



Cohort variation in individual body mass dissipates with age in large herbivores

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Abstract:	Environmental conditions experienced during early growth and development markedly shape phenotypic traits. Consequently, individuals of the same cohort may show similar life-history tactics throughout life. Conditions experienced later in life, however, could fine-tune these initial differences, either increasing (cumulative effect) or decreasing (compensatory effect) the magnitude of cohort variation with increasing age. Our novel comparative analysis that quantifies cohort variation in individual body size trajectories shows that initial cohort variation

dissipates throughout life, and that lifetime patterns change both across species with different paces of life and between sexes. We used longitudinal data on body size (mostly assessed using mass) from 11 populations of large herbivores spread along the "slow-fast" continuum of life histories. We first quantified cohort variation using mixture models to identify clusters of cohorts with similar initial size. We identified clear cohort clusters in all species except the one with the slowest pace of life, revealing that variation in early size is structured among cohorts and highlighting typological differences among cohorts. Growth trajectories differed among cohort clusters, highlighting how early size is a fundamental determinant of lifetime growth patterns. In all species, among-cohort variation in size peaked at the start of life, then quickly decreased with age and stabilized around mid-life. Cohort variation was lower in species with a slower than a faster pace of life, and vanished at prime age in species with the slowest pace of life. After accounting for viability selection, compensatory/catch-up growth in early life explained much of the decrease in cohort variation. Females showed less phenotypic variability and stronger compensatory/catch-up growth than males early in life, whereas males showed more progressive changes throughout life. These results confirm that stronger selective pressures for rapid growth make males more vulnerable to poor environmental conditions early in life and less able to recover after a poor start. Our comparative analysis illustrates how variability in growth changes over time in closely related species that span a wide range on the "slow-fast" continuum, the main axis of variation in life-history strategies of vertebrates.

1 RH: Cohort variation in body size

2

3 **Cohort variation in individual body mass dissipates with age in large herbivores**

4

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30 ABSTRACT

31 Environmental conditions experienced during early growth and development markedly
32 shape phenotypic traits. Consequently, individuals of the same cohort may show similar
33 life-history tactics throughout life. Conditions experienced later in life, however, could
34 fine-tune these initial differences, either increasing (cumulative effect) or decreasing
35 (compensatory effect) the magnitude of cohort variation with increasing age. Our novel
36 comparative analysis that quantifies cohort variation in individual body size trajectories
37 shows that initial cohort variation dissipates throughout life, and that lifetime patterns
38 change both across species with different paces of life and between sexes. We used
39 longitudinal data on body size (mostly assessed using mass) from 11 populations of large
40 herbivores spread along the “slow-fast” continuum of life histories. We first quantified
41 cohort variation using mixture models to identify clusters of cohorts with similar initial
42 size. We identified clear cohort clusters in all species except the one with the slowest
43 pace of life, revealing that variation in early size is structured among cohorts and
44 highlighting typological differences among cohorts. Growth trajectories differed among
45 cohort clusters, highlighting how early size is a fundamental determinant of lifetime
46 growth patterns. In all species, among-cohort variation in size peaked at the start of life,
47 then quickly decreased with age and stabilized around mid-life. Cohort variation was
48 lower in species with a slower than a faster pace of life, and vanished at prime age in
49 species with the slowest pace of life. After accounting for viability selection,
50 compensatory/catch-up growth in early life explained much of the decrease in cohort
51 variation. Females showed less phenotypic variability and stronger compensatory/catch-
52 up growth than males early in life, whereas males showed more progressive changes

53 throughout life. These results confirm that stronger selective pressures for rapid growth
54 make males more vulnerable to poor environmental conditions early in life and less able
55 to recover after a poor start. Our comparative analysis illustrates how variability in
56 growth changes over time in closely related species that span a wide range on the “slow-
57 fast” continuum, the main axis of variation in life-history strategies of vertebrates.

58

59 **Keywords:** Compensatory growth, catch-up growth, cumulative effects, cohort, life-
60 history tactics, mixture models, ungulates, sexual selection, “slow-fast” continuum,
61 viability selection.

62

63 INTRODUCTION

64 At the population level, the expression of life-history traits as individuals age results from
65 a combination of ontogenetic, selective (both viability and fertility selection, Fisher
66 1930), and environmental processes (Coulson and Tuljapurkar 2008, Ozgul et al. 2009).
67 Because conditions early in life usually determine juvenile body development and size
68 (Madsen and Shine 2000, Metcalfe and Monaghan 2001, Bateson et al. 2004, Solberg et
69 al. 2004), variability in early conditions often leads to phenotypic differences among
70 individuals of a population at the start of life (Lindström 1999). Conceptually, this means
71 that environmental conditions, in interaction with genotype, set the phenotypic starting
72 values of individual life-history traits (Figs. 1a, b). This variability must be considered
73 when assessing changes in a trait with age. If initial differences persist, they result in the
74 ranking of individuals for a given trait that remain constant throughout life (Lindström
75 1999, Metcalfe and Monaghan 2001, Monaghan 2008). Differences among individuals
76 that are fixed at birth are referred to as fixed or static heterogeneity (Tuljapurkar et al.
77 2009). In addition to early-life conditions, environmental conditions experienced later in
78 life also influence life-history traits (Wooller et al. 1992, McNamara 1998, Descamps et
79 al. 2008, Wilkin and Sheldon 2009, Crowley and Hopper 2015). The resulting individual
80 differences later in life are referred to as dynamic heterogeneity when they are generated
81 from a stochastic process affecting changes in life-history stages (Tuljapurkar et al.
82 2009). If individual differences later in life display positive serial auto-correlations,
83 environmental effects may cumulate with age and accentuate between-individual
84 differences over the lifetime, hereafter referred to as “cumulative effect” (Nussey et al.
85 2007, Dmitriew 2011; Fig. 1d). On the other hand, if individuals can recover from a poor

86 start (Metcalf and Monaghan 2001, Dmitriew 2011), due to improved conditions and/or
87 genetic predisposition, individual differences will decrease with increasing age, hereafter
88 referred to as “compensatory effect” (Fig. 1c). In bighorn sheep (*Ovis canadensis*) for
89 instance, lighter yearling females prolonged growth so that their size difference with
90 heavier yearling females decreased from 20 to 4% between 1 and 7 years of age (Marcil-
91 Ferland et al. 2013). Conceptually, cumulative or compensatory effects imply that
92 environmental conditions, along with genotype, not only affect the starting values (Figs.
93 1a, b), but also the rate of change of life-history traits, thereby increasing or decreasing
94 between-individual variance with age (Figs. 1c, d; Schielzeth and Forstmeier 2009, van
95 de Pol and Wright 2009). Importantly, cumulative or compensatory effects can result
96 from actual differences in ontogeny and/or from viability selection among phenotypes
97 (Fisher 1930, Vaupel et al. 1979). For instance, a reduction in the variance of mass with
98 age can result both from the selective disappearance of lighter individuals (Fig. 1e;
99 Gaillard et al. 2000a, van de Pol and Verhulst 2006, Plard et al. 2015, Théoret-Gosselin et
100 al. 2015) and from changes in the growth patterns of lighter versus heavier individuals.
101 Changes in growth patterns can occur either through compensatory growth (i.e. faster
102 growth of lighter individuals when conditions improve) or catch-up growth (i.e. lighter
103 individuals extending the growth period) (Metcalf and Monaghan 2003).

104

105 The intensity of cumulative or compensatory effects might vary among species in relation
106 to their life-history strategies (Stearns 1976). The long generation time of species with a
107 slow pace of life evolved from a strategy that promotes survival over reproduction
108 (Gaillard and Yoccoz 2003). This resulted in environmental canalization of adult

109 survival, which varies little over time or space, and in a high susceptibility of
110 reproductive traits to spatio-temporal changes in environmental conditions. The opposite
111 pattern occurs in short-lived species, with lower variance in reproductive traits and a
112 more variable adult survival (Gaillard and Yoccoz 2003). Thus, the influence of
113 environmental conditions and selection processes on life-history trait distributions is
114 likely to differ between species with slow and fast life-history strategies (Stearns 1983;
115 see Gaillard et al. 2016 for a recent review). The survival of long-lived species might be
116 buffered against environmental variation because individuals may stop allocating energy
117 to reproduction when facing harsh conditions, whereas individuals of short-lived species
118 will jeopardize survival to reproduce. Although long-lived species should be able to
119 compensate/catch-up for a bad start by restraining reproductive effort, short-lived species
120 should engage in reproduction as early as possible and might thus be less able to
121 compensate/catch-up for a bad start (Gaillard and Yoccoz 2003). Life-history tactics can
122 also markedly differ between sexes within species under sexual selection (Clutton-Brock
123 2007). Males in many species of mammals have evolved a “live fast, die young” strategy
124 (sensu Bonduriansky et al. 2008) that involves strong selection for high growth rate to
125 prevail in intra-sexual competition and increase reproductive performance (e.g. Robinson
126 et al. 2006). Therefore, we expect males of sexually dimorphic and polygynous species to
127 be more susceptible to variation in early-life conditions (Wilkin and Sheldon 2009) and
128 to be less able to compensate/catch-up for a bad start than females (Toïgo et al. 1999).

129

130 Individual variation early in life can be shaped by several factors, including genotypic
131 differences, parental effects, or early environment (Bernardo 1996, Lindström 1999,

132 Lindström and Kokko 2002, Solberg et al. 2007, Mousseau and Fox 2008, Théoret-
133 Gosselin et al. 2015). Unlike genetic and parental effects, environmental conditions
134 during early growth and development affect all individuals born the same year
135 simultaneously. Environmental variation can thus result in strong cohort effects,
136 particularly in populations with low natal dispersal, and can lead to persistent individual
137 differences throughout life, as often reported in vertebrate populations (e.g. Albon et al.
138 1987, Clutton-Brock 1988, Madsen and Shine 2000, Steinheim et al. 2002, Hastings et al.
139 2011, Douhard et al. 2013, Hayward et al. 2013, Herfindal et al. 2015). Cohort variation
140 at the start of life can result from limited resource availability in poor years (Madsen and
141 Shine 2000, Descamps et al. 2008), or from a phenological mismatch between the peak in
142 resources and that in energy demands (Thomas et al. 2001, Suarez et al. 2004, Solberg et
143 al. 2007, Plard et al. 2014a). Nutrient deficiency during development in poor years likely
144 affects growth and developmental processes, leading to body size differences among
145 cohorts born under contrasting environmental conditions (Douhard et al. 2013). Initial
146 conditions can cause a ‘silver spoon effect’ (Grafen 1988), where lasting benefits of
147 being born during a favorable year lead to positive correlations among performance traits
148 in adulthood (Madsen and Shine 2000, van de Pol et al. 2006, Descamps et al. 2008).
149 Because the influence of ontogenetic, selection, and environmental processes are likely to
150 change with individual states, defined as the physiological and environmental conditions
151 that influence survival and reproduction (McNamara and Houston 1996), cohorts born in
152 favorable and unfavorable years should display different responses to selection and
153 environmental processes (Metcalf and Monaghan 2003, Auer 2010, Douhard et al. 2014,
154 Garratt et al. 2015). Therefore, cohorts sharing similar environmental conditions may

155 show similar life-history tactics throughout lifetime, which might differ from other
156 cohorts and from the average tactic observed at the population level (see Figs. 1c, d, e).
157 They may also show different intensity of cumulative or compensatory effects depending
158 on both the ability of surviving individuals to compensate/catch-up for a poor start (Toïgo
159 et al. 1999, Metcalfe and Monaghan 2003, Auer 2010, Dmitriew 2011, Douhard et al.
160 2014), and the strength of viability selection (Fisher 1930, Vaupel et al. 1979, Ozgul et al.
161 2009). Assessing how cohort effects change throughout lifetime is crucial to understand
162 population dynamics because cohort variation can either stabilize or destabilize
163 population dynamics (Lindström and Kokko 2002).

164
165 Although the effects of environmental conditions on average population responses have
166 received considerable attention, how environmental changes shape the variability in
167 individual responses both within and among cohorts has received little attention
168 (Metcalfe and Monaghan 2003, Wilson et al. 2009). Most previous studies accounted for
169 cohort variation on life-history strategies by including birth year as a random effect to
170 obtain an unbiased assessment of life-history traits. Specific analyses of cohort variation
171 have shown that it is a key process (Metcalfe and Monaghan 2001) shaping individual
172 differences in trait values at different life stages (Albon et al. 1987, Baron et al. 2010, Le
173 Galliard et al. 2010, Douhard et al. 2013). However, how the magnitude of cohort
174 variation changes along trait trajectories over the lifespan, and whether these patterns
175 vary between sexes and among species with different paces of life remain largely
176 unexplored. Assessing the variance in life-history traits at a given life stage and its
177 change with age requires long-term monitoring of individuals over a period sufficiently

178 long to include enough variation in environmental conditions. Here, we performed a
179 comparative analysis of cohort variation based on long-term studies of different species
180 of large herbivores with up to 40 years of longitudinal data collected on body size for
181 individuals of both sexes. Large herbivores provide a unique opportunity to explore
182 cohort variation because the basic life history and ecology of many species are well
183 understood. The species included in this study vary widely in size (Supplementary
184 Material Fig. S1) and in position along the “slow-fast” continuum of life histories (Table
185 1). Box 1 presents an overview of the research questions addressed.

186

187 To quantify cohort variation in body size, we first used mixture models (McLachlan and
188 Peel 2000) to define clusters of cohorts with similar body size early in life. Although
189 between-individual variation is usually quantified from estimates of random effects
190 obtained using mixed models, random effects representing the between-individual
191 variation in mixed models are assumed to be normally distributed. This assumption is
192 often violated when clusters among subjects lead to multimodal distributions (Verbeke
193 and Lesaffre 1996, Stamps et al. 2012). This multimodality can bias the random effect
194 estimates used to quantify between-individual variance in mixed models (Verbeke and
195 Lesaffre 1996, Hamel et al 2016). Mixture models incorporate a categorical latent
196 variable that aggregates subjects into clusters sharing similar traits (McLachlan and Peel
197 2000). This latent variable captures the multimodal dimension of the variability, and
198 thereby accounts for the between-individual variance that might be present at a higher
199 level, i.e. among clusters. Mixture models are therefore particularly useful to identify
200 how ecological and evolutionary processes change over time within a population because

201 they classify individual trajectories (or traits) into clusters of mean trajectories, instead of
202 a single mean population trajectory (Hamel et al. 2016). These models are widely used in
203 psychology, sociology, and medicine to describe the diversity of trajectories within a
204 population over time, such as psychological development or growth (Jones et al. 2001,
205 Hoeksma and Kelderman 2006). They are also used in capture-recapture studies to
206 account for individual differences in survival within populations (Cubaynes et al. 2012,
207 Ford et al. 2012). Therefore, in the presence or expectation of multimodality, mixture
208 models allow determining whether there is variation in life-history tactics within a
209 population, and when there is, they provide an objective classification of subjects into
210 clusters, each representing a typological tactic within a population. Importantly, cluster
211 classification is not fixed. The classification uncertainty is accounted for when estimating
212 the parameters describing each cluster, thereby providing a more objective quantification
213 of each tactic.

214

215 Here, using mixture models allowed determining the best level of clustering between a
216 single cluster (population level) and a separate cluster for each cohort (cohort level),
217 thereby identifying typological differences among cohorts. This is a major advantage in a
218 comparative analysis of studies with different durations because the greater the number of
219 cohorts included, the more environmental variation is likely to be encountered by cohorts.
220 By focusing on the higher level of variation rather than on the specificity of each cohort,
221 mixture models allowed quantifying a standardized variance among cohort clusters
222 controlling for the different number of cohorts monitored among populations (Table 1),
223 and hence providing reliable comparisons among species. After having assessed the

224 presence of cohort clusters with mixture models, we used these cohort clusters to estimate
225 cluster-specific trajectories of body size with age, and evaluated whether the cohort
226 clusters displayed different growth trajectories later in life. Furthermore, we used these
227 growth trajectories to determine whether body size variation among cohort clusters
228 increased (cumulative effect) or decreased (compensatory effect) with increasing age. As
229 we found compensatory effects to be predominant, we accounted for the disappearance of
230 individuals with age to separate the influence of viability selection from that of
231 compensatory/catch-up growth. To contrast results among species and between sexes, we
232 developed standardized estimates to test whether generation time, a reliable measure of
233 the pace of life across mammals (Gaillard et al. 2005), and sex, affected the amount of
234 cohort variation and how this variation changed with age.

