

1 **Quantifying individual heterogeneity and its influence on life-history trajectories:**
2 **Different methods for different questions and contexts**

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15 **Abstract**

16 Heterogeneity among individuals influences the life-history trajectories we observe at the
17 population level because viability selection, selective immigration and emigration
18 processes, and ontogeny change the proportion of individuals with specific trait values
19 with increasing age. Here, we review the two main approaches that have been proposed
20 to account for these processes in life-history trajectories, contrasting how they quantify
21 ontogeny and selection, and proposing ways to overcome some of their limitations.

22 Nearly all existing approaches to model individual heterogeneity assume either a single
23 normal distribution or a priori known groups of individuals. Ontogenetic processes,
24 however, can vary across individuals through variation in life-history tactics. We show
25 the usefulness of describing ontogenetic processes by modelling trajectories with a
26 mixture model that focuses on heterogeneity in life-history tactics. Additionally, most
27 methods examine individual heterogeneity in a single trait, ignoring potential correlations
28 among multiple traits caused by latent common sources of individual heterogeneity. We
29 illustrate the value of using a joint modelling approach to assess the presence of a shared
30 latent correlation and its influence on life-history trajectories. We contrast the strengths
31 and limitations of different methods for different research questions, and we exemplify
32 the differences among methods using empirical data from long-term studies of ungulates.

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34

35 **Introduction**

36 Age-specific changes affect the evolution of traits and their influence on population
37 dynamics (Vaupel and Yashin 1985, Vindenes and Langangen 2015). It is therefore
38 essential to quantify accurately how life-history traits vary with age. Life-history
39 trajectories are usually quantified at the species or population levels (e.g. Mysterud et al.
40 2001), but changes in life-history traits with age occur at the individual level. Indeed,
41 life-history trajectories result from a combination of ontogenetic processes at the
42 individual level, selection processes leading to the appearance (through fertility selection
43 or immigration) or disappearance (through viability selection or emigration) of
44 individuals within a population, and multiple environmental influences on individuals. As
45 a result, a substantial part of the age-specific variation observed at the population level is
46 often due to heterogeneity among individuals (Service 2000, van de Pol and Verhulst
47 2006, van de Pol and Wright 2009).

48

49 Typically, ontogenetic trajectories of life-history traits display a \cap -shaped (Emlen (1970)
50 for reproductive performance) or U-shaped (Caughley (1966) for mortality = 1- survival)
51 curve with age: survival and reproductive traits increase until a plateau is reached during
52 prime-age, and then decrease until death. Variation in reproductive traits with age may
53 result from two main ontogenetic processes. First, reproductive output can increase early
54 in life as individuals gain experience or allocate more to reproduction, reflecting an
55 improvement with age (Curio 1983, Forslund and Pärt 1995) (Fig. 1A). Second,
56 reproductive output can decrease at old age as a result of senescence (see Nussey et al.
57 (2013) for a review of empirical evidence in vertebrates) (Fig. 1B), which corresponds to

58 the irreversible decline of physiological and cellular functions with increasing age (e.g.
59 Medawar 1952). Although the basic concepts behind these ontogenetic processes are
60 relatively simple, other processes such as viability and fertility selections (as defined by
61 Fisher (1930)) can have fundamental influences on the average ontogenetic patterns
62 observed at the population level. On one hand, viability selection removes certain
63 phenotypes at younger ages, typically frail individuals, leading cohort composition to
64 change with age (Vaupel et al. 1979, Newton and Rothery 1998) and thereby affecting
65 the age-specific mean and variance of a trait at the population level (Fig. 1C, D). For
66 example, in red-billed choughs (*Pyrrhocorax pyrrhocorax*), the decline in offspring
67 survival with increasing parental age observed at the population level results from the
68 disappearance of short-lived parents whose offspring have higher survival than those
69 born to long-lived parents (Reid et al. 2010) (Fig. 1D). On the other hand, fertility
70 selection leads to individual variation in reproductive performance, such that certain
71 genotypes will contribute more to reproduction than others (Wooller et al. 1992), which
72 will in turn affect the patterns observed at the population level. If selection fine-tunes first
73 reproduction according to body size or body condition, individuals with different
74 phenotypic traits will enter the breeding population at different ages (e.g. Forslund and
75 Pärt 1995 in birds, Weladji et al. 2010 in mammals) (Fig. 1E, F). For example, the
76 observation at the population level that female oystercatchers (*Haematopus ostralegus*)
77 produce larger eggs as they age is mainly the result of females producing larger eggs
78 when they delay first reproduction (van de Pol and Verhulst 2006). Thus, there is an
79 increasing proportion of females producing larger eggs in the breeding population with
80 increasing age, leading egg size to increase with age at the population level (Fig. 1E).

81

82 Other population processes including delayed recruitment and immigration/emigration
83 may also lead to age-related changes in cohort structure if these processes are biased
84 towards certain types of individuals. Finally, human harvest is often selective for body
85 size (Fenberg and Roy 2008), size of specific traits (Douhard et al. 2016) or reproductive
86 status (Rughetti and Festa-Bianchet 2014), leading to substantial changes in trait
87 distribution with age (Darimont et al. 2009), often because larger individuals are removed
88 at younger ages.

89

90 Selective disappearance and appearance of individuals of different phenotypes and
91 viability and fertility selection all influence how the mean and the variance of a
92 phenotypic trait change with age at the population level. Although ontogenetic and
93 selection processes could each explain patterns observed at the population level (as in the
94 oystercatcher example; Fig. 1E), combinations of both processes are likely to occur in
95 nature (Ozgul et al. 2009, 2010) (Fig. 1G-J), sometimes leading to interactive effects. For
96 example, Rebke et al. (2010) showed that selective disappearance leads to an
97 overestimation of the improvement of reproduction with age in young common terns
98 (*Sterna hirundo*), and to an underestimation of senescence in old ones.

99

100 Variation in environmental conditions over the lifetime can also affect each individual
101 differently depending on its state (McNamara 1998), influencing the mean and the
102 variance of the responses observed at the population level (Yashin et al. 2002, Barbraud
103 and Weimerskirch 2005, Nussey et al. 2007, Hamel et al. 2009b). While assessments of

104 environmental effects on average population responses have received considerable
105 attention in ecological research, less attention has been given to how environmental
106 conditions may lead to variation in individual responses (Wilson et al. 2009). Early
107 environment influences the condition of individuals and hence their initial trait values,
108 such as age at first reproduction (Albon et al. 1987, Lindström 1999, Forchhammer et al.
109 2001). Statistically, this means that environmental conditions affect the intercepts of
110 individual responses (Fig. 1). These effects may persist throughout the lifetime (Metcalf
111 and Monaghan 2001) or may disappear as a result of early-life selection (Vedder and
112 Bouwhuis 2017). Conditions experienced later in life, however, might affect between-
113 individual differences as individuals are ageing. If environmental effects accumulate with
114 age, they may accentuate initial between-individual differences (Nussey et al. 2007) (Fig.
115 1L). If individuals can compensate for poor early conditions, individual differences
116 should decrease with age (Hamel et al. 2016) (Fig. 1K). Statistically, environmental
117 conditions can affect not only the intercepts (i.e. variation at early age), but also the
118 slopes of individual responses, leading the variance in life-history traits to vary over age
119 (Schielzeth and Forstmeier 2009, van de Pol and Wright 2009) (Fig. 1K, L).

120

121 Previous research has shown that selection processes and environmental influences may
122 shape patterns of ontogeny observed at the population level (Sunderland et al. 1976,
123 Yashin et al. 2002). Until recently, the lack of data from individually marked animals
124 monitored from birth to death limited our ability to assess the relative importance of these
125 processes and how they varied between the individual and the population levels. In the
126 past decade, however, longitudinal studies have provided the high-quality data required

127 to assess these patterns empirically (Clutton-Brock and Sheldon 2010) and to develop
128 methods integrating these effects in analyses of life-history variation with age (Rattiste
129 2004, Nussey et al. 2006, van de Pol and Verhulst 2006, Nussey et al. 2011). For
130 instance, Rebke et al. (2010) showed that changes in annual reproduction in common
131 terns are mostly the result of ontogenetic processes, yet the smaller effects of viability
132 selection result in complex interactions with ontogeny. In great tits (*Parus major*),
133 Bouwhuis et al. (2009) showed that accounting for the selective disappearance of
134 individuals by including the age at last reproduction reveals that the onset of senescence
135 is nearly one year earlier (2.8 vs. 3.5 years of age) than what is observed at the population
136 level. The complexity of ontogenetic and selection processes means that an adequate
137 quantification of their relative contributions to life-history trajectories is of fundamental
138 importance to understand evolutionary dynamics. Furthermore, the importance of
139 individual heterogeneity in shaping population responses reveals a need to understand its
140 impact on ontogenetic processes.

141

142 Here, we review approaches to account for individual heterogeneity when
143 estimating/studying/quantifying life-history trajectories with age, demonstrating how
144 each method quantifies the ontogenetic, selection, and environmental processes taking
145 place within a population. Specifically, we compare the demographic decomposition of
146 observed changes proposed by Rebke et al. (2010) with the statistical modelling approach
147 based on random effect models proposed by van de Pol and Verhulst (2006).
148 Furthermore, we demonstrate how mixture models can quantify how population
149 processes are affected by the relative proportions of individuals displaying a given life-

150 history tactic. We also show how joint modelling of life-history traits can evaluate the
151 covariance among traits and its impact on population processes. We illustrate these
152 methods using empirical data from long-term studies of ungulates (see Appendix 1 for
153 the specific details of the study areas, data collection and analyses). We conclude by
154 contrasting the strengths and limitations of these methods in answering different
155 questions and show how combining methods can overcome some limitations. We focus
156 on methods developed for populations with individual detection probability close to 1.
157 Approaches used to account for individual heterogeneity in the context of capture-mark-
158 recapture (CMR) in populations with imperfect detection are covered in detail by
159 Gimenez et al. (2017).

