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

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Running headline: Stochastic elasticity and life history

Summary

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

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

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

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

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

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

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

Introduction

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

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 single transition matrix only includes the mean values of demographic parameters estimated throughout the study period. The elasticity of each parameter in the average transition matrix then measures the relative change in population growth rate resulting from a very small relative change in the parameter. However, lots of studies have pointed out that including temporal variation in demographic parameters can change the picture (Tuljapurkar 1989; Boyce *et al.* 2006; Morris *et al.* 2008; Morris *et al.* 2011). In stochastic environments, demographic parameters fluctuate from year to year so that the transition matrix changes from year to year (Fieberg & Ellner 2001; Boyce *et al.* 2006), leading the age structure to change from year to year as well (Coulson, Rohani & Pascual 2004). Consequently, in a stochastic world, the change in a demographic parameter impacts population growth using two different pathways. As observed in the deterministic context, changing a demographic parameter has a 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

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

Materials and methods

TRANSITION MATRICES

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

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

147 with *R* corresponding to age class-specific recruitment and *S* corresponding to age class-
148 specific survival. From the transition matrix A_1 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:

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

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 $Tb = \sum_i i * Si * mi *$

λ^{-i} with Si the probability of surviving from birth to age i, mi the number of offspring females born to a female of age i and λ the asymptotic growth rate (Leslie 1966). For each population, we also took the information about the age at first reproduction into account and estimated adult survival as the mean survival of individuals from the age at first reproduction onwards $\Psi 3$.

ELASTICITIES ESTIMATES

From these transition matrices, we measured both the direct effect of changing a demographic rate on population growth (denoted $e_{R,t}$) and the indirect effect via changes in age-structure (denoted $e_{U,t}$) (Table 2) using the procedure described by Haridas *et al.* (2009) in Matlab (Matlab version 7.11 2011). Haridas *et al.* (2009) defined annual elasticities E_t as the sum of $e_{R,t}$ 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 positive or negative.

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 was not present in some species that did reproduce as yearling. More precisely, for $\Psi 1$, we estimated the mean of $e_{R,t}$ and the mean of $E_{t'}$ over the course of the study for the yearling survival ($\Psi 1$). We calculated the ratio between the mean of $e_{R,t}$ and the mean of $E_{t'}$ to measure the relative contribution of the direct effects on population growth (i.e., caused by changing the focal demographic parameter). The division by $E_{t'}$ took into account the fact that total elasticity of $\Psi 1$ could differ from one species to another. Consequently, the division by $E_{t'}$ provided a way to standardize the measure of the contribution among different life histories, and thereby allowed comparing of the contribution of direct effects among populations with contrasted life histories. We performed the same analysis on survival of

matures ($\Psi 3$) by summing $e_{R,t}$ (respectively $E_{t'}$) of all the matrix elements containing $\Psi 3$ for each time t. Then, we estimated the mean of $e_{R,t}$ and the mean of $E_{t'}$ over the course of the study for $\Psi 3$ and calculated the ratio between these two means (i.e., the ratio $e_{R,t}/E_{t'}$).

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

To test a potential influence of generation time and its components on the relative contribution of direct effect of changing a demographic parameter on population growth, we assessed the relationship between the species-specific ratio between $e_{R,t}$ and $E_{t'}$ and generation time, for both yearling and adult survival which correspond to $\Psi 1$ and $\Psi 3$. We also assessed the relationship between the species-specific ratio between $e_{R,t}$ and $E_{t'}$ and the two biological components of generation time, namely survival and reproduction. We used adult survival and age at first reproduction, respectively, to analyze these components. Our choice was motivated by the current state of art 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. To be expressed as a biological time, adult survival was logit-transformed and interpreted as a life expectancy expressed in years (Stearns 1983, Gaillard *et al.* 1989). Generation time and age at first reproduction are already biological times expressed in years and therefore were only log-transformed in the analyses to satisfy the rules of allometry (Houle *et al.* 2011).