235

236 METHODS

237 *Study populations*

238 We compared body size of individuals in 11 populations of 8 species of large herbivores,
239 intensively monitored from birth to death for 13 - 41 years (Table 1). Using generation
240 time to assess the relative position of a given population on the “slow-fast” continuum
241 (see Gaillard et al. 2005 for a justification and e.g. Jones et al. 2008 or Sæther et al. 2013
242 for applications), these populations displayed a fivefold variation in the pace of life –
243 from about 4 years in mouflon (*Ovis gmelini*) to about 20 years in African elephant
244 (*Loxodonta africana*; Table 1). Generation time (T_b , sensu Leslie 1966) was calculated as
245 the inverse of the sum of the elasticities of the recruitment parameters (i.e. the elements
246 of the first row of a pre-breeding census Leslie matrix based on female demography and

247 calculated over all available years; Caswell 2001), according to Lebreton (2005). Body
248 size was measured as body mass, with the exception of elephants for which shoulder
249 height was used because individual masses were not recorded. Skeletal measures
250 including shoulder height strongly correlate with body mass in adult elephants ($r > 0.9$;
251 Laws et al. 1975, Christiansen 2004), and provide a reliable measure of variation in mass
252 in this species. Data were collected on a yearly basis for both sexes, except for the two
253 reindeer (*Rangifer tarandus*) populations for which only females were sampled. Mass
254 was measured at the same period of the year in each population, and when needed, it was
255 adjusted to a specific date to control for seasonal changes (see e.g. Hamel et al. 2010).
256 For elephants, shoulder height was measured throughout the year. Details on study areas
257 and populations have been published elsewhere (references in Table 1).

258

259 To assess cohort variation in body size and its changes with increasing age, the analyses
260 followed 6 steps (Box 1, Fig. 2).

261

262 *Step 1: Selecting the number of cohort clusters*

263 For each population, we first ran a mixture model to identify clusters of cohorts based on
264 body size, i.e. using individual initial body size as the response variable. Mixture models
265 classify observations into clusters based on the probability of belonging to a given
266 cluster, where each cluster is defined by a separate set of regression parameters
267 (McLachlan and Peel 2000). For data like body size, which follows a Gaussian
268 distribution N with a cluster-specific mean $\mu_k(x) = \beta_k x$ (where β_k is the vector of

269 coefficients for the effects of x specific to each cluster k , and x is a vector of predictor
 270 variables) and a variance σ_k^2 , a mixture model with K clusters takes the following form:

$$271 \quad h(y|x, \psi) = \sum_{k=1}^K \pi_k N(y | \mu_k(x), \sigma_k^2) \quad \text{eqn. 1}$$

272 where y is a vector of individual initial body sizes with a conditional density h depending
 273 on x (see below for covariate predictors included for each species) and ψ , a vector of all
 274 parameters of the mixture distribution, where $\psi = (\pi_1, \dots, \pi_K, \mu_1, \dots, \mu_K, \sigma_1^2, \dots, \sigma_K^2)$. The
 275 prior probabilities (π_1, \dots, π_K) are the proportions of each cluster k in the mixture;

276 $\sum_{k=1}^K \pi_k = 1$, $\pi_k > 0$. We refer to Hamel et al. (2016) for a detailed review of the use of

277 mixture models to separate individuals in clusters that present different life-history tactics
 278 within a population.

279

280 For each population, we ran a mixture model including only the first body size
 281 measurements collected (see “age at first measurement” in Table 1) to represent cohort
 282 measurements early in life. In some populations, the first measurements were collected
 283 during the first summer of life, referred to as age 0, whereas in other populations the first
 284 measurements were available after the first year of life, referred to as age 1 (Table 1).

285 Therefore, the first body size measurement was collected during or just after the first year
 286 of life, which corresponds to the inter-birth interval (IBI=1 year) in species with annual
 287 reproduction. For African elephants at Amboseli, however, the IBI is approximately 4.5
 288 years (Moss et al. 2011). To be comparable with the other species, we used

289 measurements between ages 0 and 4.5 to assess differences in body size among cohorts,

290 using a single measure per offspring and “age at first measurement” as a covariate to
291 account for growth between ages 0 and 4.5. This was also necessary because young
292 elephants were measured throughout the year. For each population, the model included
293 measurements of both males and females because we sought to pool cohorts that
294 experienced similar environmental conditions and not to segregate cohorts differently for
295 each sex. We therefore included “sex” as a covariate to account for sexual size
296 dimorphism in the first year of life, except for reindeer for which we only had data on
297 females. In addition, we also included covariates known to influence offspring size in
298 some species when these variables were available. Thus, for Soay sheep (*Ovis aries*), we
299 included the covariate “twin” (born as a twin vs. as a singleton) because twins are born
300 lighter and have slower early growth than singletons (Robertson et al. 1992, Clutton-
301 Brock et al. 1996). For elephants, we included the covariate “primiparity of the mother”
302 (primiparous vs. multiparous) because primiparous mothers produce smaller offspring
303 than multiparous mothers (Lee et al. 2013a).

304

305 We used the R package “FlexMix” with the “FLXMRglmfix” driver (Grün and Leisch
306 2008) to run a mixture model on each population. We thus fitted a linear mixture model
307 using “individual body size at first measurement” as the dependent variable and including
308 as a fixed covariate “sex” (all species except reindeer), “twin” (Soay sheep), “primiparity
309 of the mother” (elephants) and “age at first measurement” (elephants). We included
310 “cohort” as the latent clustering variable to segregate cohorts in distinct clusters. For each
311 run, we used a minimum of 5 repetitions with random initializations to avoid reaching a
312 local maximum (Grün and Leisch 2008). We used the “stepFlexmix” function, which fits

313 a model with increasing number of clusters (K) sequentially. We then evaluated the best
314 K based on different selection criteria. Indeed, numerous criteria have been proposed to
315 select K in finite mixture models, but there is no agreement yet on the most appropriate
316 statistical method because different selection criteria sometimes result in different K
317 being selected, with some criteria performing better than others in some situations and
318 *vice versa* (McLachlan and Peel 2000, Aitkin et al. 2009, Everitt et al. 2011, Stahl and
319 Sallis 2012, Melnykov 2013, McLachlan and Rathnayake 2014). Therefore, it has been
320 recommended to consider multiple criteria together with theoretical and practical
321 considerations, because results from a single criterion could be misleading (Everitt et al.
322 2011, Stahl and Sallis 2012; see also Hamel et al. 2016 for a review). Thereby, the K s
323 selected with different criteria represent plausible alternative typologies in a data set.
324 These alternatives can be compared a posteriori to select the best one according to the
325 research objectives, for example by examining the amount of overlap between clusters to
326 limit cases where some criteria appear to overestimate K (Hamel et al. 2016).

327 Accordingly, we compared four criteria: the bootstrap criterion provided in the package
328 FlexMix (Grün and Leisch 2008) and three of the most commonly used criteria (Everitt et
329 al. 2011, Stahl and Sallis 2012), i.e. the Akaike Information Criterion (AIC – using AICc
330 led to the same results), the Bayesian Information Criterion (BIC), and the bootstrap
331 criterion based on the likelihood ratio test statistic (McLachlan 1987). Each of these four
332 criteria has different merits for selecting K (McLachlan and Peel 2000, Brame et al. 2006,
333 Aitkin et al. 2009, Everitt et al. 2011, Cubaynes et al. 2012; Stahl and Sallis 2012, and
334 see Hamel et al. 2016 for a demonstration). Therefore, for each K selected by a given
335 criterion, we obtained the predictions and 95% confidence intervals (CI) for each cluster.

336 We then selected K as the highest plausible number of clusters with no overlap among the
337 95% CI of body size (see Fig. 2). The left panels of Fig. 2 illustrate the plausible K s
338 found for two populations: $K=2, 3$ or 4 for bighorn sheep at Ram Mountain, and $K=4$ or 6
339 for Soay sheep at St Kilda. In bighorn sheep, two clusters have overlapping 95% CI for
340 $K=4$, but all clusters are distinct for $K=3$, and so $K=3$ was selected. Similarly, $K=4$ was
341 selected for Soay sheep because the alternative with 6 clusters showed overlap among
342 clusters. We selected K accordingly for all populations. In FlexMix, a cluster needs to
343 include a minimum of 5% of observations to be identified. The minimum value for a
344 cluster was 8% in mountain goats. The number of individuals in a cluster only affects the
345 uncertainty around the estimates computed for each cluster, not the mean, and these
346 uncertainties are represented by the 95% CI in the figures. To evaluate whether the
347 magnitude in the structure of cohort variation at the initial age varied across species along
348 the “slow-fast” continuum, we determined the Pearson correlation coefficient (with its
349 95% CI) between the number of cohort clusters selected and generation time (on a log-
350 scale).

351

352 In this first step, males and females of each population were included in the same mixture
353 model because our aim was first to pool cohorts that experienced similar environmental
354 conditions, to later assess whether the same environmental conditions affected the
355 variance of males and females differently. Separate analyses for each sex could have
356 resulted in a cohort year being included in a different cluster for each sex, so that the
357 variance among clusters would be based on different environmental conditions for each
358 sex and would not be comparable. After the clustering, we modeled growth trajectories

359 separately for males and females. Therefore, each population was described by a certain
360 number of cohort clusters, with each cluster including both males and females born the
361 same years, while the difference in size between sexes was accounted for by using sex as
362 a covariate in the model. In the next 5 steps, we used the cohort classification provided by
363 the clusters of the mixture models in step 1 to determine the growth trajectory specific to
364 each cohort cluster, and this separately for each sex because growth trajectories vary
365 between sexes. Therefore, for each population, cohort years in each cluster were
366 extracted from the mixture model (e.g. cluster 1 = 1995, 1999, ..., 2005; cluster 2 = 1990,
367 1998, ..., 2010; etc.). Then, all individuals born in the years included in a cluster were
368 assigned the same cluster number. To analyze the sex-specific growth trajectory of each
369 cohort cluster (Steps 2 to 6), we used the data set including all body size measurements of
370 individuals throughout their lifetime and assigned all measurements for a given
371 individual to its respective cluster number.

372

373 *Step 2: Assessing growth trajectories of cohort clusters*

374 First, we evaluated whether cohort clusters differed in lifetime growth trajectories for
375 each population and sex. We analyzed each sex separately to account for potential
376 confounding effects of female reproductive status in capital breeding species (see below),
377 and male reproductive status was not available. Furthermore, because growth markedly
378 differs between sexes in sexually dimorphic species and was modeled with a spline,
379 analyzing sexes together would have required a three-way interaction (age, sex and
380 cluster) that would have been difficult to interpret. Our aim was not to assess whether the
381 interaction between age and cluster differed between sexes, but rather to determine

382 whether interactive effects between age and cluster occurred in each sex. We fitted linear
383 mixed models (LMMs) using the R function “lmer” of the “lme4” package (Bates et al.
384 2014), including body size as the dependent variable, and including both year and
385 individual identity as random intercepts to account for annual variation and the repeated
386 measures of individuals with age. For the selection of fixed effects, we sequentially
387 compared a model with only age (i.e. no difference among cohort clusters), a model with
388 additive effects of cluster and age (i.e. a unique growth trajectory for all cohort clusters,
389 but cluster-specific size in early life that remained unchanged throughout lifetime), and a
390 model with an interaction between cohort cluster and age (i.e. cluster-specific growth
391 trajectories). We used likelihood ratio test based on the “anova.merMod” function in
392 lme4 to select the best model, which was appropriate since we compared nested models
393 with the same random effects. Age was fitted with a B-spline (package “splines” in R),
394 using likelihood ratio tests to determine the best polynomial degree of the spline function.
395 We used this method throughout the analyses whenever we included a spline effect of
396 age. Furthermore, we pooled data from older ages so that the oldest age examined always
397 included at least 5 individuals. In addition to age and cohort cluster as fixed effects, we
398 included all the factors reported or expected to affect body mass and for which we had
399 data in each species. We did not systematically look for effects of these variables when
400 there was no biological reason to do so. We included the covariate “reproductive status”
401 for the LMMs on female mass, to account for the influence of producing an offspring on
402 female annual mass in capital breeders. Female body mass in roe deer (*Capreolus*
403 *capreolus*) is not affected by reproduction because they are income breeders (sensu
404 Jönsson 1997) that do not rely on body reserves for gestation and lactation, as previously

405 documented empirically in the two roe deer populations included in this study (Andersen
406 et al. 2000, Plard et al. 2014b). Reproductive status was thus not included in the roe deer
407 models. Furthermore, we could not include reproductive status for Wind Cave bison
408 (*Bison bison*) and mouflon because the data were not available, and for Svalbard reindeer
409 because reproductive status during the previous summer was uncertain for most females.
410 Finally, we included the covariate “twin” and “primiparity of the mother” as a fixed
411 effect in Soay sheep and elephants, respectively. We evaluated model fit by looking at
412 diagnostic plots of residuals. On two occasions a data point seemed to be an outlier, but
413 analyses with and without these points led to similar results. We also performed a visual
414 assessment of parameter estimations by looking at the shapes of the deviance profiles
415 (Bates et al. 2015).

416

417 For each sex in each population, we then extracted the expected body size, β_{ka} , and its
418 95% confidence interval (CI) at each age a from LMMs for each cohort cluster k (Step 2
419 of Fig. 2, Supplementary Material Fig. S1). These predictions (Fig. S1) were then used in
420 the next step to compare growth trajectories among cohort clusters.

421

422 *Step 3: Standardizing growth trajectories among cohort clusters*

423 We standardized the predictions and 95% CI found at Step 2 to contrast cluster-specific
424 growth trajectories and evaluate how they differed among populations and sexes. A large
425 variation in body size occurred among species, such that a 1 kg difference in female Soay
426 sheep that average 13 kg at the end of their first summer corresponds to a much larger
427 size variation than a 1 kg difference in female bison weighing on average 140 kg at the

428 same age. Therefore, we scaled the difference among cohort clusters in a given sex of a
429 given population as the relative difference from the mean population value m at each age
430 a . For each sex in each population, we used a LMM including measurements from all
431 cohort clusters but excluding the cluster effect from the model, and then extracted for
432 each age the arithmetic mean prediction, β_{ma} , and its 95% CI. We then computed the
433 relative difference at each age as $(\beta_{ka} - \beta_{ma}) / \beta_{ma}$, such that a cohort cluster had a value of 0
434 if it did not differ from the mean, and had either a positive or negative value if it was
435 higher or lower than the mean (see Step 3 in Fig. 2). These values were relative to the
436 mean body size of a specific sex in a given population (referred to as “relative
437 difference”, see Box 1) and could thus be compared among species and between sexes.
438 Performing all analyses based on scaled absolute differences instead of relative
439 differences led to similar results.

