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

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Heterogeneity among individuals influences the life-history trajectories we observe at the population level because viability selection, selective immigration and emigration processes, and ontogeny change the proportion of individuals with specific trait values with increasing age. Here, we review the two main approaches that have been proposed to account for these processes in life-history trajectories, contrasting how they quantify ontogeny and selection, and proposing ways to overcome some of their limitations. Nearly all existing approaches to model individual heterogeneity assume either a single normal distribution or a priori known groups of individuals. Ontogenetic processes, however, can vary across individuals through variation in life-history tactics. We show the usefulness of describing ontogenetic processes by modelling trajectories with a mixture model that focuses on heterogeneity in life-history tactics. Additionally, most methods examine individual heterogeneity in a single trait, ignoring potential correlations among multiple traits caused by latent common sources of individual heterogeneity. We illustrate the value of using a joint modelling approach to assess the presence of a shared latent correlation and its influence on life-history trajectories. We contrast the strengths and limitations of different methods for different research questions, and we exemplify the differences among methods using empirical data from long-term studies of ungulates.

Introduction

Age-specific changes affect the evolution of traits and their influence on population dynamics (Vaupel and Yashin 1985, Vindenes and Langangen 2015). It is therefore essential to quantify accurately how life-history traits vary with age. Life-history trajectories are usually quantified at the species or population levels (Mysterud et al. 2001), but changes in life-history traits with age occur at the individual level. Indeed, life-history trajectories result from a combination of ontogenetic processes at the individual level, selection processes leading to the appearance (through fertility

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selection or immigration) or disappearance (through viability selection or emigration) of individuals within a population, and multiple environmental influences on individuals. As a result, a substantial part of the age-specific variation observed at the population level is often due to heterogeneity among individuals (Service 2000, van de Pol and Verhulst 2006, van de Pol and Wright 2009).

Typically, ontogenetic trajectories of life-history traits display a ∩-shaped (Emlen 1970 for reproductive performance) or U-shaped (Caughley 1966 for mortality = 1 – survival) curve with age: survival and reproductive traits increase until a plateau is reached during prime-age, and then decrease until death. Variation in reproductive traits with age may result from two main ontogenetic processes. First, reproductive output can increase early in life as individuals gain experience or allocate more to reproduction, reflecting an improvement with age (Curio 1983, Forslund and Pärt 1995) (Fig. 1A). Second, reproductive output can decrease at old age as a result of senescence (see Nussey et al. 2013 for a review of empirical evidence in vertebrates) (Fig. 1B), which corresponds to the irreversible decline of physiological and cellular functions with increasing age (Medawar 1952). Although the basic concepts behind these ontogenetic processes are relatively simple, other processes such as viability and fertility selections (as defined by Fisher 1930) can have fundamental influences on the average ontogenetic patterns observed at the population level. On one hand, viability selection removes certain phenotypes at younger ages, typically frail individuals, leading cohort composition to change with age (Vaupel et al. 1979, Newton and Rothery 1998) and thereby affecting the age-specific mean and variance of a trait at the population level (Fig. 1C–D). For example, in red-billed choughs *Pyrrhocorax pyrrhocorax*, the decline in offspring survival with increasing parental age observed at the population level results from the disappearance of short-lived parents whose offspring have higher survival than those born to long-lived parents (Reid et al. 2010) (Fig. 1D). On the other hand, fertility selection leads to individual variation in reproductive performance, such that certain genotypes will contribute more to reproduction than others (Wooller et al. 1992), which will in turn affect the patterns observed at the population level. If selection fine-tunes first reproduction according to body size or body condition, individuals with different phenotypic traits will enter the breeding population at different ages (Forslund and Pärt 1995 in birds, Weladji et al. 2010 in mammals) (Fig. 1E–F). For example, the observation at the population level that female oystercatchers *Haematopus ostralegus* produce larger eggs as they age is mainly the result of females producing larger eggs when they delay first reproduction (van de Pol and Verhulst 2006). Thus, there is an increasing proportion of females producing larger eggs in the breeding population with increasing age, leading egg size to increase with age at the population level (Fig. 1E).

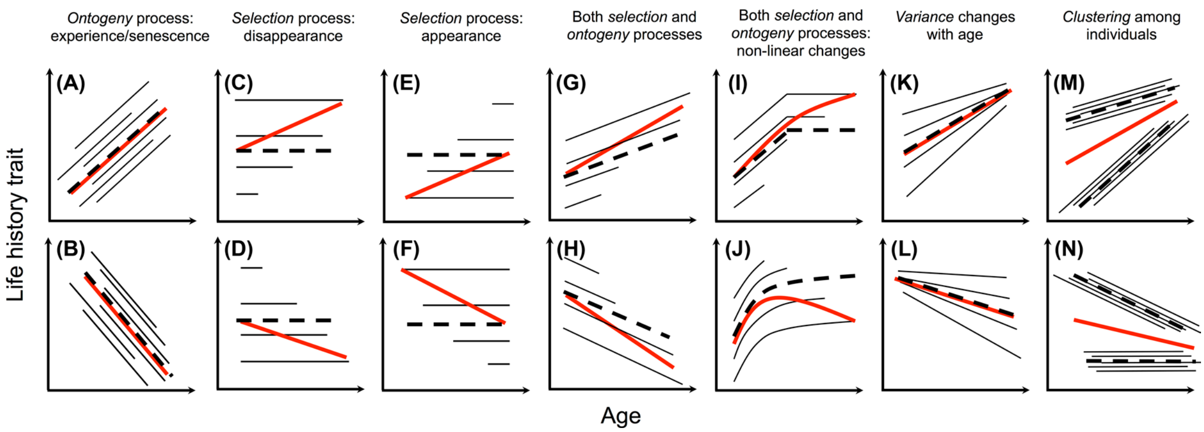

Figure 1. Potential changes in a life-history trait with age (black solid: individual responses, red solid: mean population responses, black dotted: the mean of individual responses). Upper panels: scenarios with population-level improvement with age. Lower panels (except J): scenarios with population-level deterioration with age. First column: scenarios where the *ontogeny* process occurs, with a real improvement (A: experience) or deterioration (B: senescence) with age at the individual level. Second column: scenarios where the *selection* process takes place as a result of disappearance of individuals as cohorts age (C: 'low-quality' individuals disappear, D: 'high-quality' individuals disappear). Third column: scenarios where the selection process takes place due to appearance of individuals as cohorts age, for example because of differences in age at first reproduction (E: 'high-quality' individuals appear, F: 'low-quality' individuals appear). Fourth and fifth columns: most probable scenarios, where both selection and ontogeny processes occur. Note that all curves representing changes with age could be nonlinear, as shown in the fifth column. Sixth column: potential influence of environmental conditions on the between-individual variance in a life-history trait – (K) individuals with lower intercepts (i.e. a poor start) have more positive slopes than individuals with higher intercepts, indicating that compensation reduces differences among individuals at older ages, (L) individuals with lower intercepts have steeper negative slopes than individuals with higher intercepts, as observed when effects accumulate and increase the initial differences among individuals with increasing age. Last column: clustering among individuals resulting in distinct life-history tactics within a population – (M) stronger improvement with age in the cluster that started poorly, (N) deterioration with age only in one cluster. This figure expands on Fig. 1 in van de Pol and Verhulst (2006).

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

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

Variation in environmental conditions over the lifetime can also affect each individual differently depending on its state (McNamara 1998), influencing the mean and the variance of the responses observed at the population level (Yashin et al. 2002, Barbraud and Weimerskirch 2005, Nussey et al. 2007, Hamel et al. 2009b). While assessments of environmental effects on average population responses have received considerable attention in ecological research, less attention has been given to how environmental conditions may lead to variation in individual responses (Wilson et al. 2009). Early environment influences the condition of individuals and hence their initial trait values, such as age at first reproduction (Albon et al. 1987, Lindström 1999, Forchhammer et al. 2001). Statistically, this means that environmental conditions affect the intercepts of individual responses (Fig. 1). These effects may persist throughout the lifetime (Metcalfe and Monaghan 2001) or may disappear as a result of early-life selection (Vedder and Bouwhuis 2017). Conditions experienced later in life, however, might affect between-individual differences as individuals are ageing. If environmental effects accumulate with age, they may accentuate initial between-individual differences (Nussey et al. 2007) (Fig. 1L). If individuals can compensate for poor early conditions, individual differences should decrease with age (Hamel et al. 2016) (Fig. 1K). Statistically, environmental conditions can affect not only the intercepts (i.e. variation at early age), but also the slopes of individual responses, leading the variance in life-history traits to vary over age (Schielzeth and Forstmeier 2009, van de Pol and Wright 2009) (Fig. 1K–L).