In addition, for each population, we studied the sign of the average $e_{U,t}$ corresponding to the 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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Results

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

A large range of generation time, age at first reproduction and adult survival was observed across mammalian species included in the analyses (Table 1). The relationship between the ratio $e_{R,t} / E_{t'}$ for yearling survival $\psi 1$ and generation time (on a log-scale) (Fig. 1a) showed the longer the generation time, the lower the ratio $e_{R,t} / E_{t'}$ (slope= -0.062 (SE: 0.0139), p-value<< 0.01) meaning that the relative contribution of $e_{R,t}$ to the population growth rate decreases with the generation time. The relationship between the ratio $e_{R,t} / E_{t'}$ for yearling survival $\psi 1$ and age at first reproduction (on a log-scale) (Fig. 2a) showed the later the age at first reproduction, the lower the ratio $e_{R,t} / E_{t'}$ (slope= -0.060 (SE: 0.0138), p-value<< 0.01) meaning that the relative contribution of $e_{R,t}$ to the population growth rate decreases with the age at first reproduction. Finally, the relationship between the ratio $e_{R,t} / E_{t'}$ for yearling survival $\psi 1$ and life expectancy (i.e., adult survival on a logit-scale) (Fig. 3a) showed the higher the life expectancy, the lower the ratio $e_{R,t} / E_{t'}$ (slope= -0.038 (SE: 0.0148), p-value= 0.025) meaning that the relative contribution of $e_{R,t}$ to the population growth rate decreases with the life expectancy.

By studying the sign of the average $e_{U,t}$ allows distinguishing two groups of species. A first group of species characterized by a fast pace of life, with a short generation time, an early age at first reproduction, and a low adult survival, had a positive $e_{U,t}$ on average for yearling survival $\psi 1$. For these species, the change in population structure resulting from a change in yearling survival leads to a positive contribution to population growth rate. The second group of species were characterized by a slow pace of life, with a long generation time, a late age at first reproduction and a high adult survival, had a negative $e_{U,t}$ on average yearling

survival $\psi 1$. For these species, the change in population structure resulting for a change in a yearling survival leads to a negative contribution to population growth rate.

No relationship was found between the ratio $e_{R,t} / E_{t'}$ for adult survival $\psi 3$ and generation time (on a log-scale) (Fig. 1b), age at first reproduction (on a log-scale) (Fig. 2b) and life expectancy (Fig. 3b). For all species, the relative contribution of $e_{R,t}$ to the population growth rate is thus similar. By studying the sign of the average $e_{U,t}$, we found that all species had a positive $e_{U,t}$ on average for adult survival $\psi 3$ irrespective of their pace of life, except red squirrel that exhibited a negative $e_{U,t}$ on average. On average, for all species except red squirrel, the change in population structure resulting from a change in adult survival leads to a positive contribution to population growth rate.

Discussion

STOCHASTIC VS. DETERMINISTIC ELASTICITIES

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

These deterministic elasticities usually estimated in demographic analyses, are based on the average transition matrix and correspond to $e_{R,t}$, the direct effect of changing a given demographic parameter on population growth rate. Nevertheless, in stochastic environments, demographic parameters fluctuate from year to year. In the bighorn sheep population of Sheep River for instance (*Coulson et al.* 2005), adult survival is variable from year to year because of pneumonia and predation (Festa-Bianchet 1988; Jorgenson *et al.* 1997; Ross *et al.* 1997), 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 $\psi 1$ 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 $\psi 1$ 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

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

The relative contribution of direct vs. indirect effects of changing adult survival $\psi 3$ on population growth was not associated with either generation time, age at first reproduction, or life expectancy. Irrespective of their pace of life, all species but red squirrel showed identical relative contributions of direct vs. indirect effects of changing adult survival on population growth. Increasing $\psi 3$ in a given population increased the proportion of adult individuals that are able to reproduce. Consequently, the contribution of indirect effect of an increase of adult survival to long-term population growth was positive. In the same way, decreasing survival of prime-aged females will lead to decrease the population growth rate by the direct way but also by the indirect way and such a decrease could thus affect population viability. As already reported, size-selective harvesting, where the largest and thus the prime-aged individuals are preferentially taken, in both marine and terrestrial habitats can affect the demography of populations (Fenberg & Roy 2008). This analysis of stochastic elasticity patterns provides further support of that size-selective harvesting can negatively influence the demography of populations irrespective of their pace of life.