441 *Step 4: Quantifying the magnitude of cohort variation*

442 To evaluate how the magnitude of cohort variation changed with age, we used the
443 relative differences obtained from Step 3 and calculated the range among all cohort
444 clusters at each age, i.e. the difference between the maximum and the minimum value,
445 hereafter called “range of relative differences” (see Step 4 in Fig. 2, Box 1). We did this
446 using all age-specific size data from the age at first measurement up to the last age when
447 all clusters were measured (black dots in Step 4 of Fig. 2). When at least one cohort
448 cluster was missing at a given age, all data from this age onwards were excluded from
449 analyses (grey dots in Step 4 of Fig. 2). We then evaluated whether the range of relative
450 differences varied between sexes and along the “slow-fast” continuum using a linear

451 model (LM) with a spline effect of age, sex as a factor, a linear effect of generation time,
452 and two-way interactions between age and sex and between age and generation time
453 (using the product for the latter). The data have a hierarchical structure, with population
454 nested in species, and sex crossed with population. However, accounting for this structure
455 using a nested random intercept of population within species did not capture more
456 variability (random effect variance of population within species estimated close to zero),
457 reflecting that populations within species were not strongly dependent, and that variation
458 among populations associated with generation time accounted for much of the variability.
459 We log-transformed the range of relative differences to normalize the residuals, adding
460 0.1 because some relative differences were null. We also standardized age to account for
461 differences in the length of the time series between sexes and among species generated by
462 differences in lifespan. Because there was only a single cohort cluster in elephants, we
463 replicated the analysis by including and then excluding this population. Although the
464 influence of generation time was slightly more pronounced when elephants were
465 included, the results were overall similar. We therefore only report the conservative
466 results from analyses excluding elephants. In addition, the range of relative differences
467 was influenced by the number of clusters and the age at first measurement, but including
468 or excluding these covariates in the analysis led to qualitatively similar results.

469

470 *Step 5: Quantifying cohort variation between each pair of cohort clusters*

471 In Step 4, we computed the range in relative differences among all cohort clusters for a
472 given sex and population. In the fifth step, we calculated the difference in relative
473 differences between each pair of cohort clusters, referred to as “paired relative

474 differences” (see Step 5 in Fig. 2, Box 1). This paired analysis better captured the patterns
475 of changes in cohort variation over age within a sex in a given population, illustrating
476 whether different patterns occurred among pairs of cohorts (e.g. differences between
477 cohort clusters 1 and 2 might compensate with age, whereas those between cohort
478 clusters 1 and 3 might cumulate with age). Again, we used all age-specific size
479 measurements from the age at first measurement up to the last age when all clusters were
480 measured (solid lines in Step 5 of Fig. 2).

481

482 *Step 6: Measuring cumulative vs. compensatory effects*

483 To determine whether relative cohort variation in size remained constant throughout life,
484 increased (size divergence), or decreased (size compensation), we computed the relative
485 change in paired relative differences between cohort clusters from age x to age $x+1$
486 (hereafter referred to as “relative change from age to age”, Box 1), using the paired
487 relative differences calculated at Step 5 (illustrated in Fig. 4 with their 95% CI). A
488 positive value indicated an increase in the difference between a pair of cohort clusters
489 with age, and therefore cumulative effects with age. On the other hand, a negative value
490 indicated reduced differences between pairs of cohort clusters with age, and thus
491 compensatory effects. A value of 0 indicated no change in cohort variation in size with
492 age between a pair of cohort clusters. We then evaluated whether the relative change
493 from age to age varied between sexes and along the “slow-fast” continuum using a LMM
494 including a spline effect of age, sex as a factor, a linear effect of generation time, and two
495 two-way interactions between age and sex and between age and generation time (using
496 the product for the latter). We included population as a random intercept because we had

497 repeated values. Repetitions were more numerous for populations with more cohort
498 clusters because these populations included a greater number of paired clusters (Fig. 6).
499 Again, adding a nested random intercept of population within species did not capture
500 more variability (random effect variance of population within species estimated close to
501 zero). According to the profile log-likelihood for the parameter of the Box-Cox
502 transformation (package “MASS” in R, Venables and Ripley 2002), we transformed the
503 relative change from age to age to the power 7.5 to normalize the residuals, adding 0.5 to
504 shift the distribution above zero (Supplementary Material Fig. S2). As in Step 4, we
505 standardized age to account for differences in the length of the time series between sexes
506 and among species, due to differences in lifespan. We also repeated this analysis with
507 elephants included and excluded. Again, results were similar but with a more pronounced
508 influence of generation time when elephants, the species with the longest generation time,
509 were included. We only report the conservative results from analyses excluding
510 elephants. Also, including or excluding age at first measurement as a covariate in the
511 analysis led to qualitatively similar results.

512

513 *Separating compensatory/catch-up growth from viability selection*

514 We sought to remove the influence of viability selection from that of differences in
515 growth to assess the specific influence of compensatory/catch-up growth on patterns of
516 cohort variation with age. We did this by rerunning Steps 2 to 6 while accounting for the
517 disappearance of individuals (mostly through mortality because emigration was limited or
518 absent in most populations), thereby modeling differences among cohort clusters due
519 only to differences in growth. First, we added the age at last measurement of each

520 individual as a covariate in each LMM run to estimate the growth of a cohort cluster
521 (Step 2). We fitted a LMM according to equation 1 in van de Pol and Verhulst (2006),
522 using the age at last measurement to reflect the timing of disappearance (i.e. parameter α_i
523 in van de Pol and Verhulst (2006)'s equation). We tested for both a linear and a quadratic
524 effect of age at last measurement and retained the best model based on a likelihood ratio
525 test. Then, we extracted the predicted trajectories of expected body size with age (β_{ka})
526 from these LMMs that included age at last measurement. As these LMMs provided a
527 measure of within-cohort cluster change in body size that was independent of viability
528 selection (i.e. parameter β_w in van de Pol and Verhulst (2006)'s equation), we will refer to
529 these parameters as βW_{ka} , for “within change in β_{ka} ”. The influence of age at last
530 measurement could differ among cohort clusters of a given sex and population because
531 each cluster was modeled using a different LMM. To obtain the βW_{ka} predictions,
532 however, we used the same age at last measurement for all cohort clusters of the same
533 sex and population, using the mean age at disappearance for that sex and population,
534 thereby controlling for the variation in age at disappearance among cohort clusters. Using
535 these growth trajectories adjusted for disappearance, we then computed the standardized
536 growth trajectory for each cohort cluster (Step 3). As the standardized growth trajectories
537 in Step 3 provided a measure of relative difference among cohort clusters calculated as
538 $(\beta_{ka} - \beta_{ma}) / \beta_{ma}$, we used $(\beta W_{ka} - \beta W_{ma}) / \beta W_{ma}$, where βW_{ma} was obtained from a LMM similar
539 as that for β_{ma} in Step 3, but again including age at last measurement as a covariate, with
540 either a linear or quadratic effect. We extracted βW_{ma} predictions for the mean age at
541 disappearance for each sex and population. Therefore, the relative difference calculated
542 accounted for the selective disappearance of individuals and allowed us to calculate the

543 relative change from age to age in cohort variation (Step 6) that was only due to
544 differences in growth. Next, we evaluated whether sex and generation time affected the
545 relative change from age to age that was only due to differences in growth. We did this
546 similarly to Step 6, except that we replaced the response variable “relative change from
547 age to age *due to both viability selection and growth*” with the “relative change from age
548 to age *due only to differences in growth*”. We could then compare the results for the
549 relative change from age to age that represented both viability selection and
550 compensatory/catch-up growth with those only due to differences in growth. Finally, to
551 evaluate the importance of viability selection, we used likelihood ratio tests to determine
552 whether the LMM including age at last measurement as a covariate received greater
553 support than the same model without this covariate (i.e. LMMs in Step 2 with and
554 without age at last measurement). We did this separately for each cohort cluster of a
555 given sex in a given population. Note that for the bison population at Konza,
556 disappearance was mostly the result of culling.

557

558 RESULTS

559 *Structure in body size variation among cohorts: number of cohort clusters*

560 We found statistical evidence for distinct cohort clusters in almost all populations, with
561 up to 5 clusters in the Wind Cave bison population (Table 1). Only the Amboseli
562 elephants, the species with the longest generation time, did not exhibit detectable cohort
563 variation in size. In the species with the second longest generation time, the mountain
564 goat (*Oreamnos americanus*), we found 2 cohort clusters, but one cluster only included
565 two of 25 cohorts, suggesting no structure or low cohort variation in this species. The

566 trend for the number of clusters to decrease with generation time (Table 1) was not
567 statistically significant (r [95% CI] = -0.33 [-0.78, 0.33], $p = 0.3$). The data on bison at
568 Konza were characterized by four cohort clusters, but one cluster only included recent
569 cohorts, and thus we could not examine growth trajectories in this cohort cluster because
570 no individual was monitored past age 4. For bison at Wind Cave, one of the five clusters
571 also had no individual monitored past age 4. Thus, for the bison populations, we
572 performed steps 2 to 6, which assess growth trajectories, only for clusters with enough
573 data later in life, i.e. three for Konza and four for Wind Cave.

574

575 *Growth trajectories of cohort clusters*

576 Models including an interactive effect between age and cluster received most support in
577 almost all cases (likelihood ratio p 's < 0.1, Supplementary Material Table S1), supporting
578 that growth trajectories differed substantially among cohort clusters throughout life. The
579 only exceptions were for roe deer males at Trois Fontaines and female mountain goats
580 where the additive model was retained, and for male mountain goats where the selected
581 model only included age (Supplementary Material Table S1).

582

583 *Magnitude of cohort variation in body size*

584 The standardized growth trajectories quantifying the relative difference in size (Step 3;
585 Fig. 3) illustrate that variation in size among cohort clusters was generally higher early in
586 life, with an average difference of 20% and up to 40% (Fig. 4). This early variation
587 decreased rapidly in the first few years and then stabilized (Fig. 3). The range of relative
588 differences in size among cohort clusters (Step 4; Fig. 4) was influenced by an interactive

589 effect between age and sex, and by an additive effect of generation time (Table 2a).
590 Differences among cohort clusters decreased markedly with increasing age, in both sexes
591 and for any generation time (Fig. 5). Males, however, showed about 7% greater cohort
592 variation in early life than females, while both sexes displayed similar magnitude of
593 cohort variation in size at the end of life. The decrease in the magnitude of cohort
594 variation in size with increasing age was more progressive and extended for a greater part
595 of life in males than in females, for which cohort variation stabilized just before mid-life
596 (Fig. 5). The strength of the decrease in cohort variation with increasing age was
597 independent of generation time (Table 2a). Nevertheless, populations with a short
598 generation time exhibited more cohort variation in size throughout their entire life than
599 populations with a long generation time (Fig. 5).

600

601 *Change in the magnitude of cohort variation in size: cumulative vs. compensatory effects*

602 The curves of paired relative differences (Step 5; Fig. 6) were generally similar within a
603 sex in a given population. From these curves, we computed the relative change from age
604 to age in the magnitude of cohort variation in size between paired cohorts (Step 6; Fig. 7).
605 The relative change from age to age was influenced by interactive effects between age
606 and sex and between age and generation time (Table 2b). Early in life, the relative change
607 from age to age was negative, corresponding to compensatory effects (Fig. 8). In general,
608 these compensatory effects rapidly decreased with age (sharp increase in the curves in
609 Fig. 8) and stopped just before mid-life (stabilizing around zero, implying neither
610 cumulative nor compensatory effects; Fig. 8). In males, however, compensatory effects
611 were weaker early in life compared with females, but continued throughout the lifetime,

612 decreasing only progressively with age (Fig. 8). Compensatory effects were stronger in
613 early life in species with a short generation time. In contrast, species with a long
614 generation time had a relative change from age to age that stabilized more rapidly,
615 reaching a plateau close to zero at an earlier age relative to their lifetime (Fig. 8).
616 Comparing figures 6 and 7 reveals that the stabilization in species with a long generation
617 time is mainly the result of a dissipation of cohort variation in size with increasing age,
618 whereas cohort variation in size in species with a short generation time stabilized but was
619 still present from mid-age to late life.

620

621 *Compensatory/catch-up growth vs. viability selection*

622 With the exception of mountain goats and reindeer, likelihood ratio tests revealed
623 viability selection in all species, but not necessarily in both sexes or in all cohort clusters
624 (Table 3). Overall, about half of the cohort clusters (Table 3) for both males (50%, 13 of
625 26 cases) and females (52%, 16 of 31 cases) showed evidence for viability selection.
626 With the exception of Wind Cave bison, the coefficient for the effect of age at last
627 measurement on body size (i.e. Step 2 including age at last measurement) was
628 consistently positive, suggesting disappearance of lighter individuals with increasing age
629 (e.g. males in Chizé, Fig. 9). Nevertheless, the relative change from age to age in the
630 magnitude of cohort variation that was only due to differences in growth did not differ
631 much from that due to both viability selection and growth (range of differences from 0 to
632 17.1% in the relative change from age to age after accounting for viability selection; Fig.
633 10). Overall, the change from age to age only due to differences in growth was influenced
634 by the same variables as when including viability selection (Table 2b and 2c, Fig. 10),

635 with the influence of age, sex and generation time showing very similar patterns
636 (compare Fig. 8 and 10, which are on the same scale). The main difference was early in
637 life, when the relative change from age to age only due to differences in growth was less
638 than when the data included both viability selection and growth, particularly for short-
639 lived species (blue and pink lines in Fig. 10). This effect was slightly stronger in males
640 than in females (Fig. 10).

641

642 DISCUSSION

643 Based on an exceptional set of long-term data collected in 11 populations of large
644 herbivores, we quantified cohort variation and assessed how it changed throughout life,
645 demonstrating that this fundamental biological process varied both across species in
646 relation to their pace of life and between sexes. Variation in size peaked at the start of
647 life, then quickly decreased with increasing age in all species and stabilized around mid-
648 life. Even after accounting for viability selection, compensatory/catch-up growth was still
649 a major process explaining the decrease in the amount of cohort variation with increasing
650 age. Among-cohort variation was lower in species with a slower than a faster pace of life
651 throughout the lifetime, and vanished at prime ages in the species with the slowest paces
652 of life. Females showed less phenotypic variability and stronger compensatory/catch-up
653 growth than males early in life, whereas males showed more progressive changes
654 throughout life. This resulted in old males having the same low level of cohort variation
655 as old females. Our findings concern mainly body mass variation because mass was used
656 to describe body size in all except one species.

657

658 We found large variation in body size among cohorts in all species except the slowest
659 species along the “slow-fast” continuum of life histories included in this study. Mixture
660 models (McLachlan and Peel 2000), an innovative method to assess individual
661 differences in life-history traits (Hamel et al. 2016), identified clusters of cohorts sharing
662 similar body size at the start of life. We showed that cohort variation was structured, as
663 opposed to the unstructured variation (i.e. uniform distribution) usually assumed when
664 studying cohort effects with mixed models. This structured variation led to distinct
665 growth trajectories throughout life among clusters of cohorts sharing similar initial size,
666 in all species and most often in both sexes, thereby showing that early body size is a key
667 driver of the growth trajectory later in life. Disentangling whether cohort-specific growth
668 trajectories results from early or late environmental conditions is difficult without an
669 experimental approach because individuals of the same cohort can experience the same
670 environmental conditions throughout their entire lifetime (Metcalf and Monaghan 2003).
671 In this regard, one major novelty in our study is that we showed that environmental
672 conditions experienced early in life *per se*, not just the cohort year modeled as a random
673 effect term, typically have long-term consequences irrespective of late-life conditions.
674 Indeed, cohort clusters with similar body size at the start of life included cohorts born in
675 different years, and hence individuals included in the same cluster experienced different
676 environmental conditions later in life. In many species, clusters included cohorts that
677 were more than 20 years apart. Still, cohort clusters characterized by different initial body
678 sizes displayed different growth trajectories throughout life, supporting the hypothesis
679 that individual growth trajectories in large herbivores are considerably affected by early
680 development. Of course, cohort variation does not account for all observed variation

681 among body mass trajectories in a given population. The specific early mass of an
682 individual, for instance, should markedly influence its future age-specific mass, as often
683 reported for large herbivores (Clutton-Brock and Pemberton 2004, Douhard et al. 2013).
684 Here, because individuals were not measured every year in several populations, we did
685 not assess the contribution of individual variation in early mass to observed variation in
686 age-specific mass later in life.

