



HAL
open science

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

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

► **To cite this version:**

Marlène Gamelon, Jean-Michel Gaillard, Olivier Gimenez, Tim Coulson, Shripad Tuljapurkar, et al..
Linking demographic responses and life history tactics from longitudinal data in mammals. *Oikos*,
2015, 125, pp.395 - 404. 10.1111/oik.02582 . hal-03499378

HAL Id: hal-03499378

<https://hal.science/hal-03499378>

Submitted on 4 Jan 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Marlène Gamelon^{1,2,3,4}, Jean-Michel Gaillard¹, Olivier Gimenez³, Tim Coulson⁵, Shripad
5 Tuljapurkar⁶, Serge Brandt², and Eric Baubet²

6

7 1. Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR 5558, Laboratoire
8 de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France

9 2. Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, 2 Bis
10 Rue des Religieuses, BP 19, 52 120 Châteauvillain, France

11 3. Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, campus CNRS, 1919 route de
12 Mende, 34 293 Montpellier Cedex 5, France

13 4. marlene.gamelon@univ-lyon1.fr, corresponding author

14 5. Department of Life Sciences, Imperial College London, Silwood Park SL5 7PY, UK

15 6. Biological Sciences, Stanford University, Stanford, CA 94305, USA

16

17

18

19 **Running headline:** Stochastic elasticity and life history

20

21

22

23 **Summary**

24 **1.** In stochastic environments, demographic parameters such as survival or reproduction
25 fluctuate from year to year, leading to changes in age structure. The change observed in a
26 given demographic parameter can thus influence population growth rate either directly or via
27 the resulting change in age structure. Therefore, stochastic elasticity includes both the effect
28 directly due to changing the focal demographic parameter and the effect indirectly due to
29 changes in age structure generated by changing the focal demographic parameter.

30 **2.** We investigated the role of life history traits for driving the relative contributions of direct
31 and indirect components of stochastic elasticity. We assessed stochastic elasticity patterns in
32 several mammalian species with contrasted life histories.

33 **3.** The relative contribution of direct and indirect impacts of changing yearling survival was
34 strongly associated with generation time and each of its components (i.e., age at first
35 reproduction and life expectancy), showing that stochastic elasticity patterns are shaped by
36 life-history tactics. For fast species, the change in population structure resulting from a change
37 in yearling survival leads to a positive contribution to population growth rate whereas for
38 slow species, the change in population structure resulting from a change in yearling survival
39 leads to a negative contribution to population growth rate.

40 **4.** Irrespective of the species' pace of life, the change in population structure resulting from a
41 change in adult survival (i.e., the indirect effect) leads to on average, a positive contribution to
42 population growth rate.

43 **5.** In a stochastic world, analyses of stochastic elasticity improve our understanding of
44 population dynamics in fast and slow species. These results demonstrate that the pace of life

45 of a given species dictates the pathways by which observed variation in demographic
46 parameters influence population growth.

47

48 **Key-words:** Generation time, life-history, mammals, population structure, stochastic
49 elasticity

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64 **Introduction**

65 To study population dynamics, demographic parameters such as age-specific survival and
66 reproduction can be integrated into population models, also called population projection
67 matrices (Caswell 2001). Sensitivity analyses can then be performed using different scales of
68 changes to allow identifying demographic parameters that drive population dynamics. Among
69 them, elasticity analyses are often performed in ecology and evolution to quantify the relative
70 changes in population growth rate resulting from small relative changes in the matrix
71 transition elements (de Kroon, van Groenendael & Ehrlén 2000). In evolutionary biology,
72 they are useful tools to evaluate the strength of natural (Van Tienderen 2000; Coulson *et al.*
73 2003 for an application on red deer *Cervus elaphus*) or human-induced (see Gamelon *et al.*
74 2011 for an application on wild boar *Sus scrofa scrofa*) selection on phenotypic traits.

75 Demographic analyses can be performed either in a deterministic or in a stochastic context. In
76 deterministic models, demographic parameters are assumed to be constant through time and
77 the single transition matrix only includes the mean values of demographic parameters
78 estimated throughout the study period. The elasticity of each parameter in the average
79 transition matrix then measures the relative change in population growth rate resulting from a
80 very small relative change in the parameter. However, lots of studies have pointed out that
81 including temporal variation in demographic parameters can change the picture (Tuljapurkar
82 1989; Boyce *et al.* 2006; Morris *et al.* 2008; Morris *et al.* 2011). In stochastic environments,
83 demographic parameters fluctuate from year to year so that the transition matrix changes from
84 year to year (Fieberg & Ellner 2001; Boyce *et al.* 2006), leading the age structure to change
85 from year to year as well (Coulson, Rohani & Pascual 2004). Consequently, in a stochastic
86 world, the change in a demographic parameter impacts population growth using two different
87 pathways. As observed in the deterministic context, changing a demographic parameter has a
88 direct effect on population growth rate. In addition, in a stochastic world, changing a

89 demographic parameter will also lead to change the age structure, which will have an indirect
90 effect on population growth rate. The total impact of changing a demographic rate on
91 population growth thus corresponds to the sum of these direct and indirect effects (Haridas,
92 Tuljapurkar & Coulson 2009).

