Oikos 125: 395–404, 2016
doi: 10.1111/oik.02582

Subject Editor: Dustin Marshall. Editor-in-Chief: Dries Bonte. Accepted 5 June 2015

Linking demographic responses and life history tactics from longitudinal data in mammals

Marlène Gamelon, Jean-Michel Gaillard, Olivier Gimenez, Tim Coulson, Shripad Tuljapurkar and Eric Baubet

M. Gamelon (marlene.gamelon@ntnu.no), Dept of Biology, Centre for Biodiversity Dynamics, Norwegian Univ. of Science and Technology, NO-7491 Trondheim, Norway. – J.-M. Gaillard, Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Univ. de Lyon, Université Lyon 1, FR 69 622 Villeurbanne, France. – O. Gimenez, Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, campus CNRS, 1919 Route de Mende, FR-34 293 Montpellier Cedex 5, France. – T. Coulson, Dept of Zoology, Univ. of Oxford, South Parks Road, Oxford, OX1 3PS, UK. – S. Tuljapurkar, Biological Sciences, Stanford Univ., Stanford, CA 94305, USA. – E. Baubet, Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, 2 Bis Rue des Religieuses, BP 19, FR-52 120 Châteauvillain, France.

In stochastic environments, a change in a demographic parameter can influence the population growth rate directly or via a resulting impact on age structure. Stochastic elasticity of the long-run stochastic growth rate λ_s to a demographic parameter offers a suitable way to measure the overall demographic response because it includes both the direct effect of changing the demographic parameter and its indirect effect through changes in the age structure. From 25 mammalian populations with contrasting life histories, we investigated how pace of life and population growth rate influence the demographic responses (measured as the relative contributions of the direct and indirect components of stochastic elasticity on λ_s). We found that in short-lived species, the change in population structure resulting from an increase in yearling survival leads to an additional increase in λ_s, whereas in long-lived species, the same change in population structure leads to a decrease. Short-lived species thus display a boom-bust life history strategy contrary to long-lived species, for which the long lifespan dampens the demographic consequences of changing age structure. Irrespective of the species' life history strategy, the change in population age structure resulting from an increase in adult survival leads to an additional increase in λ_s due to an increase of the proportion of mature individuals in the population. On the contrary, a change in population age structure resulting from an increase of reproductive performance leads to a decrease in λ_s that is due to the increase of the proportion of immature individuals in the population. Our comparative analysis of stochastic elasticity patterns in mammals shows the existence of different demographic responses to changes in age structure between short- and long-lived species, which improves our understanding of population dynamics in variable environments in relation to the species-specific pace of life.

To study population dynamics, age-specific survival and reproduction are usually integrated into matrix population models to project the fate of populations over time and possibly space (Caswell 2001). Sensitivity or elasticity analyses are then commonly used to identify demographic parameters with the greatest potential to affect population growth rate (de Kroon et al. 1986).

Demographic analyses can be performed either in a deterministic or in a stochastic context. In deterministic models, demographic parameters are assumed to be constant through time and the population projection matrix incorporates only one estimated value of each demographic parameter for the study period. However, numerous studies have pointed out that including process variance of demographic parameters can change biological inference (Tuljapurkar 1989, Boyce et al. 2006, Morris et al. 2008, 2011). In variable environments, demographic parameters fluctuate from year to year so that the projection matrix changes from one year to the next (Fieberg and Ellner 2001, Boyce et al. 2006), causing the age structure to change as well (Coulson et al. 2004). Consequently, in variable environments, a given change in a demographic parameter affects population growth – measured as the limit of the geometric mean of the per time step non-equilibrium growth rates and termed the long-run stochastic growth rate λ_s – using two different pathways. As in the deterministic context, changing a demographic parameter has a direct effect on the long-run stochastic growth rate. In addition, in variable environments, changing a demographic parameter will also change the age structure, which will have an indirect effect on population growth. In other words, this indirect effect corresponds to the elasticity of population growth rate due to changes in age structure when holding fixed the matrix at time *t*. The total impact of changing a demographic rate on population growth is the sum of both the direct and indirect effects (Haridas et al. 2009).

Haridas et al. (2009) proposed a method to calculate these two components and used red deer *Cervus elaphus* as an illustration. Long-lived species like red deer display relatively little temporal variation in most demographic parameters (Benton and Grant 1996, Morris et al. 2011), and not surprisingly observed changes in population growth were mainly due to the direct effects of changing demographic parameters (Haridas et al. 2009), with very little influence of indirect effects of changing age structure despite marked observed variation in age structure among years (Coulson et al. 2004). This pioneering study left several questions unanswered. In particular, whether the relative contributions of direct and indirect effects of changing a demographic parameter on population growth rate are constant or vary among species with contrasting life histories remains unknown. Here, we aim to fill this gap in our knowledge by measuring how the relative influence of direct and indirect components of stochastic elasticity on the long-run population growth rate varies across a wide range of mammalian life histories.

We organized life histories by generation time, a metric that ranks species on the so-called slow–fast continuum (Gaillard et al. 2005), which corresponds to the major axis of variation in life history tactics in mammals (Gaillard et al. 1989, Bielby et al. 2007, Jeschke and Kokko 2009, reviewed by Gaillard et al. 2015). This continuum contrasts 'fast' species, characterized with early maturity, high annual fecundity, and short lifespan, to 'slow' species with opposite characteristics (Stearns 1983, Gaillard et al. 1989, Read and Harvey 1989). The wide range of mammalian life histories along the slow–fast continuum provides a unique opportunity to investigate differences in the relative contributions of direct and indirect effects of changing a demographic parameter on population growth among species with different paces of life (sensu Hille and Cooper 2015). Indeed, in 'fast' populations with a short generation time, the contribution of indirect effects on population growth rate via changes in age structure is expected to be higher than in 'slow' populations with a long generation time. For instance, increasing the proportion of juveniles in a population with a short generation time is expected to influence population growth rate to a larger extent than doing so in a population with a long generation time because slow life histories should be buffered to changes in the relative abundance of juveniles. To explore these hypotheses, we computed the elasticity patterns in populations of mammalian species with contrasting life histories.

