

# 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.

**Key words:** catch-up growth; cohort; compensatory growth; cumulative effects; life-history tactics; mixture models; sexual selection; slow-fast continuum; ungulates; viability selection.

## INTRODUCTION

At the population level, the expression of life-history traits as individuals age results from a combination of ontogenetic, selective (both viability and fertility selection; Fisher 1930), and environmental processes

(Coulson and Tuljapurkar 2008, Ozgul et al. 2009). Because conditions early in life usually determine juvenile body development and size (Madsen and Shine 2000, Metcalfe and Monaghan 2001, Bateson et al. 2004, Solberg et al. 2004), variability in early conditions often leads to phenotypic differences among individuals of a population at the start of life (Lindström 1999). Conceptually, this means that environmental conditions, in interaction with genotype, set the phenotypic starting

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values of individual life-history traits (Fig. 1a, b). This variability must be considered when assessing changes in a trait with age. If initial differences persist, they result in the ranking of individuals for a given trait that remain constant throughout life (Lindström 1999, Metcalfe and Monaghan 2001, Monaghan 2008). Differences among individuals that are fixed at birth are referred to as fixed or static heterogeneity (Tuljapourkar et al. 2009). In addition to early-life conditions, environmental conditions experienced later in life also influence life-history traits (Wooler et al. 1992, McNamara 1998, Descamps et al. 2008, Wilkin and Sheldon 2009, Crowley and Hopper 2015). The resulting individual differences later in life are referred to as dynamic heterogeneity when they are generated from a stochastic process affecting changes in life-history stages (Tuljapourkar et al. 2009). If individual differences later in life display positive serial autocorrelations, environmental effects may cumulate with age and accentuate between-individual differences over the lifetime, hereafter referred to as “cumulative effect” (Nussey et al. 2007, Dmitriew 2011, Fig. 1d). On the other hand, if individuals can recover from a poor start (Metcalfe and Monaghan 2001, Dmitriew 2011), due to improved conditions and/or genetic predisposition, individual differences will decrease with increasing age, hereafter referred to as “compensatory effect” (Fig. 1c). In bighorn sheep (*Ovis canadensis*) for instance, lighter yearling females prolonged growth so that their size difference with heavier yearling females decreased from 20% to 4% between 1 and 7 yr of age (Marcil-Ferland et al. 2013). Conceptually, cumulative or compensatory effects imply that environmental conditions, along with genotype, not only affect the starting values (Fig. 1a, b), but also the rate of change of life-history traits, thereby increasing or decreasing between-individual variance with age (Fig. 1c, d; Schielzeth and Forstmeier 2009, van de Pol and Wright 2009). Importantly, cumulative or compensatory effects can result from actual differences in ontogeny and/or from viability selection among phenotypes (Fisher 1930, Vaupel et al. 1979). For instance, a reduction in the variance of mass with age can result both from the selective disappearance of lighter individuals (Fig. 1e; Gaillard et al. 2000a, van de Pol and Verhulst 2006, Plard et al. 2015, Théoret-Gosselin et al. 2015) and from changes in the growth patterns of lighter vs. heavier individuals. Changes in growth patterns can occur either through compensatory growth (i.e., faster growth of lighter individuals when conditions improve) or catch-up growth (i.e., lighter individuals extending the growth period; Metcalfe and Monaghan 2003).

The intensity of cumulative or compensatory effects might vary among species in relation to their life-history strategies (Stearns 1976). The long generation time of species with a slow pace of life evolved from a strategy that promotes survival over reproduction (Gaillard and Yoccoz 2003). This resulted in environmental canalization of adult survival, which varies little over time or space, and in a high susceptibility of reproductive traits