Previous research has shown that selection processes and environmental influences may shape patterns of ontogeny observed at the population level (Sunderland et al. 1976, Yashin et al. 2002). Until recently, the lack of data from individually marked animals monitored from birth to death limited our ability to assess the relative importance of these processes and how they varied between the individual and the population levels. In the past decade, however, longitudinal studies have provided the high-quality data required to assess these patterns empirically (Clutton-Brock and Sheldon 2010) and to develop methods integrating these effects in analyses of life-history variation with age (Rattiste 2004, Nussey et al. 2006, 2011, van de Pol and Verhulst 2006). For instance, Rebke et al. (2010) showed that changes in annual reproduction in common terns are mostly the result of ontogenetic processes, yet the smaller effects of viability selection result in complex interactions with ontogeny. In great tits *Parus major*, Bouwhuis et al. (2009) showed that accounting for the selective disappearance of individuals by including the age at last reproduction reveals that the onset of senescence is nearly one year earlier (2.8 versus 3.5 years of age) than what is observed at the population level. The complexity of ontogenetic and selection processes means that an adequate quantification of their relative contributions to life-history trajectories is of fundamental importance to understand evolutionary dynamics. Furthermore, the importance of individual heterogeneity in shaping population responses reveals a need to understand its impact on ontogenetic processes.

Here, we review approaches to account for individual heterogeneity when estimating/studying/quantifying life-history trajectories with age, demonstrating how each method quantifies the ontogenetic, selection, and environmental processes taking place within a population. Specifically, we compare the demographic decomposition of observed changes proposed by Rebke et al. (2010) with the statistical modelling approach based on random effect models proposed by van de Pol and Verhulst (2006). Furthermore, we demonstrate how mixture models can quantify how population processes are affected by the relative proportions of individuals displaying a given life-history tactic. We also show how joint modelling of life-history traits can evaluate the covariance among traits and its impact on population processes. We illustrate these methods using empirical data from long-term studies of ungulates (see Supplementary material Appendix 1 for the specific details of the study areas, data collection and analyses). We conclude by contrasting the strengths and limitations of these methods in answering different questions and show how combining methods can overcome some limitations. We focus on methods developed for populations with individual detection probability close to 1. Approaches used to account for individual heterogeneity in the context of capture–mark–recapture (CMR) in populations with imperfect detection are covered in detail by Gimenez et al. (2018).

Demographic decomposition

The decomposition of demographic changes based on a derivation of the Price equation (Price 1970) first appeared in studies of human demography (Vaupel and Canudas Romo 2002) and then in evolutionary ecology (Coulson and

Tuljapurkar 2008). Rebke et al. (2010) built on these previous works to present a demographic decomposition approach at the population level to disentangle within-individual trait change from changes caused by selective appearance and disappearance at each age. They quantified the selection resulting from appearance/disappearance based on differences in the mean trait between different groups of individuals rather than on the covariance (Rebke et al. 2010). It provides an exact decomposition of the average population change *P* of a trait in each age interval into average within-individual change *I* and change due to selective appearance *A* and to selective disappearance *D*, assuming that all individuals remaining in the population are measured (Fig. 2A).

Thus, the method allows quantifying directly ontogeny (*I*) and selection processes (*A* and *D*) for each age interval (Table 1). The exact decomposition at each age captures the relative importance of the different processes across the lifespan. Nevertheless, low sample sizes in late life is the rule because few individuals survive to old age, which leads to high uncertainties in late-life estimates (Rebke et al. 2010; see also the example below). The small sample of old individuals prevents an accurate assessment of senescence patterns at oldest ages, an important focus of all studies of age-specific variation in traits (Evans et al. 2011, Nussey et al. 2011, Zhang et al. 2015), and makes it difficult to compare the strength of processes between early and late life. This is not specific to this

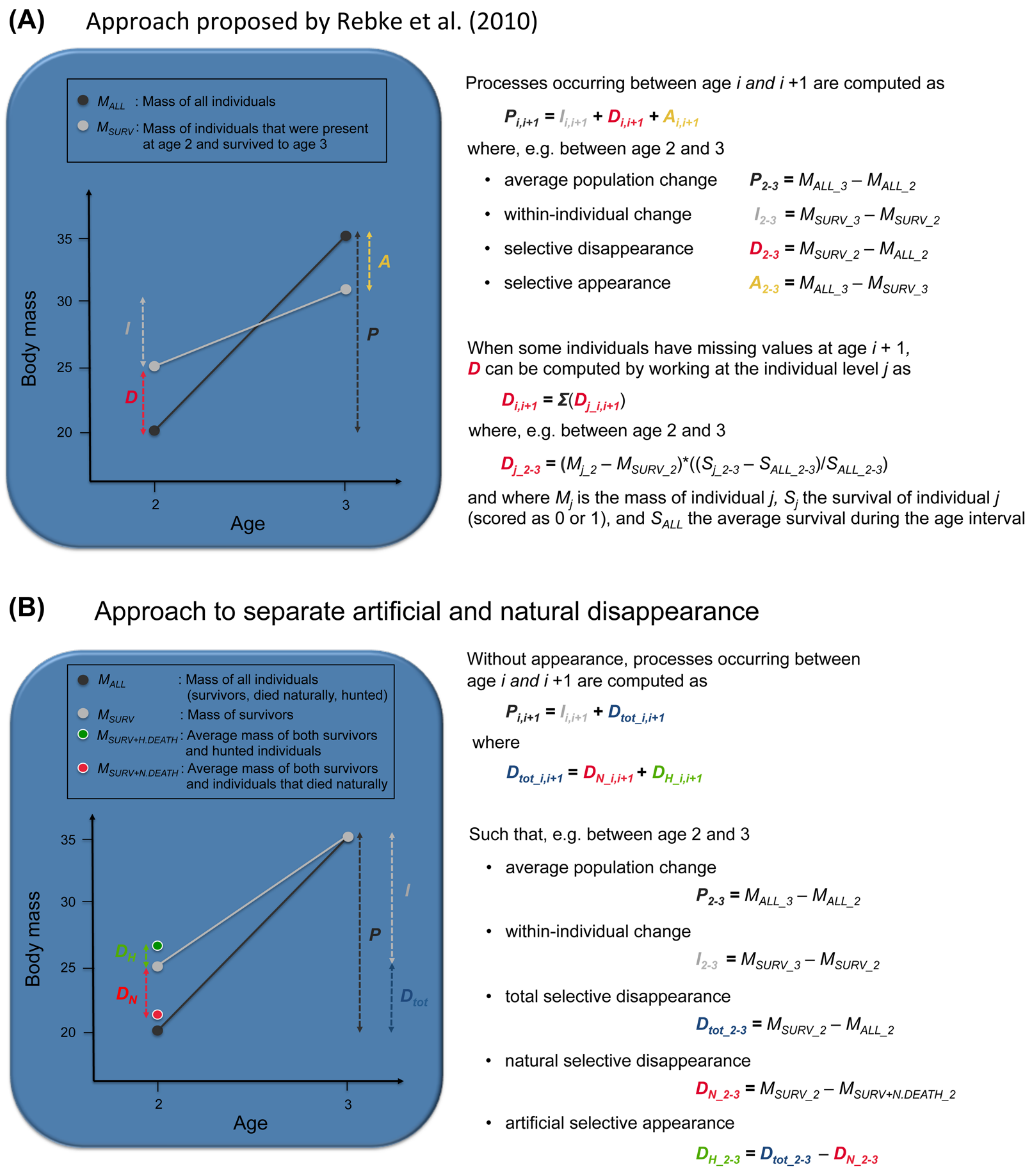

Figure 2. The demographic decomposition approach proposed by Rebke et al. (2010; A), and an extension to this approach to separate artificial and natural disappearance in harvested populations (B). This figure illustrates the average phenotypic change *P* in body mass between ages 2 and 3 observed at the population level, which is decomposed to quantify the true ontogenetic change (i.e. within-individual change *I*) and selection processes (i.e. selective appearance *A* and disappearance *D*) for that age interval.

Table 1. Pros and cons of the different approaches to quantify population processes while estimating how life-history traits change with age. The table displays in bold characteristics that are not available when using the formal approach but can be estimated when using the combined approached developed here). Latent tactics correspond to clusters of age-related changes not identified a priori (see text). Symbols match notations in Fig. 2, 4 and 6.