93 How to calculate these two components has been shown by Haridas *et al.* (2009) using red
94 deer as an illustration. As expected for a long-lived species like red deer, which displays only
95 little temporal variation in most demographic parameters (Benton & Grant 1996), Haridas *et*
96 *al.* (2009) found that most changes in population growth were generated by the direct effects
97 of changing demographic parameters, with very little influence of indirect effects of changing
98 age structure despite clear observed variation in age structure among years (Coulson *et al.*
99 2004). This pioneer study left several questions unanswered. In particular, whether the
100 relative contribution of direct and indirect effects of changing a demographic parameter on
101 population growth rate is constant or varies among species with contrasted life histories
102 remains unknown. In this study, we aim to answer this question by quantifying the relative
103 contribution of direct and indirect effects of changing a parameter on population growth in a
104 range of mammalian populations with contrasted life histories.

105 More specifically, we looked for the influence of generation time. This metric provides a
106 suitable measure of the ranking of a species on the so-called slow-fast continuum (Gaillard *et*
107 *al.* 2005) that opposes species with an early maturity, a high fecundity, and a short life span to
108 species with opposite characteristics (Eisenberg 1981; Gaillard *et al.* 1989; Read & Harvey
109 1989; Promislow & Harvey 1990). A different contribution of direct and indirect effects of
110 changing a demographic parameter on population growth can indeed be expected among
111 mammals with contrasting pace of life. In populations with a short generation time that live
112 on the fast line, the contribution of indirect effects on population growth rate via changes in
113 age structure is expected to be higher than in populations with a long generation time that live

114 on the slow line. Increasing the proportion of juveniles in a population with a short generation
115 time is then expected to influence population growth rate to a larger extent than doing the
116 same in a population with a long generation time. To test this hypothesis, we measured the
117 elasticity patterns in 14 populations belonging to 11 mammalian species with contrasting life
118 histories.

119

120

121

122

123

124

125

126

127

128

129

130

131

132

133 **Materials and methods**

134 TRANSITION MATRICES

135 We gathered yearly estimates of age-specific survival and reproduction from 14 populations
136 belonging to 11 mammalian species (Table 1) ranging widely along the fast-slow continuum
137 of life-history tactics (Gaillard *et al.* 2005). For each population, estimates of demographic
138 parameters were integrated in a female age-structured population model (Caswell 2001) based
139 on year-specific matrices. We considered a pre-breeding census model (see matrices in
140 Appendix S1). For the mountain goat *Oreamnos americanus* for example, ten age-classes
141 were used to describe its life cycle (Festa-Bianchet & Côté 2008). The first age class
142 corresponded to individuals of 1 year of age, the second age class to individuals of 2 years of
143 age, the third age class to individuals of 3 years of age... and the tenth age class to individuals
144 older than 10 years of age. The transition matrix for a given year t took thus the following
145 form:

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

146

147 with R corresponding to age class-specific recruitment and S corresponding to age class-
 148 specific survival. From the transition matrix A_t at time 1, we calculated the stable age
 149 distribution denoted W_0 . Then, for each year t , the vector of age distribution W_t was calculated
 150 such as $W_t = A_t * W_{t-1}$, then normalized (i.e., whose elements add to 1).

151 From a biological viewpoint, we defined three life history stages, with yearling survival (Ψ_1);
 152 survival of immature individuals (Ψ_2) older than 2 years that were not yet able to reproduce
 153 (this parameter corresponded to a different number of years depending on the life cycle of the
 154 species, going from 0 when yearling were able to reproduce (like eg., wild boar) to 8 years in
 155 primates for which females do not reproduce before 9 years of age); and adult survival (Ψ_3)
 156 corresponding to individuals that are able to reproduce (see matrices in Appendix S1). For
 157 example, for the mountain goat, the transition matrix for a given year t took thus the following
 158 form:

$$\begin{pmatrix} 0 & 0 & R & R & R & R & R & R & R & R \\ \Psi_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \Psi_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \Psi_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \Psi_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \Psi_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \Psi_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \Psi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \Psi_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \Psi_3 & \Psi_3 \end{pmatrix}$$

159
 160 Moreover, for each population, we calculated generation time Tb , which corresponds to the
 161 mean age of the mothers at childbirth in the population and is defined as $Tb = \sum_i i * S_i * m_i *$

162 λ^{-i} with S_i the probability of surviving from birth to age i , m_i the number of offspring females
163 born to a female of age i and λ the asymptotic growth rate (Leslie 1966). For each population,
164 we also took the information about the age at first reproduction into account and estimated
165 adult survival as the mean survival of individuals from the age at first reproduction onwards
166 Ψ_3 .

167

168 ELASTICITIES ESTIMATES

169 From these transition matrices, we measured both the direct effect of changing a demographic
170 rate on population growth (denoted $e_{R,t}$) and the indirect effect via changes in age-structure
171 (denoted $e_{U,t}$) (Table 2) using the procedure described by Haridas *et al.* (2009) in Matlab
172 (Matlab version 7.11 2011). Haridas *et al.* (2009) defined annual elasticities E_t as the sum of
173 $e_{R,t}$ and $e_{U,t}$. Here, we defined global elasticities E_t' as the sum of $e_{R,t}$ and $|e_{U,t}|$ as $e_{U,t}$ could be
174 positive or negative.

