015) The compadre Plant Matrix Database: an open online repository for plant demography. *Journal of Ecology* 103, 202–218.
- Saunders, G., Mcilroy, J., Kay, B., Gifford, E., Berghout, M. & Van De Ven, R. (2002) Demography of foxes in central-western New South Wales, Australia. *Mammalia* 66, 247–258.
- Sayer, J.A. & Lavieren, L.P. Van (1975) The ecology of the Kafue lechwe population of Zambia before the operation of hydro-electric dams on the Kafue River. *African Journal of Ecology* 13, 9–37.
- Schindler, S., Gaillard, J.-M., Grüning, A., Neuhaus, P., Traill, L.W., Tuljapurkar, S. & Coulson, T. (2015) Sex-specific demography and generalization of the Trivers–Willard theory. *Nature* 526, 249–252.
- Schradin, C., Kinahan, A.A. & Pillay, N. (2009) Cooperative Breeding in Groups of Synchronously Mating Females and Evolution of Large Testes to Avoid Sperm Depletion in African Striped Mice. *Biology of Reproduction* 81, 111–117.
- Schulte-Hostedde, A.I., Millar, J.S. & Hickling, G.J. (2001) Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79, 1021–1029.

- Schulte-Hostedde, A.I., Millar, J.S. & Hickling, G.J. (2001a) Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79, 1021–1029.
- Schulte-Hostedde, A.I., Millar, J.S. & Hickling, G.J. (2001b) Evaluating body condition in small mammals. *Canadian Journal of Zoology* 79, 1021–1029.
- Schwartz, O.A., Armitage, K.B. & Van Vuren, D. (1998) A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology* 246, S0952836998009911.
- Servanty, S., Gaillard, J.-M., Allainé, D., Brandt, S. & Baubet, E. (2007) Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behavioral Ecology* 18, 427–432.
- Sherman, P.W. & Morton, M.L. (1984) Demography of Belding's Ground Squirrels. *Ecology* 65, 1617–1628.
- Sherman, P.W. & Runge, M.C. (2002) Demography of a population collapse: the northern idaho ground squirrel (*spermophilus brunneus brunneus*). *Ecology* 83, 2816–2831.
- Sherman, P.W. & Runge, M.C. (2002a) Demography of a Population Collapse: The Northern Idaho Ground Squirrel (*spermophilus Brunneus Brunneus*). *Ecology* 83, 2816–2831.
- Sherman, P.W. & Runge, M.C. (2002b) Demography of a population collapse: the northern idaho ground squirrel (*spermophilus brunneus brunneus*). *Ecology* 83, 2816–2831.
- Siler, W. (1979) A Competing-Risk Model for Animal Mortality. *Ecology* 60, 750–757.
- Simard, M.A., Huot, J., de Bellefeuille, S. & Côté, S.D. (2014) Linking conception and weaning success with environmental variation and female body condition in a northern ungulate. *Journal of Mammalogy* 95, 311–327.
- Skibiél, A.L., Dobson, F.S. & Murie, J.O. (2009) Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* 79, 325–341.
- Skibiél, A.L., Dobson, F.S. & Murie, J.O. (2009a) Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* 79, 325–341.
- Skibiél, A.L., Dobson, F.S. & Murie, J.O. (2009b) Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* 79, 325–341.

- Soulsbury, C.D., Baker, P.J., Iossa, G. & Harris, S. (2008) Fitness costs of dispersal in red foxes (*Vulpes vulpes*). Behavioral Ecology and Sociobiology 62, 1289–1298.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Linde, A.V.D. (2002) Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 64, 583–639.
- Spinage, C.A. (1972) African Ungulate Life Tables. Ecology 53, 645–652.
- Stephens, P.A., Boyd, I.L., McNamara, J.M. & Houston, A.I. (2009) Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90, 2057–2067.
- Sullivan, K.A. (1989) Predation and Starvation: Age-Specific Mortality in Juvenile Juncos (*Junco phaeotus*). Journal of Animal Ecology 58, 275–286.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., et al. (2004) Extinction risk from climate change. Nature 427, 145–148.
- Tidière, M., Gaillard, J.-M., Berger, V., Müller, D.W.H., Bingaman Lackey, L., Gimenez, O., Clauss, M. & Lemaître, J.-F. (2016) Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. Scientific Reports 6, 36361.
- Tidière, M., Gaillard, J.-M., Berger, V., Müller, D.W.H., Bingaman Lackey, L., Gimenez, O., Clauss, M. & Lemaître, J.-F. (2016a) Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. Scientific Reports 6, 36361.
- Tidière, M., Gaillard, J.-M., Berger, V., Müller, D.W.H., Bingaman Lackey, L., Gimenez, O., Clauss, M. & Lemaître, J.-F. (2016b) Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. Scientific Reports 6, 36361.
- Tidière, M., Gaillard, J.-M., Müller, D.W.H., Lackey, L.B., Gimenez, O., Clauss, M. & Lemaître, J.-F. (2015) Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants. Evolution 69, 3123–3140.

- Trivers, R. (1985) Social evolution.
- Tuljapurkar, S. & Edwards, R.D. (2011) Variance in Death and Its Implications for Modeling and Forecasting Mortality. *Demographic research* 24, 497–526.
- Tuljapurkar, S. (2010) The final inequality: variance in age at death. In *Demography and the Economy* pp. 209–221. University of Chicago Press.
- Vaupel, J.W., Manton, K.G. & Stallard, E. (1979) The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16, 439–454.
- Viechtbauer, W. (2010) Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software* 36.
- Vindenes, Y. & Langanen, Ø. (2015) Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letters* 18, 417–432.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* 416, 389–395.
- Whitlock, M.C. (2011) Data archiving in ecology and evolution: best practices. *Trends in Ecology & Evolution* 26, 61–65.
- Willey, C.H. (1974) Aging Black Bears from First Premolar Tooth Sections. *The Journal of Wildlife Management* 38, 97–100.
- Williams, G.C. (1957) Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution* 11, 398–411.
- Wilmoth, J.R. (2000) Demography of longevity: past, present, and future trends. *Experimental Gerontology* 35, 1111–1129.
- Wilson, A.J. & Nussey, D.H. (2010) What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* 25, 207–214. Elsevier Ltd.
- Zarulli, V., Jones, J.A.B., Oksuzyan, A., Lindahl-Jacobsen, R., Christensen, K. & Vaupel, J.W. (2018) Women live longer than men even during severe famines and epidemics. *Proceedings of the National Academy of Sciences* 115, E832–E840.
- Zedrosser, A., Dahle, B., Støen, O.-G. & Swenson, J.E. (2009) The effects of primiparity on reproductive performance in the brown bear. *Oecologia* 160, 847.

Zedrosser, A., Pelletier, F., Bischof, R., Festa-Bianchet, M. & Swenson, J.E. (2013) Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. *Ecology* 94, 231–240.

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# APPENDICES

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## Assessing errors in generation time estimates to improve IUCN extinction risk assessments

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1. Generation time is a fundamental component of extinction risk assessments for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Calculation of generation time requires age-specific data on survival and fecundity rates and knowledge of population growth rates. These data are generally lacking for threatened species, so approximations including only partial demographic information have to be used leading to potential errors in generation time estimates.
2. To quantify the magnitude of potential errors in generation time estimates we compared seven approximations with exact measures of generation time, calculated either from complete life tables available for 58 mammalian species or from simulated data. We also tested the commonly used prediction of generation time based on the allometric relationship with body mass using phylogenetic generalized least squares.
3. Root-mean-square errors were largest in measures assuming constant fecundity rates with age, some of which are currently used in Red List assessments. We found that although the

measure that only ignores population growth rates performed well, it tended to under-estimate generation time for decreasing populations, and over-estimate it for increasing populations.

4. The predictive metric of body mass to estimate generation time is inaccurate. We propose an alternative improved predictive metric based on body mass, age at first reproduction, and reproductive lifespan, which markedly improves the estimation of generation time compared to measures currently used.
5. *Synthesis and applications:* Our results provide an overview of the potential errors that occur when estimating generation time in absence of key demographic information. We demonstrate that using more rigorous mathematical formulations of generation time and accounting for uncertainties in proxy measures should considerably improve current IUCN extinction risk assessments.

## Introduction

Population demography is extremely variable across species and environments, as demonstrated by the diversity of age-specific trajectories of survival and fecundity observed across the tree of life (Jones et al. 2014). Identifying these trajectories allows researchers to estimate key measures of population dynamics such as population growth rates and generation time (Caswell 2001; Gaillard et al. 2005; Tuljapurkar, Gaillard & Coulson 2009; Bienvenu & Legendre 2015; Ellner 2018). Three main definitions of generation time include: (1) the time required for a population at the stable age distribution to grow by the net reproductive rate ( $T_R$ ); (2) the mean age of the parents of offspring produced in the current time period once the population has reached the stable age distribution ( $T_b$ ); and (3) the mean age at which members of a cohort of newborns produce offspring ( $T_s$ ) (Table 1) (Coale 1972; Cochran & Ellner 1992; Caswell 2001). Generation time has been used in a wide range of applications, including measuring the pace of life across species (Gaillard et al. 2005; Baudisch 2011), ranking species along the slow-fast life history continuum (Gaillard et al. 2005), evaluating the response of species to variable environments (Tuljapurkar, Gaillard & Coulson 2009), calculating evolution rates (Evans et al. 2012), and estimating extinction risk (Mace et al. 2008). Particularly, the close association between generation time and extinction risk has led generation time to become a fundamental measure in conservation biology. For instance, generation time is now routinely used to assess species' threat status for worldwide conservation organizations such as the International Union for Conservation of Nature (IUCN 2017) or to assess bycatch limits in fisheries (Dillingham 2010). Moreover, the mutation rate strongly depends on generation time, making it an indicator for species' adaptability to climate change (Foden et al. 2013; Pearson et al. 2014). Based on such fundamental role in establishing conservation goals, it is necessary to obtain accurate estimates of generation time for endangered species. When the necessary data for such estimation are missing, it is imperative to have a clear understanding of the uncertainty in the generation time value being available.

The IUCN Red List of Threatened Species is the primary authority for extinction risk assessments. In the Red List assessment, species are categorized as threatened based on criteria related to population decline, geographic range size, fragmentation, and small population size (IUCN 2017).

In criteria related to population decline, generation time acts as a standardization for time units that allow using the same criteria on species with extremely different lifespans (Mace et al. 2008). Criteria including generation time have been used to list 41% of mammals, 33% of birds, 14% of amphibians, 19% of reptiles, and 96% of corals categorized as threatened (IUCN 2017a).

In the *IUCN Guidelines for Using the IUCN Red List Categories and Criteria* (hereafter called IUCN guidelines, IUCN, 2017b) generation time is defined based on the cohort definition ( $T_s$ ), which would only be appropriate for data collected from a single cohort, from which individuals are monitored from birth to death, or under that assumption of stationary populations (i.e. a population growth rate equal to one). In many studies of mammals in the wild, however, age-specific vital rates are calculated as averages across years on cross sectional data (i.e. including multiple cohorts). Using average vital rates leads to the strong assumption of stationary populations when the cohort approach is used (Nussey et al. 2008). Thus, the period approach to calculate generation time ( $T_b$ ) is the most general measure as it accounts for overlapping generations by including the population growth rate.

Both the cohort and the period definitions of generation time require complete age- and sex-specific data on survival and fecundity, but this detailed information is currently only available for ~1.6% of threatened tetrapod species and probably even less for other taxonomic groups (Conde et al., unpublished data). Given the scarcity of demographic data, demographic traits such as the average age at first reproduction (Tsantes & Steiper 2009) or evolutionary allometric relationships between generation time and body mass are frequently used to approximate generation time (Millar & Zammuto 1983; Gaillard et al. 2005; Cooke et al. 2018).