Characteristic	Demographic decomposition	Statistical modelling	Mixture modelling
Quantification of ontogeny			
– over the entire lifespan	Yes ($\sum I_{i,i+1}$)	Yes (β_W)	Yes (β_{Wc1}, β_{Wc2}, …)
– for specific ages/stages	Yes ($I_{i,i+1}$)	**Yes ($\boldsymbol{\beta_{Wj}}$)**	Yes (β_{Wc1_j}, β_{Wc2_j}, …)
– for latent tactics	No	No	Yes
Quantification of selection			
– over the entire lifespan	Yes ($\sum A_{i,i+1}$; $\sum D_{i,i+1}$)	Yes (β_S)	Yes (β_{Sc1}, β_{Sc2}, …)
– for specific ages/stages	Yes ($A_{i,i+1}$; $D_{i,i+1}$)	**Yes ($\boldsymbol{\beta_{Sj}}$)**	Yes (β_{Sc1_j}, β_{Sc2_j}, …)
– for latent tactics	No	No	Yes
Quantification of environmental effects			
– over the entire lifespan	No	**Yes ($\boldsymbol{\beta_E}$)**	Yes (β_{Ec1}, β_{Ec2}, …)
– for specific ages/stages	No	**Yes ($\boldsymbol{\beta_{Ej}}$)**	Yes (β_{Ec1_j}, β_{Ec2_j}, …)
– for latent tactics	No	No	Yes
Quantification of variance (frailty/latent effect)			
– latency specific to a trait	No	Yes (σ^2_u)	Yes ($\sigma^2_{u\_c1}$, $\sigma^2_{u\_c2}$, …)
– joint latency for many traits	No	Yes (see Cam et al. 2002)	Yes
– higher level of latency	No	No	Yes
Issues with data:			
– handle missing values	Not directly, more difficult	Yes, but can generate bias if values are not missing at random	Yes, but can generate bias if values are not missing at random
– handle detectability issues	No	If performed in a capture–mark–recapture context	If performed in a capture–mark–recapture context

method, but reflects the tradeoffs between analyses based on a model of the trait-age relationship, which might be biased if the model is a poor approximation but is more precise, and more descriptive approaches, which are less biased but less precise. In addition, the method requires a full detection of individuals because they have to be measured each year they were present in the population to provide an exact decomposition (Rebke et al. 2010; however see Nussey et al. (2011) and Fig. 2A for dealing with individuals that are not measured every year but their fate is known). Consequently this approach has only rarely been used to date (Evans et al. 2011, Nussey et al. 2011, Evans and Sheldon 2013, Hayward et al. 2013, Zhang et al. 2015).

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

Compared with the statistical approach presented in the next section, the demographic decomposition proposed by Rebke et al. (2010) does not need to estimate or correct for heterogeneity in individual differences. This is advantageous compared with the statistical modelling because the latter accounts for and quantifies heterogeneity using specific fixed and random effects, and the modelling choices for these effects can influence results and may not always reliably estimate heterogeneity (van de Pol and Wright 2009, Hamel et al. 2012). Still, this means that the demographic decomposition does not provide a direct quantification of individual heterogeneity, but it can be used as an initial step to describe this heterogeneity. To quantify processes within a single population, however, the results obtained from the demographic decomposition will not be affected by heterogeneity, unless one wishes to compare two distinct time periods that will be composed of different individuals.

To illustrate the method, consider the example of age-related body mass changes in male bighorn sheep *Ovis canadensis* (see Supplementary material Appendix 1 for details on data and study area). The mass observed at the population level may be affected by viability selection because smaller individuals are less likely to survive (Nussey et al. 2011, Hamel et al. 2016), particularly in early life (Gaillard et al. 1997, Théoret-Gosselin et al. 2015). In addition to this natural disappearance, selective harvesting also drives phenotypic change in this population because adult males (≥4 years) are harvested based on their horn size, which is correlated with body mass (Coltman et al. 2005, Bonenfant et al. 2009). We can therefore expect artificial disappearance of heavier males from age 4 and over. Immigration could also lead to appearance of different phenotypes, for instance if heavier males are more likely to disperse. That being said, only seven cases of male immigration have occurred over 43 years. We therefore excluded immigrants and two transplanted males and ignored appearance in this example. We decomposed the change in body mass with age as $P = I + D_N + D_H$, where D_N is the disappearance due to natural selection and D_H is the disappearance due to artificial selection (Fig. 2B). Note that because change in mass is not linear with age, we could not use annual mass to control for annual variation, and hence used absolute rather than relative change in mass as in Nussey et al. (2011; but see 'Combining approaches' section for a solution to this limitation). P showed a marked increase until four years of age, after which mass continued to increase slightly (Fig. 3A–B). Because senescence in body mass is observed in females of the same population (Nussey et al. 2011), perhaps the absence of senescence in males is due to trophy hunting removing males from the population before physiological functions begin to deteriorate. Nevertheless, the pattern of change in mass with age was similar at the individual level I, with no within-individual declines in mass at old age after accounting for artificial and natural selection (Fig. 3B).

The contribution of natural selective disappearance to age-related changes was clearly positive during the first years of life, supporting the occurrence of strong viability selection against lighter males in early life. For example, the mass difference at age 0 between males surviving to age 1 (8.9 kg) and all males (8.1 kg) indicates that selective disappearance causes an increase of 0.8 kg in mass. Later in life, natural disappearance was small and much more variable, with fluc-

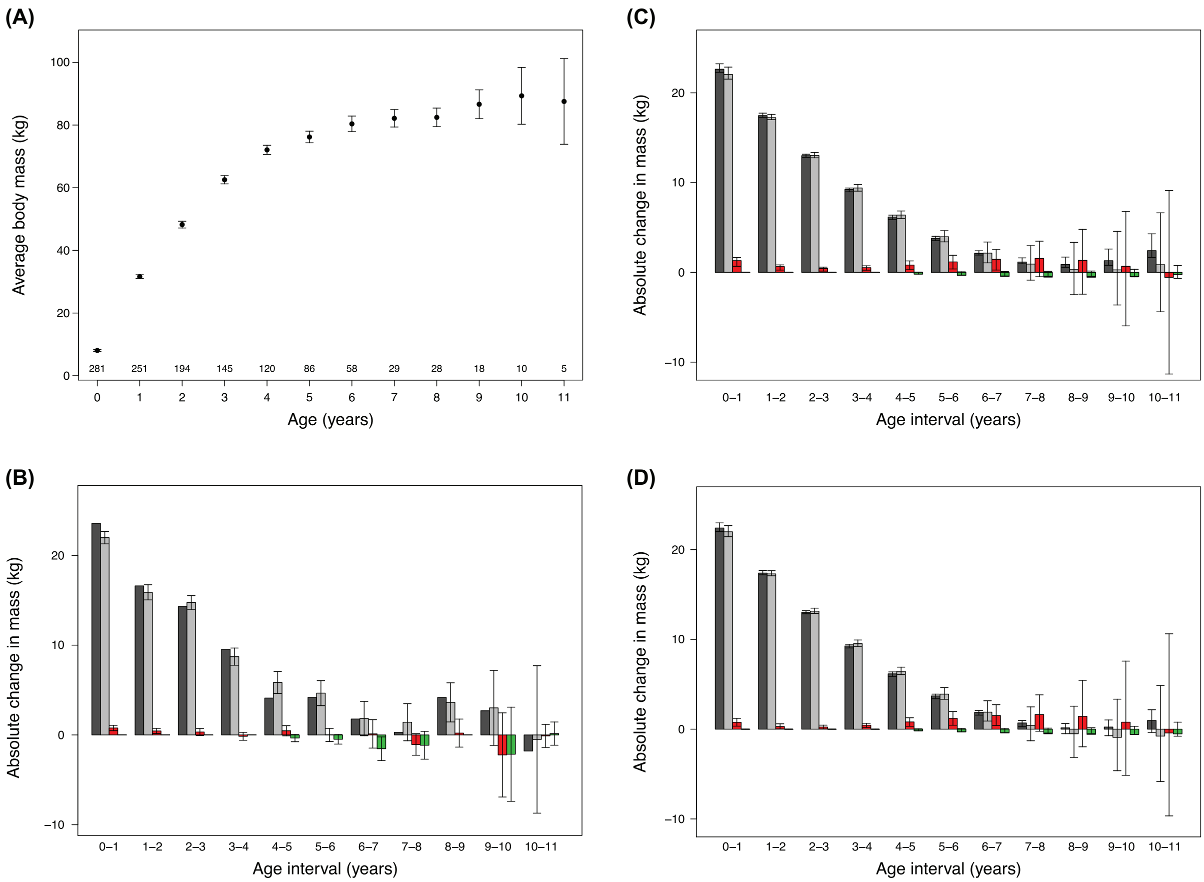

Figure 3. Growth trajectory in male bighorn sheep. (A) The observed variation in age-specific body mass, with the sample size for each age indicated at the bottom of the panel. (B to D) The relative contribution of ontogeny and selection processes to the growth trajectory. The decomposition of the absolute change in body mass at each age interval is based on the approach presented in Fig. 2B in (B), on a combination of the statistical modelling and the demographic decomposition approaches in (C) (see 'Combining approaches' section), and on the same approach as in (C) but accounting for annual environmental variation in (D). Dark grey bars represent the average population change, light grey bars the within-individual change, red bars the natural selective disappearance, and green bars the artificial selective disappearance as a result of hunting that begins at age 4. Positive disappearance values indicate selection against lighter males, whereas negative values indicate selection against heavier males. Error bars indicate the 95% confidence intervals.

tuations from positive to negative selection and vice versa from one age to the next. Estimates were also uncertain and imprecise, with confidence intervals often widely overlapping zero and widening at old ages due to low sample sizes (Fig. 3B). If we neglect the uncertainty of the estimations in late life, the absolute change in mass due to disappearance between ages 9 and 10 is greater than between ages 0 and 1 (Fig. 3B). Nonetheless, the difference of 0.8 kg at age 0 represents a 10% increase in mass induced by selective disappearance, which is larger than the 3% change in mass induced by selective disappearance at age 9. This small effect suggests little influence of natural selective disappearance in late life. On the other hand, disappearance due to artificial selection had a considerable influence in adult males, particularly those aged 4 to 8 years (Fig. 3B). Artificial disappearance due to harvesting always selected against heavier males, with survivors being up to 2 kg lighter than the whole population (Fig. 3B).