Methods

Projection matrices

From a literature survey, we gathered yearly estimates of age-specific survival and reproduction from 25 populations of 21 mammalian species (Table 1) ranging widely along the slow–fast continuum of life-histories (Gaillard et al. 2005). For each population, estimates of demographic parameters (i.e. age-specific survival and reproduction) were integrated in a female age-structured population model (Caswell 2001) based on year-specific matrices $\mathbf{A_t}$. Therefore, for each population, one matrix with age-dependent survival and reproduction was built for each year. We considered a pre-breeding census model. For example, for mountain goat *Oreamnos americanus*, 10 age classes were considered. The first age class corresponded to individuals of 1 year of age, the second age class to individuals of 2 years of age, the third age class to individuals of 3 years of age... and the tenth age class to senescent individuals of 10 years of age or older (Festa-Bianchet and Côté 2008) (see matrix structure in Supplementary material Appendix 1). Therefore, the projection matrix for a given year *t* took the following form for the mountain goat study case:

$$\mathbf{A_t} = \begin{pmatrix} 0 & 0 & R3 & R4 & R5 & R6 & R7 & R8 & R9 & R10 \\ S1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S4 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S5 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S6 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S7 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S8 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S9 & S10 \end{pmatrix}$$

with S_i the survival and R_i the realized fecundity for females of age *i* (i.e. the product of the probability of giving birth, litter size at birth, sex ratio at birth and juvenile survival between birth and one year of age). For this species, yearly demographic parameters were available for 11 years (Table 1). We thus built 11 year-specific matrices $\mathbf{A_t}$. From the projection matrix $\mathbf{A_1}$ at time 1, we calculated the stable age distribution denoted $\mathbf{w_0}$. Then, for each year *t* in the series, we used the estimated projection matrices $\mathbf{A_t}$ and computed the vector $\mathbf{A_t} \,.\, \mathbf{w_t}$ and normalized that to obtain the vector of age distribution $\mathbf{w_t}$ (i.e. whose elements sum to 1).

To compare stochastic elasticity patterns among populations with contrasting life history strategies, we defined for all the analysed populations the same life cycle graph including three different life history stages (Fig. 1). First, we defined a yearling stage corresponding to individuals of 1 year of age. Then, a second stage brought together immature individuals and corresponded to individuals greater than or equal to 2 years of age that were not yet able to reproduce. The duration of this second stage varied from 0 when yearlings were able to reproduce (as in wild boar *Sus scrofa*) to 15 years in some primates for which females do not reproduce before 16 years of age. Finally, the last stage brought together adults (pooling both prime-aged and senescent individuals when this distinction was made in the original work) that are able to reproduce. Therefore, we defined these three common stages for all the populations included in the analysis to investigate the effect of a change in yearling survival ψ_1 (corresponding to S_1 for the mountain goat study case), survival of immature individuals ψ_2 (corresponding to S_2 for the mountain goat), adult survival ψ_3 (corresponding to the sum of the contribution of prime-age survival from S_3 to S_9 and the survival of senescent females S_{10} for the mountain goat), and realized fecundity F (corresponding to the sum of the contribution from R_3 to R_{10} for the mountain goat) to the population growth rate.

Table 1. Mammal populations for which yearly estimates of age-specific survival and reproduction were available and their associated generation time (in years), age at first reproduction (AFR, in years), adult life expectancy (ALE, in years) and demographic regime (assessed using *r*, calculated as the logarithm of the dominant eigenvalue of the average matrix). Two different populations of roe deer (1: Trois Fontaines and 2: Chizé) and bighorn sheep (1: Ram Mountain and 2: Sheep River) and three different populations of mule deer (1: Bridger Mountain (PHU4), 2: Bridger Mountain (PHU2), and 3: Missouri River Breaks) were included in the analyses.

Population	Study period	Reference	Generation time	AFR	ALE	r
1. Wild boar *Sus scrofa scrofa*	1983–2005	This study	3.3	1	1.85	−0.10
2. Eastern chimpanzee *Pan troglodytes schweinfurthii*	1963–2007	Morris et al. 2008	34.0	16	18.70	−0.18
3. Mountain gorilla *Gorilla beringei beringei*	1967–2007	Morris et al. 2008	53.9	11	42.91	0.02
4. Northern muriqui *Brachyteles hypoxanthus*	1983–2007	Morris et al. 2008	70.1	9	59.50	0.05
5. Blue monkey *Cercopithecus mitis stuhlmanni*	1980–2007	Morris et al. 2008	25.1	8	17.98	0.04
6. Yellow baboon *Papio cynocephalus*	1971–2007	Morris et al. 2008	29.1	7	21.51	0.05
7. White-faced capuchin monkey *Cebus capucinus*	1986–2007	Morris et al. 2008	35.2	7	27.11	0.02
8. Verreaux's sifaka *Propithecus verreauxi*	1984–2007	Morris et al. 2008	20.5	7	13.72	−0.01
9. Red squirrel *Tamiasciurus hudsonicus*	1990–2003	Descamps et al. 2008	3.8	1	2.75	0.02
10. Mountain goat *Oreamnos americanus*	1992–2002	Festa-Bianchet and Côté 2008	9.7	3	9.55	0.06
11. Bighorn sheep 2 *Ovis Canadensis*	1983–1997	Coulson et al. 2005	7.5	2	7.69	0.00
12. Bighorn sheep 1 *Ovis canadensis*	1980–1995	Coulson et al. 2005	8.8	2	9.43	0.06
13. Roe deer 2 *Capreolus capreolus*	1985–1998	Gaillard and Yoccoz 2003	10.1	2	10.52	0.19
14. Roe deer 1 *Capreolus capreolus*	1985–1998	Gaillard and Yoccoz 2003	7.0	2	7.72	0.21
15. Soay sheep *Ovis aries*	1985–2002	Coulson et al. 2001	6.4	1	6.74	−0.08
16. Patas monkey *Erythrocebus patas*	1994–2002	Isbell et al. 2009	4.7	3	2.74	−0.22
17. Brown long-eared bat *Plecotus auritus*	1977–1985	Boyd and Stebbings 1989	5.6	2	4.63	−0.00
18. Golden-mantled ground squirrel *Spermophilus lateralis*	1990–2007	Hostetler et al. 2012	3.4	1	2.17	−0.03
19. Vervet *Chlorocebus aethiops*	1993–1998	Isbell et al. 2009	12.5	5	8.45	0.01
20. Eurasian badger *Meles meles*	1980–1993	Rogers et al. 1997	6.4	2	5.41	0.04
21. Mule deer 1 *Odocoileus hemionus*	1973–1986	Pac et al. 1991	9.3	2	8.28	−0.00
22. Mule deer 2 *Odocoileus hemionus*	1978–1986	Pac et al. 1991	6.7	2	5.67	−0.01
23. Mule deer 3 *Odocoileus hemionus*	1976–1985	Hamlin and Mackie 1989	8.0	2	6.97	0.06
24. Pronghorn *Antilocapra americana*	1981–1995	Byers 1997	8.7	2	12.15	0.05
25. Weddell seal *Leptonychotes weddellii*	1987–2001	Hadley et al. 2006	23.0	6	17.44	−0.00