The IUCN guidelines explicitly mention two approximations of generation time: The first is the ‘reproductive lifespan proxy’ that calculates generation time as the sum of age at first reproduction and the product of a variable  $z$  and the species reproductive lifespan ( $T_z$ , Table 1). This variable  $z$ , bound between 0 and 1, is estimated as the average from species for which generation time can be accurately estimated, and then used to approximate generation time for species with no demographic information. For example,  $z$  has been fixed at 0.29 (Pacifci et al. 2013) and 0.28 (Keith et al. 2015), for mammals. The  $z$ -value simply states that generation time cannot be smaller than average age at

first reproduction or larger than the average age at last reproduction and, based on the IUCN guidelines (IUCN, 2017b), scales accordingly to the relative fecundity of young vs. old individuals in the population. The second measure is the ‘adult-mortality proxy’, which is calculated as the sum of age at first reproduction and the inverse of average annual adult mortality ( $T_q$ , Table 1). Using these measures facilitates approximating generation time for a large number of species, as the required variables are more commonly available than age-specific vital rates. For example, data on age at first reproduction currently exist for at least 35% of mammalian species (Conde, et al., unpublished data). However, these measures should be applied under careful consideration as they may lead to considerable errors. For example, Cooke et al. (2018) found that calculating generation time from the ‘reproductive lifespan proxy’ for Bovidae species can lead to erroneous results when the age at last reproduction is estimated based on maximum longevity in captivity rather than in the wild. Such discrepancy comes from the consistently longer life of captive mammals compared to their wild counterparts (Tidière et al. 2016). Moreover, Fung & Waples (2017) reported that the estimation of generation time requires an adjustment that shifts ages by one year, particularly for species that start reproducing before their first year of age. Ignoring this adjustment may result in biased assessments of currently used generation time proxies. This adjustment has recently been incorporated into the IUCN guidelines (2017b). Fung and Waples (2017)’s study provides the first attempt to predict and correct for errors generated by using proxies instead of true estimates of generation time. However, their study stresses the use of approximations bearing a large number of assumptions, such as constant adult mortality and populations near stationarity (i.e. the cohort measure of generation time), rarely met in wildlife populations.

Here, we review currently used measures of generation time and compare the metric of generation time with the least number of assumptions (i.e. the period definition of generation time,  $T_b$ ) to seven metrics including only partial demographic information. We propose a new approach for estimating generation time based on allometric relationships between generation time and some key species-specific life history traits. We use complete life tables collected from studies of wild

populations belonging to 58 mammalian species spanning over nine orders, and simulated data covering a larger range of possible mortality and fecundity trajectories.

## Methods

### *Life tables from wild populations*

We obtained published life tables of wild populations for 58 terrestrial and marine mammalian species (Table S1). From these we extracted the cumulative survival probability at age  $x$  ( $l_x$ ) and the average number of female offspring born to females of age  $x$  (i.e. fecundity,  $m_x$ ). We defined  $\alpha$  as the age at first reproduction, which is the first age at which  $m_x \neq 0$ , and  $\omega$  as the age when reproduction was last observed. We equated missing values of  $m_x$  at older ages to 0 when only a handful of individuals were still alive. From the  $l_x$  and  $m_x$  data, we built population projection matrices (Caswell 2001) to calculate the asymptotic population growth rate  $\lambda$  (as the dominant eigenvalue) and the corresponding stable age distribution  $\mathbf{v}$  (as the corresponding right eigenvector). Most life tables started at birth, but in 14 species survival was lacking prior to the age at first reproduction. For these we used estimates of juvenile survival from a different population of the same species (Table S1).

### *Simulated data*

We constructed 15 mortality and 15 fecundity trajectories resulting in 225 life tables, thereby allowing us to explore a wider range of mortality and fecundity combinations than those obtained from field data. We calculated mortality trajectories by varying the mortality or hazard rate function

$$\mu(x | \theta) = \lim_{\Delta x \rightarrow 0} \frac{\Pr(x \leq X < x + \Delta x | X \geq x, \theta)}{\Delta x}, \quad (1)$$

which is the rate at which individuals die as a function of age  $x$ , given they survived to the beginning of the interval  $[x, x+\Delta x]$ , where  $x$  is age,  $X$  is a random variable for ages at death and  $\theta$  is a vector of mortality parameters. For the different shapes, we varied the parameters of the functions calculated as

$$\mu(x|\boldsymbol{\theta}) = \begin{cases} c & \text{constant mortality} \\ \exp(b_0 + b_1 x) & \text{increasing mortality} \\ \exp(a_0 - a_1 x) & \text{decreasing mortality} \\ \exp(a_0 - a_1 x) + c + \exp(b_0 + b_1 x) & \text{bathtub mortality} \\ \exp(b_0 + b_1 x) / \left[ 1 + b_2 \frac{e^{b_0}}{b_1} (e^{b_1 x} - 1) \right] & \text{logistic mortality} \end{cases} \quad (2)$$

where  $\boldsymbol{\theta}^T = [a_0, a_1, c, b_0, b_1, b_2]$  is the vector of mortality parameters, where  $\frac{1}{b_1} \times < a_0, b_0 < \times$  and  $a_1, c, b_1, b_2 \geq 0$ . The resulting mortality patterns and life expectancy at birth,  $e_0$  are depicted in Figure S1. We chose these mortality functions because they produce the most commonly encountered age-specific mortality profiles for vertebrates (Promislow, Montgomerie & Martin 1992; Ricklefs 2000; Ricklefs & Scheuerlein 2001; Bronikowski et al. 2011; Jones et al. 2014; Colchero et al. 2017).

From the hazard rate, the cumulative survival probability is calculated as

$$S(x|\boldsymbol{\theta}) = \Pr(X > x) = \exp \left[ - \int_0^x \mu(t|\boldsymbol{\theta}) dt \right]. \quad (3)$$

Here  $S(x)$  provides the expression for  $l_x$  in continuous time. From the age-structured mortality rates, we calculated survival probabilities at every age interval  $[x, x + \Delta x]$  as

$$\begin{aligned} p_x &= \Pr(X > x + \Delta x | X > x) \\ &= \exp \left[ - \int_x^{x+\Delta x} \mu(t) dt \right] \\ &= \frac{S(x + \Delta x)}{Sx}, \end{aligned} \quad (4)$$

where  $\Delta x = 1$ . We modeled the age-specific fecundity rate at birth  $m_x$  using the following flexible exponential function with a quadratic effect as a function of age (Emlen 1970)

$$m(x|\boldsymbol{\gamma}) = \gamma_0 e^{-\gamma_1(x-\gamma_2)^2}, \quad (5)$$

where  $\boldsymbol{\gamma}^T = [\gamma_0, \gamma_1, \gamma_2]$  is a vector of parameters with  $\gamma_0, \gamma_1, \gamma_2 > 0$ , where  $\gamma_0$  controls the maximum number of offspring produced when  $x = \gamma_2$ ,  $\gamma_1$  determines how fast  $m_x$  increases with age, and where  $\gamma_2$  represents the age at which maximum  $m_x$  is achieved. As with mortality, we varied the values of  $\boldsymbol{\gamma}$  to simulate a range of  $m_x$  trajectories (Figure S2). We calculated  $m_x$  for a given age interval  $[x, x + \Delta x]$  as

$$m_x = \int_x^{x+\Delta x} m(t) dt . \quad (6)$$

With the resulting age-specific fecundity rates and survival probabilities, we constructed Leslie matrices (Leslie 1945), and calculated the asymptotic population growth rate  $\lambda$  as described above and obtained the corresponding stable age distribution,  $\mathbf{v}^T = [v_0, v_1, \dots, v_\omega]$ , where  $\omega$  is the age when only 0.1% of the population remains alive (i.e.  $S(x) = 0.001$ ) (Caswell 2001).

To investigate discrepancies in the estimation of generation time for measures not considering population growth rates, we adjusted the values of  $m_x$  for all 225 simulated life tables such that the resulting population growth rate could take three values, namely  $\lambda = 0.9$ ,  $\lambda = 1$ , and  $\lambda = 1.1$ ; thus resulting in 675 populations that were either declining, stationary or increasing.

### *Calculation of generation time*

We calculated generation time  $T_b$  (sensu Leslie 1966) as the weighted mean age of the mothers at childbirth. We assumed this to be the most appropriate measure of generation time because it requires the least number of assumptions while incorporating all relevant demographic information from the population. Note that all equations calculated from life tables in Table 1 are approximations to  $T_b$ , and therefore  $T_b$  provides the closest approximation of the true generation time.

We compared  $T_b$  with seven other measures of generation time that require data from life tables, population projection matrices or are based on simpler aggregated demographic measures at the species level (Table 1). To compute IUCN's 'adult-mortality proxy',  $T_q$  we calculated the average annual adult mortality ( $\bar{q}$ ) as the complement of the weighted average age-specific survival probabilities,  $\bar{p}$ , weighted by their stable age-distribution,  $\mathbf{v}$  (see above) as

$$\bar{p} = \frac{\prod_{x=\alpha}^{\omega} l_x v_x}{\prod_{x=\alpha}^{\omega} v_x}. \quad (7)$$

For the calculation of IUCN's 'reproductive lifespan proxy',  $T_z$ , we used a  $z$  of 0.28 for mammalian and simulated life tables (Keith et al. 2015).

### *Performance of approximations based on life table information*

We fitted linear regression models of the form

$$y_{ib} = \log(T_{ib}) = \underbrace{\beta_0 + \beta_1 \log(T_{ij})}_{\hat{y}_{ibj}} + \varepsilon_i, \quad (8)$$

with  $\varepsilon_i \sim N(0, \sigma^2)$  for all  $i = 1, 2, \dots, n$ , and all  $j = 1, 2, \dots, 7$ , where  $n$  is the total number of species,  $\sigma^2$  is the residual variance,  $T_{ij}$  is generation time for each species  $i$  and approximation  $j$ , and  $\hat{y}_{ibj}$  are the fitted values. With this regression we seek to measure the accuracy with which the values of  $\log(T_{ib})$  are approximated with the different methods, represented by  $\log(T_{ij})$ . Ideally, there should be a perfect one-to-one mapping, which implies that the intercept should be  $\tilde{\beta}_0 = 0$ , and the slope  $\tilde{\beta}_1 = 1$ . We used standard hypothesis testing by means of  $t$ -tests ( $H_0: \hat{\beta}_k = \tilde{\beta}_k$  for  $k = 0, 1$ ) to determine whether the estimated values of the slope and intercept matched these expectations.

Finally, we calculated root mean square errors (RMSEs) between each approximation and the  $\log(T_{ib})$  as

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (y_{ij} - y_{ib})^2}{n}}. \quad (9)$$

### *Performance of approximations in the absence of life tables*

We implemented phylogenetic generalized least squares (PGLS) regressions between  $\log(T_{ib})$  and biological covariates that are more readily available than life tables. We started with the log of body

mass, which is allometrically related to  $T_{ib}$  (Gaillard et al. 2005, Cooke et al. 2018), and sequentially added the log of age at first reproduction and reproductive lifespan, both known to capture demographic variation among mammals (Gaillard et al. 2016). The fully parameterized regression was

$$\log(T_{ib}) = \beta_0 + \underbrace{\beta_1 \log(m_i) + \beta_2 \log(\alpha_i) + \beta_3 \log(r_i)}_{\delta_i} + \varepsilon_i, \text{ for } i = 1, \dots, n \quad (10)$$

with vector of residuals  $\boldsymbol{\varepsilon} \sim N(\mathbf{0}, \sigma^2 \lambda_p \Sigma)$ , where  $\sigma^2$  is the residual variance of the regression and  $\Sigma$  is the variance-covariance matrix. The variance-covariance matrix  $\Sigma$  is derived from the phylogenetic relationships among the 58 species that we obtained from the ‘supertree’ phylogeny of (Bininda-Emonds *et al.* 2007) hosted at the *Evo10* website ([https://www.evoio.org/wiki/File:Bininda-emonds\\_2007\\_mammals.nex](https://www.evoio.org/wiki/File:Bininda-emonds_2007_mammals.nex)). We found the maximum likelihood estimate of the coefficient  $\lambda_p$  ( $0 \leq \lambda_p \leq 1$ ) known as Pagel’s lambda, which measures the intensity of the phylogenetic signal (Harvey & Pagel, 1991).

We used the resulting coefficients to estimate the value of  $T_i$  as

$$T_{i\text{phyl}} = e^{\delta_i} \quad (11)$$

where  $T_{i\text{phyl}}$  was the median of  $T_{ib}$  under the assumption that  $T_{ib}$  is log-normally distributed.