160

161 **Demographic decomposition**

162 The decomposition of demographic changes based on a derivation of the Price equation
163 (Price 1970) first appeared in studies of human demography (Vaupel and Canudas Romo
164 2002) and then in evolutionary ecology (Coulson and Tuljapurkar 2008). Rebke et al.
165 (2010) built on these previous works to present a demographic decomposition approach
166 at the population level to disentangle within-individual trait change from changes caused
167 by selective appearance and disappearance at each age. They quantified the selection
168 resulting from appearance/disappearance based on differences in the mean trait between
169 different groups of individuals rather than on the covariance (Rebke et al. 2010). It
170 provides an exact decomposition of the average population change P of a trait in each age
171 interval into average within-individual change I and change due to selective appearance A

172 and to selective disappearance D , assuming that all individuals remaining in the
173 population are measured (Fig. 2A).
174
175 Thus, the method allows quantifying directly ontogeny (I) and selection processes (A and
176 D) for each age interval (Table 1). The exact decomposition at each age captures the
177 relative importance of the different processes across the lifespan. Nevertheless, low
178 sample sizes in late life is the rule because few individuals survive to old age, which
179 leads to high uncertainties in late-life estimates (Rebke et al. 2010; see also the example
180 below). The small sample of old individuals prevents an accurate assessment of
181 senescence patterns at oldest ages, an important focus of all studies of age-specific
182 variation in traits (Evans et al. 2011, Nussey et al. 2011, Zhang et al. 2015), and makes it
183 difficult to compare the strength of processes between early and late life. This is not
184 specific to this method, but reflects the trade-offs between analyses based on a model of
185 the trait-age relationship, which might be biased if the model is a poor approximation but
186 is more precise, and more descriptive approaches, which are less biased but less precise.
187 In addition, the method requires a full detection of individuals because they have to be
188 measured each year they were present in the population to provide an exact
189 decomposition (Rebke et al. 2010; however see Nussey et al. (2011) and Fig. 2A for
190 dealing with individuals that are not measured every year but their fate is known).
191 Consequently this approach has only rarely been used to date (Evans et al. 2011, Nussey
192 et al. 2011, Evans and Sheldon 2013, Hayward et al. 2013, Zhang et al. 2015).

193

194 To account for annual environmental effects, Rebke et al. (2010) proposed using the
195 relative value of the trait, i.e. subtracting the annual mean (see also e.g. McCleery et al.
196 (2008)). This, however, is not always intuitive for traits following a binary distribution
197 (e.g. reproduced successfully or not), and can be problematic for traits following a
198 Poisson or generalized Poisson distribution (e.g. clutch size in Kendall and Wittmann
199 (2010)). Relative values of a trait can also be influenced by the effects of the environment
200 on age structure and therefore the mean value of the trait. For example, consider a species
201 that starts breeding as one year old but with a relatively low breeding success compared
202 to older individuals, and that harsh conditions mostly affect young individuals. Following
203 a harsh winter, there will be few 1 year olds in the population, and therefore the mean
204 value for the population will be high, and the relative value of the trait will be low,
205 whereas the opposite will happen following a benign winter. Given that there are fewer
206 individuals surviving harsh than benign winters, the analyses might therefore be biased
207 towards the benign winters. In addition, the relative value of a trait cannot control for
208 fixed or lifetime environmental effects, for example if improvement with age is stronger
209 for individuals born at low density. Most importantly, it does not quantify environmental
210 effects and therefore cannot compare the relative importance of environment, ontogeny
211 and selection.

212

213 Compared with the statistical approach presented in the next section, the demographic
214 decomposition proposed by Rebke et al. (2010) does not need to estimate or correct for
215 heterogeneity in individual differences. This is advantageous compared with the
216 statistical modelling because the latter accounts for and quantifies heterogeneity using

217 specific fixed and random effects, and the modelling choices for these effects can
218 influence results and may not always reliably estimate heterogeneity (van de Pol and
219 Wright 2009, Hamel et al. 2012). Still, this means that the demographic decomposition
220 does not provide a direct quantification of individual heterogeneity, but it can be used as
221 an initial step to describe this heterogeneity. To quantify processes within a single
222 population, however, the results obtained from the demographic decomposition will not
223 be affected by heterogeneity, unless one wishes to compare two distinct time periods that
224 will be composed of different individuals.

225 To illustrate the method, consider the example of age-related body mass changes in male
226 bighorn sheep (*Ovis canadensis*; see Appendix 1 for details on data and study area). The
227 mass observed at the population level may be affected by viability selection because
228 smaller individuals are less likely to survive (Nussey et al. 2011, Hamel et al. 2016),
229 particularly in early life (Gaillard et al. 1997, Théoret-Gosselin et al. 2015). In addition to
230 this natural disappearance, selective harvesting also drives phenotypic change in this
231 population because adult males (≥ 4 years) are harvested based on their horn size, which
232 is correlated with body mass (Coltman et al. 2005, Bonenfant et al. 2009). We can
233 therefore expect artificial disappearance of heavier males from age 4 and over.
234 Immigration could also lead to appearance of different phenotypes, for instance if heavier
235 males are more likely to disperse. That being said, only seven cases of male immigration
236 have occurred over 43 years. We therefore excluded immigrants and two transplanted
237 males and ignored appearance in this example. We decomposed the change in body mass
238 with age as $P = I + D_N + D_H$, where D_N is the disappearance due to natural selection and
239 D_H is the disappearance due to artificial selection (Fig. 2B). Note that because change in

240 mass is not linear with age, we could not use annual mass to control for annual variation,
241 and hence used absolute rather than relative change in mass as in Nussey et al. (2011; but
242 see “Combining approaches” section for a solution to this limitation). *P* showed a marked
243 increase until four years of age, after which mass continued to increase slightly (Fig.
244 3A,B). Because senescence in body mass is observed in females of the same population
245 (Nussey et al. 2011), perhaps the absence of senescence in males is due to trophy hunting
246 removing males from the population before physiological functions begin to deteriorate.
247 Nevertheless, the pattern of change in mass with age was similar at the individual level *I*,
248 with no within-individual declines in mass at old age after accounting for artificial and
249 natural selection (Fig. 3B).

250

251 The contribution of natural selective disappearance to age-related changes was clearly
252 positive during the first years of life, supporting the occurrence of strong viability
253 selection against lighter males in early life. For example, the mass difference at age 0
254 between males surviving to age 1 (8.9 kg) and all males (8.1 kg) indicates that selective
255 disappearance causes an increase of 0.8 kg in mass. Later in life, natural disappearance
256 was small and much more variable, with fluctuations from positive to negative selection
257 and vice versa from one age to the next. Estimates were also uncertain and imprecise,
258 with confidence intervals often widely overlapping zero and widening at old ages due to
259 low sample sizes (Fig. 3B). If we neglect the uncertainty of the estimations in late life,
260 the absolute change in mass due to disappearance between ages 9 and 10 is greater than
261 between ages 0 and 1 (Fig. 3B). Nonetheless, the difference of 0.8 kg at age 0 represents
262 a 10% increase in mass induced by selective disappearance, which is larger than the 3%

263 change in mass induced by selective disappearance at age 9. This small effect suggests
264 little influence of natural selective disappearance in late life. On the other hand,
265 disappearance due to artificial selection had a considerable influence in adult males,
266 particularly those aged 4 to 8 years (Fig. 3B). Artificial disappearance due to harvesting
267 always selected against heavier males, with survivors being up to 2 kg lighter than the
268 whole population (Fig. 3B).

269

270 As suggested by Nussey et al. (2011), the relative contribution of selective disappearance
271 and within-individual change to the observed population-level changes of a trait can also
272 be estimated across the lifespan by calculating the proportion of absolute phenotypic
273 change due to selective disappearance as $P_D = (|D_{cum}| / (|D_{cum}| + |I_{cum}|)) * 100$, where
274 $|D_{cum}|$ and $|I_{cum}|$ are respectively the cumulative sum of absolute $D_{i,i+1}$ and $I_{i,i+1}$ values
275 (illustrated in Fig. 2A) across all ages. The proportion of absolute phenotypic change due
276 to ontogeny P_I is equal to $1 - P_D$. These proportions can also be calculated over
277 particular life stages, e.g. prime-age and senescence. Across all ages, the combined
278 disappearance effect of artificial and natural selection accounted for 9.2% of the
279 phenotypic change in body mass. This proportion was higher in adulthood (≥ 4 years, P_D
280 = 24.5%) compared to early life (0-3 years, $P_D = 2.5%$). This comparison, however, does
281 not account for uncertainty around the estimates at older ages (Fig. 3B), and for the
282 nonlinearity of the change in mass with age, which can be taken into account by working
283 on the relative rather than absolute quantification of disappearance.

284

285 **Statistical modelling**

286 In 2006, van de Pol and Verhulst proposed accounting for selection processes by using a
287 within-individual centring approach, a technique common in social sciences (Kreft et al.
288 1995, Hofmann and Gavin 1998, van de Pol and Verhulst 2006). This approach uses a
289 random effect model that specifically includes age at appearance and/or disappearance as
290 covariates, thus separating the within- and between-individual contributions to ageing. To
291 start with, a random effect model can decompose the total variance in its between- and
292 within-individual components, taking into account some of the dependence of repeated
293 measures of the same individual at different ages (eqn. 1, Fig. 4A; additional dependency
294 might be due to e.g. first-order autocorrelation, see Hamel et al. (2012)). By including
295 individual identity as a random intercept, the model provides a measure of change with
296 age (β_l , Fig. 4A) that accounts for this non-independence. If an individual has a higher
297 value for a trait than another individual, this difference in intercepts among individuals
298 will be captured by u_{0j} , which estimates the among-individual variance in intercept σ_u^2
299 (Fig. 4A). The random effects are often called latent effects (described as, e.g., “quality”)
300 because the underlying random variable is not measured.