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Tables

Table 1. Mammal populations for which yearly estimates of age-specific survival and reproduction were available and their associated generation time, age at first reproduction (in years) and adult survival. Two different populations of roe deer (1: Trois-Fontaines and 2: Chizé) 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 (*Sus scrofa scrofa*)	1983-2005	This study	2.65	1	0.458
2. Red squirrel *(Tamiasciurus hudsonicus*)	1990-2003	Descamps *et al.* 2006	2.86	1	0.512
3. Roe deer 1 (*Capreolus capreolus*)	1985-1998	Gaillard *et al.* 2003	4.33	2	0.899
4. Roe deer 2 (*Capreolus capreolus*)	1985-1998	Gaillard *et al.* 2003	5.21	2	0.923
5. Bighorn sheep 1 (*Ovis Canadensis*)	1980-1995	Coulson, Gaillard & Festa-Bianchet 2005	7.55	2	0.926
6. Bighorn sheep 2 (*Ovis Canadensis*)	1983-1997	Coulson, Gaillard & Festa-Bianchet 2005	7.72	2	0.896
7. Mountain goat (*Oreamnos americanus*)	1992-2002	Festa-Bianchet & Côté 2008	8.75	3	0.933
8. Yellow baboon (*Papio cynocephalus*)	1971-2007	Morris *et al.* 2011	16.45	7	0.920
9. Blue monkey (*Cercopithecus mitis stuhlmanni*)	1980-2007	Morris *et al.* 2011	18.05	8	0.952
10. Northern muriqui (*Brachyteles hypoxanthus*)	1983-2007	Morris *et al.* 2011	22.07	9	0.969
11. White-faced capuchin monkey (*Cebus capucinus*)	1986-2007	Morris *et al.* 2011	22.88	7	0.943
12. Verreaux's sifaka (*Propithecus verreauxi*)	1984-2007	Morris *et al.* 2011	23.69	7	0.928
13. Mountain gorilla (*Gorilla beringei beringei*)	1967-2007	Morris *et al.* 2011	30.48	11	0.975
14. Eastern chimpanzee (*Pan troglodytes schweinfurthii*)	1963-2007	Morris *et al.* 2011	40.48	16	0.951

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 $\lvert e_{U,t} \rvert$
φ_1	Yearling survival, i.e. survival of individuals between 1 and 2 years of age
φ_2	Survival of immature individuals, i.e. yearly survival of individuals, older than 2 years that are not yet able to reproduce
φ_3	Adult survival, i.e. yearly survival of individuals older than 2 years that are able to reproduce

449

Figure legends

Figure 1. Relationship between the ratio $e_{R,t} / E_{t'}$ (with $E_{t'} = e_{R,t} + |e_{U,t}|$) and generation time (on a log-scale) for the 14 populations displayed in Table 1 for **(a)** yearling survival ψ_1; **(b)** adult survival ψ_3. Filled circles correspond to a negative average $e_{U,t}$, closed circles correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the populations displayed in Table 1.

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 reproduction (on a log-scale) for the 14 populations displayed in Table 1 for **(a)** yearling survival ψ_1; **(b)** adult survival ψ_3. Filled circles correspond to a negative average $e_{U,t}$, closed circles correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the populations displayed in Table 1.

Figure 3. Relationship between the ratio $e_{R,t} / E_{t'}$ (with $E_{t'} = e_{R,t} + |e_{U,t}|$) and the adult survival (on the logit-scale) for the 14 populations displayed in Table 1 for **(a)** yearling survival ψ_1; **(b)** adult survival ψ_3. Filled circles correspond to a negative average $e_{U,t}$, closed circles correspond to a positive average $e_{U,t}$. The numbers on the graph correspond to the populations displayed in Table 1.

Fig. 1.