After selecting the model that best fitted the data by means of the Akaike’s information criterion (AIC, Akaike, 1974), we performed a cross-validation analysis to determine the predictive accuracy of the phylogenetic regression with respect to the  $z$ -approximation. We repeated the analysis for 5000 iterations where at each iteration, we randomly separated the dataset into a training subset of 53 species, and a validation subset of 5 species. We then fitted the phylogenetic regression in Eq. (10) to the training set and used the estimated parameters to predict  $\log(T_{i\text{phyl}}) \approx \delta_i$  on the validation set. We then calculated root mean square errors on the validation set between the real,  $y_{ib}$ , and estimated values,  $\delta_i$ , and, for comparison, between the real values and the  $z$ -approximation,  $y_{iz}$ .

We performed all calculations and analyses using the free-open-source software R (R Core Development Team, 2017). For the phylogenetic regressions, we used the R package ‘ape’ v.4.1

(Paradis, Claude & Strimmer 2004).

## Results

### *Performance of approximations based on life table information*

Measures of generation time that did not include  $\lambda$  showed substantial differences from the measure  $T_b$  (Fig. 1). These differences were most severe in the simulated life tables and less pronounced in the observed mammalian life tables. For decreasing populations ( $\lambda < 1$ ) generation time was underestimated using measures that neglected  $\lambda$ , whereas generation time was overestimated for increasing populations (Fig. 1,  $T_s$ ,  $T_{sc}$ ,  $T_q$ ). From observed mammalian life tables,  $\lambda$  ranged from 0.78 to 1.28 with a mean of 1.02. In simulated life tables, over- or under-estimation in  $T_s$  increased in longer-lived species (Fig. 1, b.1).

Furthermore, the assumption of constant demographic rates over the lifetime led to considerable estimation differences (Fig. 1,  $T_c$ ). This was primarily driven by constant  $m_x$  (Fig. 1,  $T_c$ ,  $T_{cm}$ ,  $T_{sc}$ ), leading to strong underestimation of generation time in shorter-lived mammal species and overestimation of longer-lived species in simulated data. The assumption of constant survival had a considerably lower effect (Fig. 1  $T_{cp}$ ). In most cases, the regression analysis yielded significant differences between the estimated intercepts and slopes with respect to the expected values of 0 and 1, respectively (Table 2). Exceptions were the intercepts of  $T_s$  and  $T_q$  for the real data, and the intercepts of  $T_{cp}$  and  $T_c$  for the simulated data. Only  $T_z$  on the real data had non-significant  $p$ -values for both parameters, but both  $p$ -values were significant for the simulated data.

Comparison of root mean square errors across different approximation of generation time for mammals (Table 2) showed that  $T_s$  performed best on the real data while  $T_c$  had the lowest RMSE on the simulated data.

### *Performance of approximations in the absence of life tables*

The phylogenetic regression that provided the best fit included all three logged variables, namely body weight, age at first reproduction and reproductive lifespan (Fig. 2). Notably, the phylogenetic regression between body mass and  $T_{bi}$  ( $T_{phyl\_1}$ ) provided the worst fit (AIC = 76.6,  $R^2 = 0.43$ ,  $\lambda_p = 0.855$ ), where  $T_b$  was markedly overestimated for shorter-lived species and strongly under-estimated for longer-lived species (Fig. 2a). The addition of age at first reproduction ( $T_{phyl\_2}$ ) improved the fit considerably (AIC = 28.2,  $R^2 = 0.87$ ,  $\lambda_p = 0.645$ ) while the model with all three covariates provided the best fit (AIC = -8.5,  $R^2 = 0.95$ ,  $\lambda_p = 0.009$ ) (Fig. 2, Table 2). Notably, the RMSE between  $y_b$  and  $\delta$  from the full regression is lower ( $RMSE_\delta = 0.167$ ) than between  $y_b$  and  $y_z$  ( $RMSE_z = 0.181$ ). The cross-validation analysis shows that the approximation based on the phylogenetic regression performs at least as well as the z-approximation (Fig. 3).

## Discussion

We show that measures of generation time are highly sensitive to the population growth rate  $\lambda$  and to the amount of age-dependence in the vital rates. Assuming stationary populations (i.e.  $\lambda = 1$ ) or constant fecundity with age ( $m_x$ ) resulted in over- or under-estimation in generation time even when high-quality life table data were available. Generation time proxies currently recommended in the IUCN guidelines performed poorly, except for the reproductive lifespan proxy,  $T_z$ , which provided a good approximation when accurate data on age at first reproduction and reproductive lifespan were available. A linear regression model based on allometric relationships can improve the estimation of generation time when age-specific vital rates and population growth rates are lacking. Furthermore, this linear model can facilitate the use of available information from related species in the estimation of generation time.

The metrics of generation time recommended by the IUCN are cohort-based and therefore do not account for non-stationarity of populations. This assumption is rarely met as illustrated from our analysis of 58 wild populations of terrestrial and marine mammals and leads to over- or under-estimation even when populations are only slightly increasing or decreasing. While  $T_b$  assumes that the

population is at the stable age distribution, which is another strong assumption that might not apply to most populations, using  $T_s$  on cross-sectional data assumes not only stable age structure, but also stationarity.

The IUCN guidelines explicitly mention that estimating generation time in populations displaying strong age-dependence in vital rates is especially difficult (IUCN 2017b). In support, we found substantial errors when assuming constant vital rates with age involving a downward bias from mammalian life tables. The assumption of constant survival with age alone provided an acceptable approximation, whereas larger errors resulted when assuming constant  $m_x$  with age. This is in line with previous results reporting that the incorrect assumption of constant fecundity rates with age led to an underestimation of generation time and thereby to an overharvesting of birds (Dillingham 2010). Considering extinction risk assessments, underestimation of generation time is especially worrisome because it can lead to wrongly assigning a species to a lower risk category. In the simulated data, we also found larger errors in longer-lived species that are especially vulnerable to extinction due to their slow life histories leading to long generation times (e.g. Cardillo et al. 2005).

Of the two IUCN proxies,  $T_z$  performed better than  $T_q$  and performed especially well in mammals for which we estimated ages at first reproduction directly from the life tables. But for most species this information is unavailable, and estimates are likely to be more severely biased. This is evident from the analysis on simulated data, where this measure performed poorly. As previously suggested (Fung & Waples 2017),  $T_z$  might only be useful when  $z$  estimates for species with similar life history are available.

Contrary to our findings in mammals, Fung & Waples (2017) found that  $T_z$  generated higher errors than  $T_q$ . These authors did, however, not account for non-stationarity of populations, which, as we demonstrated, leads to considerable errors by underestimating generation time when  $\lambda < 1$  and by overestimating it when  $\lambda > 1$ . Additionally, they calculated average mortality  $\bar{\mu}$  based on the geometric mean between the survival at  $\alpha$  and  $\omega$  (i.e.  $(l_\omega / l_\alpha)^{1/(\omega - \alpha)}$ ). We do not recommend this calculation because the geometric mean strongly depends on the mortality rates observed at first and

last reproduction and is only valid for species with constant survival with age. This is not the case in mammals (see e.g. Gaillard et al. 2017 for a recent review) and has only been reported in few species of aquatic invertebrates and a handful of plants (Roach & Gampe 2004; Dańko, Kozłowski & Schaible 2015).

The estimation of generation time from phylogenetic regression on body mass did not provide reliable results across mammals but may give some useful information if only body mass is available for the focal species. Cooke et al. (2018) recently showed that body mass and phylogeny offer a reliable predictor of generation time across Bovidae species, thus body mass might be better at predicting generation time among closely related species. We found that including two biological times, age at first reproduction and reproductive lifespan greatly improved the fit. The full model requires almost the same amount of information as the reproductive lifespan proxy,  $T_z$  recommended by the IUCN, while being more consistent with general life-history theory as it predicts generation time from species-specific values. The model only including body mass and age at first reproduction predicted generation time relatively well. This model can be used when ages at last reproduction are lacking, which are generally difficult to obtain in wild populations.

We assumed life tables provide accurate measures of species-specific generation time, but this metric can vary considerably within a species. Empirical studies have revealed an almost twofold variation in generation time within a given mammalian species (e.g. from 4.97 to 8.25 years in Pyrenean chamois (*Rupicapra rupicapra*, Crampe et al. 2006), from 3.93 to 6.80 years in roe deer (*Capreolus capreolus*, Nilsen et al. 2009), or from 2.3 to 3.6 years in wild boar (*Sus scrofa*, Servanty et al. 2011)). This further stresses that the cohort approach to calculate generation time needs to be evaluated carefully, particularly for populations exhibiting large variation in vital rates due to cohort environmental effects (e.g. Gaillard et al. 1997; Le Galliard, Marquis & Massot 2010; Gaillard et al. 2016). To benefit extinction risk assessments, studies investigating intra- vs. inter-specific variation, and variation in relation to environmental changes and increasing stressors, such as harvesting and climate change will be required.

Even the best estimation methods are only as good as the data used. A challenge will be to fill the glaring data gaps of demographic knowledge occurring even among some of the best-studied taxa like mammals. Efforts to collect age and stage-specific data across the tree of life, e.g. in the COMADRE Animal Matrix Database (Salguero-Gómez et al. 2016) will continue making these data available, which is apparent in the increasing publication record of vital rates since the 1960s (see Fig. S5, which markedly contrasts with the Fung and Waples (2017)'s statement that "Collection and publication of age-based vital-rate information peaked in the 1980s and is now uncommon" (p. 2)). Moreover, the exploration of new data sources such as captive populations in zoos, e.g. from the Zoological Information Management System (ZIMS) keeping standardized information for over 10 million individuals from 21,000 species (Species360, 2017), can provide knowledge for threatened species where no data is available yet from the wild.

Until we are able to gather sufficient demographic information for a wide range of species to estimate key demographic traits such as generation time, we will have to rely on proxies such as those provided in the IUCN guidelines. Based on our findings, we recommend improving upon this information by providing clearer guidelines on the assumptions for estimation methods on generation time. We recommend  $T_b$  as the appropriate measure of generation time to be included in the guidelines. We further recommend making assessors aware of the results obtained in this study, such as the underestimation of generation time resulting from the assumption of constant  $m_x$  and clear guidelines on the calculation of average vital rates. To spur initiatives for further research on generation time it would be desirable to include data and methods used for the estimation of generation time, where this is appropriate, in the online database of Red List assessments (<http://www.iucnredlist.org>). Further knowledge on generation times is urgently needed to design effective conservation management and prioritize species at greatest risk.

## Author contributions

FC, DAC, JMG and JS conceived and designed the study; JMG, VR, and JFL collected the data; JS and FC analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723.
- Baudisch, A. (2011) The pace and shape of ageing. *Methods in Ecology and Evolution*, *2*, 375–382.
- Bienvenu, F. & Legendre, S. (2015) A New Approach to the Generation Time in Matrix Population Models. *The American Naturalist*, **185**, 834–843.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature*, **446**, 507–512.

- Bronikowski, A.M., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A., Stoinski, T., Morris, W.F., Strier, K.B. & Alberts, S.C. (2011) Aging in the natural world: comparative data reveal similar mortality patterns across primates. *Science*, **331**, 1325–1328.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*, **309**, 1239–1241.
- Caswell, H. (2001) *Matrix Population Models*. Sunderland, MA.
- Coale, A.J. (1972) *Growth and Structure of Human Populations*. Princeton University Press.
- Cochran, M. & Ellner, S. (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs*, **62**, 345–364.
- Colchero, F., Aliaga, A.E., Jones, O.R. & Conde, D.A. (2017) Individual heterogeneity determines sex differences in mortality in a monogamous bird with reversed sexual dimorphism. (ed JM Gaillard). *The Journal of animal ecology*, **86**, 899–907.
- Cooke, R.S.C., Gilbert, T.C., Riordan, P. & Mallon, D. (2018) Improving generation length estimates for the IUCN Red List (ed L Bosso). *PLoS ONE*, **13**, e0191770.
- Crampe, J.-P., Loison, A., Gaillard, J.M., Florence, E., Caens, P. & Appolinaire, J. (2006) Patterns of reproduction of female isard (*Rupicapra pyrenaica pyrenaica*) in a non-hunted population and demographic consequences]. *Canadian Journal of Zoology/Revue Canadienne de Zoologie*, **84**, 1263–1268.
- Dańko, M.J., Kozłowski, J. & Schaible, R. (2015) Unraveling the non-senescence phenomenon in Hydra. *Journal of theoretical biology*, **382**, 137–149.
- Dillingham, P.W. (2010) Generation time and the maximum growth rate for populations with age-specific fecundities and unknown juvenile survival. *Ecological Modelling*, **221**, 895–899.