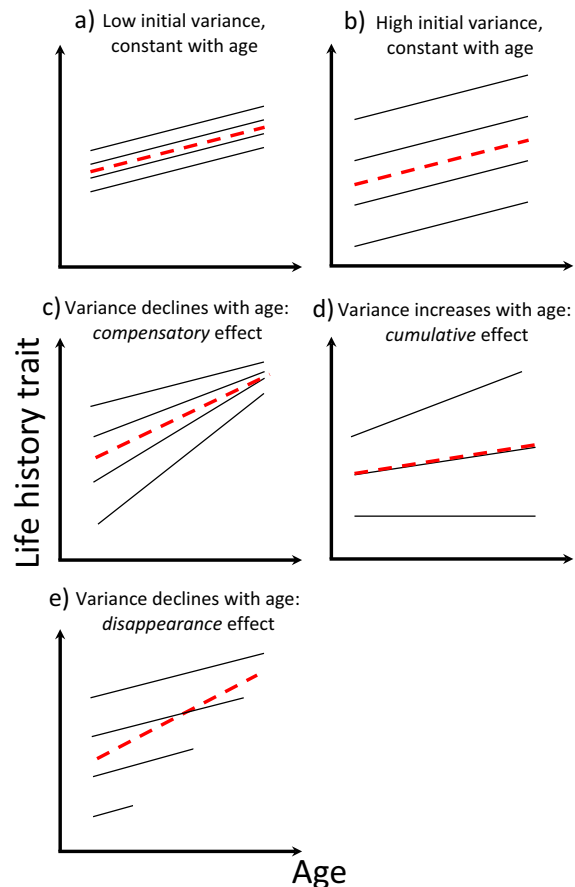


FIG. 1. Conceptualization of the potential influence of environmental conditions on the between-individual variance in a life-history trait. The black lines represent individual responses and the red dashed line is the overall population response. (a) Variance among individuals is initially low and remains 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 nonlinear trajectories.

to spatiotemporal changes in environmental conditions. The opposite pattern occurs in short-lived species, with lower variance in reproductive traits and a more variable adult survival (Gaillard and Yoccoz 2003). Thus, the influence of environmental conditions and selection processes on life-history trait distributions is likely to differ between species with slow and fast life-history strategies (Stearns 1983, see Gaillard et al. [2016] for a recent review). The survival of long-lived species might be buffered against environmental variation

because individuals may stop allocating energy to reproduction when facing harsh conditions, whereas individuals of short-lived species will jeopardize survival to reproduce. Although long-lived species should be able to compensate/catch-up for a bad start by restraining reproductive effort, short-lived species should engage in reproduction as early as possible and might thus be less able to compensate/catch-up for a bad start (Gaillard and Yoccoz 2003). Life-history tactics can also markedly differ between sexes within species under sexual selection (Clutton-Brock 2007). Males in many species of mammals have evolved a “live fast, die young” strategy (*sensu* Bonduriansky et al. 2008) that involves strong selection for high growth rate to prevail in intra-sexual competition and increase reproductive performance (e.g., Robinson et al. 2006). Therefore, we expect males of sexually dimorphic and polygynous species to be more susceptible to variation in early life conditions (Wilkin and Sheldon 2009) and to be less able to compensate/catch up for a bad start than females (Toïgo et al. 1999).

Individual variation early in life can be shaped by several factors, including genotypic differences, parental effects, or early environment (Bernardo 1996, Mousseau and Fox 1998, Lindström 1999, Lindström and Kokko 2002, Solberg et al. 2007, Théoret-Gosselin et al. 2015). Unlike genetic and parental effects, environmental conditions during early growth and development affect all individuals born the same year simultaneously. Environmental variation can thus result in strong cohort effects, particularly in populations with low natal dispersal, and can lead to persistent individual differences throughout life, as often reported in vertebrate populations (e.g., Albon et al. 1987, Clutton-Brock 1988, Madsen and Shine 2000, Steinheim et al. 2002, Hastings et al. 2011, Douhard et al. 2013, Hayward et al. 2013, Herfindal et al. 2015). Cohort variation at the start of life can result from limited resource availability in poor years (Madsen and Shine 2000, Descamps et al. 2008), or from a phenological mismatch between the peak in resources and that in energy demands (Thomas et al. 2001, Suarez et al. 2004, Solberg et al. 2007, Plard et al. 2014a). Nutrient deficiency during development in poor years likely affects growth and developmental processes, leading to body size differences among cohorts born under contrasting environmental conditions (Douhard et al. 2013). Initial conditions can cause a “silver spoon effect” (Grafen 1988), where lasting benefits of being born during a favorable year lead to positive correlations among performance traits in adulthood (Madsen and Shine 2000, van de Pol et al. 2006, Descamps et al. 2008). Because the influence of ontogenetic, selection, and environmental processes are likely to change with individual states, defined as the physiological and environmental conditions that influence survival and reproduction (McNamara and Houston 1996), cohorts born in favorable and unfavorable years should display different responses to selection and environmental processes