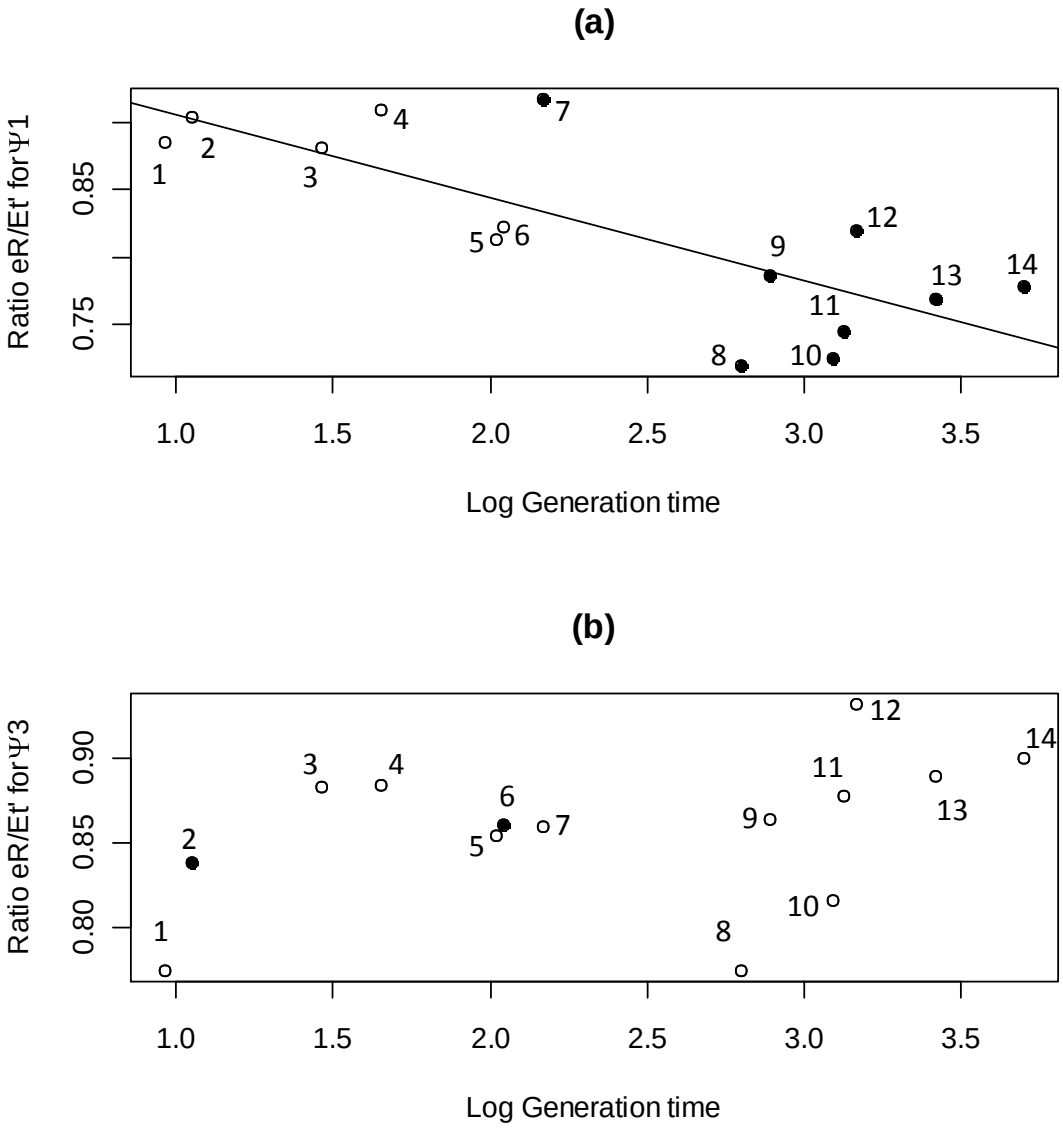

(a)
Ratio eR/Et' for Ψ1
0.75
0.85
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1.0
1.5
2.0
2.5
3.0
3.5
Log Generation time
(b)
Ratio eR/Et' for Ψ3
0.80
0.85
0.90
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1.0
1.5
2.0
2.5
3.0
3.5
Log Generation time

Fig. 2.

