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

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

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

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## 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.

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

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## 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.

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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:

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

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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 ( $\Psi_1$ );  
 152 survival of immature individuals ( $\Psi_2$ ) 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 ( $\Psi_3$ )  
 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:

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

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  $\lambda^{-i}$  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  $\lambda$  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  $\Psi_3$ .

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## 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  $\Psi_1$  and  $\Psi_3$  only (i.e., not for  $\Psi_2$ ) because this last stage  
176 was not present in some species that did reproduce as yearling. More precisely, for  $\Psi_1$ , 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 ( $\Psi_1$ ). 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  $\Psi_1$  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 ( $\Psi_3$ ) by summing  $e_{R,t}$  (respectively  $E_{t'}$ ) of all the matrix elements containing  $\Psi_3$  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  $\Psi_3$  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  $\Psi_1$  and  $\Psi_3$ . 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).

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## 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  $\psi_l$  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  $\psi_l$  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  $\psi_l$  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  $\psi_l$ . 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  $\psi_1$ . 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  $\psi_3$  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  $\psi_3$  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.

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## 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.

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#### 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  $\psi$  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.

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#### 310 SLOW SPECIES AND STOCHASTIC ELASTICITY PATTERNS

311 On the contrary, for species characterized by a slow pace of life, increasing yearling survival  
312  $\psi$  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  $\psi_3$  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  $\psi_3$  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.

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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

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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} $
$\psi_1$	Yearling survival, i.e. survival of individuals between 1 and 2 years of age
$\psi_2$	Survival of immature individuals, i.e. yearly survival of individuals, older than 2 years that are not yet able to reproduce
$\psi_3$	Adult survival, i.e. yearly survival of individuals older than 2 years that are able to reproduce

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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  $\Psi_1$ ; **(b)**  
453 adult survival  $\Psi_3$ . 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  $\Psi_1$ ; **(b)** adult survival  $\Psi_3$ . 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  $\Psi_1$ ;  
463 **(b)** adult survival  $\Psi_3$ . 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.

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471 **Fig. 1.**

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(a)

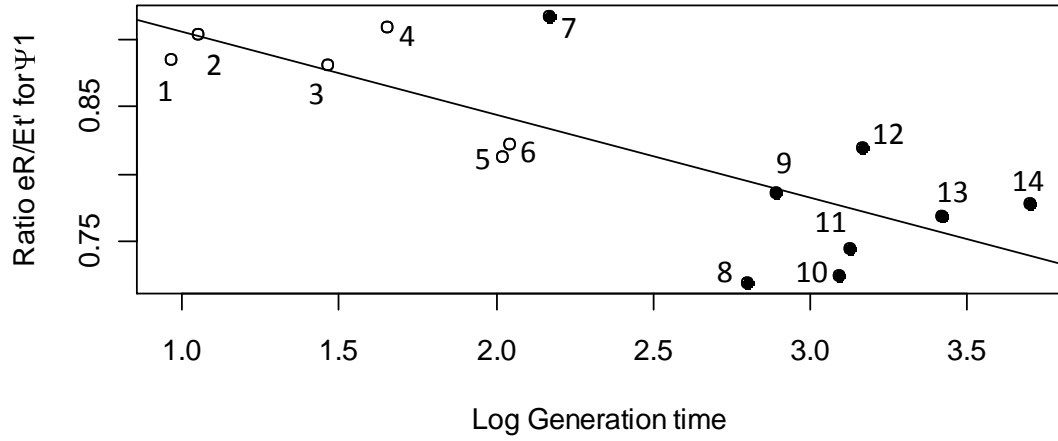
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(b)