Elasticity estimates

While elasticity estimation generally requires to generate random temporal variations in demographic rates (Tuljapurkar et al. 2003), Haridas et al. (2009) developed a method for estimating elasticities directly from time series of demographic parameters, thus liberating elasticity estimation from the need to model the environmental process. Therefore, this method is a prospective analysis (sensu Caswell 2000) in the presence of random temporal variations (Haridas et al. 2009). In short, they built annual population projection matrices and calculated annual elasticity at time *t* (E_t), which corresponds to the elasticity of the annual growth rate λ_t, as the sum of $e_{R,t}$ (i.e. the direct effect of changing a matrix element on population growth λ_t) and $e_{U,t}$ (i.e. the indirect effect via changes in age-structure on population growth rate λ_t). They showed that the long-run average of E_t converges to the stochastic elasticity, while the long-run averages of $e_{R,t}$ and $e_{U,t}$ converge to the separate limits $\overline{e_R}$ and $\overline{e_U}$.

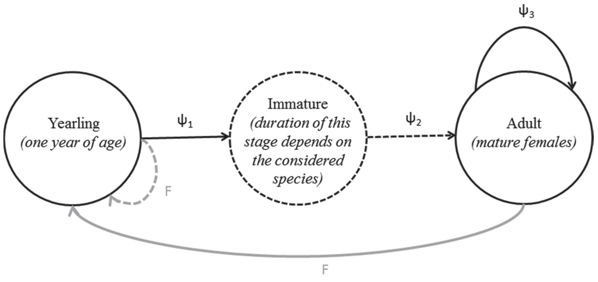

Figure 1. Life cycle graph used to standardize the measure of stochastic elasticities for the 25 populations. In black, ψ_1, ψ_2 and ψ_3 are, respectively, yearling, immature and adult survival probabilities. In grey, ***F*** corresponds to realized fecundity. Dotted lines correspond to facultative stage and transitions, depending on the considered species.

From the yearly projection matrices $\mathbf{A}_t$ built for each population, we thus measured both the direct (denoted $e_{R,t}$) and indirect (denoted $e_{U,t}$) effects on annual population growth λ_t (Table 2) using Haridas et al.'s (2009) procedure implemented in Matlab (Matlab ver. 7.11 2011). While $e_{R,t}$ (i.e. direct impact of changing the focal vital rate in year *t*) is always positive, $e_{U,t}$ (i.e. indirect impact of changing population structure via a change in the focal vital rate) can be negative. To tease apart the effect of the sign of $e_{U,t}$ from the effect of its magnitude, we defined a novel metric $|e_{U,t}|$. We then estimated $\overline{e_R}$ and $\overline{|e_U|}$ over the study period, and to estimate the relative magnitudes of direct and indirect effects on stochastic population growth rate, we calculated the ratio between these two quantities.

In practice, for each population included in the analysis, we estimated $e_{R,t}$ and $|e_{U,t}|$ for ψ_1, ψ_3 and *F* but not for ψ_2 because this latter stage varied in duration across mammal species and was not present at all when females give birth at 1 or 2 years of age (as observed in 14 out of 25 populations analyzed). For each population, we estimated the mean of $e_{R,t}$ (denoted $\overline{e_R}$) and the mean of $|e_{U,t}|$ (denoted $\overline{|e_U|}$) over the course of the study for yearling survival (ψ_1). We then calculated the ratio between $\overline{e_R}$ and $\overline{|e_U|}$ to measure the relative contribution of the direct effects on population growth

Table 2. Parameters used in the analyses and their biological meaning.

Parameters	Biological meaning
$e_{R,t}$	component of stochastic elasticity due to a change in the focal demographic parameter: measure of the direct effect of changing a given demographic parameter on population growth rate (always a positive value)
$e_{U,t}$	component of stochastic elasticity due to a change in population structure: measure of the indirect effect of changing a given demographic parameter on population growth rate (either a positive or a negative value)
ψ_1	yearling survival, i.e. yearly survival of females between one and two years of age
ψ_2	survival of immature females, i.e. yearly survival of females older than 2 years that are not yet able to reproduce
ψ_3	adult survival, i.e. yearly survival of females older than two years that are able to reproduce
F	realized fecundity, i.e. yearly fecundity of adult females

λ_s caused by changing the focal demographic parameter. We replicated this analysis on adult survival (ψ_3) by summing $e_{R,t}$ (respectively $|e_{U,t}|$) of all the matrix elements containing ψ_3 for each time *t*. For instance, for the mountain goat, for year 1, we recorded $e_{R,1}$ (respectively $|e_{U,1}|$) of ψ_3 (i.e. of S_3, S_4, S_5, S_6, S_7, S_8, S_9, S_{10}) to obtain the direct effect of changing adult survival at year 1. For year 2, we recorded $|e_{R,2}|$ (respectively $|e_{U,2}|$) of ψ_3, etc. Finally, we estimated $\overline{e_R}$ and $\left|e_U\right|$ over the course of the study for ψ_3 and calculated the ratio between these two quantities (as the ratio $\overline{e_R}/\left|e_U\right|$). We performed exactly the same analysis on the realized fecundity (*F*) by recording $e_{R,t}$ (respectively $|e_{U,t}|$) of *F* for each time *t* and by calculating the ratio $\overline{e_R}/\left|e_U\right|$.

In addition, for each population, we considered the sign of the average $\overline{e_U}$ corresponding to the component of stochastic elasticity due to change in population structure (i.e. the indirect effect). When $\overline{e_U}$ is on average positive (resp. negative), the change in population structure resulting for a change in a demographic parameter leads to a positive (resp. negative) contribution to stochastic population growth rate λ_s.

Generation time and its components

We used the generation time as a metric to rank species on the slow–fast continuum (Gaillard et al. 2005, see Sæther et al. 2013 for a similar approach). For each population, generation time was estimated from the deterministic population projection matrix built on mean demographic parameters estimated over the course of the study (see matrices in Supplementary material Appendix 1). The generation time *Tc*, corresponding to mean age of the parents of the offspring produced by a cohort over its lifetime (Caswell 2001), was calculated as $Tc = \frac{\sum_i i \times S_i \times m_i}{\sum_i S_i \times m_i}$ with m_i the number of female offspring born to a female of age *i*. A fast (resp. slow) species will thus be characterized by a short (resp. long) generation time.