- Ellner, S.P. (2018) Generation Time in Structured Populations. *The American Naturalist*, 000–000.
- Emlen, J.M. (1970) Age Specificity and Ecological Theory. *Ecology*, **51**, 588–601.
- Evans, A.R., Jones, D., Boyer, A.G., Brown, J.H., Costa, D.P., Ernest, S.K.M., Fitzgerald, E.M.G., Fortelius, M., Gittleman, J.L., Hamilton, M.J., Harding, L.E., Lintulaakso, K., Lyons, S.K., Okie, J.G., Saarinen, J.J., Sibly, R.M., Smith, F.A., Stephens, P.R., Theodor, J.M. & Uhen, M.D. (2012) The maximum rate of mammal evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 4187–4190.
- Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O’Hanlon, S.E., Garnett, S.T., Şekercioğlu, Ç.H. & Mace, G.M. (2013) Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals (ed S Lavergne). *PLoS ONE*, **8**, e65427.
- Fung, H.C. & Waples, R.S. (2017) Performance of IUCN proxies for generation length. *Conservation biology : the journal of the Society for Conservation Biology*, **18**, 273.
- Gaillard, J.M., Boutin, J.-M., Delorme, D., van Laere, G., Duncan, P. & Lebreton, J.D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.
- Gaillard, J.M., Loison, A., Toïgo, C., Delorme, D. & van Laere, G. (2016) Cohort effects and deer population dynamics. *Écoscience*, **10**, 412–420.
- Gaillard, J.M., Yoccoz, N.G., Lebreton, J.D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D. & Allaine, D. (2005) Generation Time: A Reliable Metric to Measure Life-History Variation among Mammalian Populations. *The American Naturalist*, **166**, 119–123.
- Harvey, P.H. & Pagel, M.D. *The Comparative Method in Evolutionary Biology*. 1991.

IUCN (2017a). *The IUCN Red List of Threatened Species. Version 2017-1.*

<<http://www.iucnredlist.org>>. Downloaded on 24 January 2017.

IUCN Standards and Petitions Subcommittee (2017b). Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. Downloadable from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.

Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren, J.P., Ehrlén, J., García, M.B., Menges, E.S., Quintana-Ascencio, P.F., Caswell, H., Baudisch, A. & Vaupel, J.W. (2014) Diversity of ageing across the tree of life. *Nature*, **505**, 169–173.

Keith, D., Akçakaya, H.R., Butchart, S.H.M., Collen, B., Dulvy, N.K., Holmes, E.E., Hutchings, J.A., Keinath, D., Schwartz, M.K., Shelton, A.O. & Waples, R.S. (2015) Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa. *Biological Conservation*, **192**, 247–257.

Le Galliard, J.F., Marquis, O. & Massot, M. (2010) Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology*, **79**, 1296–1307.

Leslie, P.H. (1945) On the Use of Matrices in Certain Population Mathematics. *Biometrika*, **33**, 183.

Leslie, P.H. (1966) The Intrinsic Rate of Increase and the Overlap of Successive Generations in a Population of Guillemots (*Uria aalge* Pont.). *The Journal of animal ecology*, **35**, 291.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation biology : the journal of the Society for Conservation Biology*, **22**, 1424–1442.

- Metcalfe, C.J.E. & Pavard, S. (2007) Why evolutionary biologists should be demographers. *Trends in ecology & evolution*, **22**, 205–212.
- Millar, J.S. & Zammuto, R.M. (1983) Life Histories of Mammals: An Analysis of Life Tables. *Ecology*, **64**, 631–635.
- Niel, C. & Lebreton, J.D. (2005) Using Demographic Invariants to Detect Overharvested Bird Populations from Incomplete Data. *Conservation biology : the journal of the Society for Conservation Biology*, **19**, 826–835.
- Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., van Laere, G. & Linnell, J.D.C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, **78**, 585–594.
- Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J.M. (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology*, **22**, 393–406.
- Pacifici, M., Santini, L., Di Marco, M. & Baisero, D. (2013) Generation length for mammals. *Nature*.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics (Oxford, England)*, **20**, 289–290.
- Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNeese, J. & Akçakaya, H.R. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, **4**, 217–221.
- Promislow, D.E.L., Montgomerie, R. & Martin, T.E. (1992) Mortality Costs of Sexual Dimorphism in Birds. *Proceedings of the Royal Society of London B: Biological Sciences*, **250**, 143–150.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Ricklefs, R.E. (2000) Intrinsic aging-related mortality in birds. *Journal of Avian Biology*, **31**, 103–111.
- Ricklefs, R.E. & Scheuerlein, A. (2001) Comparison of aging-related mortality among birds and mammals. *Experimental gerontology*, **36**, 845–857.
- Roach, D.A. & Gampe, J. (2004) Age-specific demography in *Plantago*: uncovering age-dependent mortality in a natural population. *The American Naturalist*, **164**, 60–69.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H. & Vaupel, J.W. (2016) COMADRE: a global data base of animal demography. (ed T Coulson). *The Journal of animal ecology*, **85**, 371–384.
- Servanty, S., Gaillard, J.M., Ronchi, F., Focardi, S., Baubet, E. & Gimenez, O. (2011) Influence of harvesting pressure on demographic tactics: implications for wildlife management. *Journal of Applied Ecology*, **48**, 835–843.
- Species360 Zoological Information Management System (ZIMS). Available at: [zims.Species360.org](https://zims.Species360.org). (2018).
- Tidière, M., Gaillard, J.M., Berger, V., Müller, D.W.H., Lackey, L.B., Gimenez, O., Clauss, M. & Lemaître, J.-F. (2016) Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific reports*, **6**, srep36361.
- Tsantes, C. & Steiper, M.E. (2009) Age at first reproduction explains rate variation in the strepsirrhine molecular clock. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 18165–18170.

Tuljapurkar, S., Gaillard, J.M. & Coulson, T. (2009) From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1499–1509.

**Tables:**

**Table 1:** Methods to estimate generation time.

	<b>Generation time formula</b>	<b>Description</b>	<b>Assumptions</b>	<b>References</b>
Life Tables	$T_b = \frac{\sum_{x=\alpha}^{\omega} x \lambda^{-x} l_x m_x}{\sum_{x=\alpha}^{\omega} \lambda^{-x} l_x m_x}$	Weighted mean age of mothers at childbirth in a population; Mean age of the parents of the offspring produced by a population at the stable stage distribution *	Population at its stable-(st-) age distribution, overlapping generations.	(Leslie 1966; Caswell 2001; Gaillard et al. 2005)
	$T_s = \frac{\sum_{x=\alpha}^{\omega} x l_x m_x}{\sum_{x=\alpha}^{\omega} l_x m_x}$	Average age of parents at childbirth in a cohort or for stationary populations	Applied to cohort life tables or stationary population ( $\lambda=1$ ).	(Caswell 2001; Metcalf & Pavard 2007; IUCN 2017)
(St)age-based matrix (not evaluated)	$T_R = \frac{\log R_0}{\log \lambda}$	The time T required for the population to increase by a factor of its net reproductive rate, $R_0$ .	Population at its stable-(st-) age distribution	(Caswell 2001)
	$T_A = \frac{\lambda \mathbf{v} \mathbf{w}}{\mathbf{v} \mathbf{F} \mathbf{w}}$	The average time between two reproductive events in the genealogy of a population	Population at its stable-(st-) age distribution, entries of matrix are normalized (sum to 1)	Bienvenu & Legendre 2015
Partial life table data/ Aggregated demographic measure at the species level	$T_c = \frac{\sum_{x=0}^{\omega} x \lambda^{-x} p^x}{\sum_{x=0}^{\omega} \lambda^{-x} p^x}$	Same as in $T_b$ but with constant fecundity and survival model	Constant survival and fecundity from onset of breeding	(Niel & Lebreton 2005; Gaillard et al. 2005)
	$T_{cp} = \frac{\sum_{x=0}^{\omega} x \lambda^{-x} p^x m_x}{\sum_{x=0}^{\omega} \lambda^{-x} p^x m_x}$	Same as in $T_b$ but with constant survival, varying fecundity model	Constant survival, fecundity can vary	(Dillingham 2010)
	$T_{cm} = \frac{\sum_{x=0}^{\omega} x \lambda^{-x} l_x}{\sum_{x=0}^{\omega} \lambda^{-x} l_x}$	Same as in $T_s$ but with constant fecundity and varying survival	Constant fecundity, survival can vary	
	$T_{sc} = \frac{\sum_{x=0}^{\omega} x p^x}{\sum_{x=0}^{\omega} p^x}$	Same as in $T_s$ but with constant fecundity and survival model for stationary populations	Constant survival and constant fecundity, stationary populations.	
	$T_z = \alpha + z(\omega - \alpha)$	Reproductive-lifespan proxy	$z$ , $\alpha$ and $\omega$ are well known	(IUCN 2017)
	$T_q = \frac{\sum_{x=\alpha}^{\omega} x l_x}{\sum_{x=\alpha}^{\omega} l_x}$	Adult-mortality proxy	Constant survival and fecundity from onset of breeding; $q$ and $\alpha$ are well known	(IUCN 2017)

$x$  = age,  $l_x$  = probability of surviving to age  $x$ ,  $m_x$  = number of offspring females born to females at age  $x$ ,  $\lambda$  =

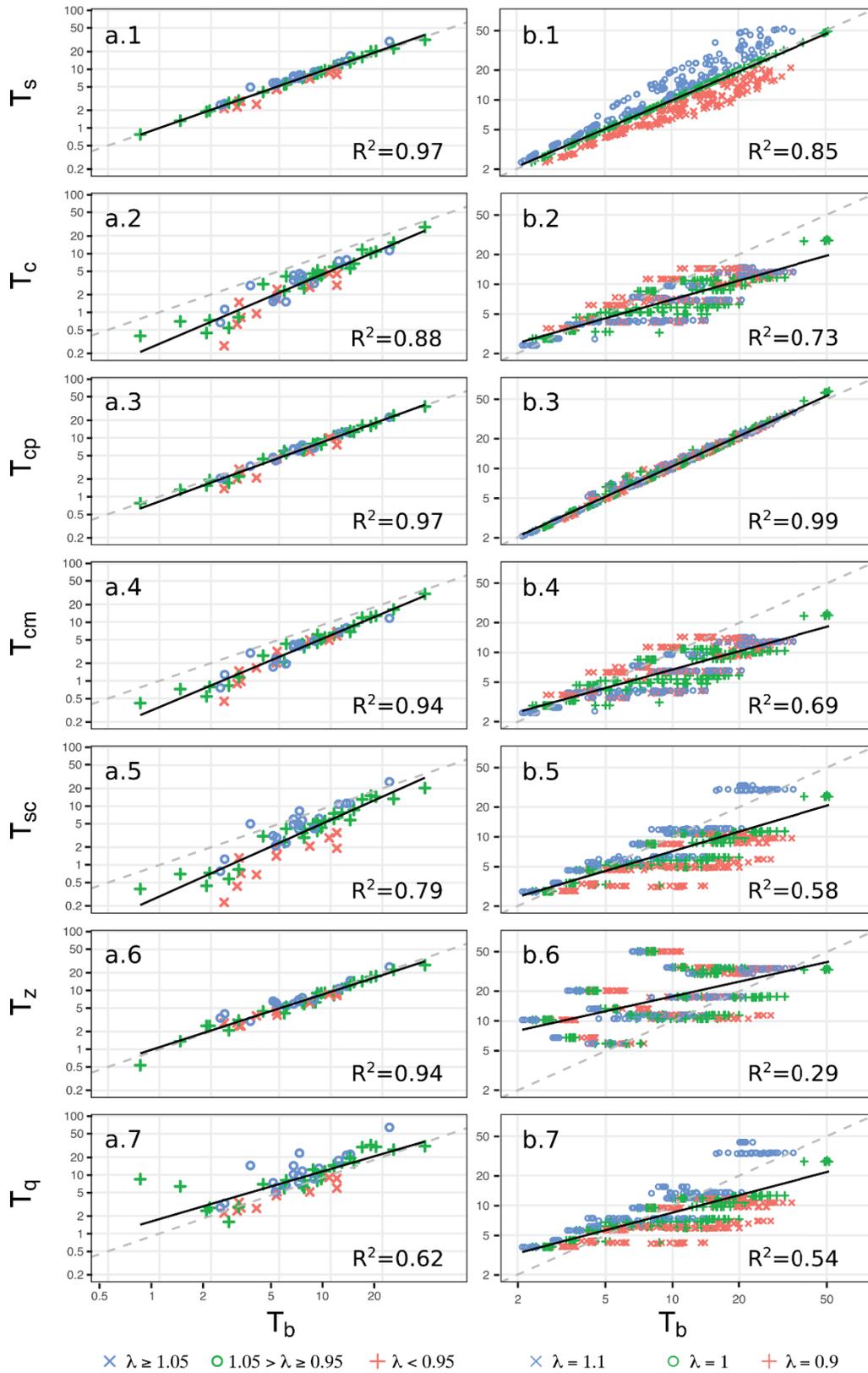
population growth rate at its stable stage distribution,  $R_0 = \prod_{x=\alpha}^{\omega} l_x m_x$  known as the net reproductive rate,  $\mathbf{F}$  = fecundity matrix of population projection matrix,  $\mathbf{v}$  reproductive value (left-eigenvector) of population projection matrix,  $\mathbf{w}$  stable stage distribution (right-eigenvector) of population projection matrix,  $\alpha$  = age at first reproduction,  $\omega$  = age at last reproduction,  $z$  = species-specific constant,  $p$  = mean annual survival,  $q$  = mean annual mortality. For  $\omega = \infty$ ,  $T_c$  becomes  $T_c = \alpha + p / (\lambda - p)$  (Gaillard et al. 2005) and  $T_q$  becomes  $T_q = \alpha + 1/q$  (IUCN 2017). \* The denominator in  $T_b$  is necessary to account for small errors in the estimation of the continuous Euler-Lotka equation from a discrete approximation.