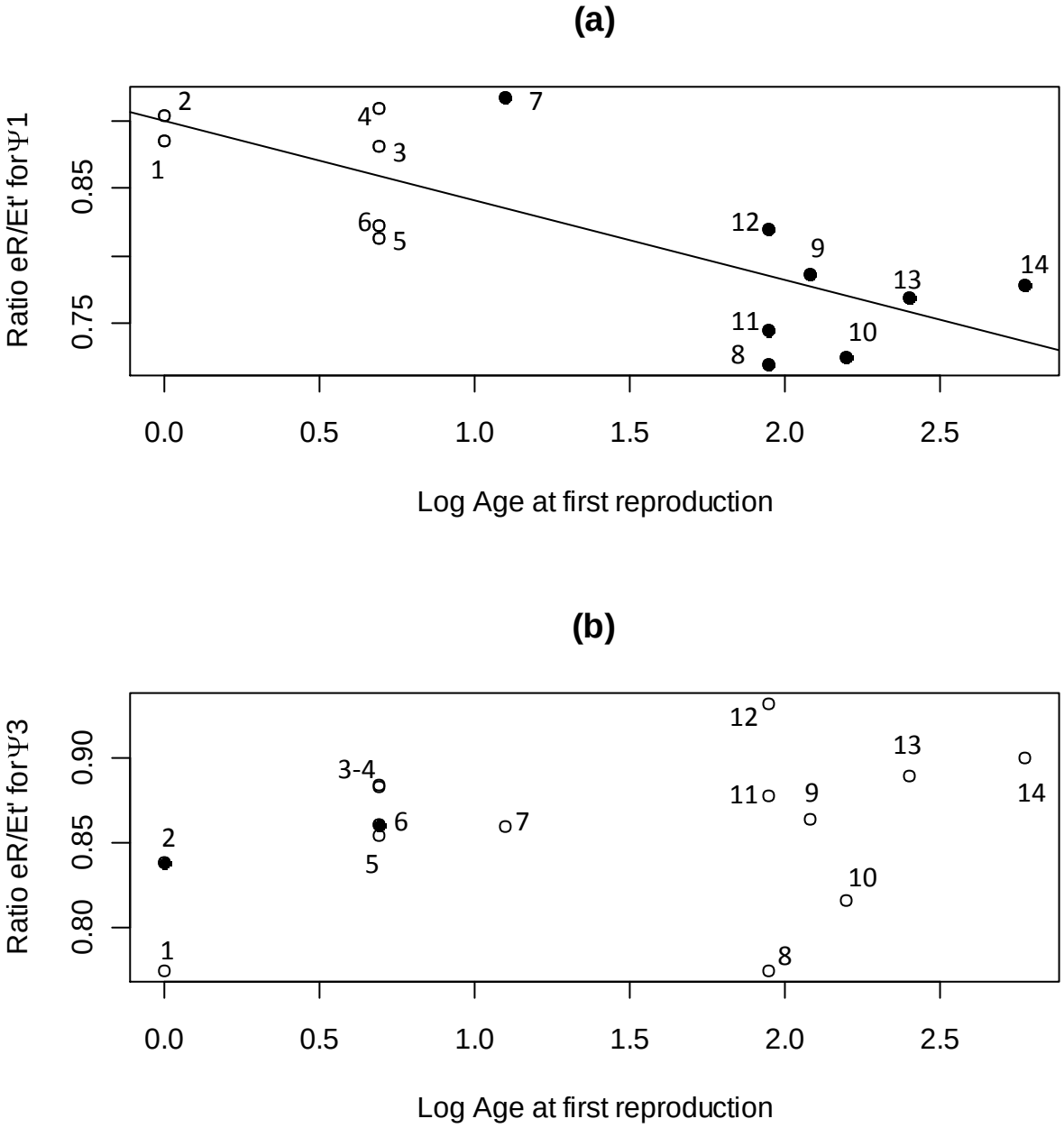
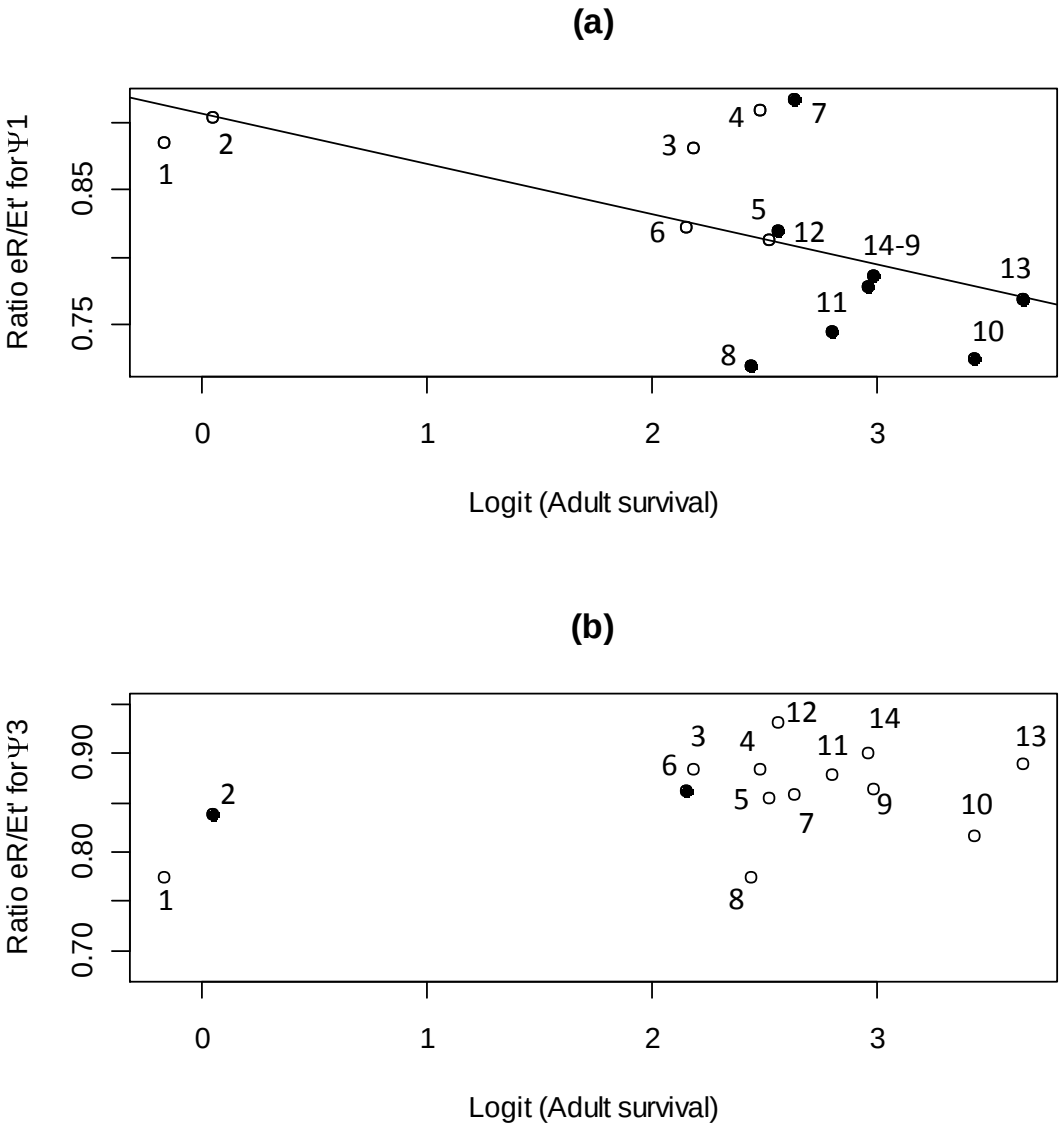

(a)
Ratio eR/Et' for Ψ1
0.75
0.85
0.0
0.5
1.0
1.5
2.0
2.5
Log Age at first reproduction
1
2
3
4
5
6
7
8
9
10
11
12
13
14
(b)
Ratio eR/Et' for Ψ3
0.80
0.85
0.90
0.0
0.5
1.0
1.5
2.0
2.5
Log Age at first reproduction
1
2
3-4
5
6
7
8
9
10
11
12
13
14

Fig. 3.


(a)
Ratio eR/Et' for Ψ1
0.75
0.85
1
2
3
4
7
5
6
12
14-9
13
11
10
8
0
1
2
3
Logit (Adult survival)
(b)
Ratio eR/Et' for Ψ3
0.70
0.80
0.90
1
2
3
6
12
14
13
4
11
5
9
10
7
8
0
1
2
3
Logit (Adult survival)