(Metcalf and Monaghan 2003, Auer 2010, Douhard et al. 2014, Garratt et al. 2015). Therefore, cohorts sharing similar environmental conditions may show similar life-history tactics throughout lifetime, which might differ from other cohorts and from the average tactic observed at the population level (see Fig. 1c–e). They may also show different intensity of cumulative or compensatory effects depending on both the ability of surviving individuals to compensate/catch up for a poor start (Toïgo et al. 1999, Metcalfe and Monaghan 2003, Auer 2010, Dmitriew 2011, Douhard et al. 2014), and the strength of viability selection (Fisher 1930, Vaupel et al. 1979, Ozgul et al. 2009). Assessing how cohort effects change throughout lifetime is crucial to understand population dynamics because cohort variation can either stabilize or destabilize population dynamics (Lindström and Kokko 2002).

Although the effects of environmental conditions on average population responses have received considerable attention, how environmental changes shape the variability in individual responses both within and among cohorts has received little attention (Metcalf and Monaghan 2003, Wilson et al. 2009). Most previous studies accounted for cohort variation on life-history strategies by including birth year as a random effect to obtain an unbiased assessment of life-history traits. Specific analyses of cohort variation have shown that it is a key process (Metcalf and Monaghan 2001) shaping individual differences in trait values at different life stages (Albon et al. 1987, Baron et al. 2010, Le Galliard et al. 2010, Douhard et al. 2013). However, how the magnitude of cohort variation changes along trait trajectories over the lifespan, and whether these patterns vary between sexes and among species with different paces of life remain largely unexplored. Assessing the variance in life-history traits at a given life stage and its change with age requires long-term monitoring of individuals over a period sufficiently long to include enough variation in environmental conditions. Here, we performed a comparative analysis of cohort variation based on long-term studies of different species of large herbivores with up to 40 years of longitudinal data collected on body size for individuals of both sexes. Large herbivores provide a unique opportunity to explore cohort variation because the basic life history and ecology of many species are well understood. The species included in this study vary widely in size (Appendix S1: Fig. S1) and in position along the “slow-fast” continuum of life histories (Table 1). Table 2 presents an overview of the research questions addressed.

To quantify cohort variation in body size, we first used mixture models (McLachlan and Peel 2000) to define clusters of cohorts with similar body size early in life. Although between-individual variation is usually quantified from estimates of random effects obtained using mixed models, random effects representing the between-individual variation in mixed models are assumed to be normally distributed. This assumption is