Generation time can be split into its two biological components, namely survival and reproduction. In particular, we used adult life expectancy (ALE) and age at first reproduction (AFR). For each population, ALE (referring more precisely to life expectancy at maturity) was estimated following the approach described in Caswell (2001) (p. 118–120) from the deterministic population projection matrix. To standardize the dimension of both ALE and AFR as times (Stahl 1962) and account for allometric constraints (Houle et al. 2011), these measures were log-transformed. Our choice was motivated by the current state of our knowledge of life history evolution: a slower life history, characterized by a long generation time, is commonly associated with delayed reproduction and high adult survival (Stearns 1992), and both age at first reproduction (Cole 1954) and adult survival (Charnov 1986) have been shown to play a major role in shaping life history strategies.

The effects of generation time, its components, and asymptotic population growth rate on stochastic elasticity patterns

To test a potential influence of generation time and of its components (i.e. ALE and AFR) on the relative magnitudes of direct and indirect effects of changing a demographic parameter on population growth λ_s, we assessed the relationship between the species-specific ratio between $\overline{e_R}$ and $\left|e_U\right|$ (on a log-scale) for yearling survival (ψ_1) and generation time, ALE and AFR (all log-scaled). Because of the concept of biological time (sensu Calder 1984), generation time, ALE and AFR are by nature positively correlated. Therefore, they were not included in the models simultaneously. Moreover, the demographic status of a population is linked to elasticity patterns in deterministic frameworks (Festa-Bianchet et al. 2006, Nilsen et al. 2009). The asymptotic growth rate λ that corresponds to the dominant eigenvalue of the average matrix usually provides an assessment of the demographic regime of the population. We thus also assessed the effect of *r*, corresponding to the logarithm of λ, on the relative magnitudes of direct and indirect effects on stochastic population growth rate, by including it in the regressions linking the ratio $\overline{e_R}/\left|e_U\right|$ (on a log-scale) to generation time and its components.

The same analyses were performed for the species-specific ratio between $\overline{e_R}$ and $\left|e_U\right|$ (on a log-scale) for adult survival (ψ_3) as well as for realized fecundity (*F*).

Instead of using linear regressions to link the species-specific ratio between $\overline{e_R}$ and $\left|e_U\right|$ to asymptotic population growth rate, generation time, ALE and AFR, we used phylogenetic generalized least-squares models (PGLS). This is because species may share similar values of stochastic elasticities and life history as a result of common ancestry (Harvey and Pagel 1991). This problem generates dependency among the data, which, when not accounted for, may lead to the detection of spurious effects (Ives and Zhu 2006). To control for this non-independence among species, a phylogeny was derived from the phylogenetic supertree of mammals with topology and branch length provided by Bininda-Emonds et al. (2007) (Supplementary material Appendix 2). We estimated an index we called Δ varying from 0 (corresponding to the complete absence of phylogenetic structure) to 1 (when the phylogenetic structure can be represented by the previously constructed tree) (Freckleton et al. 2002), which was then introduced in the model to control for the phylogenetic effect (Freckleton et al. 2002, procedure implemented in R by Gage and Freckleton 2003).

The Akaike information criterion corrected for small sample size (AICc) was used for model selection (Burnham and Anderson 2002). These analyses were performed in R ver. 2.12.2 (<www.r-project.org>).

Results

The 25 mammalian life histories included in the analyses spanned a large range of generation time (from 3.3 to 70.1 years), AFR (from 1 to 16 years), and ALE (from 1.85 to 59.5 years) (Table 1, Supplementary material Appendix 3). These populations also varied a lot in terms of demographic status, including decreasing, stationary or increasing populations (Table 1, Supplementary material Appendix 3).

For most of the models linking the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ to asymptotic population growth rate, generation time, AFR and ALE, the phylogenetic signal Δ was close to 1 except for some relationships involving the ratio for realized fecundity, meaning that there was in overall a strong phylogenetic signature (Table 3).

Taking into account the correction for phylogenetic structure, the model of the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for yearling survival ψ_1 included an effect of ALE (Fig. 2, Table 3). The higher the ALE, the lower the $\overline{e_R}/\left|\overline{e_U}\right|$ ratio (slope = –0.43 (SE: 0.20)), meaning that the relative contribution of the direct effect of elasticity $e_{R,t}$ to the population growth rate λ_s decreases with increasing ALE. It is noteworthy that the model with the second rank of lowest AICc was the constant one. Moreover, a model including an effect of generation time was close to the most parsimonious model (Table 3). Increasing generation time led to a decrease in the relative contribution of direct effects of elasticity $\overline{e_R}$ on the population growth rate of the same magnitude as increasing ALE (slope = –0.42 (SE: 0.23)). On the contrary, the model including AFR only was poorly supported (Table 3) and displayed a much weaker effect size (slope = −0.25 (SE: 0.30)). Finally, the higher *r*, the lower the relative contribution of direct effects of elasticity $\overline{e_R}$ to the population growth rate (slope = −2.64 (SE: 1.40), Table 3). Studying the sign of the average $\overline{e_U}$ allowed us to distinguish two groups of species. The first group included species characterized with a short life expectancy, which had a positive $\overline{e_U}$ on average for yearling survival ψ_1 (Fig. 2, Supplementary material Appendix 3). For those species, the change in population age structure resulting from a change in yearling survival increased the contribution of change in yearling survival to population growth rate λ_s. The second group included species characterized with a long life expectancy, which had a negative $\overline{e_U}$ on average for yearling survival ψ_1 (Fig. 2, Supplementary material Appendix 3). For those species, the change in population age structure resulting from a change in yearling survival decreased the contribution of change in yearling survival to population growth rate λ_s.

Table 3. Model selection of phylogenetic generalized least-squares models with the $\overline{e_R}/\left|\overline{e_U}\right|$ ratio as a response variable for (A) yearling survival ψ_1, (B) adult survival ψ_3, and (C) realized fecundity **F** and with the demographic regime (*r*), generation time (*Tc*), age at first reproduction (*AFR*) and adult life expectancy (*ALE*) as fixed effects. Displayed are the AICc of each model, the difference in AICc between each candidate model and the best model (Δ*AICc*) and the phylogenetic signal Δ of each tested model. The best models are in bold.