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

Statistical modelling

In 2006, van de Pol and Verhulst proposed accounting for selection processes by using a within-individual centring approach, a technique common in social sciences (Kreft et al. 1995, Hofmann and Gavin 1998, van de Pol and Verhulst 2006). This approach uses a random effect model that specifically includes age at appearance and/or disappearance as covariates, thus separating the within- and between-individual contributions to ageing. To start with, a random effect model can decompose the total variance in its between- and within-individual components, taking into account some of the dependence of repeated measures of the same individual at different ages (Eq. 1, Fig. 4A; additional dependency might be due to e.g. first-order autocorrelation, see Hamel et al. 2012). By including individual identity as a random intercept, the model provides a measure of change with age (β_1, Fig. 4A) that accounts for this non-independence. If an individual has a higher value for a trait than another individual, this difference in intercepts among individuals will be captured by u_{0j}, which estimates the among-individual variance in intercept σ_u^2 (Fig. 4A). The random effects are often called latent effects (described as, e.g. 'quality') because the underlying random variable is not measured.

As proposed by van de Pol and Verhulst (2006), adding the age of each individual at appearance and/or disappearance α_j (Eq. 2, Fig. 4B) as a covariate to this model allows evaluating the influence of timing of appearance/disappearance on within-individual changes with age. In the standard random effect model (Fig. 4A), the difference in phenotypic quality among individuals is modelled, whereas the model that includes selection (Fig. 4B) also includes the probability that phenotypic quality covaries with the chance of appearing or disappearing from the population. If one studies reproduction, for instance, age of appearance will be age at first reproduction and age at disappearance will be age at last reproduction. The random effect model that includes appearance/disappearance as a covariate provides a coefficient that measures the change in the trait intercept that results from variation in age at appearance/disappearance, β_S (Fig. 4B, 5B), thereby measuring the strength of the selection process. It also provides a coefficient that measures the within-individual change of the trait with age, β_W (Fig. 4B, 5B), a measure of ontogeny that accounts for appearance and disappearance, and therefore is not biased by selection. We can also compute the strength of the between-individual effect, which is simply the addition of the within-individual change and the selection effect, i.e. $\beta_B = \beta_W + \beta_S$ (Fig. 4B, 5B). Figure 5 illustrates how these parameters can be quantified, examining the relative change in offspring mass produced by mothers with different ages at first reproduction. The figure is based on empirical data from a long-term mountain goat population (see Supplementary material Appendix 1 for details) where females reach asymptotic mass at 7 years of age but primiparity ranges from 3 to 8 years (Festa-Bianchet and Côté 2008). We may therefore suspect the occurrence of fertility selection if mothers delaying first reproduction produce heavier offspring because the tradeoff between growth and reproduction weakens with age (Hamel and Côté 2009), or through experience, as primiparous mothers produce lighter offspring (Côté and Festa-Bianchet 2001). We grouped females aged 8 years and older because we did not expect difference in offspring mass after females had reached asymptotic mass (Côté and Festa-Bianchet 2001). To exemplify how fertility selection can be modelled, we accentuated the appearance effect by simulating a series of random values with a mean of 0.7 and a standard deviation of 0.5 (n = 196 simulated values, one for each kid mass available). We then multiplied this value by the age at first reproduction of the mother (centred) and added it to the mass of the kid.

To quantify processes, we ran mixed models ('lmer' function, 'lme4' package in R; Bates et al. 2015, <www.r-project.org>) according to Eq. 1 and 2 (Fig. 4A–B). This procedure

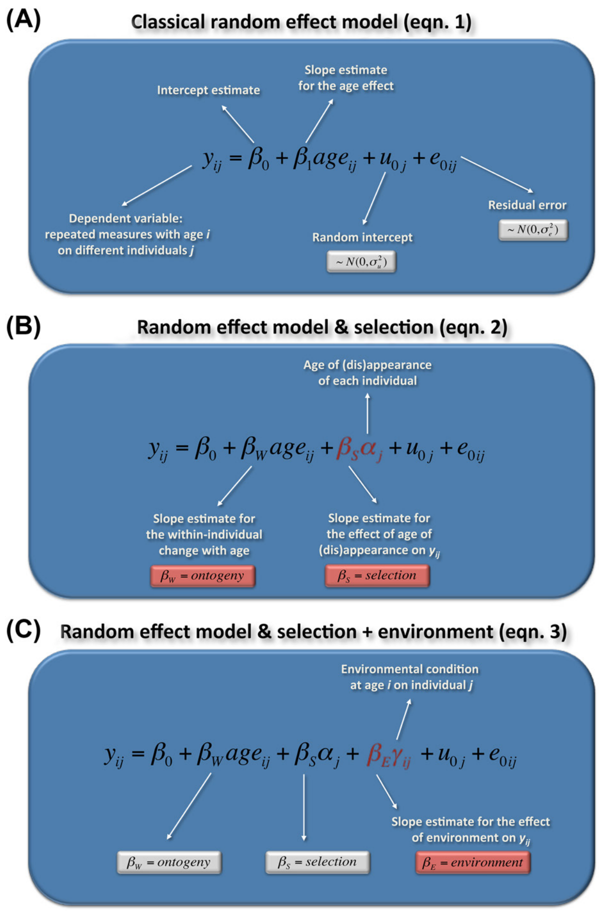

Figure 4. Different mixed models used to quantify heterogeneity among individuals, illustrating the classical random effect model that includes a random intercept to account for individual differences when assessing how a life-history trait changes with age (A), the same model but including the age at appearance or disappearance to separate and quantify the relative contribution of selection and ontogeny, i.e. the statistical modelling approach proposed by van de Pol and Verhulst (2006; B), and an extension of the approach presented in B where environmental covariates are included to quantify the influence of environmental variation on the change in trait trajectory with age (C). Equations are presented for traits following a normal distribution, and variables added from one equation to the next are highlighted in red.

estimated the relative change in kid mass with increasing maternal age at both the population level β_1 (Fig. 5A) and the individual level β_W (ontogeny; Fig. 5B), as well as the influence of appearance β_S (fertility selection; Fig. 5B). These parameters are then directly comparable and allow quantifying the relative importance of each population process (Fig. 5C). Because we forced a simulated effect of fertility selection, we see as expected that the change observed at the population level is not the result of a change with increasing age at the individual level, but is entirely caused by females that started to reproduce later and thereby produced heavier offspring. As for the demographic decomposition approach, we can obtain not only the quantification of the different processes, but also the within-individual trajectory by predicting the trajectory for the mean value of age at appearance (Fig. 5B) (but see 'Challenges' section for different ways of predicting trajectories depending on the questions of interest).

This statistical approach allows us to quantify directly ontogeny, β_W, and selection processes, β_S, over the lifespan (Table 1), but does not provide an exact decomposition at each age. The models, however, are quite flexible: they can be used when the average number of repeated measures of individuals is low (e.g. less than 2 in Class and Brommer 2016) and can account for different functions of age and age at appearance/disappearance (van de Pol and Verhulst 2006). For instance, we could model age as a factor, providing a measure of ontogeny at each age for a trait showing a nonlinear increase with age, such as growth (Fig. 3A). This, however, would assume that the effect of age at appearance/disappearance is constant with increasing age, an unjustified assumption because selection processes are likely to change at different life stages as illustrated in the bighorn sheep example (Fig. 3B). A more prudent approach would be to model the interactive effect of age and age at appearance/disappearance (see simulated example in the Supplementary material Appendix 2). In such case, age and age at appearance/disappearance cannot both be used as factors because they would not all be identifiable. An alternative would be to use age categories to estimate processes for specific life stages, e.g. to contrast growth versus senescence. An appropriate selection of age categories, however, might not always be obvious, and the choice could affect the results. If the aim is not to contrast specific life stages, then using a nonlinear effect of age could be more appropriate. Modelling age with an ordinary polynomial or a spline would also allow smoothing the unexpected fluctuations in the estimates we sometimes obtain between ages as a result of low sample size in late life (e.g. Fig. 3B). That being said, although nonlinear modelling can account for selection processes and provide unbiased predictions of phenotypic change with age, the beta estimates describing the nonlinearity cannot be directly used to quantify ontogeny and selection (but see 'Combining approaches' section for a solution).