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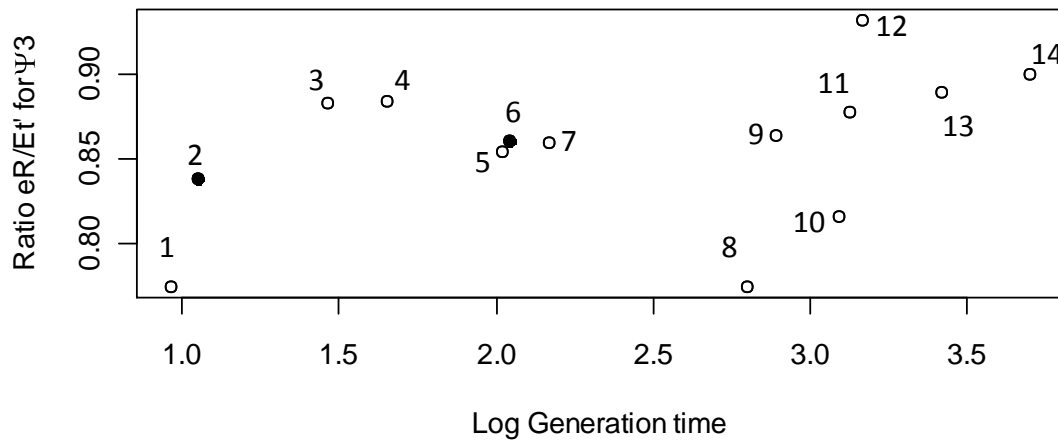
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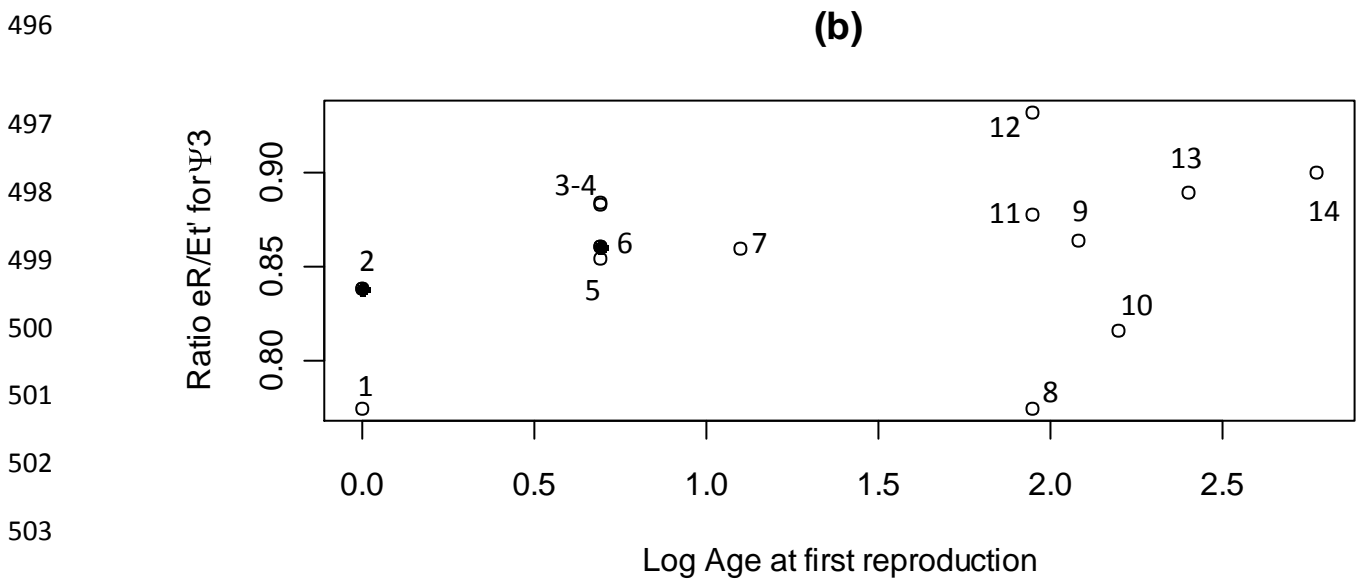
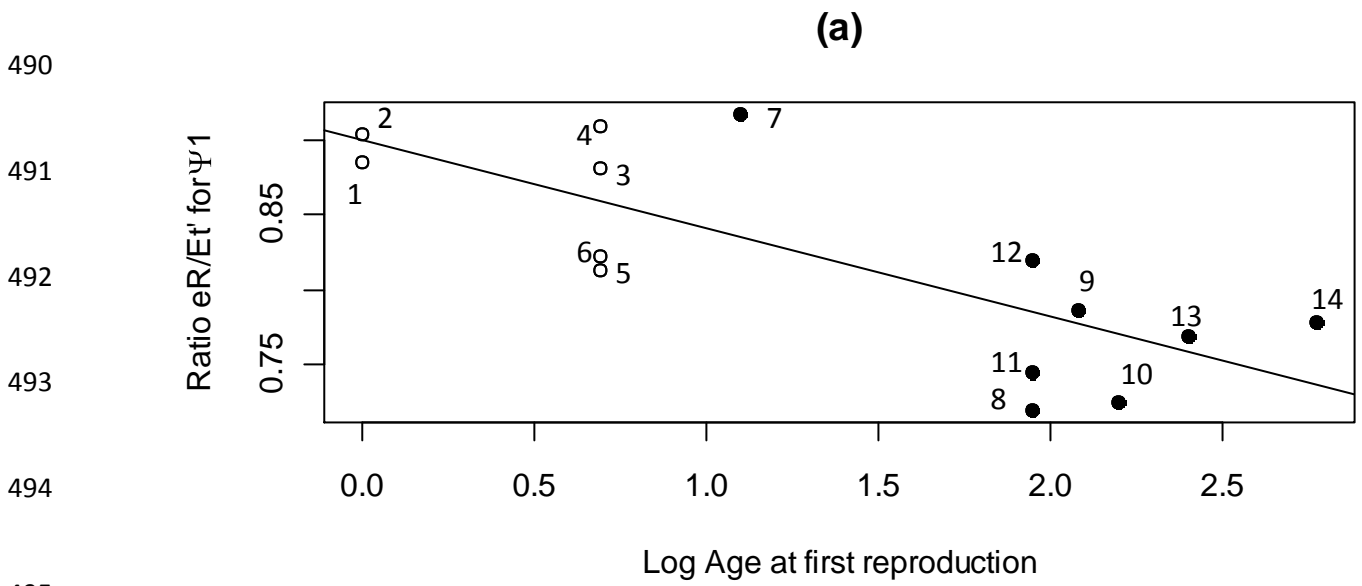
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489 **Fig. 2.**