687

688 The greatest cohort variation in size occurs at the start of life, with on average a 20% (up
689 to 40%) difference between cohort clusters. Cohort variation in size, however, decreased
690 relatively rapidly with increasing age in all species. Our results indicate much potential
691 for compensation in the magnitude of cohort variation in large herbivores despite limited
692 time to compensate due to growth cessation at maturity. Nevertheless, the meta-analysis
693 by Hector and Nakagawa (2012) pointed out that mammals and birds allocate more to
694 accelerating growth after food restriction compared to fish and arthropods, possibly
695 because species with determinate growth gain more benefits by compensating early,
696 before growth ceases (Metcalf and Monaghan 2003). The decreasing cohort variation
697 with increasing age was a consequence of both higher survival of larger individuals, and
698 compensatory/catch-up growth, which allowed some cohorts to partly make up for a poor
699 start. Our results demonstrate that viability selection resulting from the positive influence
700 of large size on individual survival is common in natural populations of large herbivores
701 (Nussey et al. 2011). Nevertheless, although viability selection was detectable in almost
702 all species and both sexes, it only explained a small fraction of the compensation in the
703 magnitude of cohort variation, affecting mostly shorter-lived species. Viability selection

704 is likely to peak during the neonatal stage in large herbivores, when survival is low and
705 most variable (Gaillard et al. 2000b), and for many of our study populations it had likely
706 already taken place when body size was first measured (Table 1). Consequently, our
707 results imply that viability selection is influential, but that compensatory/catch-up growth
708 is the main factor explaining the decrease in cohort variation with increasing age after the
709 neonatal stage.

710
711 Changes in growth patterns, either by increasing growth rate when conditions are better
712 (compensatory growth) or by extending the growth period (catch-up growth), are likely to
713 be selected whenever the ratio of benefits to costs is positive (Metcalf and Monaghan
714 2001, Metcalfe and Monaghan 2003, Dmitriew 2011). Compensatory/catch-up growth
715 should be selected when it enhances survival, both in the short-term, when it allows
716 individuals to move out of a vulnerable stage, reducing mortality risk, and in the long-
717 term, when large size buffers against environmental variation throughout life (Metcalf
718 and Monaghan 2003, Dmitriew 2011). Selection pressures for compensatory/catch-up
719 growth are also high when large size improves reproductive success (Dmitriew 2011). In
720 mammals, larger size provides competitive advantages to males of many species (Lidgard
721 et al. 2005, Pelletier and Festa-Bianchet 2006, Mainguy et al. 2009), and generally also
722 improves female reproductive success (Dobson et al. 1999, Hodge et al. 2008, Jones et al.
723 2010, Zedrosser et al. 2013, Plard et al. 2014b). On the other hand, compensatory/catch-
724 up growth can have short-term costs by reducing allocation to reproduction (Marcil-
725 Ferland et al. 2013) or by increasing predation risk because of greater foraging time, and
726 thereby exposure to predators (Dmitriew 2011). Faster or prolonged growth during

727 development can also result in detectable trade-offs in other life-history traits later in life
728 (Nussey et al. 2007, Dmitriew 2011, Douhard et al. 2014). For instance, according to the
729 disposable soma theory (Kirkwood 1977), individuals allocating more to growth early in
730 life are expected to pay a cost later in terms of reproduction or survival (Metcalfé and
731 Monaghan 2001, Lemaître et al. 2015). Indeed, an increase in oxidative stress and in the
732 repair of damaged cells can affect ageing patterns and longevity (Mangel and Munch
733 2005, Monaghan et al. 2009, Nussey et al. 2009, Dmitriew 2011), leading to subtle costs
734 that might appear only late in life and hence might be under lower selection pressure (e.g.
735 Lee et al. 2013b). The long-term trade-offs associated with growth during development
736 are a cornerstone of life-history theory (Dmitriew 2011), and hence it is essential to
737 assess how variation in individual growth changes with age to understand better its
738 impact on individual fitness (Lee et al. 2013b). However, the relevance for population
739 dynamics of subsequent changes in growth and trade-offs with life-history traits depends
740 on the survival of individuals from different cohorts. Given the documented potential
741 negative long-term fitness consequences of a poor start (reviewed in Metcalfé and
742 Monaghan 2001), the benefits, and thereby selection pressures, of compensating for a bad
743 start are likely to be high. This is supported by our finding that compensatory/catch-up
744 growth is a key process in the dissipation of cohort variation with increasing age. Hence,
745 the benefits/costs ratio for compensatory/catch-up growth is likely high in large
746 herbivores, with strong selection pressures for compensatory/catch-up growth in all
747 species irrespective of their pace of life.

748

749 Although compensatory effects were detected in all species, we found important
750 differences among species in relation to their ranking on the “slow-fast” continuum of
751 life histories. Cohort variation in size in early life was greater in species with a fast than a
752 slow pace of life. This was supported by *i-* our inability to detect any cohort variation in
753 size in the African elephant, which had the longest generation time, *ii-* the tendency to
754 identify more cohort clusters in species with a fast than a slow pace of life, and *iii-* the
755 greater relative differences in size among cohort clusters in species with a fast pace of life
756 than in species with a slow pace of life. Long-lived species have evolved a slow pace of
757 life: individuals generally show a conservative reproductive tactic that favors their own
758 survival over that of their offspring because longevity increases fitness (Clutton-Brock
759 1988, Newton 1989). In these species, selection pressures have resulted in environmental
760 canalization of adult survival, which shows lower variance than reproductive traits across
761 a wide range of environmental conditions (Gaillard and Yoccoz 2003). Conversely, short-
762 lived species have evolved a faster life-history strategy in which individuals allocate a
763 high reproductive effort to each reproductive occasion, and environmental canalization
764 has led to a lower variance in reproductive traits compared with long-lived species
765 (Gaillard and Yoccoz 2003). The lower variance in growth at the start of life in long-lived
766 than short-lived species suggests that initial growth is more affected by fluctuations in
767 environmental conditions in species with a fast than a slow pace of life. This lower
768 variance might also result from maternal effects, for example if mothers of longer-lived
769 species provided more care to offspring, thereby buffering against environmental
770 fluctuations. Although elephant mothers allocate to maternal care for a much longer
771 period than any other large herbivore, the absolute time devoted to offspring by female

772 elephant corresponds to the same allocation relative to their pace of life as other large
773 herbivores included in our analysis (Langer 2008). Therefore, the lower variance in initial
774 growth in long-lived species does not correspond to higher maternal investment in
775 response to potentially higher time constraints. Moreover, maternal effects are unlikely to
776 have a strong influence because mothers of long-lived species tend to favor their own
777 survival at the expense of their offspring when resources are scarce (Sæther et al. 1993,
778 Festa-Bianchet and Jorgenson 1998, Therrien et al. 2007, Martin and Festa-Bianchet
779 2010). Because body size is one of the main determinants of juvenile survival in most
780 vertebrates including large herbivores (Plard et al. 2015, Théoret-Gosselin et al. 2015),
781 our results suggest that body growth during development is likely to have been under
782 strong selective pressures to promote survival, particularly in long-lived species.

783

784 Although cohort variation in size decreased markedly with increasing age and the
785 strength of this decrease was similar across species, body size still varied among cohorts
786 in short-lived species when they reached prime ages. In long-lived species, cohort
787 variation almost totally vanished at the same life stage. Although compensatory/catch-up
788 growth is relatively common, it is often incomplete (Metcalf and Monaghan 2001,
789 Dmitriew 2011). This is likely because of physiological constraints, where individuals are
790 trapped in a developmental trajectory, or because the benefits/costs ratio is not high
791 enough, and so growth rates are usually not maximal (Metcalf and Monaghan 2003,
792 Dmitriew 2011). Our results further suggest that there is a limited time window for
793 compensatory/catch-up growth before prime age in species with determinate growth.
794 Furthermore, cohorts of species with a fast pace of life were more variable in size early in

795 life and, as the rate of decrease in cohort variation with increasing age was similar across
796 species, they did not fully compensate/catch-up for initial size differences compared with
797 species with a slow pace of life. With a limited time window and the costs paid later in
798 life, the advantages of compensatory/catch-up growth should depend on its timing, with
799 earlier compensatory/catch-up growth likely to be selected because of its direct benefits
800 to survival and lifetime reproductive success (Dmitriew 2011).

801

802 In addition to differences in cohort variation in size across species, we highlighted
803 between-sex differences in cohort variation of large herbivores. Cohort variation in size
804 was higher in early life in males than in females. Although the magnitude of cohort
805 variation stabilized at mid-life in females, it continued to decrease progressively
806 throughout lifetime in males, reaching the same level as that of females only at the end of
807 life. Compensatory/catch-up growth, however, was stronger early in life in females and
808 stopped at mid-life compared with males that showed a weaker but constant
809 compensatory/catch-up growth throughout lifetime. These results likely emerged from
810 the contrasted sexual selection pressures in males and females in relation with sex
811 differences in intra-sexual competition (Bonduriansky et al. 2008). Indeed, although
812 sexual selection can be strong in females (Clutton-Brock 2007), selection for traits
813 affecting competitive abilities is generally stronger in males than in females, especially in
814 sexually size dimorphic and polygynous species such as large herbivores (Orians 1969,
815 Clutton-Brock 2007). Males and females adopt different tactics to increase their lifetime
816 reproductive success. The reproductive success of males is often highly skewed and
817 dependent on their ability to compete for reproductive opportunities (Orians 1969,

818 Trivers 1972). Thus, males often must fight to reproduce, and body size is a major
819 determinant of fighting and reproductive success (Lidgard et al. 2005, Pelletier and Festa-
820 Bianchet 2006, Mainguy et al. 2009). Females, on the other hand, usually compete for
821 resources (Orians 1969, Trivers 1972, Clutton-Brock 1991). Body size can therefore have
822 a stronger influence on the reproductive success of males than females, as shown in red
823 deer (*Cervus elaphus*; Kruuk et al. 1999). As a result of these differences in sexual
824 selection, males often evolve a “grow fast, die young” life-history strategy (Bonduriansky
825 et al. 2008), allocating more resources to rapid growth and fewer to maintenance (see e.g.
826 Toïgo et al. 1999 and Robinson et al. 2006). Males will therefore grow faster early in life
827 and for longer compared with females (Garel et al. 2006), thereby requiring more
828 nutrients than females (Michener and Locklear 1990, Landete-Castillejos et al. 2005).
829 Consequently, males are more sensitive to food shortage during early life and often show
830 greater juvenile mortality than females (Clutton-Brock et al. 1985). Greater vulnerability
831 to nutritional stress in males likely explains the larger cohort variation and the slightly
832 stronger viability selection found in males than in females. Furthermore, even though
833 males should have a shorter catch-up time window than females because they grow faster
834 and die younger, compensatory/catch-up growth was much weaker and slower in males
835 than in females. This pattern seems to confirm that even though it would be beneficial for
836 males to compensate early in life, they have a lower ability to compensate/catch-up for a
837 bad start than females (Toïgo et al. 1999, Festa-Bianchet et al. 2000, but see Solberg et al.
838 2008 and Rughetti and Festa-Bianchet 2010). Perhaps the costs of compensation/catch-up
839 growth are greater for males, or small females can allocate more resources to growth by

840 postponing primiparity (Martin and Festa-Bianchet 2012), an option that is not available
841 to males.

842

843 CONCLUSION

844 The role of cohort variation as a process in life-history variation has often been explored.

845 Our study, however, provides novel results on how the magnitude of cohort variation

846 changes over the lifespan, and how these patterns vary among species in relation to the

847 pace of life and between sexes. These topics have been neglected in previous studies

848 likely because the required data for a comparative analysis were lacking until recently.

849 We found that cohort variation in size decreased markedly during the first half of life and

850 then almost vanished, particularly in species with a slow pace of life. Both

851 compensatory/catch-up growth and viability selection dampened cohort variation in size

852 with ageing, but compensatory/catch-up growth was the main underlying process beyond

853 the neonatal stage. Our findings suggest that the costs associated with

854 compensatory/catch-up growth are not necessarily high, at least early in life and

855 particularly in females, or that the benefits are high. It remains to be determined whether

856 differences in growth trajectories are adaptive. For instance, no study has yet tested

857 whether delayed costs of rapid or prolonged early growth exist in wild vertebrates (see

858 Lemaître et al. 2015 for a review). As fitness mostly depends on survival and

859 reproductive success, which are both linked with body size (Dmitriew 2011), it is

860 fundamental to evaluate the degree to which body size early in life and variability in

861 developmental patterns among cohorts influence other traits later in life.

862

863 Our study has shown that understanding how cohort variation changes over the lifetime
864 in wild populations reveals how selective forces affect populations and trait evolution.
865 Even though compensation is often assumed to occur in most species, its extent and the
866 eco-evolutionary mechanisms behind this process are often overlooked despite their
867 fundamental importance in population ecology (Metcalf and Monaghan 2001, Metcalfe
868 and Monaghan 2003, Dmitriew 2011). For instance, climate change is predicted to result
869 in greater variability in environmental conditions (Easterling et al. 2000), likely
870 increasing variation among cohorts at the start of life (Stenseth et al. 2002). In this
871 context, only long-term studies can determine whether individuals within populations can
872 adapt to the increasing environmental variability brought by climate change. Unraveling
873 how variation changes with age, to what extent compensation occurs within populations,
874 and which eco-evolutionary processes are responsible for compensatory effects will
875 further our understanding of how future environmental changes may impact the
876 phenotypic composition of wild populations. Our comparative analysis provides the first
877 answers to these questions, by demonstrating the pervasiveness of cohort variation in size
878 in both sexes in populations of large herbivores distributed widely over the “slow-fast”
879 continuum of life histories, and by identifying how this cohort variation in size varies
880 with increasing age, highlighting the importance of both compensatory/catch-up growth
881 and viability selection.

882

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900

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Box 1. Overview of the research questions about cohort effects in large herbivores, the methods applied to answer these questions, and the variables used at each step of this study.

Question	Method	Step	Description of the variable	Name of the variable
A Is there a structure in body size variation among cohorts within a population or does body size variation follow a normal distribution over all cohorts?	We ran mixture models on body size at first measurement to assess the existence of cohort clusters in each population.	1	Clusters of cohorts with similar body size	<i>"cohort clusters"</i>
B Do cohort clusters show different growth trajectories?	We fitted linear mixed models and tested for an interaction between age and cluster. From these growth trajectories, we then extracted expected body size at each age for each cohort cluster.	2	Growth trajectory of each cohort cluster, i.e. mean body size at each age (Fig. S1)	<i>"body size"</i>
C How does the magnitude of cohort variation in body size change with age? Does this differ among species and between sexes?	From the "body size" measures obtained for each cohort cluster (Step 2), we scaled the difference among cohort clusters as the relative difference from the mean population value at each age.	3	Standardized growth trajectory of each cohort cluster, i.e. relative difference in body size at each age (Fig. 3)	<i>"relative difference"</i>
	From the "relative difference" measures (Step 3), we calculated the range in relative differences among all cohort clusters at each age. Then, we assessed the influence of age, sex and generation time on this variable.	4	Magnitude of cohort variation in size at each age (Fig. 4)	<i>"range of relative differences"</i>
D Does the change with age in cohort body size variation result from cumulative or compensatory effects? Does this differ among species and between sexes?	From the "relative difference" measures (Step 3), we calculated the difference in relative differences between each pair of cohort clusters for a given sex in a given population.	5	Magnitude of cohort variation in size at each age computed for each pair of cohort clusters (Fig. 6)	<i>"paired relative differences"</i>

From the "paired relative difference" measures (Step 5), we computed the relative change in paired relative differences between cohort clusters from age x to age $x+1$. Then, we assessed the influence of age, sex and generation time on this variable.

6 Relative change with age in cohort variation between each pair of cohort cluster (Fig. 7)

"relative change from age to age"

Table 1. Summary of populations monitored and data available for the comparative analysis of cohort variation in size in large herbivores.