301

302 As proposed by van de Pol and Verhulst (2006), adding the age of each individual at
303 appearance and/or disappearance α_j (eqn. 2, Fig. 4B) as a covariate to this model allows
304 evaluating the influence of timing of appearance/disappearance on within-individual
305 changes with age. In the standard random effect model (Fig. 4A), the difference in
306 phenotypic quality among individuals is modelled, whereas the model that includes
307 selection (Fig. 4B) also includes the probability that phenotypic quality covaries with the
308 chance of appearing or disappearing from the population. If one studies reproduction, for

309 instance, age of appearance will be age at first reproduction and age at disappearance will
310 be age at last reproduction. The random effect model that includes
311 appearance/disappearance as a covariate provides a coefficient that measures the change
312 in the trait intercept that results from variation in age at appearance/disappearance, β_S
313 (Figs 4B, 5B), thereby measuring the strength of the selection process. It also provides a
314 coefficient that measures the within-individual change of the trait with age, β_W (Figs 4B,
315 5B), a measure of ontogeny that accounts for appearance and disappearance, and
316 therefore is not biased by selection. We can also compute the strength of the between-
317 individual effect, which is simply the addition of the within-individual change and the
318 selection effect, i.e. $\beta_B = \beta_W + \beta_S$ (Figs 4B, 5B). Figure 5 illustrates how these parameters
319 can be quantified, examining the relative change in offspring mass produced by mothers
320 with different ages at first reproduction. The figure is based on empirical data from a
321 long-term mountain goat population (see Appendix 1 for details) where females reach
322 asymptotic mass at 7 years of age but primiparity ranges from 3 to 8 years (Festa-
323 Bianchet and Côté 2008). We may therefore suspect the occurrence of fertility selection if
324 mothers delaying first reproduction produce heavier offspring because the trade-off
325 between growth and reproduction weakens with age (Hamel and Côté 2009), or through
326 experience, as primiparous mothers produce lighter offspring (Côté and Festa-Bianchet
327 2001). We grouped females aged 8 years and older because we did not expect difference
328 in offspring mass after females had reached asymptotic mass (Côté and Festa-Bianchet
329 2001). To exemplify how fertility selection can be modelled, we accentuated the
330 appearance effect by simulating a series of random values with a mean of 0.7 and a
331 standard deviation of 0.5 (n=196 simulated values, one for each kid mass available). We

332 then multiplied this value by the age at first reproduction of the mother (centred) and
333 added it to the mass of the kid.

334

335 To quantify processes, we ran mixed models (“lmer” function, “lme4” package in R;
336 Bates et al. (2015), R Development Core Team (2016)) according to eqn. 1 and 2 (Fig.
337 4A,B). This procedure estimated the relative change in kid mass with increasing maternal
338 age at both the population level β_l (Fig. 5A) and the individual level β_w (ontogeny; Fig.
339 5B), as well as the influence of appearance β_s (fertility selection; Fig. 5B). These
340 parameters are then directly comparable and allow quantifying the relative importance of
341 each population process (Fig. 5C). Because we forced a simulated effect of fertility
342 selection, we see as expected that the change observed at the population level is not the
343 result of a change with increasing age at the individual level, but is entirely caused by
344 females that started to reproduce later and thereby produced heavier offspring. As for the
345 demographic decomposition approach, we can obtain not only the quantification of the
346 different processes, but also the within-individual trajectory by predicting the trajectory
347 for the mean value of age at appearance (Fig. 5B) (but see “Challenges” section for
348 different ways of predicting trajectories depending on the questions of interest).

349

350 This statistical approach allows us to quantify directly ontogeny, β_w , and selection
351 processes, β_s , over the lifespan (Table 1), but does not provide an exact decomposition at
352 each age. The models, however, are quite flexible: they can be used when the average
353 number of repeated measures of individuals is low (e.g. less than 2 in Class and Brommer
354 (2016)) and can account for different functions of age and age at

355 appearance/disappearance (van de Pol and Verhulst 2006). For instance, we could model
356 age as a factor, providing a measure of ontogeny at each age for a trait showing a
357 nonlinear increase with age, such as growth (Fig. 3A). This, however, would assume that
358 the effect of age at appearance/disappearance is constant with increasing age, an
359 unjustified assumption because selection processes are likely to change at different life
360 stages as illustrated in the bighorn sheep example (Fig. 3B). A more prudent approach
361 would be to model the interactive effect of age and age at appearance/disappearance (see
362 simulated example in Appendix 2). In such case, age and age at
363 appearance/disappearance cannot both be used as factors because they would not all be
364 identifiable. An alternative would be to use age categories to estimate processes for
365 specific life stages, e.g. to contrast growth vs. senescence. An appropriate selection of age
366 categories, however, might not always be obvious, and the choice could affect the results.
367 If the aim is not to contrast specific life stages, then using a nonlinear effect of age could
368 be more appropriate. Modelling age with an ordinary polynomial or a spline would also
369 allow smoothing the unexpected fluctuations in the estimates we sometimes obtain
370 between ages as a result of low sample size in late life (e.g. Fig. 3B). That being said,
371 although nonlinear modelling can account for selection processes and provide unbiased
372 predictions of phenotypic change with age, the beta estimates describing the nonlinearity
373 cannot be directly used to quantify ontogeny and selection (but see “Combining
374 approaches” section for a solution).

375

376 To account for environmental effects, van de Pol and Verhulst (2006) also suggested
377 using the relative value of the trait, which suffers from the same limitations as with the

378 demographic decomposition method. Other studies used year as a fixed factor in
379 statistical models (e.g., Nussey et al. 2011). This completely accounts for annual
380 variation, but cannot quantify the influence of the environment on phenotypic change to
381 compare its relative importance with ontogeny and selection. One solution would be to
382 incorporate environmental effects directly in the models (e.g. Bouwhuis et al. 2009).
383 Environmental covariates added directly in the model can estimate β_E (eqn. 3; Fig. 4C),
384 thereby quantifying the ontogeny that is independent of the environmental effect as well
385 as quantifying the environmental effect itself. In Figure 4C, we illustrated an example
386 with an environmental condition that can vary at each age, but we could also replace
387 $\beta_E \gamma_{ij}$ with $\beta_E \gamma_j$ to model a static/fixed environmental condition (e.g. cohort effect;
388 Descamps et al. 2008). Because individual heterogeneity could also change with age or
389 depend on environmental conditions (Schielzeth and Forstmeier 2009, Cam et al. 2016),
390 we could model a dynamic heterogeneity by adding a random slope with either age, i.e.
391 $(\beta_W + u_{Aij})age_{ij}$ (Pennell and Dunson 2006, Morrongiello and Thresher 2015), or
392 environment, i.e. $(\beta_E + u_{Eij})\gamma_{ij}$ (Dingemanse and Dochtermann 2013; see also Chambert et
393 al. (2013) for an example with a binary environmental covariate).

394

395 To illustrate the quantification of environmental effects, we used the November-March
396 anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994) as a measure of
397 the annual environmental variation in winter conditions during the gestation of female
398 mountain goats to assess this environmental influence on offspring mass. NPI is a global
399 climate index with higher anomalies characterising colder and snowier winters than lower
400 anomalies in this study area (Hamel et al. 2009c). Adding this variable to the model

401 according to eqn. 3 (Fig. 4C) with standardized predictors, we can obtain β_E and compare
402 its relative influence with that of ontogeny and selection (Fig. 5D). This simulated case
403 shows that NPI tends to have a negative relative influence, such that harsh winters might
404 reduce offspring mass (Fig. 5D). Including this environmental variable supported that
405 selection was a dominant process over ontogeny (Fig. 5C), but also allowed us to assess
406 that selection was three times more important than environmental variation in explaining
407 the phenotypic changes of offspring mass as mothers are ageing (Fig. 5D). Obviously,
408 this approach is highly dependent on the choice of the environmental variable. In this
409 case, the model including NPI had 30% greater residual variance than a model including
410 year as a factor, and the latter also provided a better fit according to a likelihood ratio
411 test, suggesting NPI only captured a limited part of annual variation. The interpretation of
412 the relative influences should therefore be made specific to the environmental factor
413 measured unless the factor is shown to capture most of the annual variation in the studied
414 trait. One advantage of working with covariates, however, is that other factors that might
415 influence traits can also be included and their relative influence can be compared. For
416 instance, the body condition of an individual often affects its reproduction, and including
417 condition as a covariate can account for such a correlation and allow quantifying its
418 effect. Correlations among traits can alternatively be accounted for by using a joint
419 modelling approach, which will be more appropriate to use when aiming to quantify the
420 dependency among traits and to identify tactics related to this dependency (see “Joint
421 modelling” section).

422

423 One major advantage of the statistical modelling approach is that it can handle a large
424 proportion of missing values, such as when traits are only measured for a fraction of the
425 individual lifetime, and results will be robust as long as the occurrence of missing values
426 is not dependent on the process being estimated, such as individuals with a low weight
427 not being measured. Missing values in some independent variables will reduce the power
428 of assessing selection and environmental processes (van de Pol and Verhulst 2006), an
429 important limitation in the quantification of these processes. Another advantage of these
430 models is that they can also be performed in a capture-mark-recapture (CMR)
431 framework, thereby providing a way to account for the probability of detection when it is
432 below 1 (see review on CMR models by Gimenez et al. (2017)). One issue, however, is
433 the correlation between fixed factors in the models (van de Pol and Verhulst 2006),
434 because longevity will inevitably be higher and less variable at older than at younger ages
435 of trait measures, and one must check that the parameter estimates are not affected by this
436 potential correlation.

437

438 **Combining approaches**

439 The statistical modelling approach presented by van de Pol and Verhulst (2006) and the
440 demographic decomposition approach presented by Rebke et al. (2010) are the two main
441 methods that have been used up to now. Statistical modelling has been preferred (e.g. 187
442 citations for van de Pol and Verhulst vs. 71 for Rebke et al., Web of Knowledge accessed
443 8. Aug. 2017). In the few cases when both approaches have been used (Evans et al. 2011,
444 Nussey et al. 2011, Evans and Sheldon 2013, Hayward et al. 2013, Zhang et al. 2015),
445 studies have first used a statistical model to test for the structure of the selection process

446 and then performed the demographic decomposition to illustrate the different
447 contributions at each age. This two-step approach is interesting because it uses the
448 strengths of each method. Still, the number of studies with the data required to perform
449 the second step remains rather limited. Furthermore, for traits that change nonlinearly
450 with age such as mass, the annual mean will vary with age structure, and hence cannot be
451 used to control for annual variation in the second step. To solve both issues, we propose
452 combining the two methods, which means performing the demographic decomposition
453 using the predictions obtained from a statistical model that can include environmental
454 covariates. This combined approach allows quantifying ontogeny and selection for
455 specific ages or stages in cases where the data prevent from using the demographic
456 decomposition (e.g. incomplete data), as well as quantifying environmental effects. The
457 new parameters the combined approach allows us to estimate are highlighted in bold in
458 Table 1.