To account for environmental effects, van de Pol and Verhulst (2006) also suggested using the relative value of the trait, which suffers from the same limitations as with the demographic decomposition method. Other studies used year as a fixed factor in statistical models (Nussey et al. 2011). This completely accounts for annual variation, but cannot quantify the influence of the environment on phenotypic change to compare its relative importance with ontogeny and selection. One solution would be to incorporate environmental effects directly in the models (Bouwhuis et al. 2009). Environmental covariates added directly in the model can estimate β_E (Eq. 3; Fig. 4C), thereby quantifying the ontogeny that is independent of the environmental effect as well as quantifying the environmental effect itself. In Fig. 4C, we illustrated an example with an environmental condi-

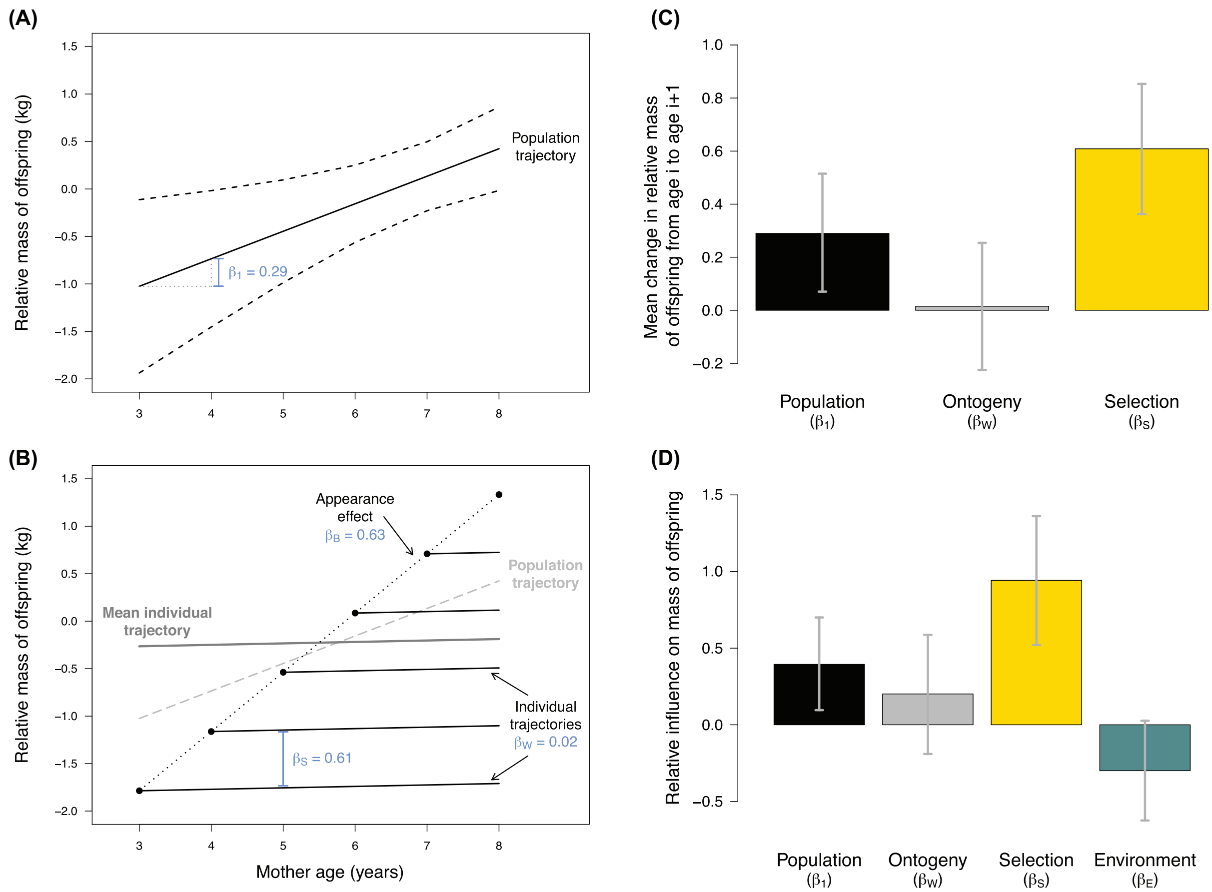

Figure 5. Illustration of the statistical modelling approach proposed by van de Pol and Verhulst (2006; A, B, C), and the extension of this approach for quantifying environmental influence (D). The figure uses empirical data on the relative change of offspring mass with maternal age in mountain goats for which we simulated an increase in offspring mass with increasing age at first reproduction (i.e. an appearance effect) to exemplify better this approach (see 'Statistical modelling' section). (A) illustrates the relative change in offspring mass with maternal age at the population level, with the population trajectory and its 95% confidence interval estimated according to Eq. 1 (Fig. 4A). (B) illustrates the individual trajectories for the relative change in offspring mass with maternal age when accounting for the appearance effect (estimated according to Eq. 2 in Fig. 4B), contrasting the mean within-individual change to the change observed at the population level. (C) contrasts the relative influence of ontogeny and selection to the mean change in relative mass of offspring (parameters estimated according to Eq. 1 and 2 in Fig. 4). (D) contrasts the relative influence of ontogeny, selection, and environment on the mass of offspring (parameters estimated according to Eq. 1 and 3 in Fig. 4). Bars in (C) and (D) refers to the 95% confidence intervals. Symbols refer to notations used in the equations presented in Fig. 4.

tion that can vary at each age, but we could also replace $\beta_E\gamma_{ij}$ with $\beta_E\gamma_j$ to model a static/fixed environmental condition (e.g. cohort effect; Descamps et al. 2008). Because individual heterogeneity could also change with age or depend on environmental conditions (Schielzeth and Forstmeier 2009, Cam et al. 2016), we could model a dynamic heterogeneity by adding a random slope with either age, i.e. $(\beta_W + u_{Aij})age_{ij}$ (Pennell and Dunson 2006, Morrongiello and Thresher 2015), or environment, i.e. $(\beta_E + u_{Eij})\gamma_{ij}$ (Dingemanse and Dochtermann 2013; see also Chambert et al. (2013) for an example with a binary environmental covariate).

To illustrate the quantification of environmental effects, we used the November–March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994) as a measure of the annual environmental variation in winter conditions during the gestation of female mountain goats to assess this environmental influence on offspring mass. NPI is a global climate index with higher anomalies characterising colder and snowier winters than lower anomalies in this study area (Hamel et al. 2009c). Adding this variable to the model according to Eq. 3 (Fig. 4C) with standardized predictors, we can obtain β_E and compare its relative influence with that of ontogeny and selection (Fig. 5D). This simulated case shows that NPI tends to have a negative relative influence, such that harsh winters might reduce offspring mass (Fig. 5D). Including this environmental variable supported that selection was a dominant process over ontogeny (Fig. 5C), but also allowed us to assess that selection was three times more important than environmental variation in explaining the phenotypic changes of offspring mass as mothers are ageing (Fig. 5D). Obviously, this approach is highly dependent on the choice of the environmental variable. In this case, the model including

NPI had 30% greater residual variance than a model including year as a factor, and the latter also provided a better fit according to a likelihood ratio test, suggesting NPI only captured a limited part of annual variation. The interpretation of the relative influences should therefore be made specific to the environmental factor measured unless the factor is shown to capture most of the annual variation in the studied trait. One advantage of working with covariates, however, is that other factors that might influence traits can also be included and their relative influence can be compared. For instance, the body condition of an individual often affects its reproduction, and including condition as a covariate can account for such a correlation and allow quantifying its effect. Correlations among traits can alternatively be accounted for by using a joint modelling approach, which will be more appropriate to use when aiming to quantify the dependency among traits and to identify tactics related to this dependency (see 'Joint modelling' section).

One major advantage of the statistical modelling approach is that it can handle a large proportion of missing values, such as when traits are only measured for a fraction of the individual lifetime, and results will be robust as long as the occurrence of missing values is not dependent on the process being estimated, such as individuals with a low weight not being measured. Missing values in some independent variables will reduce the power of assessing selection and environmental processes (van de Pol and Verhulst 2006), an important limitation in the quantification of these processes. Another advantage of these models is that they can also be performed in a capture–mark–recapture (CMR) framework, thereby providing a way to account for the probability of detection when it is below 1 (see review on CMR models by Gimenez et al. 2018). One issue, however, is the correlation between fixed factors in the models (van de Pol and Verhulst 2006), because longevity will inevitably be higher and less variable at older than at younger ages of trait measures, and one must check that the parameter estimates are not affected by this potential correlation.

Combining approaches

The statistical modelling approach presented by van de Pol and Verhulst (2006) and the demographic decomposition approach presented by Rebke et al. (2010) are the two main methods that have been used up to now. Statistical modelling has been preferred (e.g. 187 citations for van de Pol and Verhulst versus 71 for Rebke et al., Web of Knowledge accessed 8 Aug. 2017). In the few cases when both approaches have been used (Evans et al. 2011, Nussey et al. 2011, Evans and Sheldon 2013, Hayward et al. 2013, Zhang et al. 2015), studies have first used a statistical model to test for the structure of the selection process and then performed the demographic decomposition to illustrate the different contributions at each age. This two-step approach is interesting because it uses the strengths of each method. Still, the number of studies with the data required to perform the second step remains rather limited. Furthermore, for traits that change nonlinearly with age such as mass, the annual mean will vary with age structure, and hence cannot be used to control for annual variation in the second step. To solve both issues, we propose combining the two methods, which means performing the demographic decomposition using the predictions obtained from a statistical model that can include environmental covariates. This combined approach allows quantifying ontogeny and selection for specific ages or stages in cases where the data prevent from using the demographic decomposition (e.g. incomplete data), as well as quantifying environmental effects. The new parameters the combined approach allows us to estimate are highlighted in bold in Table 1.