508 **Fig. 3.**

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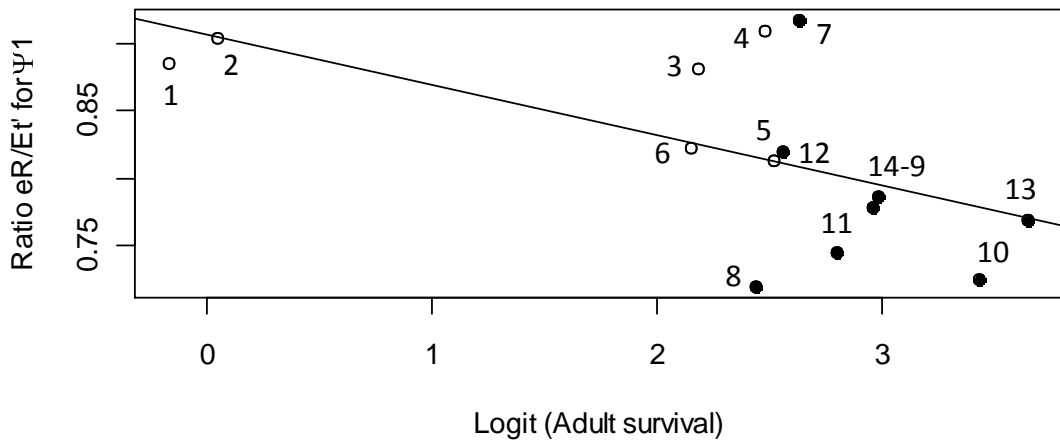
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(a)



(b)