459
460 We illustrate the approach with the example on mass in male bighorn sheep (see also
461 Appendix 2 for an example with simulated data). First, to compare with the results
462 obtained with the decomposition method that did not account for environmental variation
463 (Fig. 3B), we ran a set of statistical models without controlling for annual variation. The
464 first model was built according to eqn. 1 (Fig. 4A), but with age entered as a cubic
465 polynomial. The best polynomial degree was determined based on likelihood ratio tests,
466 and was the same for all statistical models used in this example. We extracted mass
467 predictions from this model, which provided body mass values at each age at the
468 population level, i.e. average mass of all individuals (M_{ALL} , in black in Fig. 2B). Hence, P

469 at each age interval was the difference between M_{ALL} at age $i + 1$ and at age i (Fig. 2B).
470 The second model was built according to eqn. 2 (Fig. 4B), but using longevity in
471 interaction with age. The predictions obtained at each age from this model provided mass
472 values at each age at the individual level, i.e. average mass of surviving individuals
473 (M_{SURV} , in grey in Fig. 2B). Thus, I at each age interval was the difference between M_{SURV}
474 at age $i + 1$ and at age i , and the difference between M_{SURV} and M_{ALL} at age i was the total
475 disappearance (D_{tot} , in blue in Fig. 2B) for both natural and artificial selection. To
476 separate the effect of these two types of disappearance, we ran a third model exactly as
477 the first one but on a data set that excluded the mass in the last year of life for individuals
478 that were shot. This model provided mass predictions at each age for both survivors and
479 individuals that died from natural causes ($M_{SURV+N.DEATH}$, in red in Fig. 2B). Thus, the
480 disappearance due to natural causes at each age D_N was the difference between M_{SURV} and
481 $M_{SURV+N.DEATH}$ at each age, and the disappearance due to hunting at each age D_H was
482 equal to $D_{tot} - D_N$ (see Fig. 2B). To calculate the uncertainty on parameters P , I , D_N , and
483 D_H , we performed a bootstrap (n=1000 simulations) where we used the first model to
484 simulate new response values conditional on the individuals already in the data set (i.e.
485 re.form=NULL in the “simulate” function in R). We conditioned the simulations on the
486 same individuals because our goal is to explain the contribution to ontogeny and selection
487 observed in these individuals. We then reran the three models with the simulated mass
488 responses, estimated P , I , D_N , and D_H for each simulation, and used the 0.025 and 0.975
489 percentiles of each parameter to represent the 95% confidence interval. The results from
490 this combined approach (Fig. 3C) showed similar patterns of ontogeny, natural and
491 artificial selection as the demographic decomposition (Fig. 3B). The main difference was

492 that at older ages the changes were smoother across ages with the combined method
493 because we modelled age as a polynomial, which is less sensitive to age-specific
494 fluctuations in late life. This is advantageous in this case because age-specific changes in
495 body mass are expected to be smaller once males have reached asymptotic body mass
496 than during the growing period. Although senescence in body mass occurs in male
497 ungulates (e.g. Carranza et al. 2004, Mainguy and Côté 2008, Jégo et al. 2014), the large
498 age-specific changes obtained from the demographic decomposition were most likely due
499 to low sample sizes.

500 Then, to illustrate the potential influence of environmental variation in the different
501 contributions, we repeated the combined approach, but included in each statistical model
502 the average mass of yearlings each year as a covariate to account for annual variation in
503 mass (i.e. following eqn. 3 instead of eqn. 2, Fig. 4). Yearling mass is an index of annual
504 resource availability in this bighorn population (Festa-Bianchet et al. 2004), and in this
505 case it provided a reliable metric to control for annual variation because these models
506 were equivalent to models including year as a factor (likelihood ratio tests equal to 1).
507 Extracting the predictions from these models allowed calculating contributions to P , I ,
508 D_N , and D_H that accounted for environmental effects (Fig. 3D). Interestingly, the
509 disappearance caused by viability selection in the three first age intervals was reduced by
510 half when controlling for annual variation. This suggests that environmental variation is a
511 determinant mechanism that drives viability selection in young male bighorn sheep, and
512 illustrates the importance of accounting for environmental variation.

513

514 **Mixture modelling**

515 The statistical modelling approach assumes that the variability representing individual
516 heterogeneity, σ_u^2 , is normally distributed (Fig. 4). That assumption, however, is violated
517 when different life-history tactics coexist within a population, resulting in multimodal
518 distributions (Verbeke and Lesaffre 1996, Stamps et al. 2012). Indeed, the response of
519 individuals sharing similar trait trajectories is likely to differ from that of individuals with
520 different trait trajectories, as well as from the population mean response (Fig. 1M, N). For
521 instance, individuals born in years with favourable or unfavourable conditions could form
522 clusters with distinct growth tactics throughout the lifetime, as shown in large herbivores
523 (Hamel et al. 2016, 2017). Life-history tactics represent distinct ontogenetic patterns that
524 might be influenced differently by selection processes and environmental effects, such
525 that the relative contributions of these processes are likely to differ across tactics.

526

527 A mixture modelling approach is particularly useful to tackle life-history tactics
528 (McLachlan and Peel 2000; see Hamel et al. (2017) for a review). These models have
529 been used widely in psychology, sociology, and medicine (Farewell 1982, Jones et al.
530 2001, Hoeksma and Kelderman 2006, Karlis and Meligkotsidou 2007, Curran et al.
531 2010), and are now increasingly used to model individual heterogeneity in survival in
532 capture-mark-recapture studies (Cubaynes et al. 2012, Ford et al. 2012, see Gimenez et
533 al. (2017) for a review). Finite mixture models (Fig. 6) allow assessing whether there is
534 structured variation in life-history tactics within a population and provide an objective
535 classification of individual trajectories into clusters, each representing a life-history tactic
536 that differs from the mean trajectory of the population (see e.g. Fig. 7). These models
537 identify the best level of clustering between a single cluster (i.e. the population level) and

538 a cluster for each individual (i.e. a classical random effect), thereby working on a higher
539 level of individual heterogeneity by focusing on the cluster level (Hamel et al. 2017).
540 Essentially, each cluster is defined by a separate set of regression parameters (McLachlan
541 and Peel 2000) (Fig. 6). If two clusters are found within a population, parameters from
542 two regressions will be estimated, where the regression for a specific cluster contains
543 observations from all individuals weighted by their probability of belonging to this
544 cluster. If clusters are well defined (i.e. the individual probability of belonging to a given
545 cluster is either 0 or 1), then it will be like running a separate regression on each cluster.
546
547 Mixture models allow us to compare the general ontogenetic curve of clusters with that of
548 the population, thereby determining how processes vary across clusters and how this can
549 affect what we observe at the population level. For example, mixture models fitted on
550 body mass data of different ungulate populations revealed that the ontogenetic pattern of
551 growth varies across clusters, and that the rate observed at the population level might not
552 always be representative of all clusters (see Appendix 1 for modelling details). The model
553 for male bighorn sheep (Fig. 7A) shows that there are three growth tactics within the
554 population and that growth rate differs among tactics before the prime-age stage, leading
555 to distinct asymptotic body mass across tactics during the prime-age stage. Overall, only
556 one growth tactic would be well represented by ontogenetic changes measured at the
557 population level (shown as the red curve in Fig. 7A). Note that there is almost no
558 difference at age 0 because annual environmental conditions were included in the model,
559 thereby accounting for differences among cohorts due to conditions in the year of birth.
560 In male roe deer (Fig. 7B), three very different growth tactics exist, which vary in terms

561 of the onset of senescence, but the strength of senescence (slope of the decrease) is
562 similar across growth tactics. In female bighorn sheep (Fig. 7C), the four growth tactics
563 illustrate not only a difference in the onset of senescence, but also in the rate of
564 senescence. These examples demonstrate that, by concentrating on the cluster level,
565 mixture models allow assessing a different level of individual heterogeneity that
566 corresponds to life-history tactics when analysing life-history trajectories.

567

568 Essentially, any parameter describing ontogeny, selection, and environmental processes
569 that can be included in the statistical modelling approach (i.e. β_W , β_S , β_E , Fig. 4) can also
570 be included in the mixture modelling approach to quantify these processes specifically for
571 each cluster trajectory (e.g. β_{Wc1} , β_{Wc2} , β_{Sc1} , β_{Sc2} , β_{Ec1} , β_{Ec2} , Fig. 6). This allows
572 quantifying the relative importance of these processes for each cluster and contrasting
573 them within a population. For example, if we run again the mixture model on mass in
574 male bighorn sheep including age at disappearance to segregate the clusters (assuming a
575 linear effect of disappearance for the sake of simplicity), we observe that the
576 disappearance of light individuals varies across the three clusters, being 5 times stronger
577 in one cluster out of the two that showed a strong support for disappearance
578 (disappearance estimate [95% confidence interval]: $\beta_{Sc1} = 0.05$ [0.00; 0.10], $\beta_{Sc2} = 1.03$
579 [0.89; 1.17], $\beta_{Sc3} = 0.21$ [0.07; 0.35]).

580

581 Although multimodality resulting from the occurrence of different clusters corresponding
582 to different tactics within a population violates the assumption of normality, this does not
583 affect fixed effects at the population level (Verbeke and Lesaffre 1997, Hamel et al.