**Table 2:** Results of the regression analysis and root mean square errors (*RMSE*) between  $T_b$  and the different approximations on log-log scale for 58 mammalian life tables (upper panel) and simulated life tables (lower panel). Values include estimated regression coefficients with standard errors in parentheses,  $p$ -values for the hypothesis described in the methods, and ranks based on *RMSEs*.

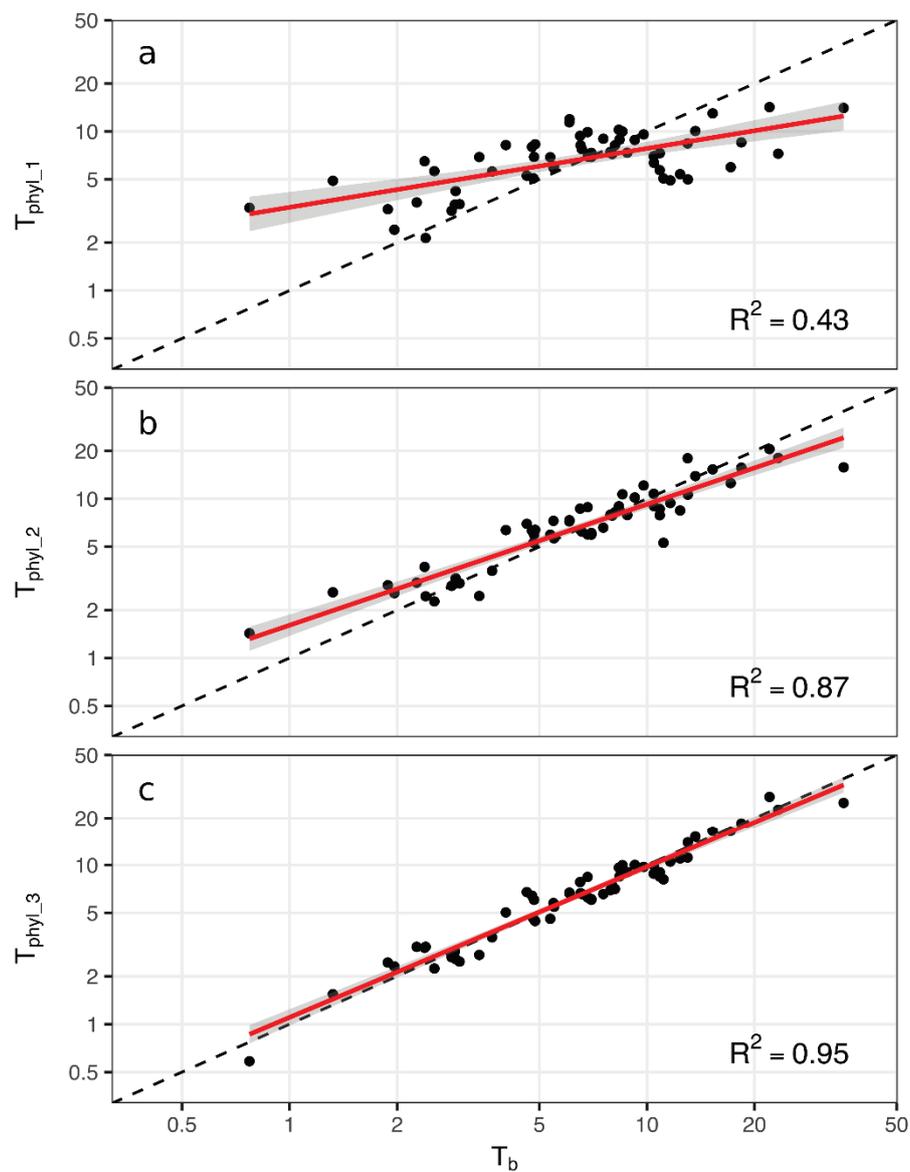
<b>Approx.</b>	<b>Intercept (SE)</b>	<b>Slope (SE)</b>	<b><math>p</math>-val. Interc.</b>	<b><math>p</math>-val. Slope</b>	<b>RMSE</b>	<b>R<sup>2</sup></b>	<b>Rank</b>
<i>Real data</i>							
$T_s$	0.05 (0.04)	0.95 (0.02)	0.225	<b>0.028</b>	0.132	0.97	<b>1</b>
$T_c$	1.10 (0.05)	0.71 (0.04)	< <b>0.001</b>	< <b>0.001</b>	0.879	0.88	7
$T_{cp}$	0.23 (0.04)	0.92 (0.02)	< <b>0.001</b>	< <b>0.001</b>	0.163	0.97	2
$T_{cm}$	0.91 (0.04)	0.77 (0.03)	< <b>0.001</b>	< <b>0.001</b>	0.682	0.94	5
$T_{sc}$	1.13 (0.07)	0.61 (0.04)	< <b>0.001</b>	< <b>0.001</b>	0.861	0.79	6
$T_z$	0.04 (0.06)	1.01 (0.03)	0.561	0.679	0.181	0.95	3
$T_q$	0.28 (0.17)	0.73 (0.08)	0.112	<b>0.001</b>	0.578	0.62	4
<i>Simulated data</i>							
$T_s$	0.26 (0.03)	0.89 (0.01)	< <b>0.001</b>	< <b>0.001</b>	0.272	0.85	2
$T_c$	0.05 (0.05)	1.15 (0.03)	0.337	< <b>0.001</b>	0.493	0.72	4
$T_{cp}$	0.02 (0.01)	0.98 (0.01)	<b>0.020</b>	< <b>0.001</b>	0.068	0.99	<b>1</b>
$T_{cm}$	0.12 (0.06)	1.13 (0.03)	<b>0.028</b>	< <b>0.001</b>	0.524	0.69	5
$T_{sc}$	0.55 (0.06)	0.88 (0.03)	< <b>0.001</b>	< <b>0.001</b>	0.545	0.58	6
$T_z$	0.60 (0.10)	0.58 (0.04)	< <b>0.001</b>	< <b>0.001</b>	0.857	0.28	7
$T_q$	0.30 (0.07)	0.93 (0.03)	< <b>0.001</b>	<b>0.023</b>	0.481	0.54	3

**Figures:**

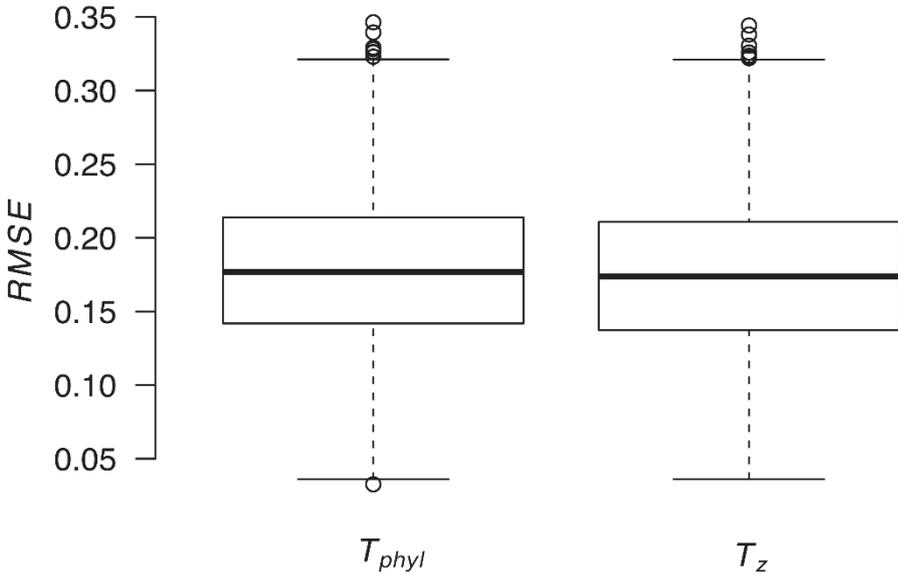
**Figure 1:** Comparison between  $T_b$  and seven approximations of generation time calculated from 58 mammalian life tables (a.1-a.7) and simulated life tables (b.1-b.7) on log-log-scale. The grey dashed line represents isometry (i.e. the equation  $y = x$ ). The black solid line shows the fitted regression of the data points. Color and shape indicate population growth rates. For interpretability we inverted the axes whereby  $\log(T_b)$  is on the x-axis and  $\log(T_j)$  on the y-axis.



**Figure 2:** Relationship between  $T_b$  and generation time fitted values from three phylogenetic generalized least squares including either body mass only (a), body mass and age at first reproduction (b), or body mass, age at first reproduction, and reproductive lifespan (c). Linear regression (on a log-log scale) was fitted to life tables from 58 mammalian populations. The black dashed line represents isometry (i.e. the equation  $y = x$ ). The red solid line represents the best regression line fitted to the data points. Grey shaded areas correspond to standard errors.



**Figure 3:** Boxplots of the RMSE between the  $\log(T_{ib})$  and the predicted  $\delta_i$  values ( $T_p$ , left) and the z-approximation  $\log(T_{iz})$  ( $T_z$ , right) on the validation set.



## Supplementary

**Table S1:** References for survival, juvenile survival (if missing in survival data) and reproduction used to calculate the generation time for each mammalian species.