175 We thus estimated $e_{R,t}$ and E_t' for Ψ_1 and Ψ_3 only (i.e., not for Ψ_2) because this last stage
176 was not present in some species that did reproduce as yearling. More precisely, for Ψ_1 , we
177 estimated the mean of $e_{R,t}$ and the mean of E_t' over the course of the study for the yearling
178 survival (Ψ_1). We calculated the ratio between the mean of $e_{R,t}$ and the mean of E_t' to
179 measure the relative contribution of the direct effects on population growth (i.e., caused by
180 changing the focal demographic parameter). The division by E_t' took into account the fact that
181 total elasticity of Ψ_1 could differ from one species to another. Consequently, the division by
182 E_t' provided a way to standardize the measure of the contribution among different life
183 histories, and thereby allowed comparing of the contribution of direct effects among
184 populations with contrasted life histories. We performed the same analysis on survival of

185 matures (Ψ_3) by summing $e_{R,t}$ (respectively $E_{t'}$) of all the matrix elements containing Ψ_3 for
186 each time t . Then, we estimated the mean of $e_{R,t}$ and the mean of $E_{t'}$ over the course of the
187 study for Ψ_3 and calculated the ratio between these two means (i.e., the ratio $e_{R,t}/E_{t'}$).

188

189 THE ROLE OF GENERATION TIME AND ITS COMPONENTS ON STOCHASTIC 190 ELASTICITY PATTERNS

191 To test a potential influence of generation time and its components on the relative
192 contribution of direct effect of changing a demographic parameter on population growth, we
193 assessed the relationship between the species-specific ratio between $e_{R,t}$ and $E_{t'}$ and generation
194 time, for both yearling and adult survival which correspond to Ψ_1 and Ψ_3 . We also assessed
195 the relationship between the species-specific ratio between $e_{R,t}$ and $E_{t'}$ and the two biological
196 components of generation time, namely survival and reproduction. We used adult survival and
197 age at first reproduction, respectively, to analyze these components. Our choice was
198 motivated by the current state of art of our knowledge of life history evolution. A slower life
199 history, characterized by a long generation time, is commonly associated with delayed
200 reproduction and high adult survival (Stearns 1992), and both age at first reproduction (Cole
201 1954) and adult survival (Charnov 1986) have been shown to play a major role in shaping life
202 history strategies. To be expressed as a biological time, adult survival was logit-transformed
203 and interpreted as a life expectancy expressed in years (Stearns 1983, Gaillard *et al.* 1989).
204 Generation time and age at first reproduction are already biological times expressed in years
205 and therefore were only log-transformed in the analyses to satisfy the rules of allometry
206 (Houle *et al.* 2011).

207 In addition, for each population, we studied the sign of the average $e_{U,t}$ corresponding to the
208 component of stochastic elasticity due to change in population structure (i.e., the indirect

209 effect). When $e_{U,t}$ is in average positive, the change in population structure resulting for a
210 change in a demographic parameter leads to a positive contribution to population growth rate.
211 On the contrary, when $e_{U,t}$ is in average negative, the change in population structure resulting
212 for a change in a demographic parameter leads to a negative contribution to population
213 growth rate.

214 These analyses were performed with R 2.12.2 (R Development Core Team 2011).

215

216

217

218

219

220

221

222

223

224

225

226

227

228 **Results**

229 THE ROLE OF GENERATION TIME, AGE AT FIRST REPRODUCTION AND LIFE 230 EXPECTANCY ON STOCHASTIC ELASTICITY PATTERNS

231 A large range of generation time, age at first reproduction and adult survival was observed
232 across mammalian species included in the analyses (Table 1). The relationship between the
233 ratio $e_{R,t} / E_t$ for yearling survival ψ_l and generation time (on a log-scale) (Fig. 1a) showed
234 the longer the generation time, the lower the ratio $e_{R,t} / E_t$ (slope= -0.062 (SE: 0.0139), p-
235 value \ll 0.01) meaning that the relative contribution of $e_{R,t}$ to the population growth rate
236 decreases with the generation time. The relationship between the ratio $e_{R,t} / E_t$ for yearling
237 survival ψ_l and age at first reproduction (on a log-scale) (Fig. 2a) showed the later the age at
238 first reproduction, the lower the ratio $e_{R,t} / E_t$ (slope= -0.060 (SE: 0.0138), p-value \ll 0.01)
239 meaning that the relative contribution of $e_{R,t}$ to the population growth rate decreases with the
240 age at first reproduction. Finally, the relationship between the ratio $e_{R,t} / E_t$ for yearling
241 survival ψ_l and life expectancy (i.e., adult survival on a logit-scale) (Fig. 3a) showed the
242 higher the life expectancy, the lower the ratio $e_{R,t} / E_t$ (slope= -0.038 (SE: 0.0148), p-value=
243 0.025) meaning that the relative contribution of $e_{R,t}$ to the population growth rate decreases
244 with the life expectancy.

245 By studying the sign of the average $e_{U,t}$ allows distinguishing two groups of species. A first
246 group of species characterized by a fast pace of life, with a short generation time, an early age
247 at first reproduction, and a low adult survival, had a positive $e_{U,t}$ on average for yearling
248 survival ψ_l . For these species, the change in population structure resulting from a change in
249 yearling survival leads to a positive contribution to population growth rate. The second group
250 of species were characterized by a slow pace of life, with a long generation time, a late age at
251 first reproduction and a high adult survival, had a negative $e_{U,t}$ on average yearling

252 survival Ψ_1 . For these species, the change in population structure resulting for a change in a
253 yearling survival leads to a negative contribution to population growth rate.

254 No relationship was found between the ratio $e_{R,t} / E_t$ for adult survival Ψ_3 and generation
255 time (on a log-scale) (Fig. 1b), age at first reproduction (on a log-scale) (Fig. 2b) and life
256 expectancy (Fig. 3b). For all species, the relative contribution of $e_{R,t}$ to the population growth
257 rate is thus similar. By studying the sign of the average $e_{U,t}$, we found that all species had a
258 positive $e_{U,t}$ on average for adult survival Ψ_3 irrespective of their pace of life, except red
259 squirrel that exhibited a negative $e_{U,t}$ on average. On average, for all species except red
260 squirrel, the change in population structure resulting from a change in adult survival leads to a
261 positive contribution to population growth rate.