Models	AICc	ΔAICc	Δ
(A)			
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~log (Tc)	60.42	1.06	0.85
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~log (AFR)	63.02	3.66	0.86
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~log (ALE)	**59.36**	**0**	**0.85**
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~r	60.57	1.21	0.93
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~log (Tc)+ r	63.40	4.04	0.88
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~r+ log (AFR)	64.25	4.89	0.93
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~r+ log (ALE)	62.77	3.41	0.87
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_1~1	60.30	0.94	0.89
(B)			
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~log (Tc)	57.32	4.12	0.93
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~log (AFR)	58.00	4.8	0.93
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~log (ALE)	56.81	3.61	0.93
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~r	**53.20**	**0**	**0.95**
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~log (Tc)+ r	56.58	3.38	0.95
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~r+ log (AFR)	55.83	2.63	0.95
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~r+ log (ALE)	56.74	3.54	0.95
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for ψ_3~1	54.62	1.42	0.92
(C)			
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ log (Tc)	**13.66**	**0**	**0.26**
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ log (AFR)	18.46	4.80	6.61×10^{-5}
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ log (ALE)	14.98	1.32	0.52
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ r	22.11	8.45	0.76
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ log (Tc)+ r	16.37	2.71	6.61×10^{-5}
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ r+ log (AFR)	22.10	8.44	6.61×10^{-5}
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ r+ log (ALE)	18.25	4.59	0.40
$\log\left(\overline{e_R}/\left\|\overline{e_U}\right\|\right)$ for **F** ~ 1	20.29	6.63	0.72

The model retained for the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for adult survival ψ_3 included an effect of the demographic status *r* (Fig. 3, Table 3). The higher *r*, the lower the $\overline{e_R}/\left|\overline{e_U}\right|$ ratio (slope = –2.76 (SE: 1.23)), meaning that the relative contribution of $\overline{e_R}$ to the population growth rate decreased with increasing *r*. More generally, all the retained models, except the constant one, included an effect of *r*. In contrast, models including an effect of generation time (slope = –0.18

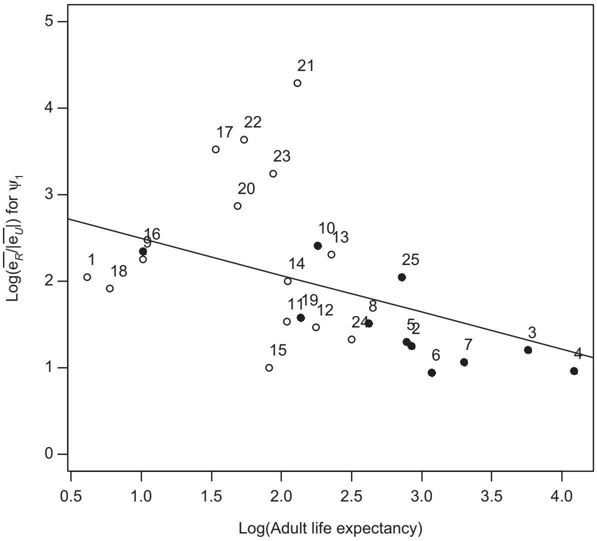

Figure 2. Relationship between the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for yearling survival ψ_1 (log-transformed) and adult life expectancy (log-transformed) for the 25 populations displayed in Table 1. Filled circles correspond to a negative average $\overline{e_U}$, open circles correspond to a positive average $\overline{e_U}$. The numbers on the graph correspond to the populations displayed in Table 1.

(SE: 0.22)) or of any of its components (ALE: slope = –0.21 (SE: 0.19), AFR: slope = –0.06 (SE: 0.28)) were poorly supported (Table 3). When considering the sign of the average $\overline{e_U}$, most of the populations (i.e. 22/25) had a positive $\overline{e_U}$ for adult survival ψ_3 irrespective of *r* (Fig. 3, Supplementary material Appendix 3). Therefore, for all these populations, the change in population age structure resulting from a change in adult survival increases the contribution of a change in adult survival to population growth rate λ_s.

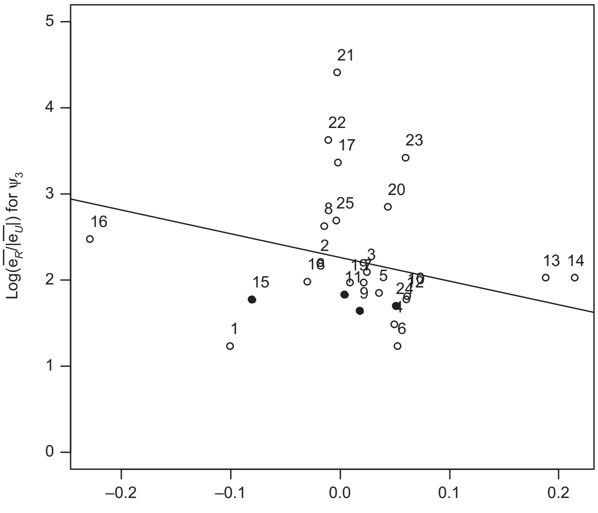

Figure 3. Relationship between the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for adult survival ψ_3 (log-transformed) and demographic status *r* for the 25 populations displayed in Table 1. Filled circles correspond to a negative average $\overline{e_U}$, open circles correspond to a positive average $\overline{e_U}$. The numbers on the graph correspond to the populations displayed in Table 1.

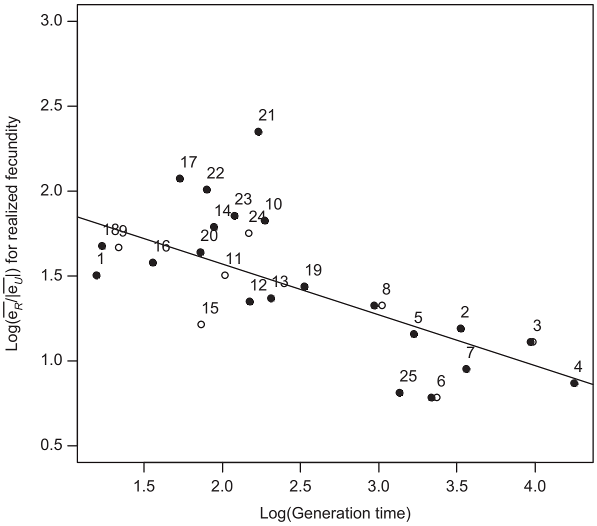

Figure 4. Relationship between the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for realized fecundity (log-transformed) and generation time (on a log-scale) for the 25 populations displayed in Table 1. Filled circles correspond to a negative average $\overline{e_U}$, open circles correspond to a positive average $\overline{e_U}$. The numbers on the graph correspond to the populations displayed in Table 1.