We illustrate the approach with the example on mass in male bighorn sheep (see also Supplementary material Appendix 2 for an example with simulated data). First, to compare with the results obtained with the decomposition method that did not account for environmental variation (Fig. 3B), we ran a set of statistical models without controlling for annual variation. The first model was built according to Eq. 1 (Fig. 4A), but with age entered as a cubic polynomial. The best polynomial degree was determined based on likelihood ratio tests, and was the same for all statistical models used in this example. We extracted mass predictions from this model, which provided body mass values at each age at the population level, i.e. average mass of all individuals (M_{ALL}, in black in Fig. 2B). Hence, P at each age interval was the difference between M_{ALL} at age $i + 1$ and at age i (Fig. 2B). The second model was built according to Eq. 2 (Fig. 4B), but using longevity in interaction with age. The predictions obtained at each age from this model provided mass values at each age at the individual level, i.e. average mass of surviving individuals (M_{SURV}, in grey in Fig. 2B). Thus, I at each age interval was the difference between M_{SURV} at age $i + 1$ and at age i, and the difference between M_{SURV} and M_{ALL} at age i was the total disappearance (D_{tot}, in blue in Fig. 2B) for both natural and artificial selection. To separate the effect of these two types of disappearance, we ran a third model exactly as the first one but on a data set that excluded the mass in the last year of life for individuals that were shot. This model provided mass predictions at each age for both survivors and individuals that died from natural causes ($M_{SURV+N.DEATH}$, in red in Fig. 2B). Thus, the disappearance due to natural causes at each age D_N was the difference between M_{SURV} and $M_{SURV+N.DEATH}$ at each age, and the disappearance due to hunting at each age D_H was equal to $D_{tot} - D_N$ (Fig. 2B). To calculate the uncertainty on parameters P, I, D_N and D_H, we performed a bootstrap (n = 1000 simulations) where we used the first model to simulate new response values conditional on the individuals already in the data set (i.e. re.form = NULL in the 'simulate' function in R). We conditioned the simulations on the same individuals because our goal is to explain the contribution to ontogeny and selection observed in these individuals. We then reran the three models with the simulated mass responses, estimated P, I, D_N and D_H for each simulation, and used the 0.025 and 0.975 percentiles of each parameter to represent the 95% confidence interval. The results from this combined approach (Fig. 3C) showed similar patterns of ontogeny, natural and artificial selection as the demographic decomposition (Fig. 3B). The main difference was that at older ages the changes were smoother across ages with the combined method because we modelled age as a polynomial, which is less sensitive to age-specific fluctuations in late life. This is advantageous in this case because age-specific changes in body mass are expected to be smaller once males have reached asymptotic body mass than during the growing period. Although senescence in body mass occurs in male ungulates (Carranza et al. 2004, Mainguy and Côté 2008, Jégo et al. 2014), the large age-specific changes obtained from the demographic decomposition were most likely due to low sample sizes.

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

Mixture modelling

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

A mixture modelling approach is particularly useful to tackle life-history tactics (McLachlan and Peel 2000; reviewed by Hamel et al. 2017a). These models have been used widely in psychology, sociology, and medicine (Farewell 1982, Jones et al. 2001, Hoeksma and Kelderman 2006, Karlis and Meligkotsidou 2007, Curran et al. 2010), and are now increasingly used to model individual heterogeneity in survival in capture–mark–recapture studies (Cubaynes et al. 2012, Ford et al. 2012, reviewed by Gimenez et al. 2018). Finite mixture models (Fig. 6) allow assessing whether there is structured variation in life-history tactics within a population and provide an objective

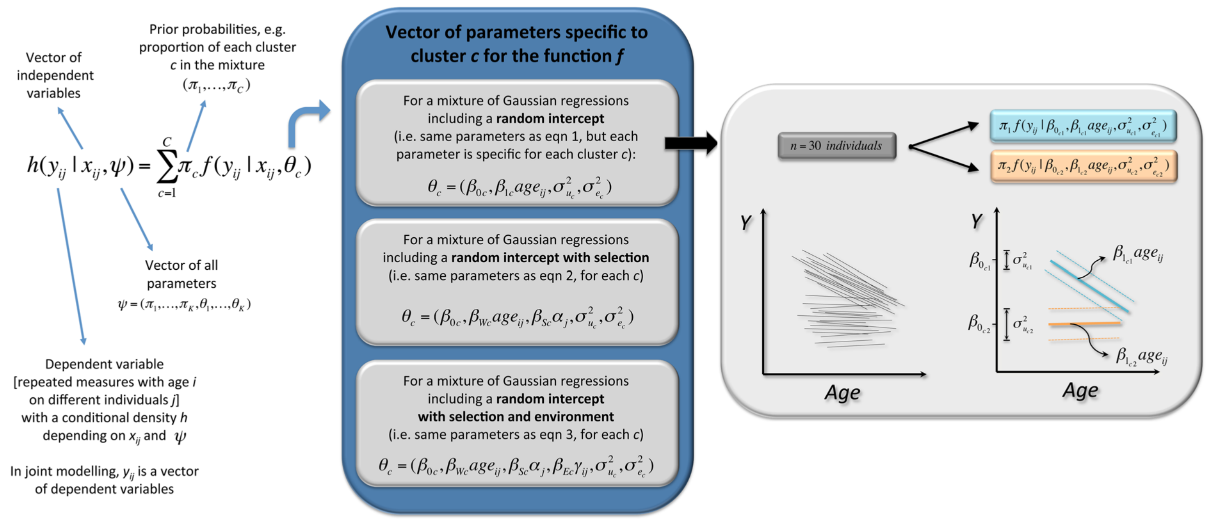

Figure 6. Illustration of the mixture modelling approach. Mixture models can detect the presence of clusters within a population, and thereby characterise different life-history tactics. The general formula for a finite mixture model is presented on the left. A finite mixture model will provide parameters that are specific to each cluster, meaning that if we model the same parameters as those used in the statistical modelling approach (i.e. Eq. 1 to 3 in Fig. 4) within a mixture framework, we can obtain parameters quantifying ontogeny, selection, and environmental processes for each tactic (as presented in the blue box in the middle of the panel). On the right, a population with two clusters (c_1 in blue and c_2 in orange) is illustrated, where a mixture model with a random intercept is fitted. This means that the mixture model estimates the same parameters as those in Eq. 1 (Fig. 4A), but each parameter is estimated specifically for each cluster.

classification of individual trajectories into clusters, each representing a life-history tactic that differs from the mean trajectory of the population (Fig. 7). These models identify the best level of clustering between a single cluster (i.e. the population level) and a cluster for each individual (i.e. a classical random effect), thereby working on a higher level of individual heterogeneity by focusing on the cluster level (Hamel et al. 2017a). Essentially, each cluster is defined by a separate set of regression parameters (McLachlan and Peel 2000) (Fig. 6). If two clusters are found within a population, parameters from two regressions will be estimated, where the regression for a specific cluster contains observations from all individuals weighted by their probability of belonging to this cluster. If clusters are well defined (i.e. the individual probability of belonging to a given cluster is either 0 or 1), then it will be like running a separate regression on each cluster.

Mixture models allow us to compare the general ontogenetic curve of clusters with that of the population, thereby determining how processes vary across clusters and how this can affect what we observe at the population level. For example, mixture models fitted on body mass data of different ungulate populations revealed that the ontogenetic pattern of growth varies across clusters, and that the rate observed at the population level might not always be representative of all clusters (see Supplementary material Appendix 1 for modelling details). The model for male bighorn sheep (Fig. 7A) shows that there are three growth tactics within the population and that growth rate differs among tactics before the prime-age stage, leading to distinct asymptotic body mass across tactics during the prime-age stage. Overall, only one growth tactic would be well represented by ontogenetic changes measured at the population level (shown as the red curve in Fig. 7A). Note that there is almost no difference at age 0 because annual environmental conditions were included in the model, thereby accounting for differences among cohorts due to conditions in the year of birth. In male roe deer (Fig. 7B), three very different growth tactics exist, which vary in terms of the onset of senescence, but the strength of senescence (slope of the decrease) is similar across growth tactics. In female bighorn sheep (Fig. 7C), the four growth tactics illustrate not only a difference in the onset of senescence, but also in the rate of senescence. These examples demonstrate that, by concentrating on the cluster level, mixture models allow assessing a different level of individual heterogeneity that corresponds to life-history tactics when analysing life-history trajectories.