262

263

264

265

266

267

268

269

270

271

272 **Discussion**

273 STOCHASTIC VS. DETERMINISTIC ELASTICITIES

274 Classically, in demographic analyses, deterministic elasticity are used to quantify the effect on
275 population growth rate of a proportional change in a given fitness component (de Kroon *et al.*
276 1986). For species characterized by a fast pace of life, elasticity of yearling survival is
277 generally higher than that of adult survival. For instance, in a heavily hunted wild boar
278 population characterized by a short generation time of 2.3 years, elasticity of yearling survival
279 is higher than that of adult survival (Servanty *et al.* 2011; Gamelon *et al.* 2011), meaning that
280 population growth rate in fast species is much more sensitive to a given variation in yearling
281 survival than to the same relative variation in adult survival. On the contrary, in large
282 herbivores, i.e. for species characterized by a slow pace of life, these deterministic analyses
283 reveal that the elasticity of adult survival is higher than that of yearling survival (Gaillard *et*
284 *al.* 2000). For these species, adult survival thus drives the demography of the population.
285 Indeed, in ungulate females for instance, females skip a reproductive event instead of
286 jeopardizing their own survival (Gaillard & Yoccoz 2003). Population growth rate in slow
287 species is much more sensitive to a given variation in adult survival than to the same relative
288 variation in yearling survival.

289 These deterministic elasticities usually estimated in demographic analyses, are based on the
290 average transition matrix and correspond to $e_{R,t}$, the direct effect of changing a given
291 demographic parameter on population growth rate. Nevertheless, in stochastic environments,
292 demographic parameters fluctuate from year to year. In the bighorn sheep population of Sheep
293 River for instance (Coulson *et al.* 2005), adult survival is variable from year to year because
294 of pneumonia and predation (Festa-Bianchet 1988; Jorgenson *et al.* 1997; Ross *et al.* 1997),
295 leading to change in the age structure. In addition to $e_{R,t}$, stochastic elasticity allows estimating

296 $e_{U,t}$, the indirect effect of changing a given demographic parameter on population growth rate,
297 via the change in population structure. Analyses of stochastic elasticity thus improve our
298 understanding of population dynamics in fast and slow species in a stochastic world.

299

300 FAST SPECIES AND STOCHASTIC ELASTICITY PATTERNS

301 The mean ratio $e_{R,t} / E_t$ provided a simple metric to evaluate the relative contribution of the
302 direct effects of changing a given demographic parameter on population growth rate, which is
303 standardized across species when life cycle are defined on a similar basis. For species
304 characterized by a fast pace of life, increasing yearling survival ψ increased the proportion
305 of yearlings in the population that are able to recruit, as for instance in wild boar being able to
306 reproduce at 1 year of age (Servanty *et al.* 2011). Consequently, the change in population
307 structure resulting from a change in yearling survival leads to a positive contribution to
308 population growth rate.

309

310 SLOW SPECIES AND STOCHASTIC ELASTICITY PATTERNS

311 On the contrary, for species characterized by a slow pace of life, increasing yearling survival
312 ψ increased the proportion of yearlings in these slow populations as it does in fast ones, but
313 individuals will not recruit before 3 years of age or more. For instance, in the white rhinoceros
314 *Ceratotherium simens*, reproduction starts at 6 years of age (Owen-Smith 1988).
315 Consequently, increasing yearling survival in rhinoceros would increase the population
316 growth rate only via direct way, because individuals less than 1 year of age are not able to
317 reproduce thus explaining why $e_{U,t}$ was negative for slow species. In other words, the change
318 in population structure due to an increase of yearling survival will negatively contribute to

319 population growth rate for species characterized by a slow pace of life. More precisely, the
320 slower the species, the stronger the negative contribution of indirect effect due to change in
321 yearling survival on population growth rate. This result provides further support for the theory
322 of “malediction of long-lived species” (Lebreton 2006) predicting higher extinction rates for
323 long-lived species.

324

325 The relative contribution of direct vs. indirect effects of changing adult survival ψ_3 on
326 population growth was not associated with either generation time, age at first reproduction, or
327 life expectancy. Irrespective of their pace of life, all species but red squirrel showed identical
328 relative contributions of direct vs. indirect effects of changing adult survival on population
329 growth. Increasing ψ_3 in a given population increased the proportion of adult individuals that
330 are able to reproduce. Consequently, the contribution of indirect effect of an increase of adult
331 survival to long-term population growth was positive. In the same way, decreasing survival of
332 prime-aged females will lead to decrease the population growth rate by the direct way but also
333 by the indirect way and such a decrease could thus affect population viability. As already
334 reported, size-selective harvesting, where the largest and thus the prime-aged individuals are
335 preferentially taken, in both marine and terrestrial habitats can affect the demography of
336 populations (Fenberg & Roy 2008). This analysis of stochastic elasticity patterns provides
337 further support of that size-selective harvesting can negatively influence the demography of
338 populations irrespective of their pace of life.

339

340

341

342 **Acknowledgments**

343 This work was supported by the French National Agency for Wildlife (ONCFS). We warmly
344 thank Rob Salguero-Gómez and Douglas Morris for their helpful comments on a previous
345 draft.