584 2017). Thus, the overall influence of these processes at the population level will not differ
585 whether a random effect model or a mixture model is used in the presence of clusters.
586 The interest in using mixture models lies in quantifying and comparing these processes
587 within each cluster, such that the details of the relative contribution for distinct types of
588 individuals provide a better understanding of how ontogeny, selection, and environmental
589 variation might interact within a population. Furthermore, although fixed effects are not
590 biased at the population level in the presence of clusters, the variance describing
591 individual heterogeneity can be greatly overestimated (Hamel et al. 2017). By
592 incorporating a categorical latent variable that aggregates subjects into clusters sharing
593 similar traits, mixture models capture the multimodal dimension that structures individual
594 heterogeneity (McLachlan and Peel 2000). Hence, by estimating the between-individual
595 variance present at the cluster level, mixture models can better quantify the variance
596 within a population and its stratification. For instance, variance in the ontogenetic pattern
597 of growth in male bighorn sheep at the population level (σ_u^2) was 25.8, whereas it was
598 much lower within clusters and varied among clusters ($\sigma_{u_c1}^2 = 3.2$, $\sigma_{u_c2}^2 = 14.9$, and
599 $\sigma_{u_c3}^2 = 13.0$). The high variance at the population level mainly resulted from the large
600 dispersion among the three main tactics rather than the dispersion among individuals
601 within a tactic. Essentially, this means that individual trait distribution can be
602 heterogeneous, and mixture modelling is a powerful approach to account for this
603 structured heterogeneity. That being said, these models are much more complex and
604 much longer to run than mixed models, and determining the number of clusters can be
605 particularly challenging, especially for traits following a binary distribution (see Hamel et
606 al. (2017) for a review of the challenges with mixture modelling). If one is not interested

607 in obtaining cluster-specific parameters to contrast life-history tactics, then one
608 alternative is to use infinite mixture models in a Bayesian framework, which does not
609 require settling the number of clusters (Rasmussen 2000, Manrique-Vallier 2016).
610 Obviously, different methods offer different possibilities for quantifying variance within
611 a population, and the choice will depend on the question addressed and the biological
612 knowledge acquired so far for the trait studied.

613

614 **Joint modelling**

615 One major finding in the study of life-history strategies and individual heterogeneity is
616 that many traits are likely to be interdependent (van Noordwijk and de Jong 1986, Lindén
617 and Møller 1989, Dobson et al. 1999, Rollinson and Rowe 2016), such that their
618 covariance should be considered to assess reliably the evolutionary forces shaping these
619 traits and their influence on population dynamics. Indeed, life-history theory predicts
620 trade-offs among traits such as survival, reproduction, and growth, with expectations of
621 negative correlations between traits (see e.g. Roff (1992) and Stearns (1992) for reviews).
622 Yet, many studies have shown that individual heterogeneity can mask these trade-offs
623 and lead to positive correlations because the best individuals always do better (van
624 Noordwijk and de Jong 1986, Cam et al. 2002, Weladji et al. 2006, Hamel et al. 2009a).
625 Joint modelling is an approach perfectly suited to account for such dependency because it
626 quantifies the covariance across life-history traits. Thus, a joint modelling approach
627 directly models the latent correlation that commonly occurs across traits as a result of
628 individual heterogeneity and provides more precise estimates of age-related changes in
629 traits.

630

631 For instance, Cam et al. (2002) modelled simultaneously the probability of survival and
632 reproduction of kittiwakes (*Rissa tridactyla*). They combined these two dependent
633 variables by modelling their variance-covariance matrix to estimate the correlation
634 between individual effects. They found a strong positive correlation between
635 reproduction and survival, and the joint analysis estimated the probability of reproduction
636 while accounting for its correlation with disappearance. Their results provided clear
637 evidence that age-specific probability of reproduction observed at the population level
638 showed weaker senescence compared with estimates at the individual level. That
639 difference increased with age as a result of the strong positive correlation between
640 reproduction and survival. Cam et al. (2002) worked on two traits, but more traits could
641 be included in a joint model (see e.g. Browne et al. 2007, Cam et al. 2013). Of course, the
642 greater the number of traits included, the more complex the variance-covariance matrix,
643 and more data are needed to estimate all parameters. Furthermore, the joint modelling
644 approach can account for imperfect detection by using a capture-mark-recapture
645 framework.

646

647 Similarly, mixture models can provide a suitable integrating approach to model the
648 covariance among traits at the cluster level. For example, we used joint modelling to
649 determine the covariance among body growth, relative reproduction (the number of
650 offspring produced at age i for individual j /total number of offspring produced by all
651 individuals that year), and the probability of survival in bighorn sheep males (see
652 Appendix 1 for details on data and description of the analysis). We included age at

653 appearance and disappearance to account for selection processes, and mean yearling mass
654 to account for annual variation in environmental conditions. We found three clusters
655 corresponding to three life-history tactics (Fig. 8). In the tactic illustrated in red (Fig. 8)
656 males do well in all traits. They have a very strong growth early in life and reach the
657 highest asymptotic mass as adults. They also obtain the highest reproductive output,
658 particularly at old ages, and have a fairly high survival that does not seem to decrease
659 with increasing age as fast as for individuals playing other tactics. Males playing the two
660 other tactics perform generally less well on most traits, and the performance of these
661 males differs among traits. Males have similar growth early in life in both tactics, but
662 males in black (Fig. 8) allocate to growth for a longer period and attain a larger
663 asymptotic mass than those males in blue (Fig. 8). The males playing the "black tactic"
664 almost never manage to reproduce successfully during their lifetime (Fig. 8).
665 Interestingly, the decrease in growth rate observed around age 4 in the males playing the
666 "blue tactic" corresponds to the time when these males started allocating to reproduction
667 (Fig. 8). These results suggest that mass is unlikely to be the only determinant of
668 reproduction. Indeed, males playing the "red tactic" achieve greater reproduction likely
669 because they have reached a higher mass, which is positively correlated with social rank
670 (Pelletier and Festa-Bianchet 2006) and thereby with mating effort (Pelletier et al. 2006).
671 Males playing the "black tactic" allocate to growth and reach a higher asymptotic mass
672 than males playing the "blue tactic", which started allocating to reproduction from age 4,
673 but they have very low reproductive success compared to males playing the "blue tactic".
674 Therefore, the higher asymptotic mass achieved by males playing the "black tactic" is
675 likely due to a much lower allocation to reproduction compared to males playing the

676 "blue tactic". Finally, males playing the "blue tactic" also had a very low early survival
677 (i.e. at ages 0 and 1) compared with males playing the two other tactics. This might have
678 selected against lower quality males, and may explain the higher reproduction of males
679 playing the "blue tactic" compared to males playing the "black tactic". In such long-lived
680 and sexually dimorphic species, body mass is a fundamental determinant of fitness
681 (Pigeon et al. 2017), having a strong influence on both survival, particularly in early life
682 (Plard et al. 2015, Théoret-Gosselin et al. 2015), and reproduction (Pelletier and Festa-
683 Bianchet 2006, Pelletier et al. 2006, Mainguy et al. 2009). Therefore, these different life-
684 history tactics might be maintained because the fitness costs and benefits of each tactic
685 likely vary during a male's lifetime.

686 **Remaining challenges**

687 *Missing values*

688 In most studies, recapture/resighting rates are less than 1, meaning that not all surviving
689 individuals are measured at all ages, and therefore the within-individual changes I , the
690 appearance A , and disappearance D do not represent an exact decomposition of P . For
691 instance, even though the resighting probability of surviving male bighorn sheep was
692 $>95\%$, the average recapture probability of surviving males was 77% , meaning that the
693 data set on body mass includes more than 20% missing values. Missing values are
694 common in life-history studies, and bias may arise if the probability that a value is
695 missing is associated with the trait studied. For example, comparing the average mass in
696 each age class for male bighorn sheep measured at age i and $i + 1$ with the average mass
697 for males that survived from age i to $i + 1$ but were only measured at age i (i.e. males
698 with missing values), we see a tendency for missing values to occur in heavier males

699 (Fig. 9). Larger males were thus less likely to be weighed the following year than lighter
700 males, meaning that the within-individual changes across these ages may be biased.
701 Removing bias requires modelling the missing value process (Little 1995).

702

703 *Imperfect detectability*

704 In addition to missing values, imperfect detection probability is the rule in most studies
705 and is therefore another major challenge when quantifying the contribution of ontogeny
706 and selection to phenotypic changes. This problem is directly linked with the missing
707 value issue because the detection probability will directly determine the rate of missing
708 values, as well as the survival estimates. This problem is addressed in detail in Gimenez
709 et al. (2017).

710

711 *Standardization*

712 For comparing responses among traits within a population or for comparing the same trait
713 among populations or species, one is confronted with issues of standardization – i.e.,
714 finding a common measurement scale (Hamel et al. 2014). This can result from the
715 variable type (e.g. numeric vs. binary, with implicit differences in variances that are used
716 for standardizing variables; Gelman (2008)), or from different transformations associated
717 with the statistical analyses (e.g. logit vs. log for proportions; Link and Doherty (2002)).
718 Analyses have also used proportional changes (see the discussion of Rebke’s method, and
719 Hamel et al. (2016)), which might be sensitive to the reference value used. One must also
720 remember that inferences are model-dependent, meaning that the choice of the model
721 structure can influence effect sizes (e.g. Knappe et al. 2011). This makes comparisons

722 among study systems challenging because different systems often require different
723 modelling structures. Moreover, the variability of a trait might reflect evolutionary
724 changes (e.g. environmental canalization as for adult survival in long-lived vertebrates;
725 Gaillard and Yoccoz (2003)), or differences in environmental variability. There is no
726 simple solution to this problem (Greenland et al. 1986), except that it requires careful
727 consideration of both what causes variation in heterogeneity, and of its consequences.

728

729 Standardization issues also arise when comparing the strength of different predictors, for
730 instance among ontogeny, selection, and environmental processes or for a given process –
731 e.g. contrasting natural versus artificial selection across different environmental
732 conditions. Predictors need to be standardized (Schielzeth 2010) to provide estimates of
733 the relative influence of ontogeny, selection, and environmental variation that are
734 comparable, but estimates are then not comparable in terms of units of change of the trait
735 with age. This may be problematic when the aim is to compare how these processes
736 change at each age, and in such cases keeping the units of change with age might be more
737 appropriate to contrast the relative influence of ontogeny and selection processes. When
738 comparing the relative influence of various environmental variables, however,
739 standardizing the environmental estimates is recommended. Standardization depends on
740 the reference value used, and the choice of the reference level to measure climate
741 variability is fundamental but far from simple (Harris et al. 2014). When the aim is to
742 evaluate whether the variability observed during the ecological study is affecting the
743 traits observed, using the variability observed in the data would be appropriate.
744 Nevertheless, variability observed in climatic data (i.e. historical variability) could be

745 useful to determine how climate change has affected traits over time. Essentially,
746 standardization requires specifying what kind of question we are trying to answer to
747 insure valid comparisons (Nakagawa and Cuthill 2007), and effect sizes should be
748 interpreted with careful considerations of the reference value used. Above all, authors
749 should present the standard deviations used for standardizing variables in order to retrieve
750 the unstandardized estimates.