Species	Reference Survival	Reference Reproduction	Reference Juvenile survival
<i>Alces alces</i>	(Ericsson et al. 2001)	(Ericsson et al. 2001)	(Ericsson et al. 2001)
<i>Arctocepalus gazella</i>	(Boyd et al. 1995)	(Boyd et al. 1995)	(Payne 1977)
<i>Arctocepalus pusillus</i>	(Gibbens & Arnould 2009)	(Gibbens et al. 2010)	
<i>Arctocepalus tropicalis</i>	(Dabin et al. 2004)	(Dabin et al. 2004)	(Bester 1980)
<i>Bison bison</i>	(Millspaugh et al. 2008)	(Millspaugh et al. 2008)	
<i>Brachyteles hypoxanthus</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Callospermophilus lateralis</i>	(Bronson 1979)	(Bronson 1979)	
<i>Capra ibex</i>	(Toigo et al. 2007)	(Toigo et al. 2007)	(Rughetti et al. 2015)
<i>Capreolus capreolus</i>	(Gaillard et al. 2017 Unpublished)	(Gaillard et al. 2017 Unpublished)	
<i>Cebus capucinus</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Cebus olivaceus</i>	(Robinson 1988)	(Robinson 1988)	
<i>Cercopithecus mitis</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Cervus elaphus</i>	(Benton et al. 1995)	(Benton et al. 1995)	(Moyes et al. 2011)
<i>Cervus nippon</i>	(Minami et al. 2009b)	(Minami et al. 2009a)	
<i>Cynomys ludovicianus</i>	(Hoogland 1995)	(Hoogland 1995)	
<i>Delphinapterus leucas</i>	(Burns & Seaman 1986)	(Burns & Seaman 1986)	
<i>Didelphis aurita</i>	(Kajin et al. 2008)	(Kajin et al. 2008)	(Ferreira et al. 2013)
<i>Dipodomys spectabilis</i>	(Waser & Jones 1991)	(Waser & Jones 1991)	(Waser et al. 2013)
<i>Elephas maximus</i>	(Mar 2002)	(Mar 2002)	
<i>Enhydra lutris</i>	(Monson et al. 2000)	(Monson et al. 2000)	
<i>Gorilla beringei</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Kobus leche</i>	(Sayer & Lavieren 1975)	(Rees 1978)	(Rees 1978)
<i>Liomys adspersus</i>	(Fleming, 1971)	(Fleming, 1971)	
<i>Loxodonta africana</i>	(Moss 2001)	(Moss 2001)	
<i>Lycaon pictus</i>	(Creel & Creel 2002)	(Creel & Creel 2002)	
<i>Mandrillus sphinx</i>	(Setchell et al. 2005)	(Setchell et al. 2005)	
<i>Marmota baibacina</i>	(Yang et al. 1988)	(Yang et al. 1988)	
<i>Marmota flaviventris</i>	(Schwartz et al. 1998)	(Schwartz et al. 1998)	
<i>Marmota marmota</i>	(Berger et al. 2016)	(Berger et al. 2015)	(Cohas et al. 2009)
<i>Meles meles</i>	(Dugdale et al. 2011)	(Dugdale et al. 2011)	(Wilkinson et al. 2000)
<i>Mirounga angustirostris</i>	(Le Boeuf & Laws 1994)	(Le Boeuf & Laws 1994)	(Hindell 1991)
<i>Mirounga leonina</i>	(Le Boeuf & Laws 1994)	(Le Boeuf & Laws 1994)	
<i>Nyctereutes procyonoides</i>	(Helle & Kauhala, 1993)	(Helle & Kauhala, 1993)	
<i>Odocoileus virginianus</i>	(Delgiudice et al. 2006)	(DelGiudice et al. 2007)	
<i>Oreamnos americanus</i>	(Festa-Bianchet & Côté 2012)	(Festa-Bianchet & Côté 2012)	(Côté & Festa-Bianchet 2001)
<i>Otaria flavescens</i>	(Grandi et al. 2016)	(Grandi et al. 2016)	
<i>Ovis aries</i>	(Clutton-Brock, T. H. Pemberton 2004)	(Clutton-Brock, T. H. Pemberton 2004)	
<i>Ovis canadensis</i>	(Festa-Bianchet et al. 2006)	(Bérubé et al. 1999)	(Rioux-Paquette et al. 2011)
<i>Pan troglodytes</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Panthera leo</i>	(Packer et al. 1998)	(Packer et al. 1998)	
<i>Panthera pardus</i>	(Balme et al. 2013)	(Balme et al. 2013)	
<i>Papio cynocephalus</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Proechimys semispinosus</i>	(Fleming, 1971)	(Fleming, 1971)	
<i>Propithecus diadema</i>	(Pochron et al. 2004)	(Pochron et al. 2004)	
<i>Propithecus verreauxi</i>	(Bronikowski et al. 2016)	(Bronikowski et al. 2016)	
<i>Rangifer tarandus</i>	(Messier et al. 1988)	(Messier et al. 1988)	
<i>Rhinoceros unicornis</i>	(Dinerstein & Price 1991)	(Dinerstein & Price 1991)	

<i>Rucervus eldii</i>	(Nie et al. 2011)	(Nie et al. 2011)	
<i>Saccopteryx bilineata</i>	(Greiner et al. 2014)	(Greiner et al. 2014)	(Young 1972)
<i>Sciurus carolinensis</i>	(Barkalow et al. 1970)	(Barkalow et al. 1970)	
<i>Spermophilus dauricus</i>	(Luo & Fox 1990)	(Luo & Fox 1990)	
<i>Tamasciurus hudsonicus</i>	(McAdam et al. 2007)	(McAdam et al. 2007)	
<i>Urocitellus beldingi</i>	(Sherman & Morton 1984)	(Sherman & Morton 1984)	
<i>Urocitellus brunneus</i>	(Sherman & Runge 2002)	(Sherman & Runge 2002)	
<i>Ursus arctos</i>	(Zedrosser et al. 2013)	(Zedrosser et al. 2013)	
<i>Vulpes vulpes</i>	(Saunders et al. 2002)	(Saunders et al. 2002)	
<i>Zalophus californianus</i>	(Hernández Camacho 2001)	(Hernández-Camacho et al. 2008)	
<i>Zapus princeps</i>	(Falk & Millar 1987)	(Falk & Millar 1987)	

Amaya JN, Alsina MG, Brandani AA. 1979. Ecología de la liebre europea. Pages 1–36 *Lepus europaeus*.

Balme GA, Batchelor A, de Woronin Britz N, Seymour G, Grover M, Hes L, Macdonald DW, Hunter LTB. 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* **43**:221–237. Available from <http://doi.wiley.com/10.1111/j.1365-2907.2012.00219.x>.

Barkalow Jr, FS, Hamilton, RB, & Soots Jr, RF. 1970. The vital statistics of an unexploited gray squirrel population. *The Journal of Wildlife Management*, 489-500.

Benton TG, Grant A, Clutton-Brock TH. 1995. Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. *Evolutionary Ecology* **9**:559–574. Available from <http://link.springer.com/10.1007/BF01237655>.

Berger V, Lemaître J-F, Dupont P, Allainé D, 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. Available from <https://academic.oup.com/jmammal/article-lookup/doi/10.1093/jmammal/gyw028>.

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. Available from <http://doi.wiley.com/10.1890/14-0774.1>.

Bérubé CH, Festa-Bianchet M, Jorgenson JT. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**:2555–2565. Available from [http://doi.wiley.com/10.1890/0012-9658\(1999\)080\[2555:IDLARS\]2.0.CO;2](http://doi.wiley.com/10.1890/0012-9658(1999)080[2555:IDLARS]2.0.CO;2).

Bester MN. 1980. Population Increase in the Amsterdam Island Fur Seal *Arctocephalus Tropicalis* at Gough Island. *South African Journal of Zoology* **15**:229–234. Available from <http://www.tandfonline.com/doi/full/10.1080/02541858.1980.11447716>.

Boyd IL, Croxall JP, Lunn NJ, Reid K. 1995. Population Demography of Antarctic Fur Seals: The Costs of Reproduction and Implications for Life-Histories. *The Journal of Animal Ecology* **64**:505. Available from <http://www.jstor.org/stable/5653?origin=crossref>.

Brandani A, Alsina MG, Amaya J. 1977. Ecología de la liebre europea. I. Estimadores de edad y estructura de una población de SC de Bariloche. *Physis* **36**:305–320.

Bronikowski AM, Cords M, Alberts SC, Altmann J, Brockman DK, Fedigan LM, Pusey A, Stoinski T, Strier KB, Morris WF. 2016. Female and male life tables for seven wild primate species. *Scientific Data* **3**:160006. Available from <http://www.nature.com/articles/sdata20166>.

Bronson MT. 1979. Altitudinal Variation in the Life History of the Golden-Mantled Ground Squirrel (*Spermophilus Lateralis*). *Ecology* **60**:272–279. Available from <http://doi.wiley.com/10.2307/1937655>.

Burns JJ, Seaman GA. 1986. Investigations of belukha whales in coastal waters of western

- and northern Alaska. II. Biology and ecology.
- Clutton-Brock, T. H. Pemberton JM. 2004. Soay sheep: dynamics and selection in an island population. Cambridge University Press.
- COHAS A, BONENFANT C, KEMPENAEERS B, ALLAINÉ D. 2009. Age-specific effect of heterozygosity on survival in alpine marmots, *Marmota marmota*. *Molecular Ecology* **18**:1491–1503. Available from <http://doi.wiley.com/10.1111/j.1365-294X.2009.04116.x>.
- Côté SD, Festa-Bianchet M. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**:230–8. Available from <http://www.ncbi.nlm.nih.gov/pubmed/24577654> (accessed October 24, 2014).
- Creel S, Creel NM. 2002. The African wild dog: behavior, ecology, and conservation. Princeton University Press.
- Dabin W, Beauplet G, Crespo EA, Guinet C. 2004. Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology* **82**:1043–1050. Available from <http://www.nrcresearchpress.com/doi/abs/10.1139/z04-079>.
- Delgiudice GD, Fieberg J, Riggs MR, Powell MC, Pan W. 2006. A Long-Term Age-Specific Survival Analysis of Female White-Tailed Deer. *Journal of Wildlife Management* **70**:1556–1568. Available from <http://www.bioone.org/doi/abs/10.2193/0022-541X%282006%2970%5B1556%3AALASAO%5D2.0.CO%3B2>.
- DelGiudice GD, Lenarz MS, Powell MC. 2007. Age-Specific Fertility and Fecundity in Northern Free-Ranging White-Tailed Deer: Evidence for Reproductive Senescence? *Journal of Mammalogy* **88**:427–435. Available from <https://academic.oup.com/jmammal/article-lookup/doi/10.1644/06-MAMM-A-164R.1>.
- Dinerstein E, Price L. 1991. Demography and Habitat Use by Greater One-Horned Rhinoceros in Nepal. *The Journal of Wildlife Management*:401–411.
- Dugdale HL, Pope LC, Newman C, Macdonald DW, Burke T. 2011. Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence. *Molecular Ecology* **20**:3261–3274. Available from <http://doi.wiley.com/10.1111/j.1365-294X.2011.05167.x>.
- Ericsson G, Wallin K, Ball JP, Broberg M. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* **82**:1613–1620.
- Falk JW, Millar JS. 1987. Reproduction by female *Zapus princeps* in relation to age, size, and body fat. *Canadian Journal of Zoology* **65**:568–571. Available from <http://www.nrcresearchpress.com/doi/abs/10.1139/z87-088>.
- Ferreira MS, Kajin M, Vieira MV, Zangrandi PL, Cerqueira R, Gentile R. 2013. Life history of a neotropical marsupial: Evaluating potential contributions of survival and reproduction to population growth rate. *Mammalian Biology - Zeitschrift für Säugetierkunde* **78**:406–411. Available from <http://linkinghub.elsevier.com/retrieve/pii/S1616504713000372>.
- Festa-Bianchet M, Côté SD. 2012. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press.
- Festa-Bianchet M, Coulson T, Gaillard J-M, Hogg JT, Pelletier F. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* **273**:1537–1543. Available from <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2006.3467>.
- Fleming TH. 1971. Population ecology of three species of Neotropical rodents. *Miscellaneous publications, Museum of Zoology, University of Michigan*, 143.