346

347

348 **References**

- 349 Benton, T. G. & Grant, A. (1996) How to keep fit in the real world: Elasticity analyses and
350 selection pressures on life histories in a variable environment. *American Naturalist*, **147**, 115–
351 139.
- 352 Boyce, M. S., Haridas, C. V., Lee, C. T., Boggs, C., Bruna, E. & Coulson, T. (2006)
353 Demography in an increasingly variable world. *Trends in Ecology & Evolution*, **21**, 141–148.
- 354 Caswell, H. (2001) Matrix population models. 2nd ed. Sinauer, MA.
- 355 Charnov, E. L. (1986) Life history evolution in a "recruitment population": Why are adult
356 mortality rates constant? *Oikos*, **47**, 129–134.
- 357 Cole, L. M. C. (1954) Some features of random population cycles. *The Journal of Wildlife*
358 *Management*, **18**, 2–24.
- 359 Coulson, T., Gaillard, J.-M. & Festa-Bianchet, M. (2005) Decomposing the variation in
360 population growth into contributions from multiple demographic rates. *Journal of Animal*
361 *Ecology*, **74**, 789–801.
- 362 Coulson, T., Kruuk, L. E. B., Tavecchia, G., Pemberton, J. M. & Clutton-Brock, T. H. (2003)
363 Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, **57**,
364 2879–2892.
- 365 Coulson, T., Rohani, P. & Pascual, M. (2004) Skeletons, noise and population growth: the end
366 of an old debate? *Trends in Ecology & Evolution*, **19**, 359–364.
- 367 Descamps, S. (2006) Stratégies d’histoire de vie dans une population d’écureuils roux
368 d’Amérique du Nord. Master’s thesis, Université du Québec à Rimouski - Université Claude

- 369 Bernard Lyon 1.
- 370 Eisenberg, J.F. (1981) *The Mammalian Radiation*. Athlone Press, London.
- 371 Fenberg, P. B. & Roy, K. (2008) Ecological and evolutionary consequences of size-selective
372 harvesting: how much do we know? *Molecular Ecology*, **17**, 209-220.
- 373 Festa-Bianchet, M. (1988) A pneumonia epizootic in bighorn sheep, with comments on
374 preventive management. *Proceedings of the Northern Wild Sheep and Goat Council*, **6**, 66-76.
- 375 Festa-Bianchet, M. & Côté, S. D. (2008) *Mountain goats: ecology, behavior, and conservation*
376 of an alpine ungulate. Island Press, Washington, DC.
- 377 Fieberg, J. & Ellner, S. P. (2001) Stochastic matrix models for conservation biology: a
378 comparative review of methods. *Ecology Letters*, **4**, 244–266.
- 379 Gaillard, J.-M., Yoccoz, N. G., Lebreton, J.-D., Bonenfant, C., Devillard, S., Loison, A.,
380 Pontier, D. & Allaine, D. (2005) Generation time: A reliable metric to measure life-history
381 variation among mammalian populations. *American Naturalist*, **166**, 119–123.
- 382 Gaillard, J.-M., Pontier, D., Allaine, D., Lebreton, J.D., Trouvilliez, J. & Clobert, J. (1989) An
383 analysis of demographic tactics in birds and mammals. *Oikos*, **56**, 59–76.
- 384 Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toïgo, C. (2000) Temporal
385 variation in fitness components and population dynamics of large herbivores. *Annual Review*
386 *of Ecological Systems*, **31**, 367-393.
- 387 Gaillard, J.-M. & Yoccoz, N. G. (2003) Temporal variation in survival of mammals: a case of
388 environmental canalization? *Ecology*, **84**, 3294-3306.
- 389 Gamelon, M., Besnard, A., Gaillard, J.-M., Servanty, S., Baubet, E., Brandt, S. & Gimenez,

390 O. (2011) High hunting pressure selects for earlier birth date: wild boar as a case study.
391 *Evolution*, **65**, 3100–3112.

392 Haridas, C. V., Tuljapurkar, S. & Coulson, T. (2009) Estimating stochastic elasticities directly
393 from longitudinal data. *Ecology letters*, **12**, 806–812.

394 Houle, D., Pélabon, C., Wagner, G. P. & Hansen, T. (2011) Measurement and meaning in
395 biology. *The Quarterly Review of Biology*, **86**, 3–34.

396 Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J. M. & Wishart, W. D. (1997) Effects of age,
397 sex, disease, and density on survival of bighorn sheep. *Ecology*, **78**, 1019–1032.

398 de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. (1986) Elasticity: the relative
399 contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.

400 de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: A review of methods and
401 model limitations. *Ecology*, **81**, 607–618.

402 Lebreton, J.-D. (2006) Dynamical and statistical models of vertebrate population dynamics.
403 *Comptes Rendus Biologies*, **329**, 804–812.

404 Leslie, P. H. (1966) The intrinsic rate of increase and the overlap of successive generations in
405 a population of guillemots (*Uria aalge pont.*). *Journal of Animal Ecology*, **35**, 291–301.

406 Matlab version 7.11 2011. The Mathworks. Nantick, Massachusetts, USA.

407 Morris, W. F., Altmann, J., Brockman, D. K., Cords, M., Fedigan, L. M., Pusey, A. E.,
408 Stoinski, T. S., Bronikowski, A. M., Alberts, S. C. & Strier, K. B. (2011) Low demographic
409 variability in wild primate populations: fitness impacts of variation, covariation, and serial
410 correlation in vital rates. *The American Naturalist*, **177**, E14–E28.