Essentially, any parameter describing ontogeny, selection, and environmental processes that can be included in the statistical modelling approach (i.e. β_W, β_S, β_E, Fig. 4) can also be included in the mixture modelling approach to quantify these processes specifically for each cluster trajectory (e.g. β_{Wc1}, β_{Wc2}, β_{Sc1}, β_{Sc2}, β_{Ec1}, β_{Ec2}, Fig. 6). This allows quantifying the relative importance of these processes for each cluster and contrasting them within a population. For example, if we run again the mixture model on mass in male bighorn sheep including age at disappearance to segregate the clusters (assuming a linear effect of disappearance for the sake of simplicity), we observe that the disappearance of light

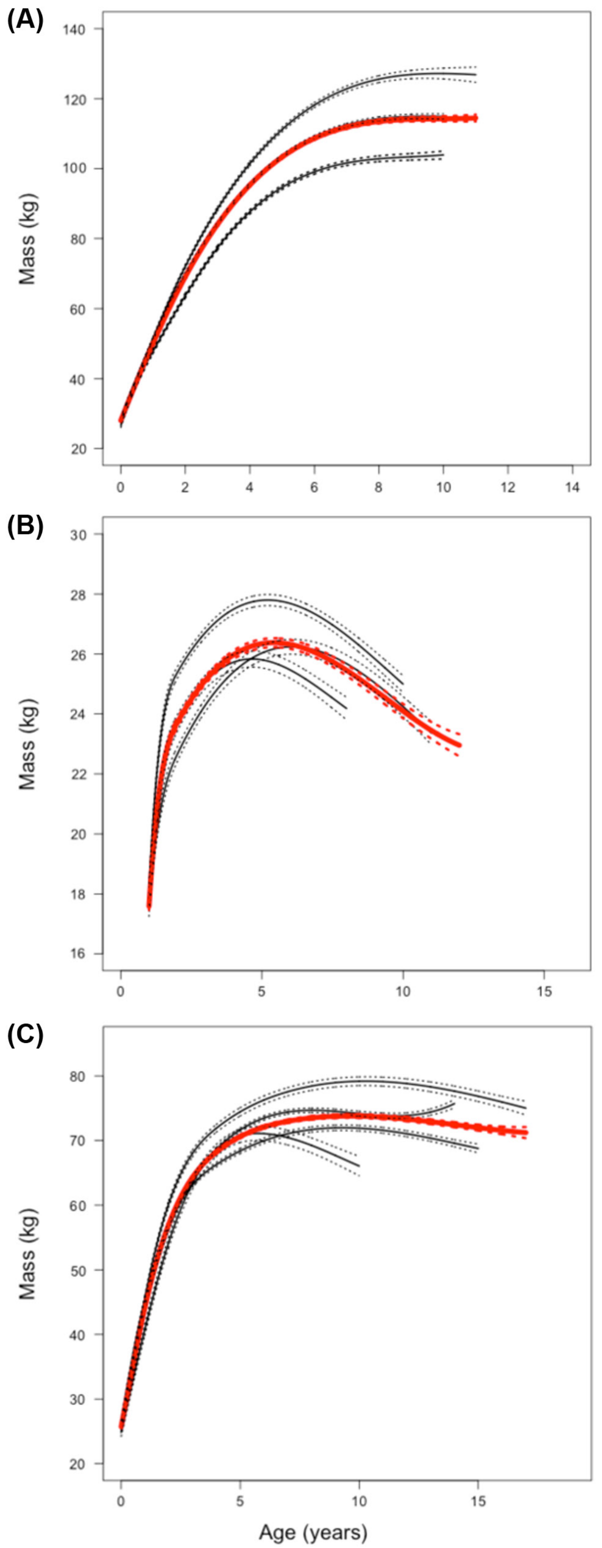

Figure 7. Growth tactics determined by finite mixture modelling on body mass of male bighorn sheep (A), male roe deer (B), and female bighorn sheep (C), illustrating how different ontogenetic tactics can co-exist within a population and differ substantially from the overall ontogenetic pattern observed at the population level. The solid lines represent the mean predictions and the dotted lines the 95% confidence intervals, with the predictions in red for the whole population and in black for the different tactics within a population.

individuals varies across the three clusters, being five times stronger in one cluster out of the two that showed a strong support for disappearance (disappearance estimate [95% confidence interval]: $\beta_{Sc1}=0.05$ [0.00; 0.10], $\beta_{Sc2}=1.03$ [0.89; 1.17], $\beta_{Sc3}=0.21$ [0.07; 0.35]).

Although multimodality resulting from the occurrence of different clusters corresponding to different tactics within a population violates the assumption of normality, this does not affect fixed effects at the population level (Verbeke and Lesaffre 1997, Hamel et al. 2017a). Thus, the overall influence of these processes at the population level will not differ whether a random effect model or a mixture model is used in the presence of clusters. The interest in using mixture models lies in quantifying and comparing these processes within each cluster, such that the details of the relative contribution for distinct types of individuals provide a better understanding of how ontogeny, selection, and environmental variation might interact within a population. Furthermore, although fixed effects are not biased at the population level in the presence of clusters, the variance describing individual heterogeneity can be greatly overestimated (Hamel et al. 2017a). By incorporating a categorical latent variable that aggregates subjects into clusters sharing similar traits, mixture models capture the multimodal dimension that structures individual heterogeneity (McLachlan and Peel 2000). Hence, by estimating the between-individual variance present at the cluster level, mixture models can better quantify the variance within a population and its stratification. For instance, variance in the ontogenetic pattern of growth in male bighorn sheep at the population level (σ_u^2) was 25.8, whereas it was much lower within clusters and varied among clusters ($\sigma_{u\_c1}^2=3.2$, $\sigma_{u\_c2}^2=14.9$, and $\sigma_{u\_c3}^2=13.0$). The high variance at the population level mainly resulted from the large dispersion among the three main tactics rather than the dispersion among individuals within a tactic. Essentially, this means that individual trait distribution can be heterogeneous, and mixture modelling is a powerful approach to account for this structured heterogeneity. That being said, these models are much more complex and much longer to run than mixed models, and determining the number of clusters can be particularly challenging, especially for traits following a binary distribution (see Hamel et al. 2017a for a review of the challenges with mixture modelling). If one is not interested in obtaining cluster-specific parameters to contrast life-history tactics, then one alternative is to use infinite mixture models in a Bayesian framework, which does not require settling the number of clusters (Rasmussen 2000, Manrique-Vallier 2016). Obviously, different methods offer different possibilities for quantifying variance within a population, and the choice will depend on the question addressed and the biological knowledge acquired so far for the trait studied.

Joint modelling

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

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

Similarly, mixture models can provide a suitable integrating approach to model the covariance among traits at the cluster level. For example, we used joint modelling to determine the covariance among body growth, relative reproduction (the number of offspring produced at age *i* for individual *j*/total number of offspring produced by all individuals that year), and the probability of survival in bighorn sheep males (see Supplementary material Appendix 1 for details on data and description of the analysis). We included age at appearance and disappearance to account for selection processes, and mean yearling mass to account for annual variation in environmental conditions. We found three clusters corresponding to three life-history tactics (Fig. 8). In the tactic illustrated in red (Fig. 8) males do well in all traits. They have a very strong growth early in life and reach the highest asymptotic mass as adults. They also obtain the highest reproductive output, particularly at old ages, and have a fairly high survival that does

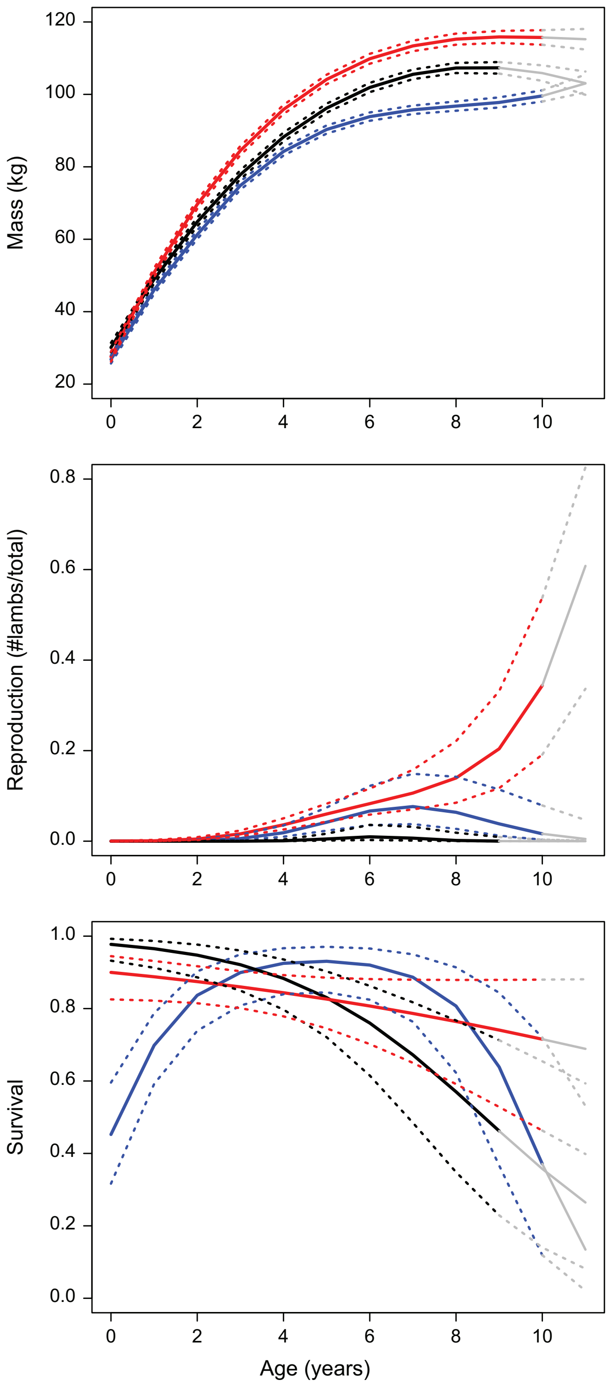

Figure 8. Life-history tactics in male bighorn sheep, illustrating trajectories in terms of body growth, relative reproduction (number of lambs produced by a male in a given year/total number of lambs produced that year), and survival probability. The three tactics illustrated with different colours were determined using a joint mixture modelling, which clustered individuals by estimating the joint latency in the three traits. The colours in each panel correspond to the same cluster of individuals and illustrate the interdependency among the three traits studied. Note there is little variation in body mass at the start of life because the model includes an environmental covariate that accounts for most variation in mass among cohorts early in life. The solid lines are the predictions and dotted lines the 95% confidence intervals. Both solid and dotted lines fade to grey at ages with less than five individuals sampled.