Finally, the model retained for the ratio $\overline{e_R}/\left|\overline{e_U}\right|$ for realized fecundity *F* (Fig. 4, Table 3) showed that the longer the generation time, the lower the $\overline{e_R}/\left|\overline{e_U}\right|$ ratio (slope = –0.30 (SE: 0.08)), meaning that the relative contribution of $\overline{e_R}$ to the population growth rate decreases with increasing generation time. Similarly, the model including both generation time and *r* was well supported (Table 3). Interestingly, once the models including generation time were discarded, the models including AFR (slope = –0.31 (SE: 0.08)) and ALE (slope = –0.25 (SE: 0.08)) were well supported (Table 3) and, as expected for measures of time, provided effect sizes of similar magnitude. All these models outperformed the constant model (Table 3). Finally, the model including an effect of *r* was less well supported (slope = –0.94 (SE: 0.75)) than ones including generation time or its components. When considering the sign of the average $\overline{e_U}$, most of the populations (i.e. 21/25) have a negative $\overline{e_U}$ for realized fecundity *F* irrespective of their pace of life (Fig. 4, Supplementary material Appendix 3). Therefore, for all these populations, the change in population age structure resulting from a change in fecundity decreases the contribution of changing fecundity to population growth rate λ_s.

Discussion

Taking advantage of long-term monitoring of 25 populations belonging to 21 species, we built year-dependent projection matrices for each population. From these matrices, we estimated $\overline{e_R}$ and $\left|\overline{e_U}\right|$, the direct and the indirect effects of changing a focal demographic parameter on stochastic growth rate λ_s, and we found that the relative contribution of these two components strongly depends on life-history tactics and demographic status displayed by the focal population.

Stochastic elasticity patterns and life history tactics

The mean ratio $\overline{e_R} / \left|\overline{e_U}\right|$ provides a simple metric to evaluate the relative magnitude of direct and indirect effects of changing a given demographic parameter on population growth rate while teasing apart the effect of the sign of $\overline{e_U}$ from the effect of its magnitude.

The relative contribution of direct versus indirect effects of changing realized fecundity on population growth is the highest for species characterized with a short generation time (Fig. 4). The long-run stochastic growth rate λ_s of fast populations is thus more influenced by a change of fecundity than the λ_s of slow populations. This result echoes previous findings from deterministic frameworks (Heppell et al. 2000). More interestingly, we found that the contribution of indirect effects to long-term population growth of increasing realized fecundity was negative for most populations we analyzed. Although being counter-intuitive at first sight, this negative indirect impact of increasing fecundity in mammalian populations can easily be explained. Indeed, increasing realized fecundity directly increases the proportion of young in the population, which had lower reproductive value. This thus leads to a negative long-term indirect contribution of increasing fecundity to population growth rate. Although the young produced are often able to reproduce the next year as yearling in species with a short generation time, recruitment is generally higher in adults than in yearlings, like observed in wild boar for instance. This thus explains why on average, increasing fecundity has a negative long-term indirect contribution to λ_s.

The relative contribution of direct versus indirect effects of changing adult survival on population growth did not depend on the pace of life, being associated with neither generation time, AFR, nor ALE. Most mammalian populations showed remarkably similar relative contributions of direct versus indirect effects of changing adult survival on population growth. However, we found that the relative contribution of direct versus indirect effects of changing adult survival on population growth depended on the demographic status of the population (Fig. 3). In declining populations (i.e. $r < 0$), the positive direct effect of increasing adult survival on population growth rate is higher than in increasing populations. Once again, this result echoes previous findings from deterministic frameworks. Indeed, adult survival generally has the highest deterministic elasticity in declining populations (Festa-Bianchet et al. 2006, Nilsen et al. 2009). For instance, a comparative study among five roe deer populations has highlighted that adult survival generally has a higher contribution in populations with low mean population growth rate (Nilsen et al. 2009). More importantly, regarding the sign of $\overline{e_U}$, increasing adult survival in a given population leads to an increase in the proportion of individuals with high reproductive value. Consequently, indirect effects of increasing adult survival almost consistently amplify the overall contribution of change in that parameter to long-term population growth λ_s. Thus, increasing (resp. decreasing) survival of mature females should lead to increase (resp. decrease) population growth rate by both direct and indirect pathways. Such stochastic elasticity patterns obviously have important practical implications in terms of management and conservation. Indeed, size-selective harvesting where the largest and thereby adult individuals are preferentially taken, negatively affects the demography of populations (Fenberg and Roy 2008). Our analysis of stochastic elasticity patterns demonstrates that such a negative influence involves both a direct decrease of survival but also associated changes in age structure, irrespective of their pace of life. Therefore, these long-lasting effects of changes in age structure will generate a lagged demographic response after a ban of selective hunting.

The relative contribution of direct versus indirect effects of changing yearling survival on population decreases with increasing ALE (Fig. 2). The long-run stochastic growth rate λ_s of short-lived populations is thus more influenced by a change of yearling survival than the λ_s of long-lived populations. Other works in deterministic frameworks have shown that the deterministic population growth rate in short-lived species is very sensitive to change in yearling survival. For instance, in a heavily hunted wild boar population suffering from a reduced ALE, the elasticity of yearling survival was 0.30 versus 0.26 for a weakly hunted population with higher ALE (Servanty et al. 2011). On the contrary, in long-lived large herbivores, deterministic analyses have revealed that the elasticity of adult survival is consistently higher than that of yearling survival (Gaillard et al. 2000). For these species, adult survival has thus the greatest potential to affect the population growth rate. In those species, females skip a reproductive event rather than jeopardizing their own survival (Gaillard and Yoccoz 2003). Population growth rate in these species is much more sensitive to a given relative change in adult survival than to the same change in yearling survival. The negative relationship we found between the relative contribution of direct versus indirect effects of changing yearling survival on population and ALE is thus not surprising. However, by investigating the sign of the mean $\overline{e_U}$, we highlighted that for short-lived species, increasing yearling survival increases the proportion of adults that are able to recruit the next year. Consequently, in short-lived species, the change in population age structure caused by changing yearling survival amplifies the contribution of that parameter to population growth rate λ_s compared to the deterministic case. Indeed, for wild boar for example, we found that $\overline{e_U}$ equals on average 0.03 while $\overline{e_R}$ equals on average 0.26 (Supplementary material Appendix 3). Thus, a short-lived species faced with disturbances causing a decrease (resp. increase) of yearling survival will experience a larger decrease (resp. increase) in the population growth rate caused by additional contribution of changing the age structure. Short-lived species thus display a boom-bust life history strategy. These findings provide a mechanistic demographic explanation for the empirical observation that short-lived species have large variation in population size over time compared to long-lived ones (Sinclair 1996). A retrospective analysis may provide insights on the mechanism driving past population variations. While increasing yearling survival also increases the proportion of yearlings in long-lived species, females in these latter species often will not recruit before 3 years of age or older. For instance, in the long-lived mountain gorilla *Gorilla beringei beringei*, females start giving birth only at 11 years of age (Morris et al. 2011). Consequently, increasing yearling survival in gorilla will lead to increase the average fraction of the population that is immature, and thereby to reduce population growth rate, explaining why $\overline{e_U}$ is negative for such species. Indeed, for mountain gorilla, we found that $e_{U,t}$ equals on average –0.014 while $\overline{e_R}$ equals on average 0.046. Thus, in long-lived species, an increase in yearling survival produces a change in age structure that reduces the overall elasticity of growth rate. It is well known that in a variable environment, the growth rate of a long-lived species is less affected by variability than is the growth rate of a short-lived species. This is a kind of buffering effect of adult life expectancy on variation in population growth (Morris et al. 2008, Tuljapurkar et al. 2009, Tuljapurkar 2010). The dampening effect of adult life expectancy on demographic variation has also been reported in Sinclair's (1996) review showing that the coefficient of variation of the number of individuals over time decreases with body size, a good proxy for life expectancy within a mammalian lineage (Gaillard et al. 2003, Speakman 2005). Our results demonstrate a different dampening effect of longevity (measured here as ALE) on the elasticity of stochastic growth rate to an increase in juvenile survival. Nevertheless, because of the dampening effect of longevity, a long-lived species faced with good environmental conditions allowing for an increase of yearling survival will experience a damped increase of population growth rate.