411 Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S.,
412 Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F. *et al.* (2008) Longevity can buffer plant
413 and animal populations against changing climatic variability. *Ecology*, **89**, 19–25.

414 Owen-Smith, R. N. (1988) Megaherbivores: the influence of very large body size on ecology.
415 Cambridge: Cambridge University Press.

416 Promislow, D.E.L. & Harvey, P.H. (1990) Living fast and dying young: a comparative
417 analysis of life-history variation among mammals. *Journal of Zoology*, **220**, 417–437.

418 R Development Core Team 2011. R: A language and environment for statistical computing. R
419 Foundation for Statistical Computing, Vienna, Austria.

420 Read, A.F. & Harvey, P.H. (1989) Life-history differences among the eutherian radiations.
421 *Journal of Zoology*, **219**, 329–353.

422 Ross, P. I., Jalkotzy, M. G. & Festa-Bianchet, M. (1997) Cougar predation on bighorn sheep
423 in southwestern Alberta during winter. *Canadian Journal of Zoology*, **75**, 771–775.

424 Servanty, S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baubet, E. & Gimenez, O. (2011)
425 Influence of harvesting pressure on demographic tactics: implications for wildlife
426 management. *Journal of Applied Ecology*, **48**, 835–843.

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

429 Stearns, S. C. (1992) The evolution of life histories. vol. 248. Oxford University Press
430 Oxford.

431 van Tienderen, P. H. (2000) Elasticities and the link between demographic and evolutionary

432 dynamics. *Ecology*, **81**, 666–679.

433 Tuljapurkar, S. (1989) An uncertain life: Demography in random environments. *Theoretical*

434 *Population Biology*, **35**, 227–294.

435

436

437

438

439

440

441

442 **Tables**443 **Table 1.** Mammal populations for which yearly estimates of age-specific survival and reproduction were available and their associated

444 generation time, age at first reproduction (in years) and adult survival. Two different populations of roe deer (1: Trois-Fontaines and 2: Chizé)

445 and bighorn sheep (1: Ram Mountain and 2: Sheep River) were included in the analyses.

Population	Study period	Reference	Generation time	Age at first reproduction	Adult survival
1. Wild boar (<i>Sus scrofa scrofa</i>)	1983-2005	This study	2.65	1	0.458
2. Red squirrel (<i>Tamiasciurus hudsonicus</i>)	1990-2003	Descamps <i>et al.</i> 2006	2.86	1	0.512
3. Roe deer 1 (<i>Capreolus capreolus</i>)	1985-1998	Gaillard <i>et al.</i> 2003	4.33	2	0.899
4. Roe deer 2 (<i>Capreolus capreolus</i>)	1985-1998	Gaillard <i>et al.</i> 2003	5.21	2	0.923
5. Bighorn sheep 1 (<i>Ovis Canadensis</i>)	1980-1995	Coulson, Gaillard & Festa-Bianchet 2005	7.55	2	0.926
6. Bighorn sheep 2 (<i>Ovis Canadensis</i>)	1983-1997	Coulson, Gaillard & Festa-Bianchet 2005	7.72	2	0.896
7. Mountain goat (<i>Oreamnos americanus</i>)	1992-2002	Festa-Bianchet & Côté 2008	8.75	3	0.933
8. Yellow baboon (<i>Papio cynocephalus</i>)	1971-2007	Morris <i>et al.</i> 2011	16.45	7	0.920
9. Blue monkey (<i>Cercopithecus mitis stuhlmanni</i>)	1980-2007	Morris <i>et al.</i> 2011	18.05	8	0.952
10. Northern muriqui (<i>Brachyteles hypoxanthus</i>)	1983-2007	Morris <i>et al.</i> 2011	22.07	9	0.969
11. White-faced capuchin monkey (<i>Cebus capucinus</i>)	1986-2007	Morris <i>et al.</i> 2011	22.88	7	0.943
12. Verreaux's sifaka (<i>Propithecus verreauxi</i>)	1984-2007	Morris <i>et al.</i> 2011	23.69	7	0.928
13. Mountain gorilla (<i>Gorilla beringei beringei</i>)	1967-2007	Morris <i>et al.</i> 2011	30.48	11	0.975
14. Eastern chimpanzee (<i>Pan troglodytes schweinfurthii</i>)	1963-2007	Morris <i>et al.</i> 2011	40.48	16	0.951

446

447

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

Parameters	Biological meaning
$e_{R,t}$	Component of stochastic elasticity due to change in the demographic parameters: measure of the direct effect of changing a given demographic parameter on population growth rate
$e_{U,t}$	Component of stochastic elasticity due to change in population structure: measure of the indirect effect of changing a given demographic parameter on population growth rate
E_t	Global elasticity corresponding to the sum of $e_{R,t}$ and $ e_{U,t} $
ψ_1	Yearling survival, i.e. survival of individuals between 1 and 2 years of age
ψ_2	Survival of immature individuals, i.e. yearly survival of individuals, older than 2 years that are not yet able to reproduce
ψ_3	Adult survival, i.e. yearly survival of individuals older than 2 years that are able to reproduce

449

450 **Figure legends**

451 **Figure 1.** Relationship between the ratio $e_{R,t} / E_t$ (with $E_t = e_{R,t} + |e_{U,t}|$) and generation time
452 (on a log-scale) for the 14 populations displayed in Table 1 for **(a)** yearling survival Ψ_1 ; **(b)**
453 adult survival Ψ_3 . Filled circles correspond to a negative average $e_{U,t}$, closed circles
454 correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the populations
455 displayed in Table 1.