751

752 **Summary**

753 Understanding how life-history traits vary as individuals age is central to life-history
754 theory because age-specific variability influences the evolution of traits and their effects
755 on population dynamics. Therefore, heterogeneity resulting from individual differences
756 affects our perception of how life-history traits change with age at the population level
757 because selection leads to an overrepresentation of specific individuals at certain ages,
758 and because ontogenetic processes themselves can vary across individuals owing to
759 heterogeneity in life-history tactics. We have presented the most recent and common
760 methods used to account for individual heterogeneity when estimating changes in life-
761 history traits with age (Table 1) and proposed a method that combines approaches to take
762 benefit from their strengths while also overcoming many of their limitations. Our
763 combined approach can also be used in the context of mixture modelling, which looks at
764 different levels of individual heterogeneity, and thereby allows assessing the influences
765 of heterogeneity in life-history tactics on the relative contribution of ontogeny, selection,
766 and environmental variation to population trajectories. Finally, we showed that using a
767 joint mixture modelling approach is valuable because it uses the latent correlation shared

768 among multiple traits to identify ontogenetic tactics with dependency among multiple
769 life-history traits. Overall, all approaches have their strengths and limitations. The best
770 method should be chosen in perspective with the question we aim to answer, and, as
771 suggested by Nussey et al. (2011), complementary approaches will sometimes be
772 necessary to obtain a better understanding of the system.

773

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783

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Fig. 1

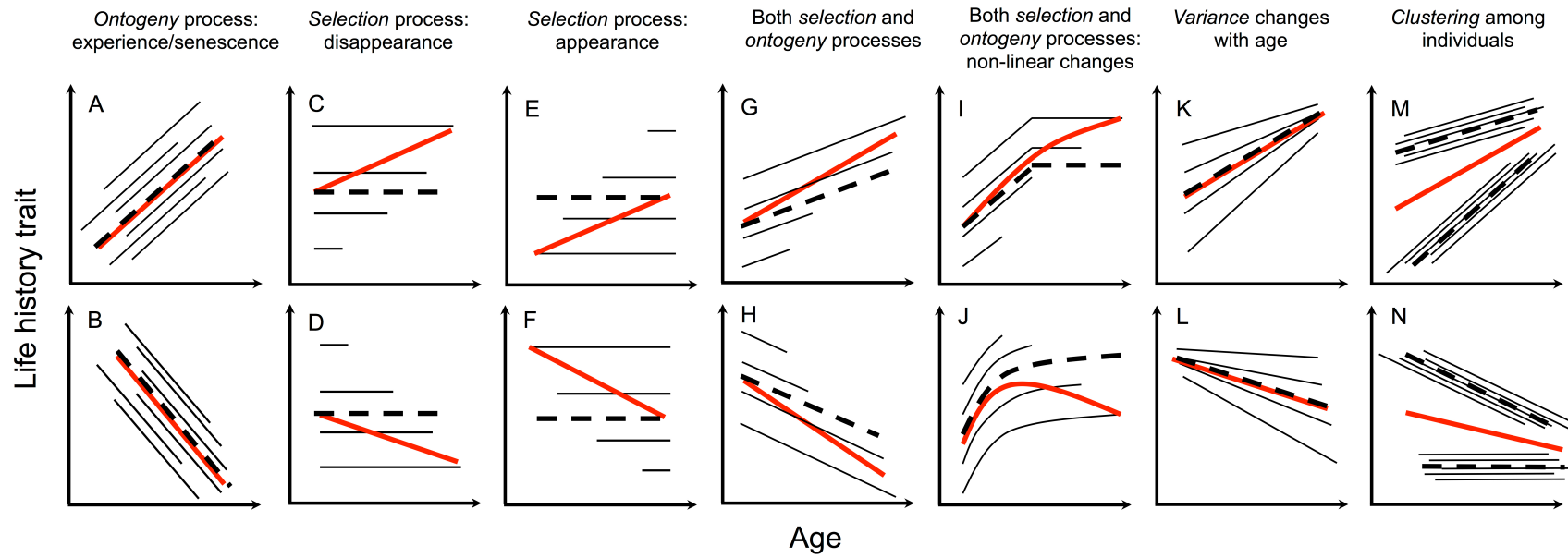
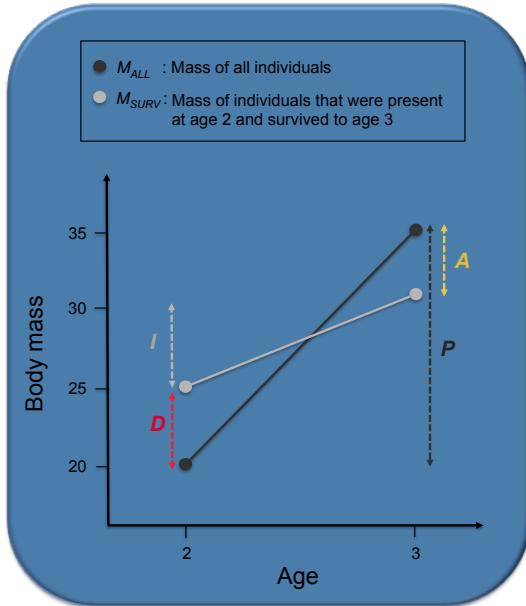


Fig. 2

A. Approach proposed by Rebke et al. (2010)



Processes occurring between age i and $i + 1$ are computed as

$$P_{i,i+1} = I_{i,i+1} + D_{i,i+1} + A_{i,i+1}$$

where, e.g. between age 2 and 3

- average population change $P_{2-3} = M_{ALL_3} - M_{ALL_2}$
- within-individual change $I_{2-3} = M_{SURV_3} - M_{SURV_2}$
- selective disappearance $D_{2-3} = M_{SURV_2} - M_{ALL_2}$
- selective appearance $A_{2-3} = M_{ALL_3} - M_{SURV_3}$

When some individuals have missing values at age $i + 1$, D can be computed by working at the individual level j as

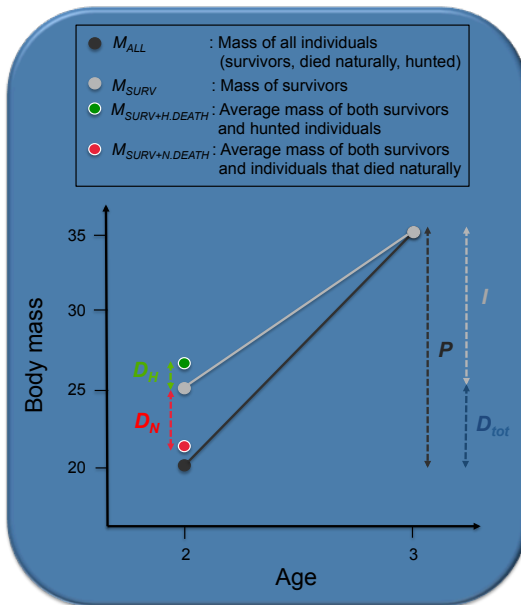
$$D_{i,i+1} = \sum(D_{j,i,i+1})$$

where, e.g. between age 2 and 3

$$D_{j,2-3} = (M_{j,2} - M_{SURV,2}) * ((S_{j,2-3} - S_{ALL,2-3}) / S_{ALL,2-3})$$

and where M_j is the mass of individual j , S_j the survival of individual j (scored as 0 or 1), and S_{ALL} the average survival during the age interval

B. Approach to separate artificial and natural disappearance



Without appearance, processes occurring between age i and $i + 1$ are computed as

$$P_{i,i+1} = I_{i,i+1} + D_{tot,i,i+1}$$

where

$$D_{tot,i,i+1} = D_{N,i,i+1} + D_{H,i,i+1}$$

Such that, e.g. between age 2 and 3

- average population change $P_{2-3} = M_{ALL_3} - M_{ALL_2}$
- within-individual change $I_{2-3} = M_{SURV_3} - M_{SURV_2}$
- total selective disappearance $D_{tot,2-3} = M_{SURV_2} - M_{ALL_2}$
- natural selective disappearance $D_{N,2-3} = M_{SURV_2} - M_{SURV+N.DEATH_2}$
- artificial selective appearance $D_{H,2-3} = D_{tot,2-3} - D_{N,2-3}$