- Gibbens J, Arnould JPY. 2009. Age-specific growth, survival, and population dynamics of female Australian fur seals. *Canadian Journal of Zoology* **87**:902–911. Available from <http://www.nrcresearchpress.com/doi/abs/10.1139/Z09-080>.
- Gibbens J, Parry LJ, Arnould JPY. 2010. Influences on fecundity in Australian fur seals (*Arctocephalus pusillus doriferus*). *Journal of Mammalogy* **91**:510–518. Available from <https://academic.oup.com/jmammal/article-lookup/doi/10.1644/08-MAMM-A-377.1>.
- Grandi MF, Dans SL, Crespo EA. 2016. Improvement in Survivorship: The Key for Population Recovery? *Zoological Studies* **55**.
- Greiner S, Nagy M, Mayer F, Knörnschild M, Hofer H, Voigt CC. 2014. Sex-Biased Senescence in a Polygynous Bat Species. *Ethology* **120**:197–205. Available from <http://doi.wiley.com/10.1111/eth.12193>.
- Helle E, Kauhala K. 1993. Age Structure, Mortality, and Sex Ratio of the Raccoon Dog in Finland. *Journal of Mammalogy* **74**(4): 936-942
- Hernández-Camacho CJ, Auriolles-Gamboa D, Gerber LR. 2008. Age-specific birth rates of California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico. *Marine Mammal Science* **24**:664–676. Available from <http://doi.wiley.com/10.1111/j.1748-7692.2008.00199.x>.
- Hernández Camacho CJ. 2001. Tabla de vida del lobo marino de California *Zalophus californianus californianus* en la lobera Los Islotes, BCS, México. Instituto Politécnico Nacional. Centro Interdisciplinario de Ciencias Marinas.
- Hindell MA. 1991. Some Life-History Parameters of a Declining Population of Southern Elephant Seals, *Mirounga leonina*. *The Journal of Animal Ecology* **60**:119. Available from <http://www.jstor.org/stable/5449?origin=crossref>.
- Hoogland JL. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press.
- Johannesen E, Andreassen HP. 1998. Survival and reproduction of resident and immigrant female root voles (*Microtus oeconomus*). *Canadian Journal of Zoology* **76**:763–766. Available from <http://www.nrcresearchpress.com/doi/abs/10.1139/z97-249>.
- Kajin M, Cerqueira R, Vieira M V., Gentile R. 2008. Nine-year demography of the black-eared opossum *Didelphis aurita* (Didelphimorphia: Didelphidae) using life tables. *Revista Brasileira de Zoologia* **25**:206–213. Available from [http://www.scielo.br/scielo.php?script=sci\\_arttext&pid=S0101-81752008000200007&lng=en&tlng=en](http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0101-81752008000200007&lng=en&tlng=en).
- Le Boeuf B, Laws R. 1994. Elephant seals population ecology behavior and physiology. Univ of California Press.
- Liang JR, Sun RY. 1985. Studies on the life table and reproduction of the root vole *Microtus oeconomus*. *Acta Zoologica Sinica* **31**:170–177.
- Luo J, Fox BJ. 1990. Life-Table Comparisons between Two Ground Squirrels. *Journal of Mammalogy* **71**:364–370. Available from <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1381947>.
- Mar KU. 2002. The demography and life history strategies of timber elephants in Myanmar. University of London.
- McAdam AG, Boutin S, Sykes AK, Humphries MM. 2007. Life histories of female red squirrels and their contributions to population growth and lifetime fitness. *Ecoscience* **14**:362. Available from [http://www.bioone.org/perlserv/?request=get-abstract&doi=10.2980%2F1195-6860\(2007\)14%5B362%3ALHOFRS%5D2.0.CO%3B2](http://www.bioone.org/perlserv/?request=get-abstract&doi=10.2980%2F1195-6860(2007)14%5B362%3ALHOFRS%5D2.0.CO%3B2).
- Messier F, Huot J, Le Henaff D, Luttich, S. 1988. Demography of the George River caribou

- herd: evidence of population regulation by forage exploitation and range expansion. *Arctic*, 279-287.
- Millspaugh JJ et al. 2008. Effects of Culling on Bison Demographics in Wind Cave National Park, South Dakota. *Natural Areas Journal* **28**:240–250. Available from <http://www.bioone.org/doi/abs/10.3375/0885-8608%282008%2928%5B240%3AEOCOBD%5D2.0.CO%3B2>.
- Minami M, Ohnishi N, Higuchi N, Okada A, Takatsuki S. 2009a. Life-Time Reproductive Success of Female Sika Deer on Kinkazan Island, Northern Japan. Pages 319–326 *Sika Deer*. Springer Japan, Tokyo. Available from [http://www.springerlink.com/index/10.1007/978-4-431-09429-6\\_23](http://www.springerlink.com/index/10.1007/978-4-431-09429-6_23).
- Minami M, Ohnishi N, Takatsuki S. 2009b. Survival Patterns of Male and Female Sika Deer on Kinkazan Island, Northern Japan. Pages 375–384 *Sika Deer*. Springer Japan, Tokyo. Available from [http://www.springerlink.com/index/10.1007/978-4-431-09429-6\\_27](http://www.springerlink.com/index/10.1007/978-4-431-09429-6_27).
- Monson DH, Estes JA, Bodkin JL, Siniff DB. 2000. Life history plasticity and population regulation in sea otters. *Oikos* **90**:457–468. Available from <http://doi.wiley.com/10.1034/j.1600-0706.2000.900304.x>.
- Moss CJ. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* **255**:S0952836901001212. Available from <http://doi.wiley.com/10.1017/S0952836901001212>.
- Moyes K, Nussey DH, Clements MN, Guinness FE, Morris A, Morris S, Pemberton JM, Kruuk LEB, Clutton-Brock TH. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology* **17**:2455–2469.
- Nie H, Song Y, Zeng Z, Zhang Q. 2011. Life history pattern and fitness of an endangered Hainan Eld's deer population. *Integrative Zoology* **6**:63–70. Available from <http://doi.wiley.com/10.1111/j.1749-4877.2010.00232.x>.
- Packer C, Tatar M, Collins A. 1998. Reproductive cessation in female mammals. *Nature* **392**:807–811. Available from <http://www.nature.com/doi/finder/10.1038/33910>.
- Payne MR. 1977. Growth of a Fur Seal Population. *Philosophical Transactions of the Royal Society B: Biological Sciences* **279**:67–79. Available from <http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.1977.0072>.
- Pochron ST, Tucker WT, Wright PC. 2004. Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* **125**:61–72. Available from <http://doi.wiley.com/10.1002/ajpa.10266>.
- Rees WA. 1978. The Ecology of the Kafue Lechwe: As Affected by the Kafue Gorge Hydroelectric Scheme. *The Journal of Applied Ecology* **15**:205. Available from <http://www.jstor.org/stable/2402931?origin=crossref>.
- Rieger JF. 1996. Body size, litter size, timing of reproduction, and juvenile survival in the Unita ground squirrel, *Spermophilus armatus*. *Oecologia* **107**:463–468. Available from <http://link.springer.com/10.1007/BF00333936>.
- Rioux-Paquette E, Festa-Bianchet M, Coltman DW. 2011. Sex-differential effects of inbreeding on overwinter survival, birth date and mass of bighorn lambs. *Journal of Evolutionary Biology* **24**:121–131.
- Robinson JG. 1988. Demography and Group Structure in Wedge-capped Capuchin Monkeys, *Cebus Olivaceus*. *Behaviour* **104**:202–232. Available from <http://booksandjournals.brillonline.com/content/journals/10.1163/156853988x00520>.

- Rughetti M, Dematteis A, Meneguz PG, Festa-Bianchet M. 2015. Age-specific reproductive success and cost in female Alpine ibex. *Oecologia* **178**:197–205. Available from <http://link.springer.com/10.1007/s00442-014-3192-3>.
- Saunders G, Mcilroy J, Kay B, Gifford E, Berghout M, Van de Ven R. 2002. Demography of foxes in central-western New South Wales, Australia. *Mammalia* **66**. Available from <https://www.degruyter.com/view/j/mamm.2002.66.issue-2/mamm.2002.66.2.247/mamm.2002.66.2.247.xml>.
- Sayer JA, Lavieren LP Van. 1975. The ecology of the Kafue lechwe population of Zambia before the operation of hydro-electric dams on the Kafue River. *African Journal of Ecology* **13**:9–37. Available from <http://doi.wiley.com/10.1111/j.1365-2028.1975.tb00121.x>.
- Schwartz OA, Armitage KB, Van Vuren D. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology* **246**:S0952836998009911. Available from <http://doi.wiley.com/10.1017/S0952836998009911>.
- Setchell JM, Charpentier M, Wickings EJ. 2005. Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). *Behavioral Ecology and Sociobiology* **58**:474–485. Available from <http://link.springer.com/10.1007/s00265-005-0946-2>.
- Sherman PW, Morton ML. 1984. Demography of Belding's Ground Squirrels. *Ecology* **65**:1617–1628. Available from <http://doi.wiley.com/10.2307/1939140>.
- Sherman PW, Runge MC. 2002. Demography of a population collapse: the northern idaho ground squirrel (*spermophilus brunneus brunneus*). *Ecology* **83**:2816–2831. Available from [http://doi.wiley.com/10.1890/0012-9658\(2002\)083\[2816:DOAPCT\]2.0.CO;2](http://doi.wiley.com/10.1890/0012-9658(2002)083[2816:DOAPCT]2.0.CO;2).
- Slade NA, Balph DF. 1974. Population Ecology of Uinta Ground Squirrels. *Ecology* **55**:989–1003. Available from <http://doi.wiley.com/10.2307/1940350>.
- SMITH RK, VAUGHAN JENNINGS N, HARRIS S. 2005. A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Review* **35**:1–24. Available from <http://doi.wiley.com/10.1111/j.1365-2907.2005.00057.x>.
- Smuts GL. 1976a. Population characteristics of Burchell's zebra (*Equus burchelli antiquorum*. H. Smith, 1841) in the Kruger National Park. *South African Journal of Wildlife Research* **6**:99–112.
- Smuts GL. 1976b. Reproduction in the zebra mare *Equus burchelli antiquorum* from the Kruger National Park. *Koedoe* **19**. Available from <http://koedoe.co.za/index.php/koedoe/article/view/1186>.
- Spinage CA. 1972. African Ungulate Life Tables. *Ecology* **53**:645–652. Available from <http://doi.wiley.com/10.2307/1934778>.
- Toïgo C, Gaillard J, Festa-bianchet M, Largo E, Michallet J, Maillard D. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology* **76**:679–686. Available from <http://doi.wiley.com/10.1111/j.1365-2656.2007.01254.x>.
- Waser PM, Jones WT. 1991. Survival and Reproductive Effort in Banner-Tailed Kangaroo Rats. *Ecology* **72**:771–777. Available from <http://doi.wiley.com/10.2307/1940579>.
- Waser PM, Nichols KM, Hadfield JD. 2013. Fitness consequences of dispersal: Is leaving home the best of a bad lot? *Ecology* **94**:1287–1295. Available from <http://doi.wiley.com/10.1890/12-1037.1>.
- Wilkinson D, Smith GC, Delahay RJ, Rogers LM, Cheeseman CL, Clifton-Hadley RS. 2000. The effects of bovine tuberculosis (*Mycobacterium bovis*) on mortality in a badger (*Meles*

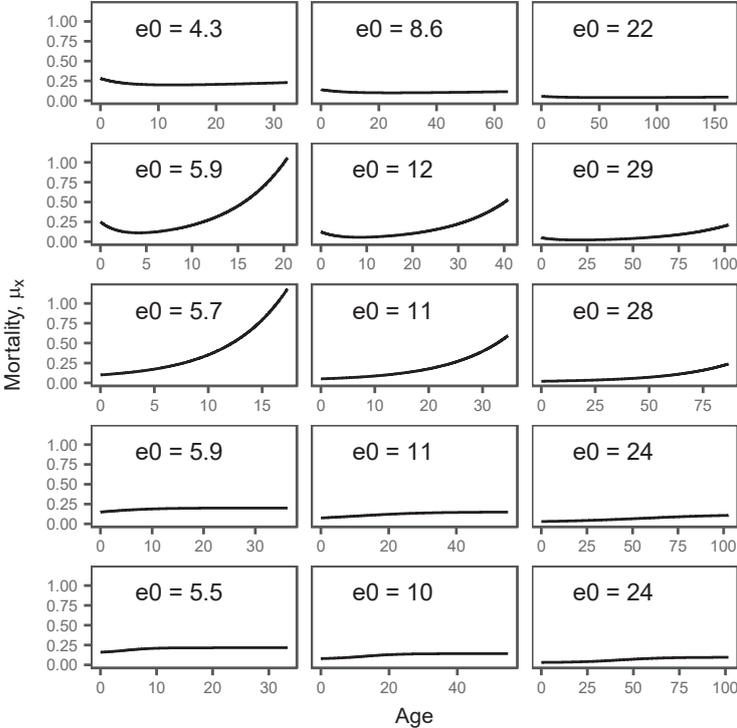
- meles) population in England. *Journal of Zoology* **250**:389–395. Available from <http://doi.wiley.com/10.1111/j.1469-7998.2000.tb00782.x>.
- Yang X, Zhang G, Chen L. 1988. A preliminary study on the life table and reproduction of the marmota baibacina. *Acta Theriologica Sinica* **2**:10.
- Young AM. 1972. An Experimental Study on the Relation of Mortality of Young to Adult Numbers in Colonies of the Lesser Sac-Winged Bat, *Saccopteryx bilineata perspicillifer*. *American Midland Naturalist* **87**:158. Available from <http://www.jstor.org/stable/2423889?origin=crossref>.
- Zedrosser A, Pelletier F, Bischof R, Festa-Bianchet M, Swenson JE. 2013. Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. *Ecology* **94**:231–240. Available from <http://doi.wiley.com/10.1890/12-0229.1>.