456 **Figure 2.** Relationship between the ratio $e_{R,t} / E_t$ (with $E_t = e_{R,t} + |e_{U,t}|$) and the age at first
457 reproduction (on a log-scale) for the 14 populations displayed in Table 1 for **(a)** yearling
458 survival Ψ_1 ; **(b)** adult survival Ψ_3 . Filled circles correspond to a negative average $e_{U,t}$, closed
459 circles correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the
460 populations displayed in Table 1.

461 **Figure 3.** Relationship between the ratio $e_{R,t} / E_t$ (with $E_t = e_{R,t} + |e_{U,t}|$) and the adult survival
462 (on the logit-scale) for the 14 populations displayed in Table 1 for **(a)** yearling survival Ψ_1 ;
463 **(b)** adult survival Ψ_3 . Filled circles correspond to a negative average $e_{U,t}$, closed circles
464 correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the populations
465 displayed in Table 1.

466

467

468

469

470

471 **Fig. 1.**

472

(a)

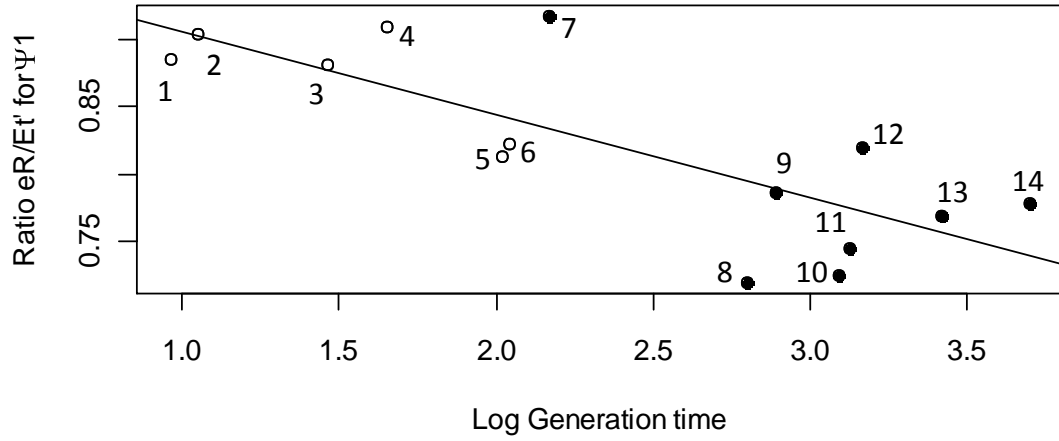
473

474

475

476

477



478

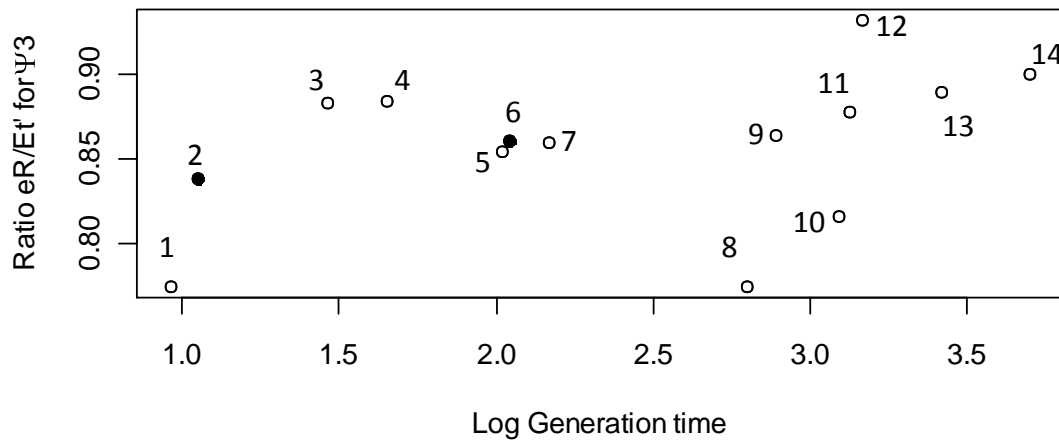
(b)