Fig. 3

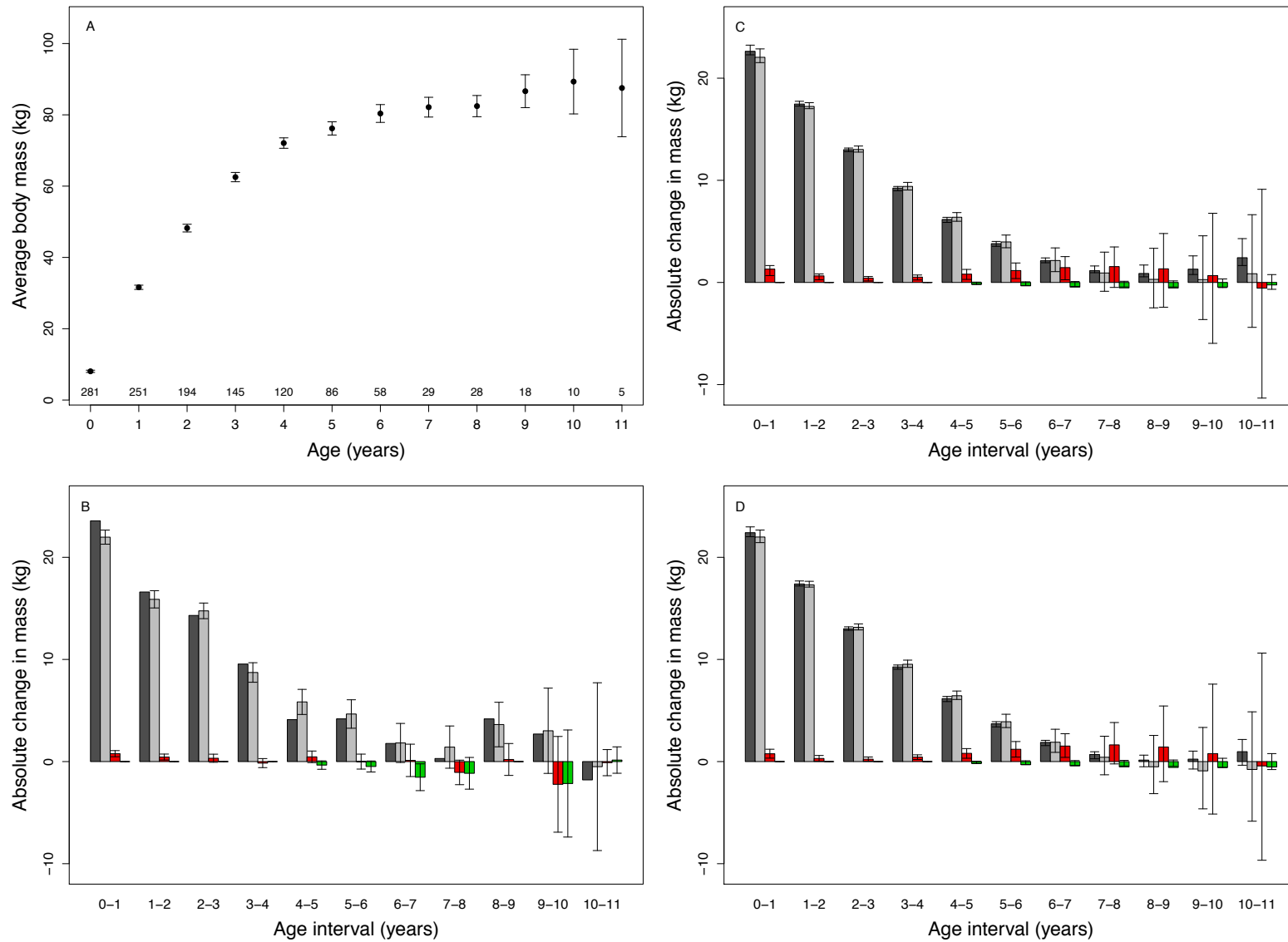
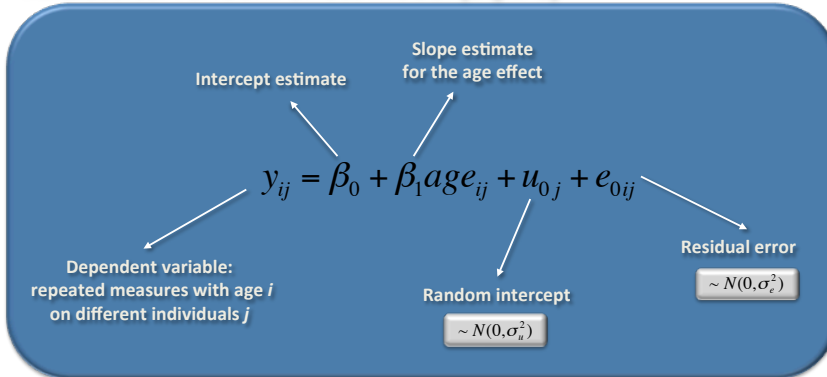
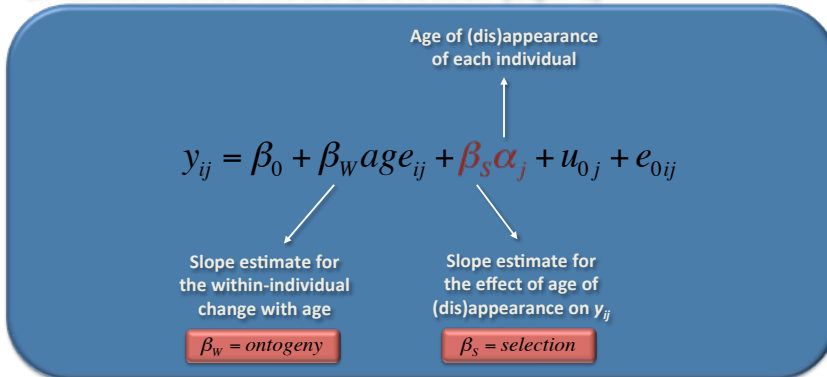


Fig. 4

A. Classical random effect model (eqn. 1)



B. Random effect model & selection (eqn. 2)



C. Random effect model & selection + environment (eqn. 3)

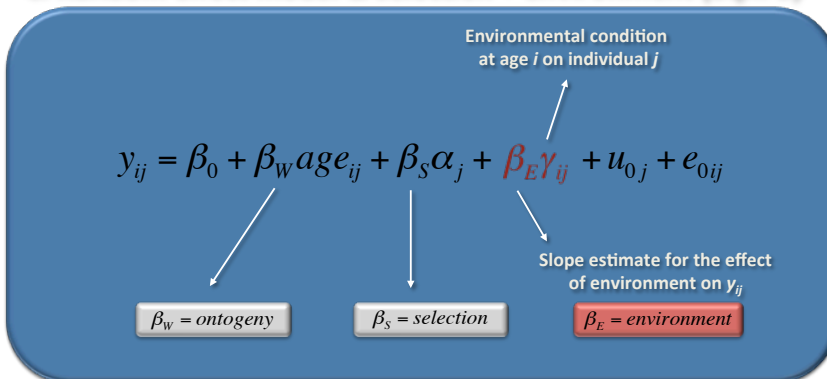


Fig. 5

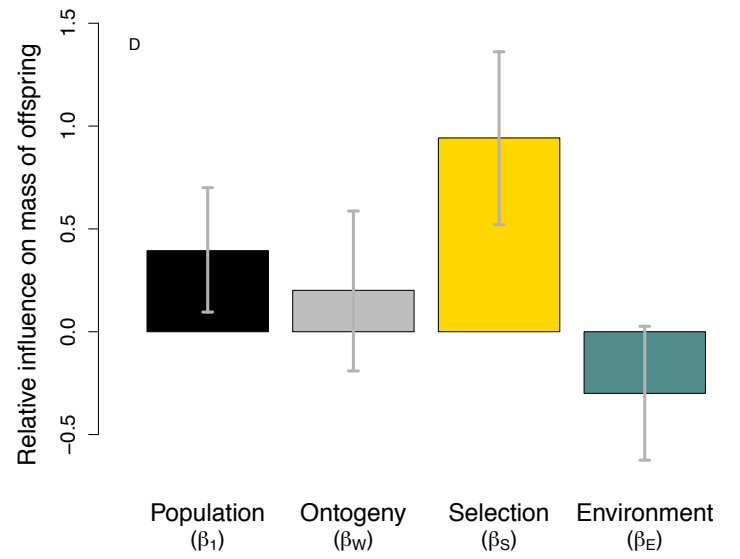
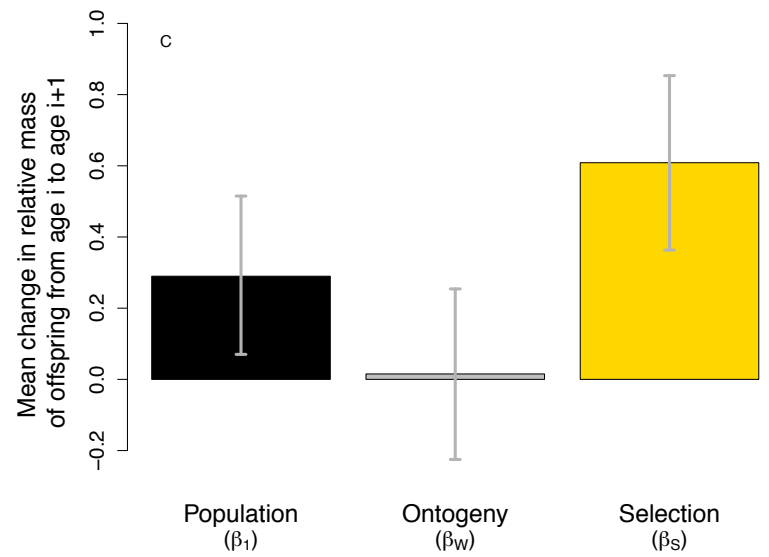
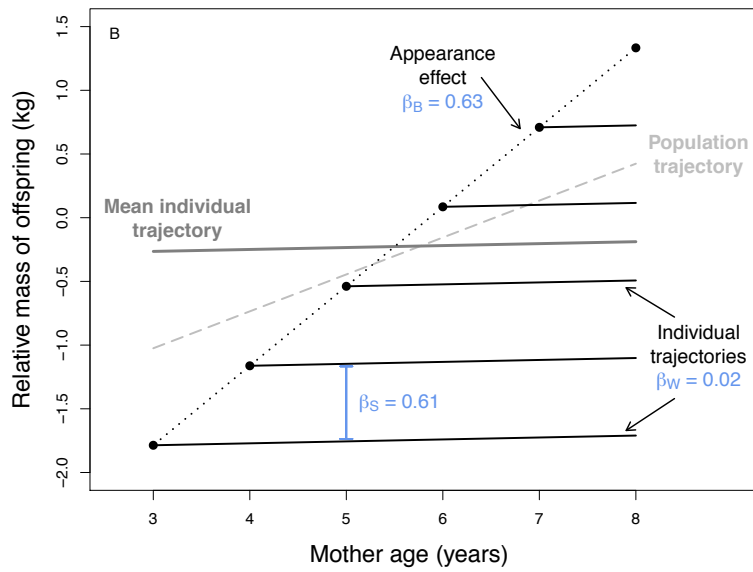
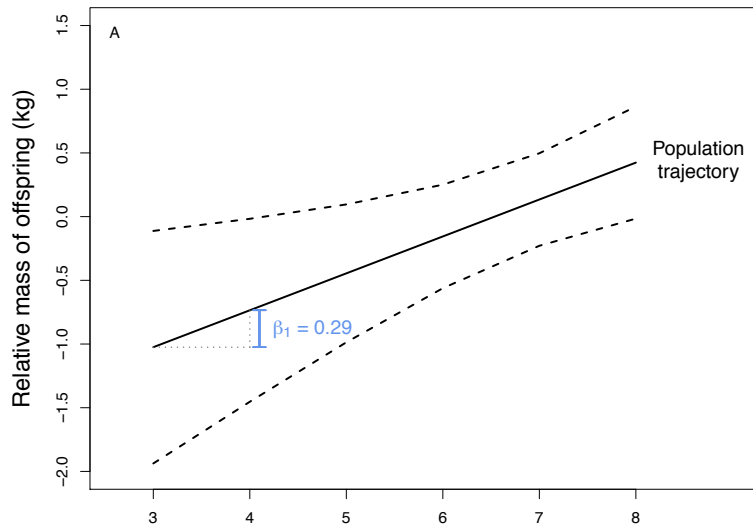