Population	Species	Location	Years	N males ^{&}	N females ^{&}	Body size measure	Age ^o	N	$\frac{K}{[R^2]}$	GT	References
Amboseli	African elephants <i>Loxodonta africana</i>	Kenya	1972-2008*	88	87	Shoulder	0-4.5 [^]	25	1	19.78	1
				249 [319]	280 [440]	height			[0]		
				1.3 [1-5]	1.6 [1-5]						
Caw Ridge	Mountain goats <i>Oreamnos americanus</i>	Alberta, Canada	1989-2013	132	124	Mass in	1	25	2	10.96	2, 3
				164 [453]	159 [761]	July			[0.28]		
				2.8 [1-8]	4.8 [1-13]						
Konza Prairie	Plains bison <i>Bison bison</i>	Kansas, USA	1994-2012	664	634	Mass in	0	19	4	9.37	4
				709 [2074]	709 [2714]	November			[0.87]		
				2.9 [1-9]	3.8 [1-17]						
Wind Cave	Plains bison <i>Bison bison</i>	South Dakota, USA	1966-2008*	931	868	Mass in	1	26	5	9.37	5
				1251 [1509]	1187 [2491]	November			[0.93]		
				1.2 [1-5]	2.1 [1-18]						
Ram Mountain	Bighorn sheep <i>Ovis canadensis</i>	Alberta, Canada	1973-2013	268	299	Mass in	1	41	3	8.57	6
				477 [1511]	484 [2369]	September			[0.65]		
				3.2 [1-13]	4.9 [1-20]						
Svalbard	Svalbard reindeer <i>Rangifer tarandus platyrhynchus</i>	Svalbard	1994-2013	-	552	Mass in	0	20	3	6.67	7
				-	618 [1953]	Feb-May			[0.58]		
				-	3.2 [1-10]						
Ravdol	Reindeer <i>Rangifer tarandus</i>	Finnmark, Norway	2002-2014	-	330	Mass in	0	13	2	5.15	8
				-	374 [1298]	September			[0.40]		
				-	3.5 [1-12]						
Chizé	Roe deer <i>Capreolus capreolus</i>	Southwestern France	1977-2012	571	510	Mass in	1	36	3	4.6	9, 10, 11
				607 [1447]	543 [1682]	Jan-Feb			[0.47]		
				2.4 [1.13]	3.1 [1-14]						
Trois Fontaines	Roe deer	Northeastern	1975-2012	361	365	Mass in	1	38	3	4.6	9, 10, 12

	<i>Capreolus capreolus</i>	France		465 [1055]	450 [1352]	Jan-Feb				[0.43]	
				2.3 [1-9]	3.0 [1-10]						
St. Kilda	Soay sheep	Hirta Island,	1985-2013*	943	982	Mass in	0	28	4	4.47	13
	<i>Ovis aries</i>	Scotland		1364 [2097]	1565 [3940]	August				[0.34]	
				1.5 [1-11]	2.5 [1-14]						
Caroux	Mouflon	Massif Central,	1995-2014	459	401	Mass in	0	20	3	4.21	14, 15
	<i>Ovis gmelini musimon</i>	France		643 [850]	523 [757]	May-June				[0.27]	
	× <i>Ovis</i> sp.			1.3 [1-7]	1.4 [1-10]						

* The range of years is higher than the number of cohorts available (N) either because data were not collected in all years, or because measurements at first age were not collected in all years.

& Top row is the number of individuals measured at first age (i.e. used in Step 1, see Methods). The second row is the number of individuals measured when including all age measurements, with the total number of observations (including repetitions on individuals) in brackets. The third row is the mean number of repetitions per individual, with the range for all individuals in brackets. The total number of individuals in row 2 is larger than the number of individuals measured at first age in row 1 because some individuals were not measured at first age but their cohort year was known and thus they could be assigned to a cohort cluster and added to the analyses starting from Step 2.

^o In some populations, the first body size measurements were collected after the first summer of life, which we referred to as age 0, whereas in other populations the first measurements were available after the first year of life only, which we referred to as age 1. The exact timing when measurements were taken each year is specified in the column "Body size measure".

[^] In elephants, age at which cohort was measured is over a longer period because of the longer inter-birth interval (IBI) compared with the other species (see Methods).

Age = the age when the body size of the cohort was measured (in years).

N = the number of cohorts available.

K = the number of cohort clusters selected by the mixture models.

R² = the coefficient of determination for the mixture model with K clusters, computed as the complement of the within cluster/total variance ratio to 1 (i.e. 1 – (within-cluster variance/total variance)), where the total variance is the sum of the between- and within-cluster variance (equation 6.5 p. 170 in Frühwirth-Schnatter 2006).

GT = the generation time, in years, computed as T_b according to Lebreton (2005).

1: Lee et al. (2013), 2: Festa-Bianchet and Côté (2008), 3: Hamel et al. (2010), 4: Hamel et al. (2012), 5: Green and Rothstein (1991), 6: Festa-Bianchet et al. (2000), 7: Stien et al. (2002), 8: Bårdsen and Tveraa (2012), 9: Gaillard et al. (2003a), 10: Gaillard et al. (2003b), 11: Pettorelli et al. (2002), 12: Plard et al. (2014), 13: Clutton-Brock and Pemberton (2004), 14: Garel et al. (2005), 15: Garel et al. (2007).

Table 2. ANOVA table for the sequential^Δ effects of age, sex, generation time, and their interactions on a) the range of relative differences in size among cohort clusters, b) the relative change from age to age in cohort variation in size (i.e. relative change in paired relative differences, see Box 1), and c) the relative change from age to age in cohort variation in size excluding the influence of viability selection, thereby representing differences in growth only.

Variables	SS	MSS	Num DF	Den DF*	F value	P value
a) Range of relative difference (Step 4)						
Age	9.93	3.31	3	192	59.0	<0.001
Sex	2.39	2.39	1	192	42.5	<0.001
GT	2.70	2.70	1	192	48.0	<0.001
Age * Sex	0.61	0.20	3	192	3.6	0.01
Age * GT	0.15	0.05	3	192	0.9	0.4
b) Relative change from age to age (Step 6)						
Age	1.18 ⁻⁴	0.39 ⁻⁴	3	400.8	22.3	<0.001
Sex	0.10 ⁻⁴	0.10 ⁻⁴	1	396.3	5.9	0.02
GT	0.08 ⁻⁴	0.08 ⁻⁴	1	41.4	4.7	0.04
Age * Sex	0.33 ⁻⁴	0.11 ⁻⁴	3	400.5	6.2	<0.001
Age * GT	0.32 ⁻⁴	0.11 ⁻⁴	3	400.5	6.0	<0.001
c) Relative change from age to age – differences in growth only						
Age	0.49 ⁻⁴	0.16 ⁻⁴	3	401.7	12.1	<0.001
Sex	0.13 ⁻⁴	0.13 ⁻⁴	1	397.9	9.5	0.002
GT	0.01 ⁻⁴	0.01 ⁻⁴	1	37.3	1.1	0.3
Age * Sex	0.30 ⁻⁴	0.10 ⁻⁴	3	401.2	7.2	<0.001
Age * GT	0.11 ⁻⁴	0.04 ⁻⁴	3	401.7	2.7	0.04

^Δ Variables were assessed sequentially in the ANOVA in the order they are presented. In such cases, when interactions are statistically significant, the strength of the main effects needs to be assessed considering the influence of interactions by comparing the estimates for the interactions as well as the sum of squares of the main effects. In “a” for instance, the interaction of age with sex is statistically significant, but it is clear from both the estimates of the interaction (Fig. 5) and the

high sum of squares for age compared with the interaction that the decrease with age corresponds to a strong main effect irrespective of the differences between sexes.

* For the linear mixed model (i.e. in b and c), the ANOVA table was computed with the Satterthwaite approximation for the degrees of freedom.

SS = Sum of squares.

MSS = Mean sum of squares.

Num DF = degrees of freedom at the numerator.

Den DF = degrees of freedom at the denominator.

GT = generation time, in years, computed as T_b according to Lebreton (2005).

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Table 3. Likelihood ratio tests evaluating whether the LMM on body size trajectories including age at last measurement as a covariate received more support than the same LMM excluding this covariate. We present the P-value of the likelihood test for each cohort cluster for a given sex and population, with the number of individuals included in each cluster (Nb ID). In grey, we highlight support or a tendency to support the model including age at last measurement, and thereby the presence of viability selection.

		Males		Females	
		P value	Nb ID	P value	Nb ID
African elephants	Gr 1	0.3	249	0.07	280
Mountain goats	Gr 1	0.6	153	0.4	138
	Gr 2	0.7	11	0.9	21
Plain bison (Konza)	Gr 1	< 0.001	105	< 0.001	83
	Gr 2	< 0.001	184	< 0.001	172
	Gr 3	< 0.001	274	< 0.001	300
Plain bison (Wind Cave)	Gr 1	< 0.001	236	0.1	248
	Gr 2	0.6	238	1	203
	Gr 3	0.04	149	0.5	165
	Gr 4	0.01	385	0.8	317
Bighorn sheep	Gr 1	0.2	60	0.2	88
	Gr 2	0.3	83	0.01	82
	Gr 3	0.8	136	< 0.001	134
Svalbard reindeer	Gr 1	-	-	0.3	173
	Gr 2	-	-	0.2	273
	Gr 3	-	-	0.6	172
Reindeer (Ravdol)	Gr 1	-	-	0.9	218
	Gr 2	-	-	0.3	156
Roe deer (Chizé)	Gr 1	< 0.001	183	0.002	173
	Gr 2	0.02	175	< 0.001	168
	Gr 3	< 0.001	251	0.004	203
Roe deer (Trois Fontaines)	Gr 1	0.8	66	< 0.001	84
	Gr 2	0.8	298	0.01	280
	Gr 3	< 0.001	101	1	86
Soay sheep	Gr 1	< 0.001	401	< 0.001	475
	Gr 2	0.3	167	0.002	203
	Gr 3	< 0.001	185	0.2	243
	Gr 4	< 0.001	611	< 0.001	644
Mouflon	Gr 1	0.8	177	0.02	139
	Gr 2	0.7	83	0.01	81
	Gr 3	1	383	0.9	303

Fig 1. Conceptualization of the potential influence of environmental conditions on the between-individual variance in a life-history trait. The black curves represent individual responses and the red dotted curve is the overall population response. A: Variance among individuals is initially low and remains constant with age. B: Variance is initially high and remains constant with age. C: The trait of individuals with a low initial value (a bad start in life) increases faster than that of individuals with higher initial trait values, which indicates a compensatory effect resulting in smaller differences among individuals at older ages. D: The trait of individuals with a low initial trait value increases less than that of individuals with higher initial trait values: individual differences for the trait accumulate over ages, resulting in a cumulative effect. E: Individuals with a low initial value die earlier than individuals with a high initial value, viability selection leads to a decrease in the initial differences through selective disappearance. For simplicity, trajectories are assumed to be linear, but the patterns are similar for non-linear trajectories.

Fig. 2. Summary of the 6 steps to analyze cohort variation and its change throughout lifetime, illustrating two contrasting examples: bighorn sheep in the top two rows and Soay sheep in the bottom two rows. In Step 1, the number of clusters is selected based on a mixture model including body size measures from both sexes at the first age of measurement (see Table 1): only one measurement is included per individual. In this step, different selection criteria provided different plausible numbers of clusters, K , which are illustrated in the different panels, and the best alternative (in color) was determined as the highest alternative without cluster overlap in the 95% confidence intervals (CI). In Step 2, growth trajectory for each cluster presents the mean prediction and 95% CI extracted from a model using all body size measurements. Step 3 illustrates the standardized growth trajectories of cohort clusters, which is the difference of each trajectory obtained in Step 2 in relation to the predicted mean trajectory for a given population and sex. The dots are the mean relative differences and the bars their 95% CI. Grey bars indicate ages when not all clusters were measured. The same clusters are represented with the same colors in Steps 1, 2 and 3. In Step 4, the magnitude of cohort variation in size was calculated using the range of relative differences among all cohort clusters as a metric. The dots are the mean relative differences and the bars are their 95% CI, with grey symbols for ages when at least one cohort cluster was missing because no individual of that age or older was sampled. In bighorn sheep for example, the magnitude of cohort

variation in size remained high at all ages in males, but decreased rapidly to near 0 in females. In Step 5, the relative difference between each pair of cohort clusters was calculated. A given color illustrates a given pair, with dotted lines from ages when at least one cohort cluster was missing. In Step 6, the relative change from age to age in cohort variation in body size was computed from the values obtained at Step 5, i.e. the paired relative differences. A positive value represents increased size variation between a pair of cohort clusters, indicating a cumulative effect, whereas a negative value represents decreased size variation between a pair of cohort clusters, and hence a compensatory effect. A value of 0 indicates that variation in size between a pair of cohort clusters remains similar with increasing age. The colors in Step 6 match the trajectories representing the different pairs of cohort clusters in Step 5. For example, compensation was stronger in Soay sheep than in bighorn sheep, particularly in males, and differences remained relatively stable with age in male bighorn sheep compared with other sex-species cases.

Fig. 3. The difference in the trajectory of each cohort cluster relative to the predicted mean (specific to each population and sex), illustrating the standardized growth of the different cohort clusters (Step 3) for each population (ordered from a long (left) to a short (right) generation time, corresponding to the “slow-fast” continuum of life histories) and sex (females: top, males: bottom). The dots are the mean relative differences and the bars represent the 95% confidence intervals. Grey bars correspond to ages from which at least one cohort cluster was missing.

Fig. 4. The magnitude of cohort variation in size at each age (Step 4), i.e. the range of relative differences among all cohort clusters (computed from the standardized growth, Step 3; Fig. 3), for each population (ordered from a long (left) to a short (right) generation time, corresponding to the “slow-fast” continuum of life histories) and sex (females: top, males: bottom). The dots are the means and the bars represent the 95% confidence intervals. Grey symbols correspond to ages when data were missing for at least one cohort cluster.

Fig. 5. Change with age in the range of relative differences in size (Step 4) in relation to sex (males: dotted lines, light grey zones, blue dots; females: solid lines, dark grey zones, pink dots) and generation time

(GT). The lines are the mean predictions and the zones are the 95% confidence intervals. The dots show the partial residuals, which account for the effects of other variables in the model. Age was standardized to account for differences in the length of the time series among populations and sexes.

Fig. 6. The paired relative differences in size between cohort clusters (Step 5) in relation to age (computed from the standardized growth trajectories, Step 3; Fig. 3), for each population (ordered from a long (left) to a short (right) generation time, corresponding to the “slow-fast” continuum of life histories) and sex (females: top, males: bottom). Each color corresponds to a specific pair, with dotted lines at ages when data for some cohort clusters were not available.

Fig. 7. The relative change from age to age in cohort variation in size between each pair of cohort clusters (Step 6) in relation to age (computed from the values compiled at Step 5; Fig. 6), for each population (ordered from a long (left) to a short (right) generation time, corresponding to the “slow-fast” continuum of life histories) and sex (females: top, males: bottom). A positive value indicates an increase in the difference in size between a pair of cohort clusters, and thereby a cumulative effect, whereas a negative value indicates a decrease in the difference in size between a pair of cohort clusters, and hence a compensatory effect. A value of 0 indicates that the difference in size between a pair of cohort clusters remains constant with age. The colors match the trajectories representing the different pairs of cohort clusters in Fig. 6.

Fig. 8. Variation in the relative change from age to age (Step 6) in relation to sex (males: dotted lines, light grey zones, blue dots; females: solid lines, dark grey zones, pink dots) and generation time (GT). The lines are the mean predictions and the zones are the 95% confidence intervals. The dots show the partial residuals, which account for the effects of other variables in the model. The red line at 0 separates compensatory effects below and cumulative effects above. Age was standardized to account for differences in the length of the time series among populations and sexes.

Fig. 9. Effect of viability selection on growth trajectories in three cohort clusters of male roe deer at Chizé. Each color represents a different cohort cluster. A: Trajectories with the same colors represent mean growth

predictions for individuals of the same cohort cluster but with different ages at last measurement, with the age at last measurement illustrated by the dot. B: The mean growth trajectory for each cohort cluster adjusted for age at last measurement (dotted lines) compared with the unadjusted growth trajectories (i.e. Step 2; continuous lines).