479

480

481

482



483

484

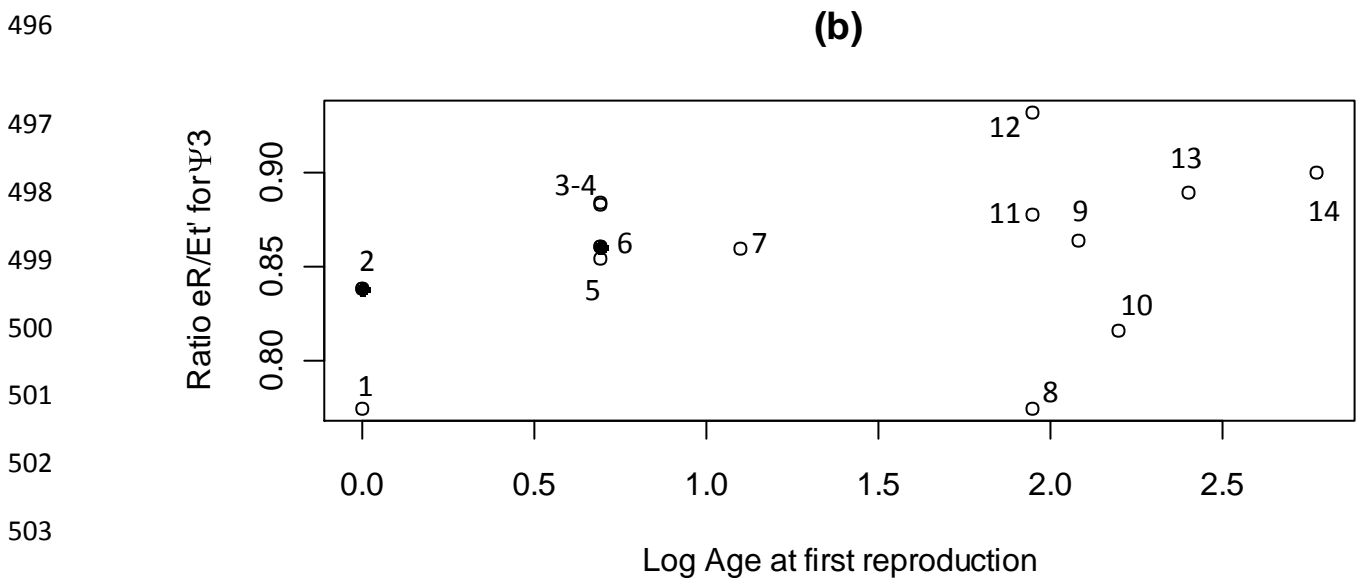
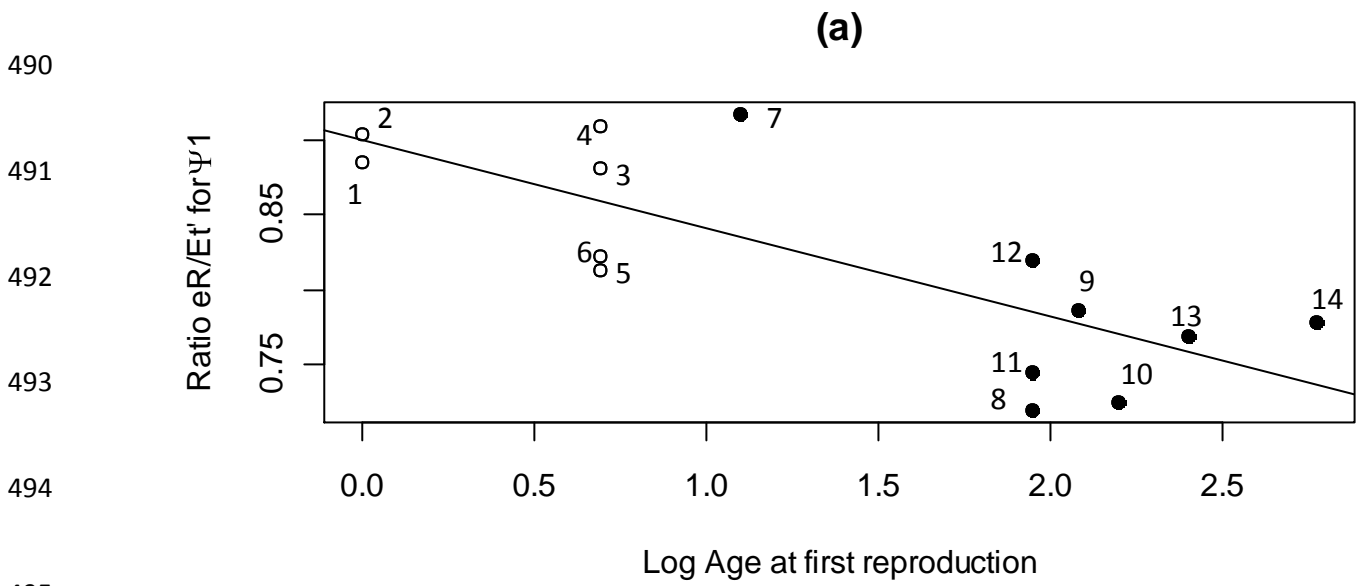
485

486

487

488

489 Fig. 2.



508 **Fig. 3.**

509

510

511

512

513

514

515

516

517

518

519

520

521

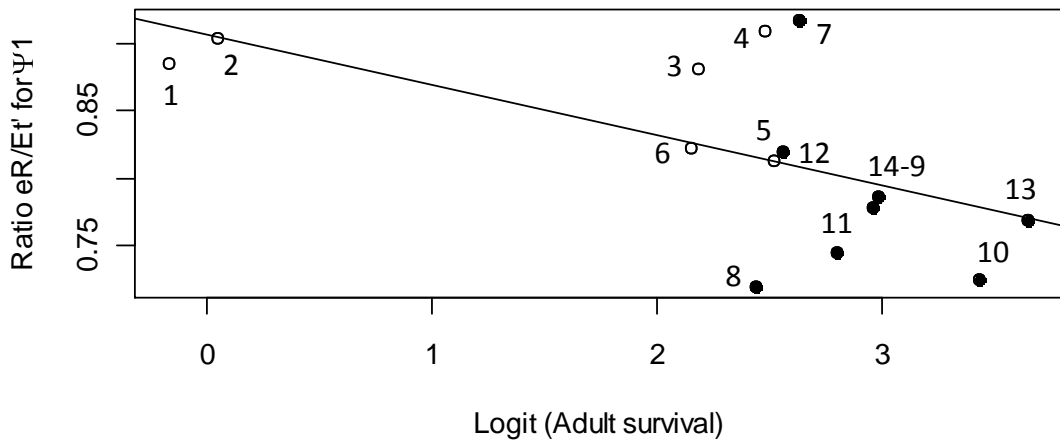
522

523

524

525

(a)



(b)