not seem to decrease with increasing age as fast as for individuals playing other tactics. Males playing the two other tactics perform generally less well on most traits, and the performance of these males differs among traits. Males have similar growth early in life in both tactics, but males in black (Fig. 8) allocate to growth for a longer period and attain a larger asymptotic mass than those males in blue (Fig. 8). The males playing the 'black tactic' almost never manage to reproduce successfully during their lifetime (Fig. 8). Interestingly, the decrease in growth rate observed around age 4 in the males playing the 'blue tactic' corresponds to the time when these males started allocating to reproduction (Fig. 8). These results suggest that mass is unlikely to be the only determinant of reproduction. Indeed, males playing the 'red tactic' achieve greater reproduction likely because they have reached a higher mass, which is positively correlated with social rank (Pelletier and Festa-Bianchet 2006) and thereby with mating effort (Pelletier et al. 2006). Males playing the 'black tactic' allocate to growth and reach a higher asymptotic mass than males playing the 'blue tactic', which started allocating to reproduction from age 4, but they have very low reproductive success compared to males playing the 'blue tactic'. Therefore, the higher asymptotic mass achieved by males playing the 'black tactic' is likely due to a much lower allocation to reproduction compared to males playing the 'blue tactic'. Finally, males playing the 'blue tactic' also had a very low early survival (i.e. at ages 0 and 1) compared with males playing the two other tactics. This might have selected against lower quality males, and may explain the higher reproduction of males playing the 'blue tactic' compared to males playing the 'black tactic'. In such long-lived and sexually dimorphic species, body mass is a fundamental determinant of fitness (Pigeon et al. 2017), having a strong influence on both survival, particularly in early life (Plard et al. 2015, Théoret-Gosselin et al. 2015), and reproduction (Pelletier and Festa-Bianchet 2006, Pelletier et al. 2006, Mainguy et al. 2009). Therefore, these different life-history tactics might be maintained because the fitness costs and benefits of each tactic likely vary during a male's lifetime.

Remaining challenges

Missing values

In most studies, recapture/resighting rates are less than 1, meaning that not all surviving individuals are measured at all ages, and therefore the within-individual changes I, the appearance A, and disappearance D do not represent an exact decomposition of P. For instance, even though the resighting probability of surviving male bighorn sheep was >95%, the average recapture probability of surviving males was 77%, meaning that the data set on body mass includes more than 20% missing values. Missing values are common in life-history studies, and bias may arise if the probability that a value is missing is associated with the trait studied. For example, comparing the average mass in each age class for male bighorn sheep measured at age i and $i+1$ with the average mass for males that survived from age i to $i+1$ but were only measured at age i (i.e. males with missing values), we see a tendency for missing values to occur in heavier males (Fig. 9). Larger males were thus less likely to be weighed the following year than lighter males, meaning that the within-individual changes across these ages may be biased. Removing bias requires modelling the missing value process (Little 1995).

Imperfect detectability

In addition to missing values, imperfect detection probability is the rule in most studies and is therefore another major challenge when quantifying the contribution of ontogeny and selection to phenotypic changes. This problem is directly linked with the missing value issue because the detection probability will directly determine the rate of missing values, as well as the survival estimates. This problem is addressed in detail in Gimenez et al. (2018).

Standardization

For comparing responses among traits within a population or for comparing the same trait among populations or species, one is confronted with issues of standardization – i.e. finding a common measurement scale (Hamel et al. 2014). This can result from the variable type (e.g. numeric versus binary, with implicit differences in variances that are used for standardizing variables; Gelman 2008), or from different transformations associated with the statistical analyses (e.g. logit versus log for proportions; Link and Doherty (2002)). Analyses have also used proportional changes (see the discussion of Rebke's method, and Hamel et al. 2016), which might be sensitive to the reference value used. One must also remember that

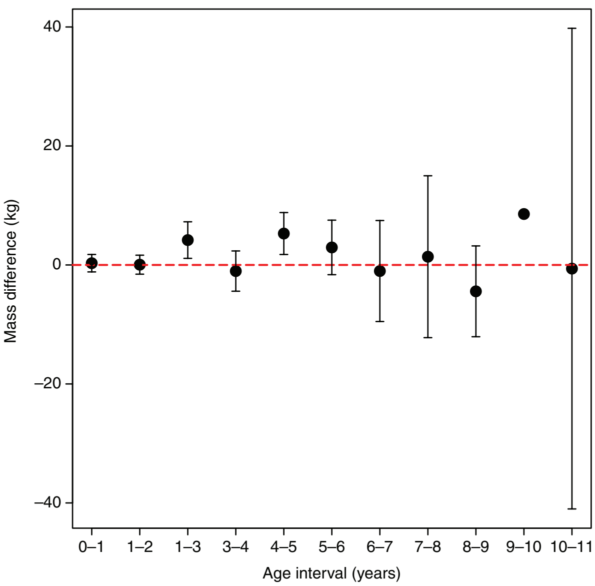

Figure 9. Difference (95% confidence intervals) between average mass for males that survived from age i to $i+1$ but were only measured at age i, which leads to missing values, and average mass for males measured at age i and $i+1$, without missing values, for each age interval in bighorn sheep. Positive values indicate missing values occurred in heavier males. There is no confidence interval for the age interval 9–10 because there is only one missing value.

inferences are model-dependent, meaning that the choice of the model structure can influence effect sizes (Knape et al. 2011). This makes comparisons among study systems challenging because different systems often require different modelling structures. Moreover, the variability of a trait might reflect evolutionary changes (e.g. environmental canalization as for adult survival in long-lived vertebrates; Gaillard and Yoccoz 2003), or differences in environmental variability. There is no simple solution to this problem (Greenland et al. 1986), except that it requires careful consideration of both what causes variation in heterogeneity, and of its consequences.

Standardization issues also arise when comparing the strength of different predictors, for instance among ontogeny, selection, and environmental processes or for a given process – e.g. contrasting natural versus artificial selection across different environmental conditions. Predictors need to be standardized (Schielzeth 2010) to provide estimates of the relative influence of ontogeny, selection, and environmental variation that are comparable, but estimates are then not comparable in terms of units of change of the trait with age. This may be problematic when the aim is to compare how these processes change at each age, and in such cases keeping the units of change with age might be more appropriate to contrast the relative influence of ontogeny and selection processes. When comparing the relative influence of various environmental variables, however, standardizing the environmental estimates is recommended. Standardization depends on the reference value used, and the choice of the reference level to measure climate variability is fundamental but far from simple (Harris et al. 2014). When the aim is to evaluate whether the variability observed during the ecological study is affecting the traits observed, using the variability observed in the data would be appropriate. Nevertheless, variability observed in climatic data (i.e. historical variability) could be useful to determine how climate change has affected traits over time. Essentially, standardization requires specifying what kind of question we are trying to answer to insure valid comparisons (Nakagawa and Cuthill 2007), and effect sizes should be interpreted with careful considerations of the reference value used. Above all, authors should present the standard deviations used for standardizing variables in order to retrieve the unstandardized estimates.

Summary

Understanding how life-history traits vary as individuals age is central to life-history theory because age-specific variability influences the evolution of traits and their effects on population dynamics. Therefore, heterogeneity resulting from individual differences affects our perception of how life-history traits change with age at the population level because selection leads to an overrepresentation of specific individuals at certain ages, and because ontogenetic processes themselves can vary across individuals owing to heterogeneity in life-history tactics. We have presented the most recent and common methods used to account for individual heterogeneity when estimating changes in life-history traits with age (Table 1) and proposed a method that combines approaches to take benefit from their strengths while also overcoming many of their limitations. Our combined approach can also be used in the context of mixture modelling, which looks at different levels of individual heterogeneity, and thereby allows assessing the influences of heterogeneity in life-history tactics on the relative contribution of ontogeny, selection, and environmental variation to population trajectories. Finally, we showed that using a joint mixture modelling approach is valuable because it uses the latent correlation shared among multiple traits to identify ontogenetic tactics with dependency among multiple life-history traits. Overall, all approaches have their strengths and limitations. The best method should be chosen in perspective with the question we aim to answer, and, as suggested by Nussey et al. (2011), complementary approaches will sometimes be necessary to obtain a better understanding of the system.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.5fm52> (Hamel et al. 2017b).

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Supplementary material (available online as Appendix oik-04725 at <www.oikosjournal.org/appendix/oik-04725>). Appendix 1–2.