Fig. 10. Variation in the relative change from age to age only due to differences in growth, in relation to sex (males: black dotted lines, light grey zones; females: black solid lines, dark grey zones) and generation time (GT). The black lines are the mean predictions and the zones are the 95% confidence intervals (for clarity, the partial residuals are not shown, see Fig. 8). The red line at 0 separates compensatory effects below and cumulative effects above. The blue (males) and pink (females) lines represent the difference between the mean predictions of the relative change from age to age due to both viability selection and growth (black lines in Fig. 8) minus those only due to differences in growth (the black lines in this figure), thereby highlighting the influence of viability selection on the relative change from age to age for each sex. Age was standardized to account for differences in the length of the time series among populations and sexes.

Fig. 1

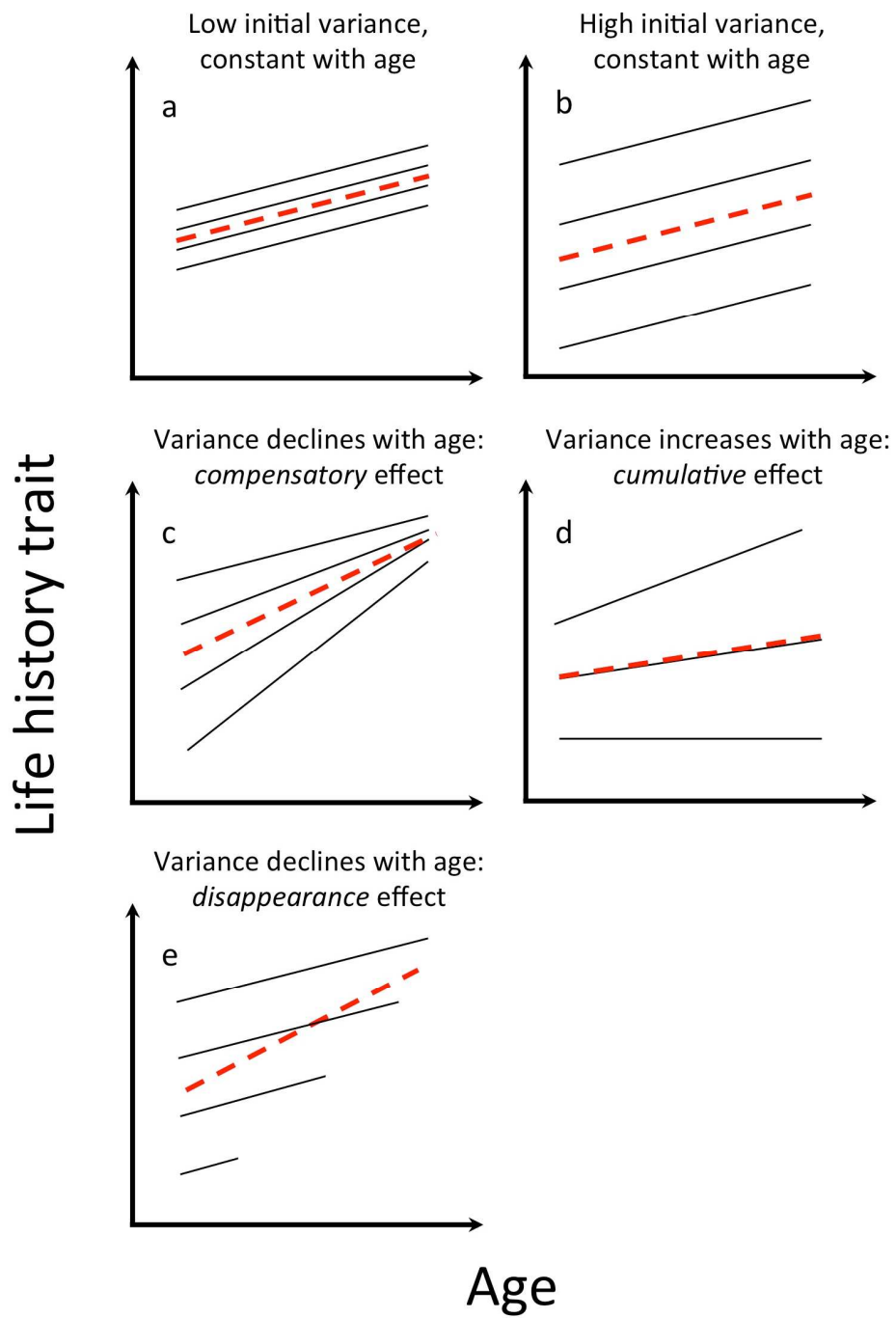


Fig. 2

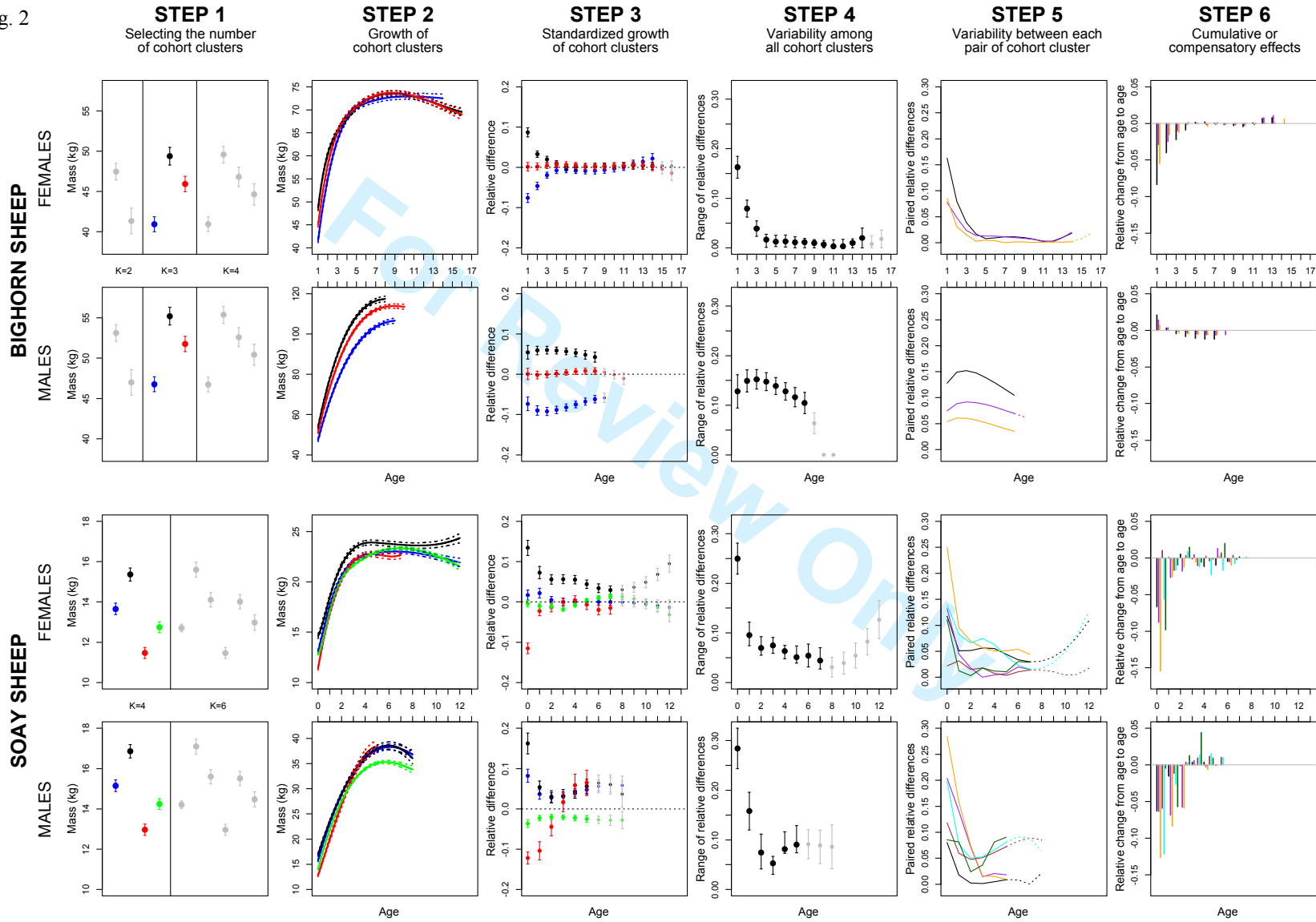


Fig. 3

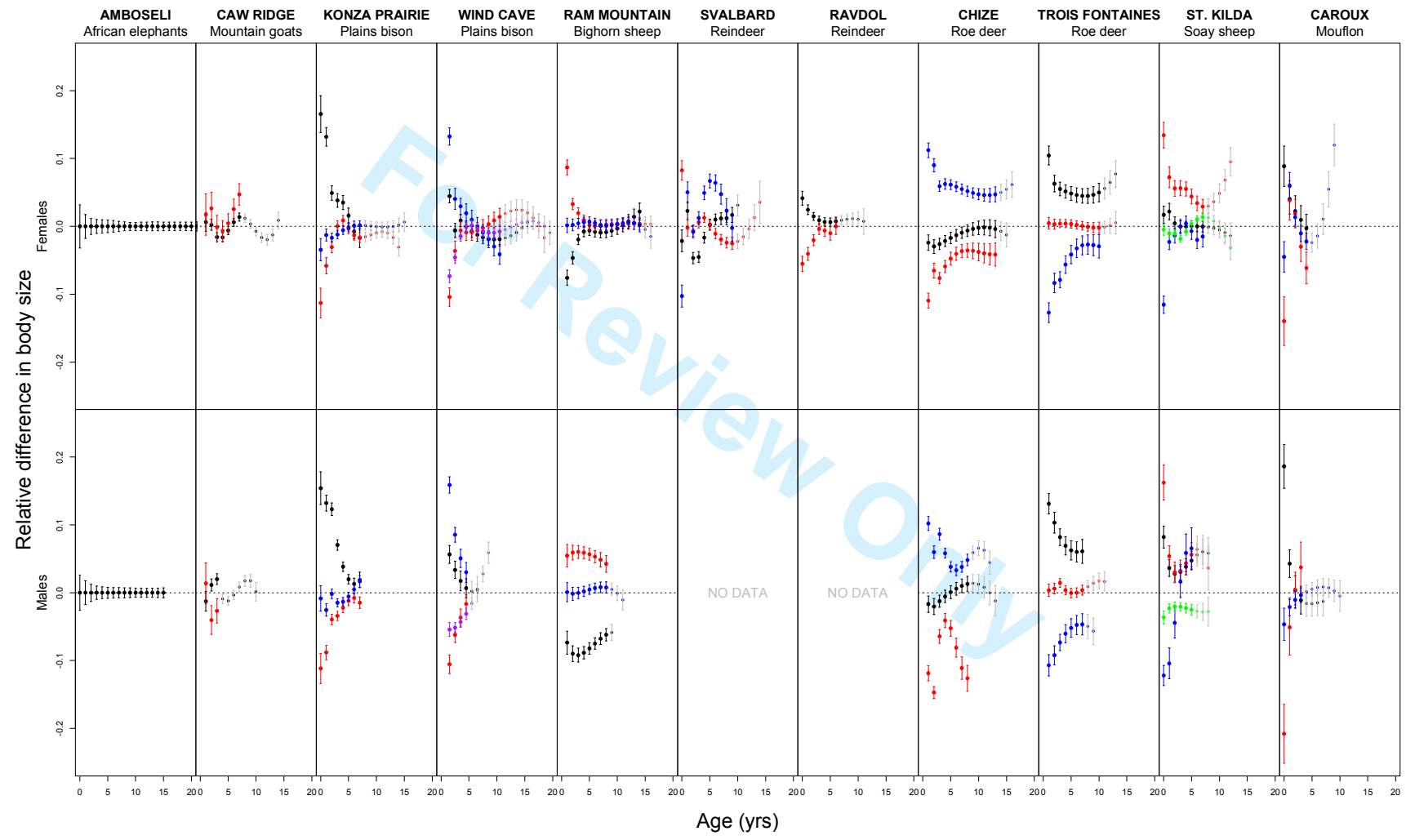


Fig. 4

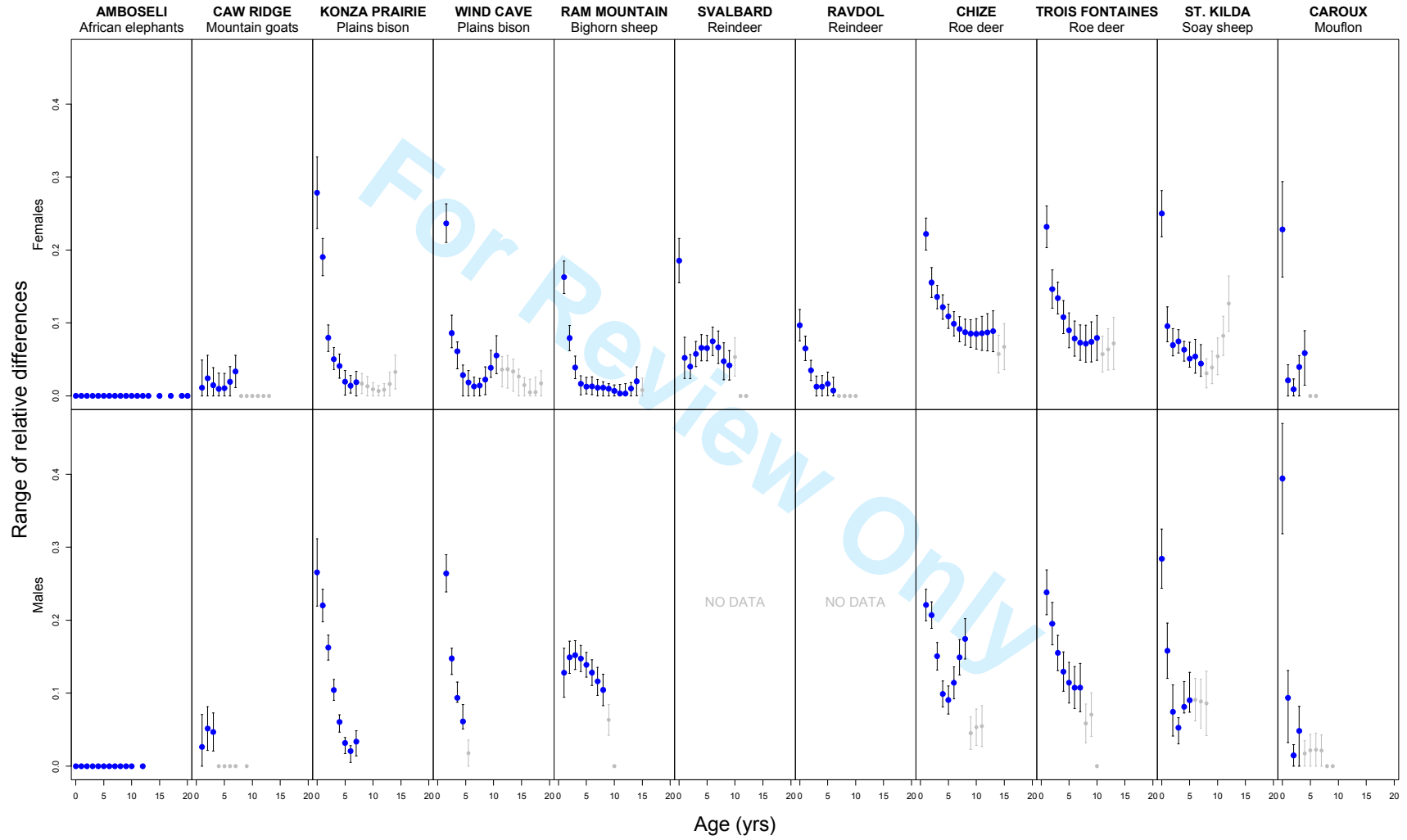


Fig. 5

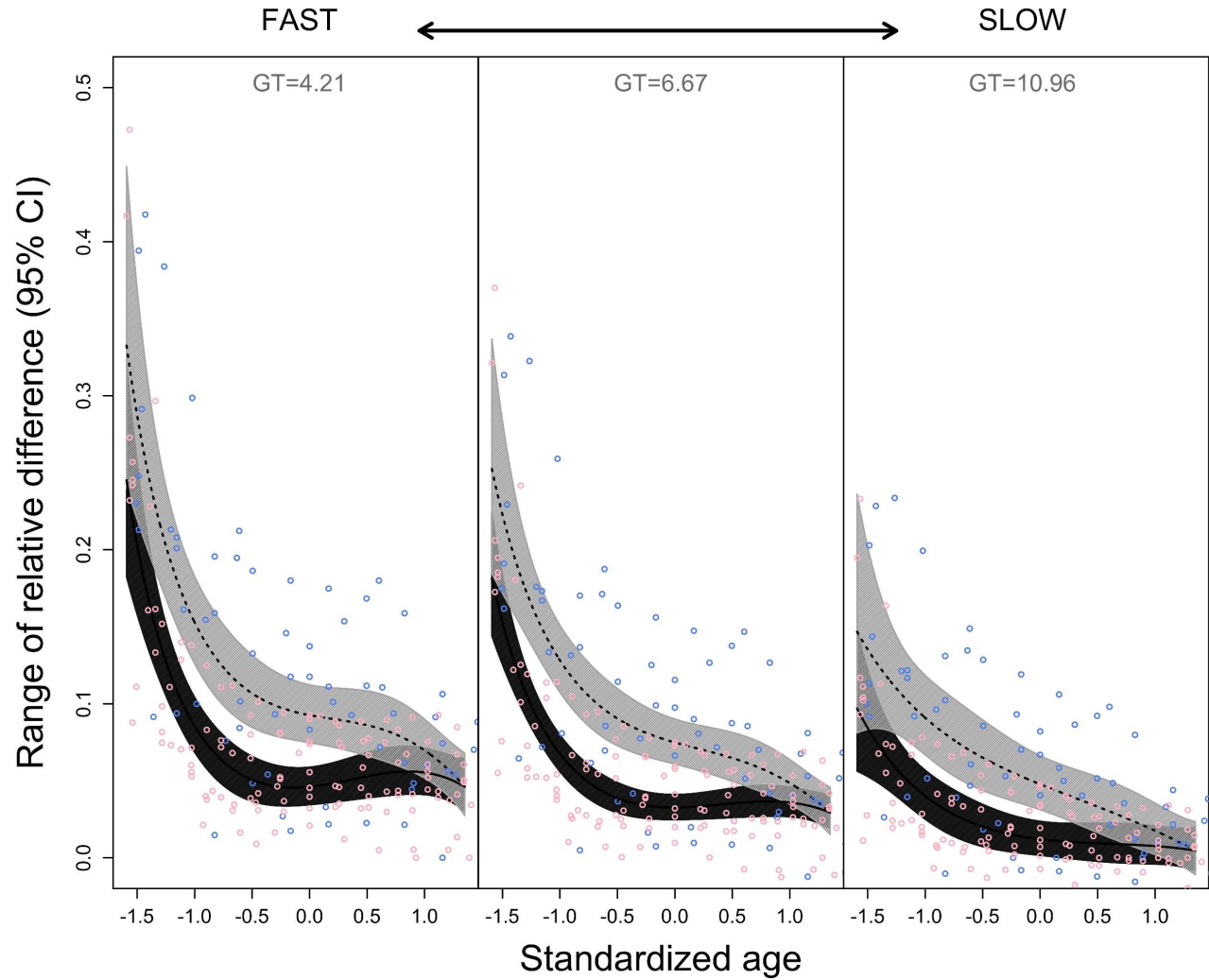


Fig. 6

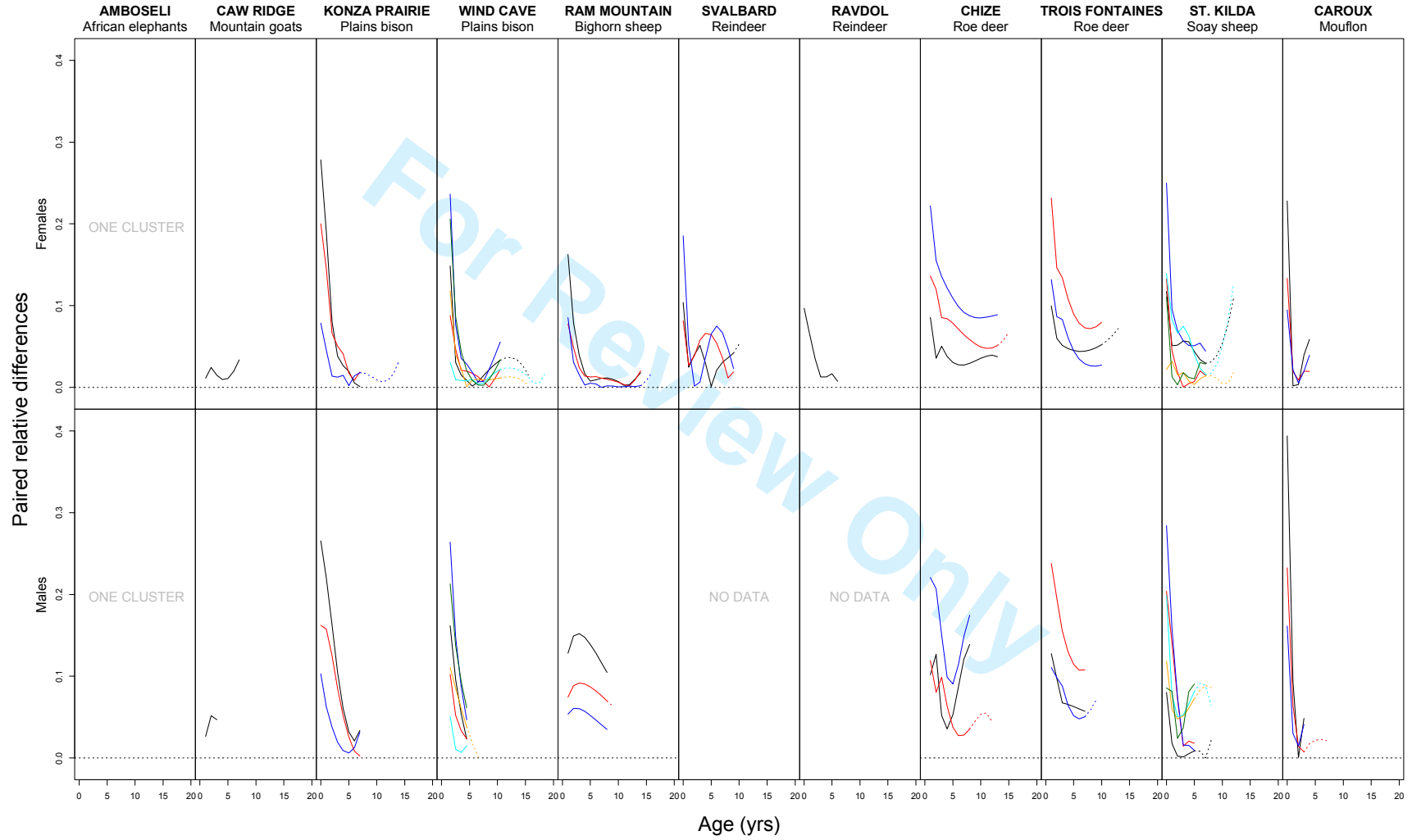


Fig. 7

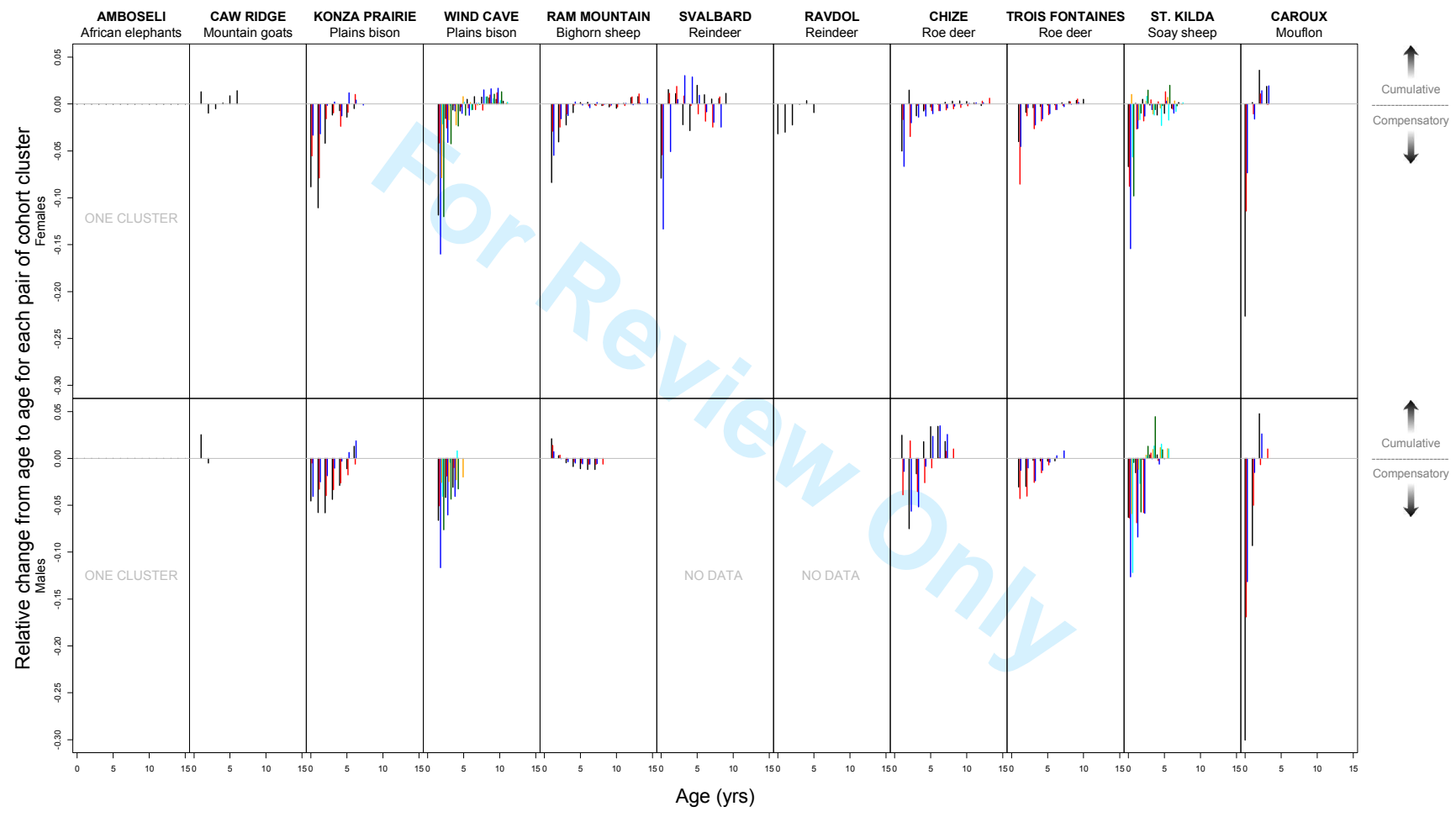


Fig. 8

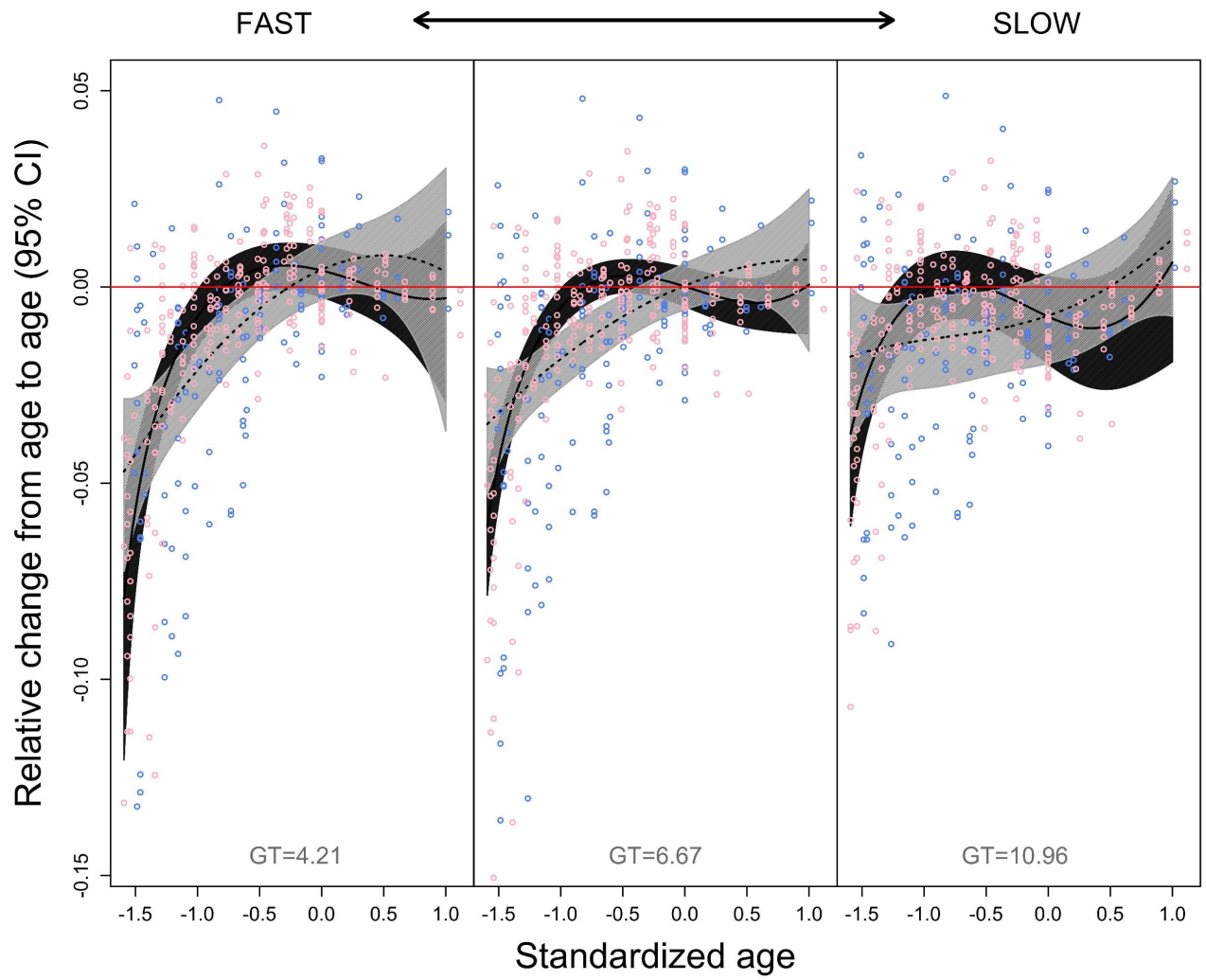


Fig. 9.