It is noteworthy that some populations consistently displayed a high relative contribution of direct effects of changing survival on population growth rate (populations numbered 17, 20, 21, 22, 23 on Fig. 2 and 3). All these populations (brown long-eared bat *Plecotus auritus*, Eurasian badger *Meles meles* and all the three populations of mule deer *Odocoileus hemionus*) have a demographic regime close to stationary, give birth for the first time at 2 years of age and have intermediate ALE (Table 1, Supplementary material Appendix 3). For these populations, the long-run stochastic growth rate λ_s is mainly influenced by the direct change of survival (either yearling or adult) and very little by the resulting change in age structure. Interestingly, by investigating the sign of the mean $\overline{e_U}$, we found that for all these populations, the change of age structure caused by an increase in survival amplifies the contribution of that parameter to population growth rate λ_s. Therefore, it seems that species with intermediate life expectancy display a life history strategy (in the sense discussed above) closer to the short-lived species than the long-lived ones. However, investigating the relative contribution of direct versus indirect effects of changing survival on λ_s for additional species with intermediate life expectancy is now required to confirm this pattern.

Stochastic versus deterministic elasticities

By analyzing the stochastic elasticity of growth rate from long-term demographic data of species belonging to different mammalian lineages and by taking into account different demographic status (declining, increasing and stationary populations) in our comparative analysis, we were able to estimate both the direct ($\overline{e_R}$) and the indirect ($\overline{e_U}$) effects of changing a focal demographic parameter. Regarding the relationship between the $\overline{e_R}/\left|e_U\right|$ ratio and generation time, its survivorship and reproductive components, and demographic status, we first provided support for previous findings from deterministic demographic analyses. However, importantly, we were also able to quantify the overall effect of changing a focal demographic parameter on population growth rate by investigating the sign of the indirect effect $\overline{e_U}$ resulting from the change caused in age structure. This allowed us to link for the first time demographic elasticities and key demographic output like demographic regime, generation time, ALE, and AFR across a wide range of mammalian life histories. Such an assessment of the impact of changing age structure through changes of demographic rates on population growth rate would have been impossible without decomposing elasticity between its two direct and indirect components using a stochastic framework. It is noteworthy that the assumption of a stable population structure rarely holds in free-ranging populations. Natural or human-induced disturbances can indeed affect population structure. There is nowadays a growing interest in relaxing the assumption of equilibrium, like illustrated by recent analyses of transient dynamics (Ezard et al. 2010, Stott et al. 2010, Gamelon et al. 2014). Stochastic models improve on deterministic models by allowing population structure and population growth to vary over time, and hence can explicitly provide an estimate of the indirect demographic impact of changing population structure (measured here by $\overline{e_U}$).

Even though stochastic models improve on deterministic models, they rarely include density-dependence (but see Koons et al. 2008) that is often reported among mammalian species (see Bonenfant et al. 2009 for a review on ungulates). In addition, stochastic models are data-demanding, explaining the limited dataset analyzed here. However, thanks to the increased availability of long-term detailed monitoring at the individual level (Clutton-Brock and Sheldon 2010), required data are accumulating rapidly, which should allow assessing how density-dependence influences the demographic responses in relation to life history tactics in the future.

Acknowledgements – This work was supported by the French National Agency for Wildlife (ONCFS). TC is funded by an ERC advanced grant. ST and JMG were supported from US National Institute of Aging grant R24AG039345 to ST. We warmly thank Roberto Salguero-Gómez, Dave Koons, Douglas Morris, Bernt-Erik Sæther and Brett Sandercock for their helpful comments on previous drafts of this paper.

References

Benton, T. G. and Grant, A. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. – Am. Nat. 147: 115–139.

Bielby, J. et al. 2007. The fast–slow continuum in mammalian life history: an empirical reevaluation. – Am. Nat. 169: 748–757.

Bininda-Emonds, O. R. P. et al. 2007. The delayed rise of present-day mammals. – Nature 446: 507–512.

Bonenfant, C. et al. 2009. Empirical evidence of density dependence in populations of large herbivores. – Adv. Ecol. Res. 41: 314–345.

Boyce, M. S. et al. 2006. Demography in an increasingly variable world. – Trends Ecol. Evol. 21: 141–148.

Boyd, I. L. and Stebbings, R. E. 1989. Population changes of brown long-eared bats (*Plecotus auritus*) in bat boxes at Thetford Forest. – J. Appl. Ecol. 26: 101–112.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. – Univ. of Chicago Press.

Calder, W. A. 1984. Size, function and life history. – Harvard Univ. Press.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. – Ecology 81: 619–627.

Caswell, H. 2001. Matrix population models, 2nd edn. – Sinauer.

Charnov, E. L. 1986. Life history evolution in a "recruitment population": why are adult mortality rates constant? – Oikos 47: 129–134.