Fig. 6

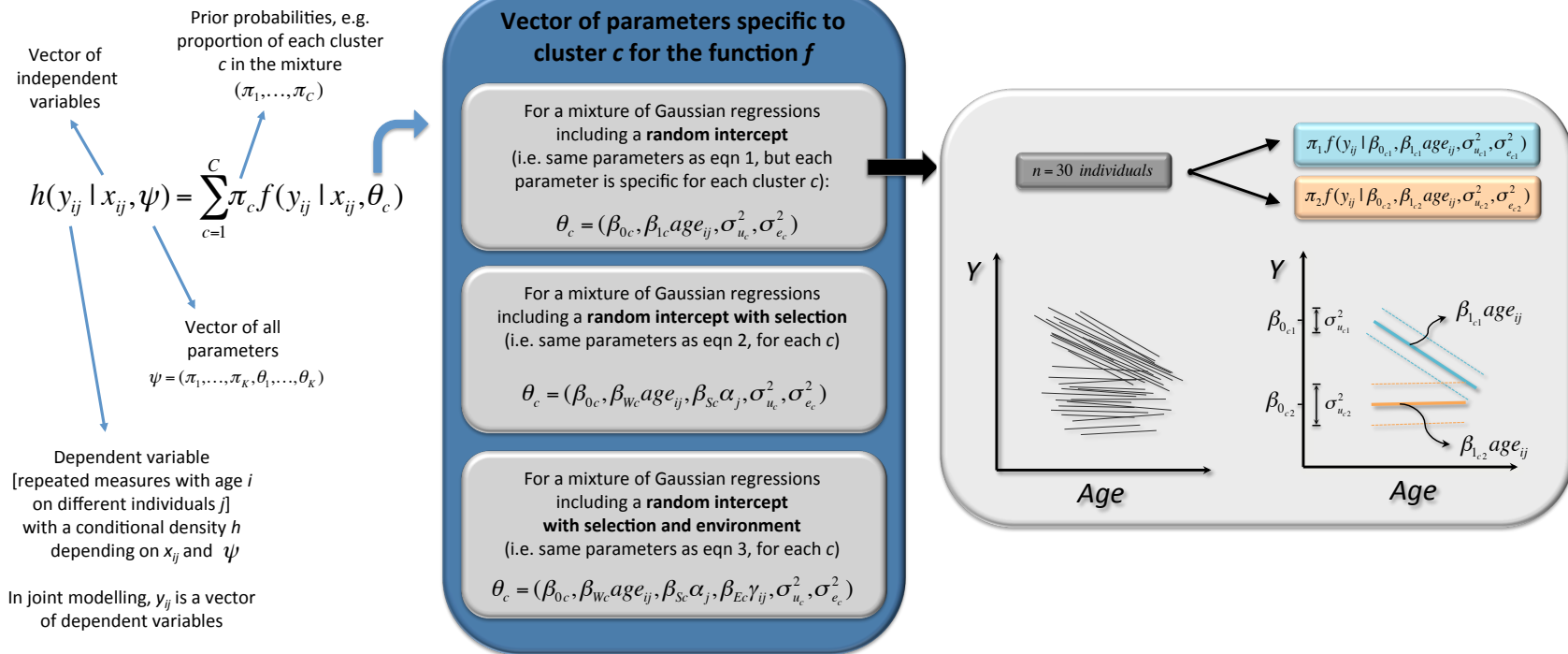


Fig. 7

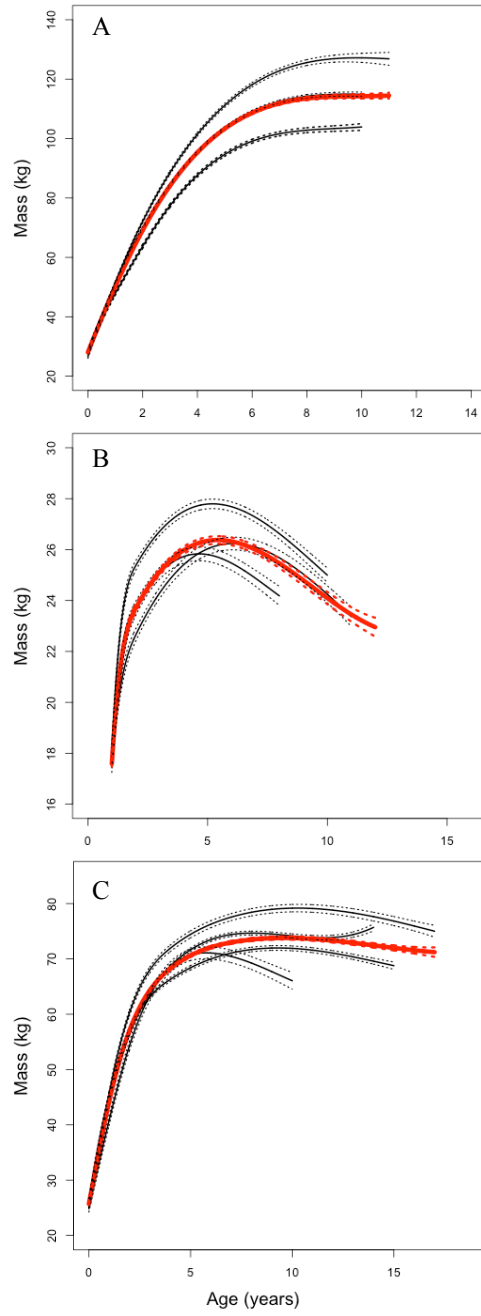


Fig. 8

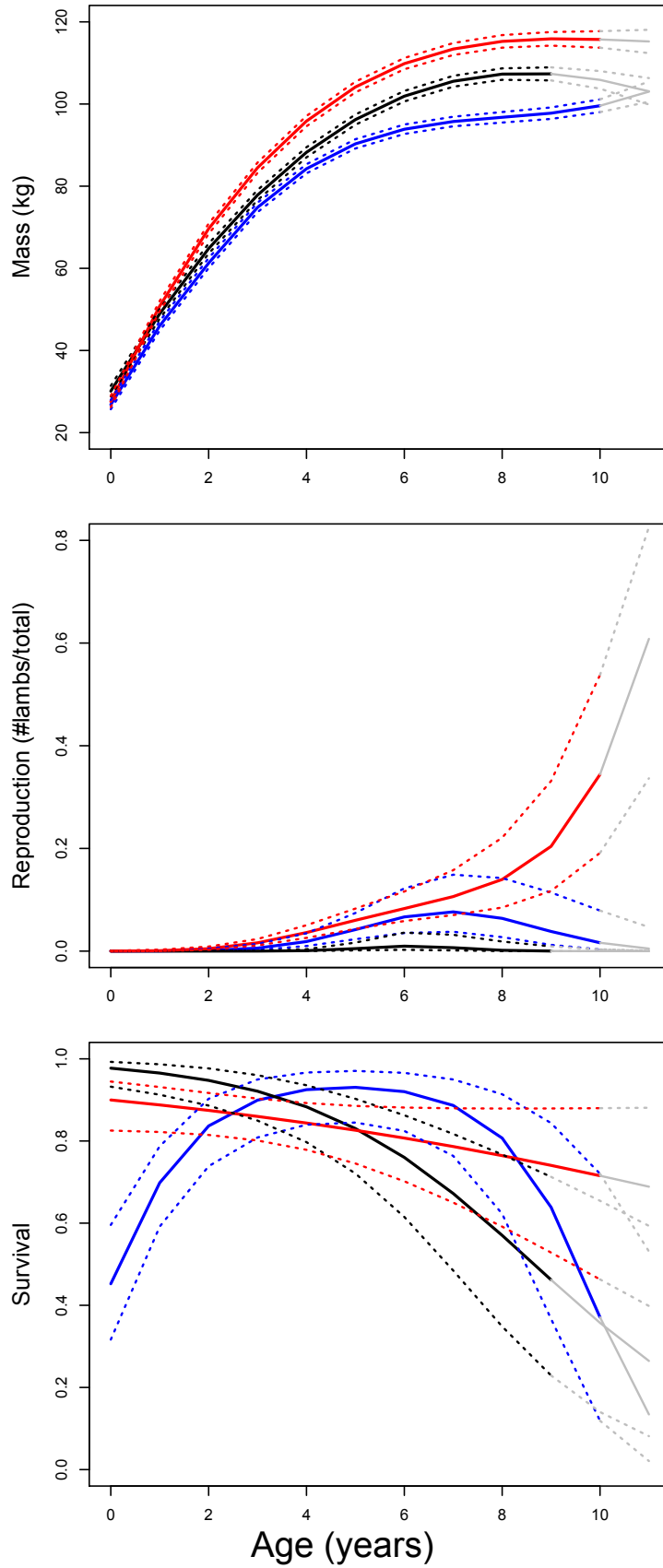


Fig. 9