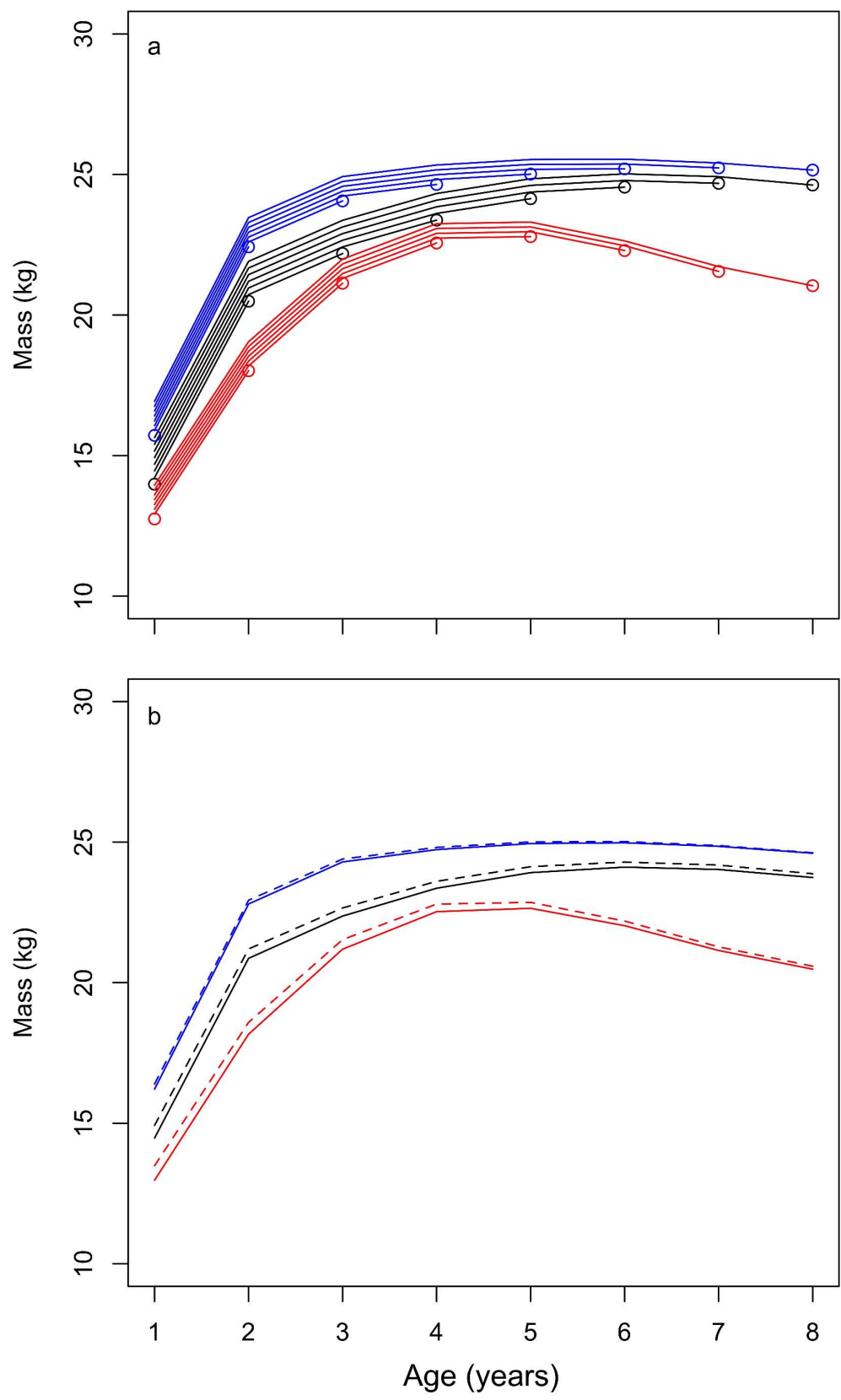
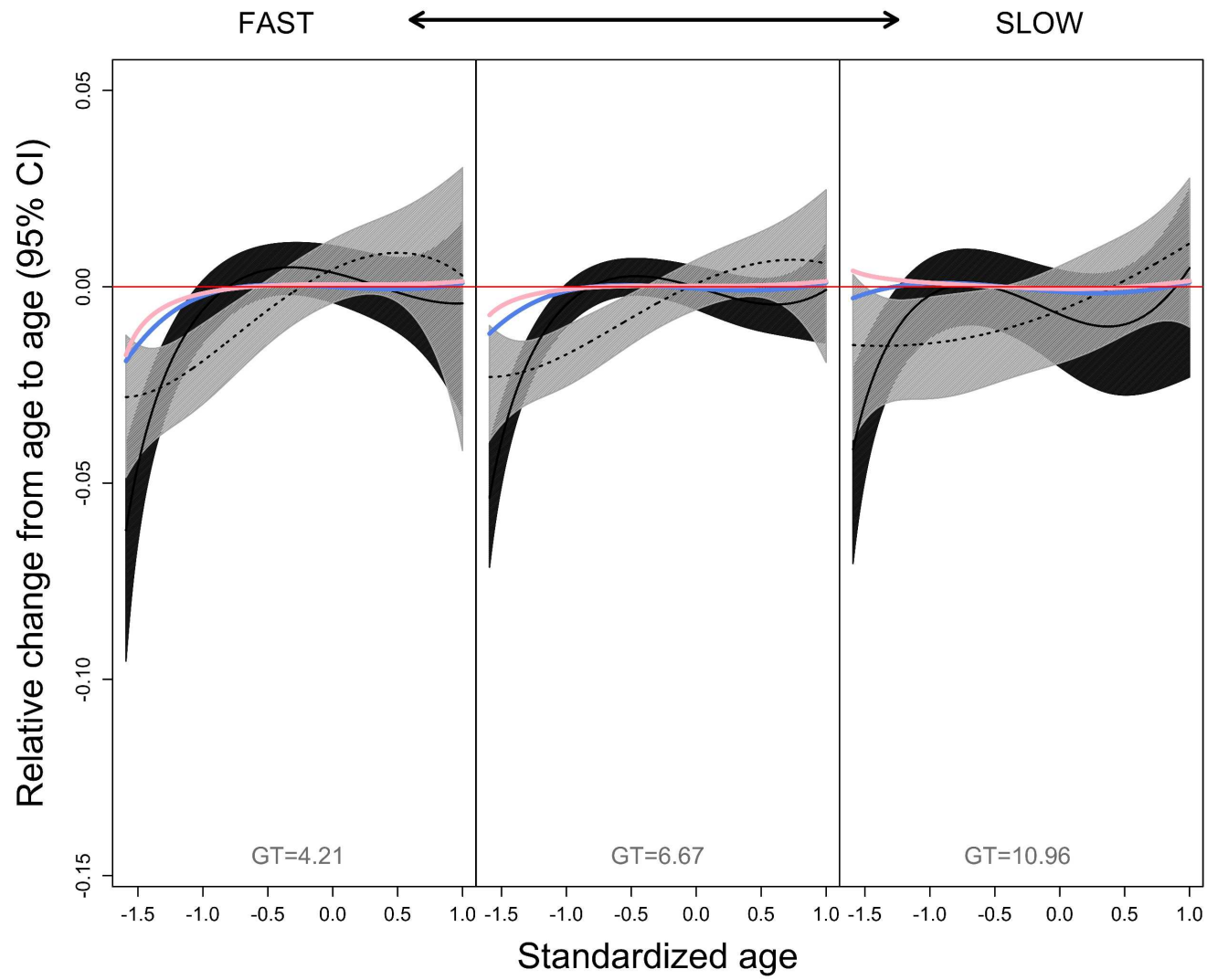


Fig. 10



Supplementary Material

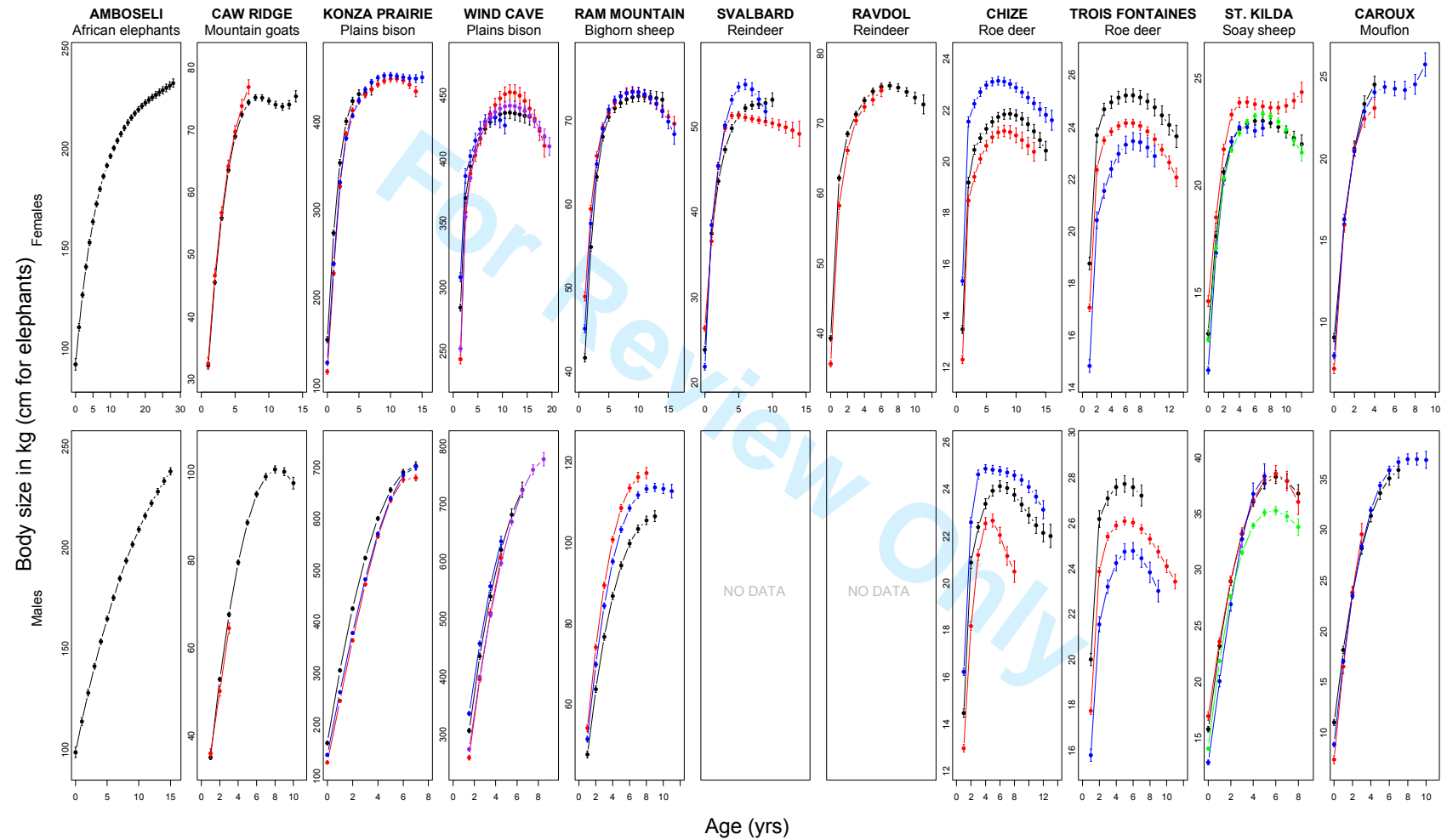


Fig. S1: Growth trajectory of each cohort cluster (Step 2) for each population (ordered from a long (left) to a short (right) generation time) and sex (females: top, males: bottom). The dots are the means and the bars represent the 95% confidence intervals.

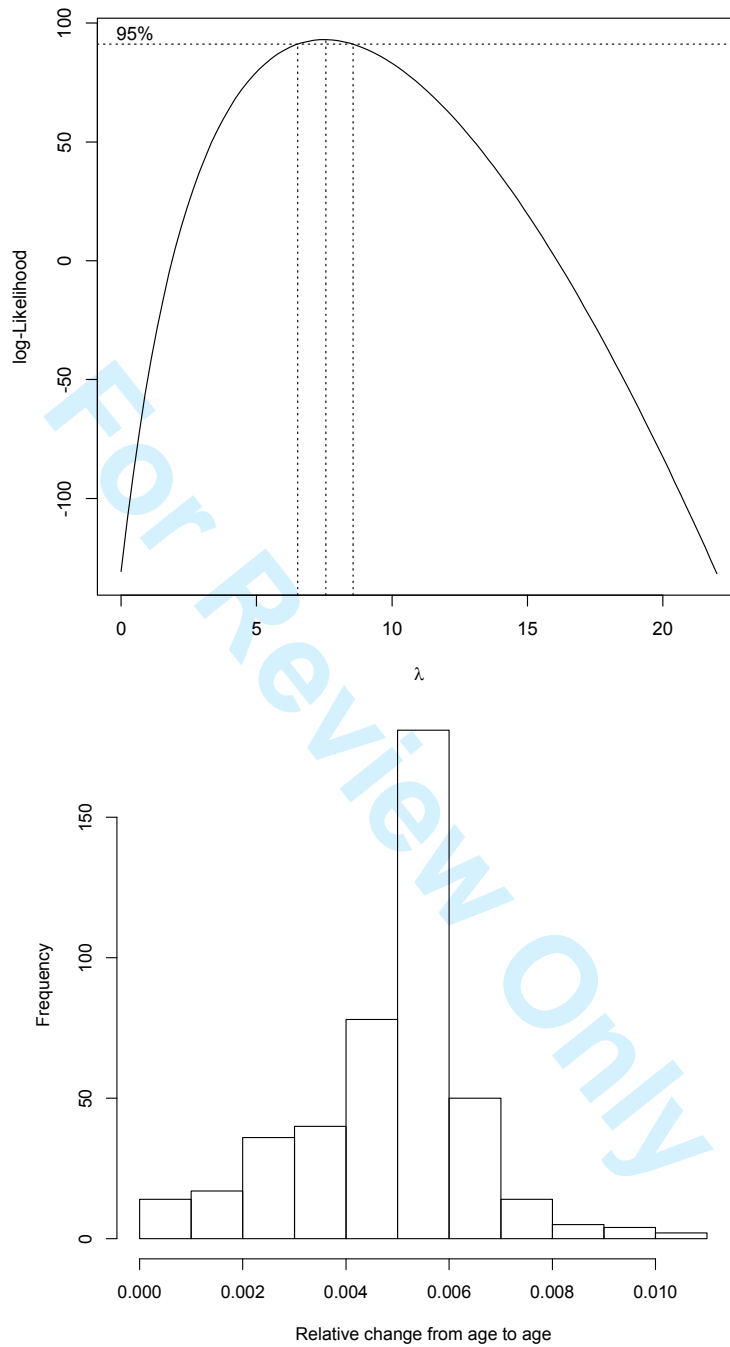


Fig. S2. Profile log-likelihood for the parameter of the Box-Cox transformation (λ) for the relative change from age to age (top panel), and distribution of the transformed data (bottom panel). Before transformation, the relative change from age to age was right-skewed and ranged from -0.31 to 0.05, and we thus added 0.5 to shift the distribution above zero to evaluate the power transformation needed to normalise the data.

Table S1. Likelihood ratio tests evaluating whether cohort clusters differed in lifetime growth trajectories for each population and each sex. We sequentially compared a model with only age (i.e. no difference among cohort clusters), a model with additive effects of cluster and age (i.e. a unique growth trajectory for all cohort clusters, but cluster-specific size in early life that remained unchanged throughout lifetime), and a model with an interaction between cohort cluster and age (i.e. cluster-specific growth trajectories). We present the P-value of the likelihood test for each sex and population, highlighting in grey cases demonstrating support for the most complex model out of the two compared. No values are presented for elephants because they had only one cluster.

		Age vs. Age + Cluster	Age + Cluster vs. Age * Cluster
African elephants	Females	--	--
	Males	--	--
Mountain goats	Females	0.05	0.39
	Males	0.39	0.14
Plain bison (Konza)	Females	0.002	<0.001
	Males	<0.001	<0.001
Plain bison (Wind Cave)	Females	<0.001	<0.001
	Males	0.41	<0.001
Bighorn sheep	Females	0.14	<0.001
	Males	<0.001	<0.001
Svalbard reindeer	Females	<0.001	0.04
Reindeer (Ravdol)	Females	<0.001	<0.001
Roe deer (Chizé)	Females	<0.001	0.02
	Males	<0.001	0.004
Roe deer (Trois Fontaines)	Females	<0.001	0.002
	Males	<0.001	0.12
Soay sheep	Females	<0.001	<0.001
	Males	<0.001	0.004
Mouflon	Females	0.12	0.09
	Males	0.05	0.02