Clutton-Brock, T. H. and Sheldon, B. 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.

Cole, L. M. C. 1954. Some features of random population cycles. – J. Wildl. Manage. 18: 2–24.

Coulson, T. et al. 2001. Age, sex, density, winter weather and population crashes in soay sheep. – Science 292: 1528–1531.

Coulson, T. et al. 2004. Skeletons, noise and population growth: the end of an old debate? – Trends Ecol. Evol. 19: 359–364.

Coulson, T. et al. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. – J. Anim. Ecol. 74: 789–801.

de Kroon, H. et al. 1986 Elasticity: the relative contribution of demographic parameters to population growth rate. – Ecology 67: 1427–1431.

Descamps, S. et al. 2008. Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. – Oikos 117: 1406–1416.

Ezard, T. et al. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. – J. Appl. Ecol. 47: 515–523.

Fenberg, P. B. and Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? – Mol. Ecol. 17: 209–220.

Festa-Bianchet, M. and Côté, S. D. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. – Island Press, Washington, DC.

Festa-Bianchet, M. et al. 2006. Stochastic predation events and population persistence in bighorn sheep. – Proc. R. Soc. B 273: 1537–1543.

Fieberg, J. and Ellner, S. P. 2001. Stochastic matrix models for conservation biology: a comparative review of methods. – Ecol. Lett. 4: 244–266.

Freckleton, R. et al. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

Gage, M. J. G. and Freckleton, R. P. 2003. Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. – Proc. R. Soc. B 270: 625–632.

Gaillard, J. M. and Yoccoz, N. G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? – Ecology 84: 3294–3306.

Gaillard, J. M. et al. 1989. An analysis of demographic tactics in birds and mammals. – Oikos 56: 59–76.

Gaillard, J. M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – Annu. Rev. Ecol. Syst. 31: 367–393.

Gaillard, J. M. et al. 2003. Ecological correlates of life span in populations of large herbivorous mammals. – Popul. Dev. Rev. 29: 39–56.

Gaillard, J. M. et al. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. – Am. Nat. 166: 119–123.

Gaillard, J. M. et al. 2015. Axes of variation in life histories. – In: Coulson, T. (ed.), Encyclopedia of evolutionary biology. – Elsevier.

Gamelon, M. et al. 2014. Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. – Am. Nat. 184: 673–683.

Hadley, G. L. et al. 2006. Variation in probability of first reproduction of Weddell seals. – J. Anim. Ecol. 75: 1058–1070.

Hamlin, K. L. and Mackie, R. J. 1989. Mule deer in the Missouri River Breaks, Montana: a study of population dynamics in a fluctuating environment (Final report, Federal aid in wildlife restoration project W-120-R). – Montana Dept of Fish, Wildlife and Parks, Helena, MT.

Haridas, C. V. et al. 2009. Estimating stochastic elasticities directly from longitudinal data. – Ecol. Lett. 12: 806–812.

Harvey, P. H. and Pagel, M. D. 1991. The comparative method in evolutionary biology, 1st edn. – Oxford Univ. Press.

Heppell, S. S. et al. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. – Ecology 8: 654–665.

Hille, S. M. and Cooper, C. B. 2015. Elevational trends in life histories: revising the pace-of-life framework. – Biol. Rev. 90: 204–213.

Hostetler, J. A. et al. 2012. Stochastic population dynamics of a montane ground-dwelling squirrel. – PloS ONE 7:e34379.

Houle, D. et al. 2011. Measurement and meaning in biology. – Q. Rev. Biol. 86: 3–34.

Isbell, L. A. et al. 2009. Demography and life histories of sympatric patas monkeys, *Erythrocebus patas*, and vervets, *Cercopithecus aethiops*, in Laikipia, Kenya. – Int. J. Primatol. 30: 103–124.

Ives, A. R. and Zhu, J. 2006. Statistics for correlated data: phylogenies, space and time. – Ecol. Appl. 16: 20–32.

Jeschke, J. and Kokko, H. 2009. The roles of body size and phylogeny in fast and slow life histories. – Evol. Ecol. 23: 867–878.

Koons, D. et al. 2008. Evolution of delayed reproduction in uncertain environments: a life-history perspective. – Am. Nat. 172: 797–805.

Morris, W. F. et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. – Ecology 89: 19–25.

Morris, W. F. et al. 2011. Low demographic variability in wild primate populations: fitness impacts of variation, covariation and serial correlation in vital rates. – Am. Nat. 177: E14–E28.

Nilsen, E. B. et al. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. – J. Anim. Ecol. 78: 585–594.

Pac, D. F. et al. 1991. Mule deer population organization, behavior and dynamics in a Rocky Mountain environment. – Montana Dept of Fish, Wildlife and Park.

Read, A. F. and Harvey, P. H. 1989. Life-history differences among the eutherian radiations. – J. Zool. 219: 329–353.

Rogers, L. M. et al. 1997. The demography of a high-density badger (*Meles meles*) population in the west of England. – J. Zool. Lond. 242: 705–728.

Sæther, B-E. et al. 2013. How life history influences population dynamics in fluctuating environments. – Am. Nat. 182: 743–759.

Servanty, S. et al. 2011. Influence of harvesting pressure on demographic tactics: implications for wildlife management. – J. Appl. Ecol. 48: 835–843.

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. – In: Floyd, R. B. et al. (eds), Frontiers of population ecology. CSIRO, pp. 127–154.

Speakman, J. R. 2005. Body size, energy metabolism and lifespan. – J. Exp. Biol. 208: 1717–1730.

Stahl W. R. 1962. Similarity and dimensional methods in biology. – Science 137: 205–212.

Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. – Oikos 41: 173–187.

Stearns, S. C. 1992. The evolution of life histories. Vol. 248. – Oxford Univ. Press.

Stott, I. et al. 2010. Boom or bust? a comparative analysis of transient population dynamics in plants. – J. Ecol. 98: 302–311.

Tuljapurkar, S. 1989. An uncertain life: demography in random environments. – Theor. Popul. Biol. 35: 227–294.

Tuljapurkar, S. 2010. Environmental variance, population growth and evolution. – J. Anim. Ecol. 79: 1–3.

Tuljapurkar, S. et al. 2003. The many growth rates and elasticities of populations in random environments. – Am. Nat. 162: 489–502.

Tuljapurkar, S. et al. 2009. From stochastic environments to life histories and back. – Phil. Trans. R. Soc. B 364: 1499–1509.

Supplementary material (available online as Appendix oik-02582 at <www.oikosjournal.org/appendix/oik-02582>). Appendix 1–3.