**Table S3:** Coefficient estimates, standard errors (SE) and p-values from the three phylogenetic regression models.

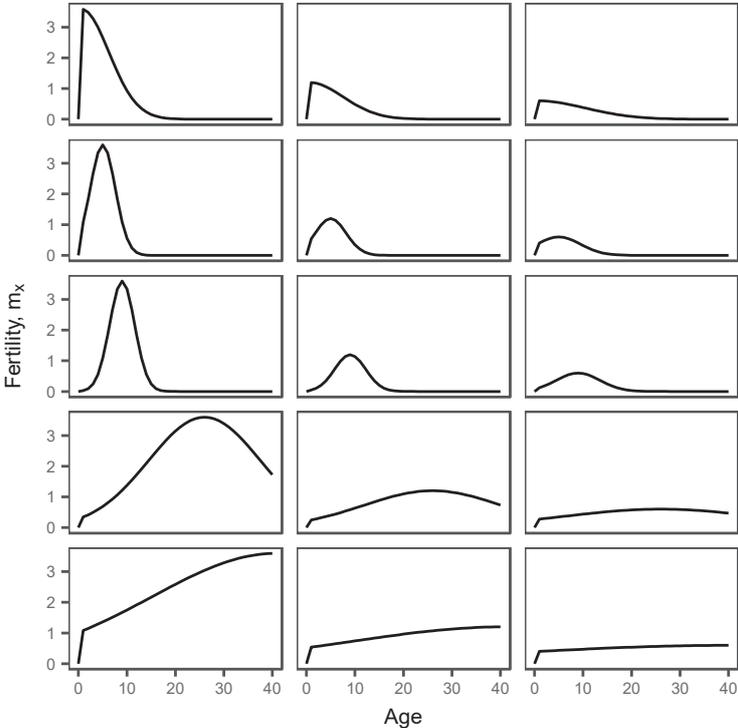
Coefficient	Estimate	SE	P-value
<i>T<sub>phyl_1</sub></i>			
Intercept	0.45	0.34	0.19
Log(Body mass)	0.15	0.03	***
<i>T<sub>phyl_2</sub></i>			
Intercept	0.78	0.19	***
Log(Body mass)	0.06	0.02	**
Log( $\alpha$ )	0.64	0.07	***
<i>T<sub>phyl_3</sub></i>			
Intercept	0.04	0.12	0.73
Log(Body mass)	0.03	0.01	*
Log(Rspan)	0.44	0.05	***
Log( $\alpha$ )	0.49	0.05	***

\*p<0.05, \*\*p <0.01, \*\*\*p <0.001.

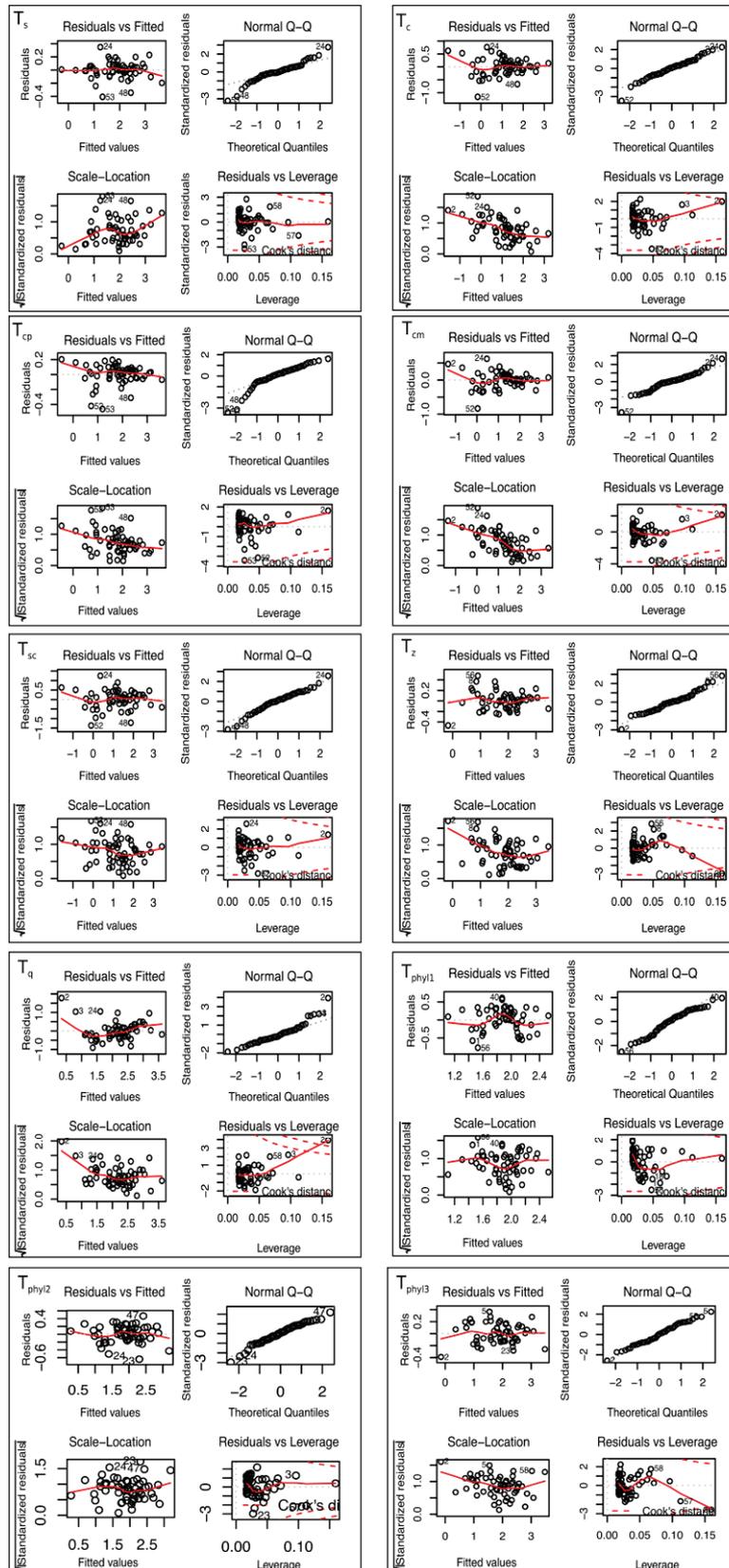
**Figure S1:** Fifteen mortality trajectories calculated from simulated data representing common mortality patterns across the tree of life, such as decreasing, increasing and bathtub shaped mortality.  $E_0$  = life expectancy at birth.



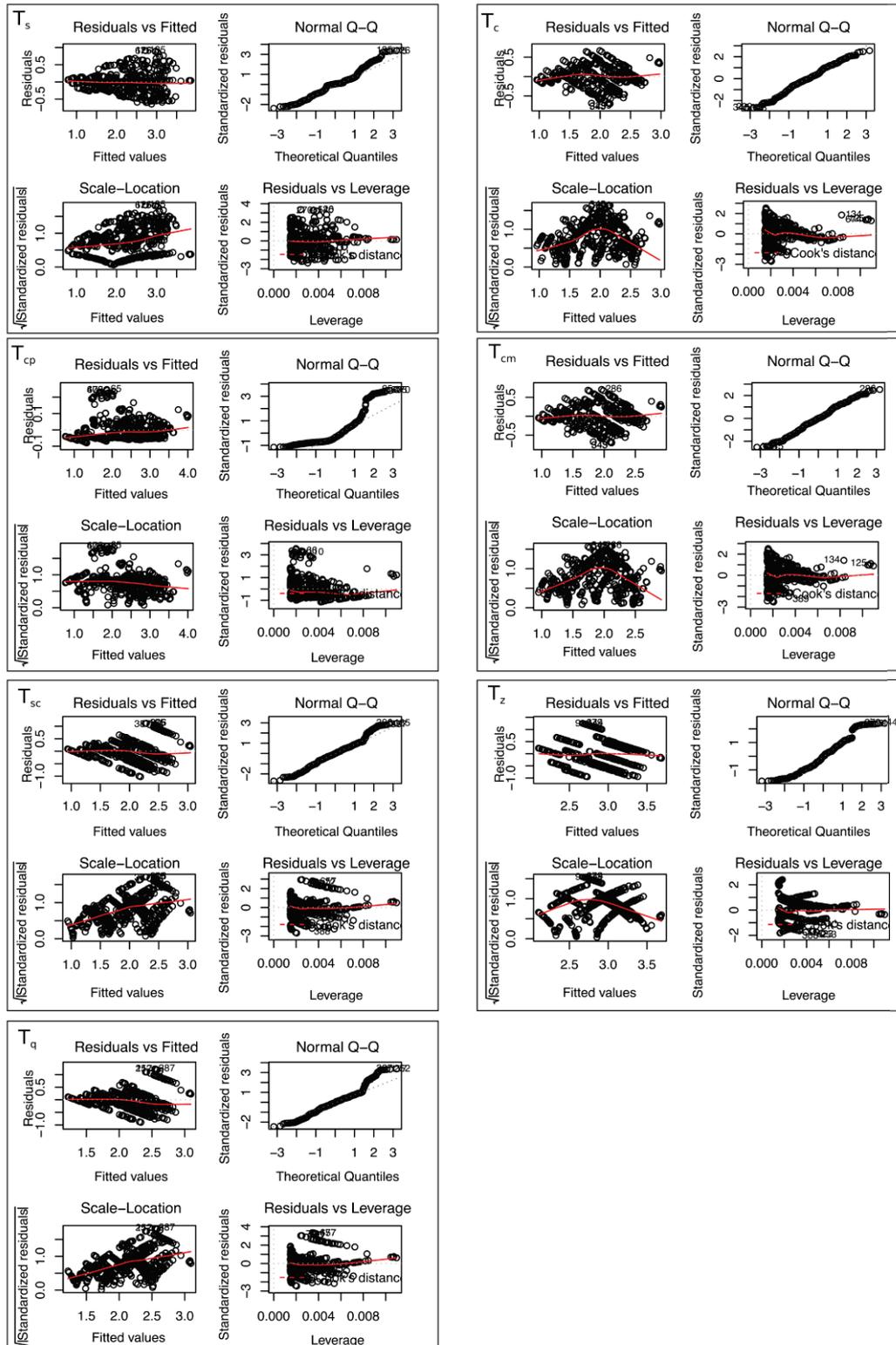
**Figure S2:** Fifteen fertility trajectories calculated from simulated data representing common fertility patterns across the tree of life.



**Figure S3:** Diagnostic plots of the linear relationship between various measures of generation time using life table data of 58 mammalian populations.



**Figure S4:** Diagnostic plots of relationship between various measures of generation time using simulated data of 225 populations (Figure 1 b.1 - b.7) and Table 2 of main text.



**Figure S5:** Number of publications of life tables and matrices per year. **A:** Number of matrices that are age-based (black) and stage-based (grey) in the COMADRE database for publication years from 1957 – 2016 in 5-year intervals as compared to **B:** modified from Fig. 1 p. 2 in Fung & Waples (2017).