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	<i>N</i> males†	<i>N</i> females†	Body size measure	Age‡	<i>N</i>	<i>K</i> [ <i>R</i> <sup>2</sup> ]	GT	Sources
Amboseli	African elephants, <i>Loxodonta africana</i>	Kenya	1972–2008§	88 249 [319] 1.3 [1–5]	87 280 [440] 1.6 [1–5]	shoulder height	0–4.5¶	25	1 [0]	19.78	1
Caw Ridge	Mountain goats, <i>Oreamnos americanus</i>	Alberta, Canada	1989–2013	128 164 [453] 2.8 [1–8]	121 159 [761] 4.8 [1–13]	mass in Jul	1	25	2 [0.28]	10.96	2, 3
Konza Prairie	Plains bison, <i>Bison bison</i>	Kansas, USA	1994–2012	664 709 [2,074] 2.9 [1–9]	634 709 [2,714] 3.8 [1–17]	mass in Nov	0	19	4 [0.87]	9.37	4
Wind Cave	Plains bison, <i>Bison bison</i>	South Dakota, USA	1966–2008§	931 1222 [1,394] 1.2 [1–5]	868 1,143 [2,330] 2.1 [1–18]	mass in Nov	1	26	5 [0.93]	9.37	5
Ram Mountain	Bighorn sheep, <i>Ovis canadensis</i>	Alberta, Canada	1973–2013	264 279 [1,096] 3.2 [1–13]	296 304 [1,942] 4.9 [1–20]	mass in Sep	1	41	3 [0.65]	8.57	6
Svalbard	Svalbard reindeer, <i>Rangifer tarandus platyrhynchus</i>	Svalbard	1994–2013	— — —	552 618 [1,953] 3.2 [1–10]	mass in Feb–May	0	20	3 [0.58]	6.67	7
Ravdol	Reindeer, <i>Rangifer tarandus</i>	Finnmark, Norway	2002–2014	— — —	330 367 [1,041] 3.5 [1–12]	mass in Sep	0	13	2 [0.40]	5.15	8
Chiz��	Roe deer, <i>Capreolus capreolus</i>	Southwestern France	1977–2012	571 607 [1,447] 2.4 [1.13]	510 543 [1,682] 3.1 [1–14]	mass in Jan–Feb	1	36	3 [0.47]	4.6	9, 10, 11
Trois Fontaines	Roe deer, <i>Capreolus capreolus</i>	Northeastern France	1975–2012	361 465 [1,055] 2.3 [1–9]	365 450 [1,352] 3.0 [1–10]	mass in Jan–Feb	1	38	3 [0.43]	4.6	9, 10, 12
St. Kilda	Soay sheep, <i>Ovis aries</i>	Hirta Island, Scotland	1985–2013§	943 1,093 [1,723] 1.5 [1–11]	982 1,284 [3,324] 2.5 [1–14]	mass in Aug	0	28	4 [0.34]	4.47	13
Caroux	Mouflon, <i>Ovis gmelini musimon</i> × <i>Ovis sp.</i>	Massif Central, France	1995–2014	459 643 [850] 1.3 [1–7]	401 523 [757] 1.4 [1–10]	mass in May–Jun	0	20	3 [0.27]	4.21	14, 15

Notes: Age is the age when the body size of the cohort was measured (in years). *N* is the number of cohorts available. *K* is the number of cohort clusters selected by the mixture models. *R*<sup>2</sup> is 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 (Eq. 6.5 in Fr  hwirth-Schnatter [2006: 170]). GT is the generation time, in years, computed as *T*<sub>b</sub> according to Lebreton (2005).

†First entry is the number of individuals measured at first age (i.e., used in Step 1, see *Methods*). The second entry 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 entry is the mean number of repetitions per individual, with the range for all individuals in brackets. The total number of individuals in entry 2 is larger than the number of individuals measured at first age in entry 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. Dashes indicate no data.

‡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.”

§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.

¶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*). Sources: 1, Lee et al. (2013a); 2, Festa-Bianchet and C  t   (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, B  rdsen and Tveraa (2012); 9, Gaillard et al. (2003a); 10, Gaillard et al. (2003b); 11, Pettorelli et al. (2002); 12, Plard et al. (2014b); 13, Clutton-Brock and Pemberton (2004); 14, Garel et al. (2005); 15, Garel et al. (2007).

often violated when clusters among subjects lead to multimodal distributions (Verbeke and Lesaffre 1996, Stamps et al. 2012). This multimodality can bias the random effect estimates used to quantify between-individual variance in mixed models (Verbeke and

Lesaffre 1996, Hamel et al. 2016). Mixture models incorporate a categorical latent variable that aggregates subjects into clusters sharing similar traits (McLachlan and Peel 2000). This latent variable captures the multimodal dimension of the variability, and thereby accounts



for the between-individual variance that might be present at a higher level, i.e., among clusters. Mixture models are therefore particularly useful to identify how ecological and evolutionary processes change over time within a population because they classify individual trajectories (or traits) into clusters of mean trajectories, instead of a single mean population trajectory (Hamel et al. 2016). These models are widely used in psychology, sociology, and medicine to describe the diversity of trajectories within a population over time, such as psychological development or growth (Jones et al. 2001, Hoeksma and Kelderman 2006). They are also used in capture–recapture studies to account for individual differences in survival within populations (Cubaynes et al. 2012, Ford et al. 2012). Therefore, in the presence or expectation of multimodality, mixture models allow determining whether there is variation in life-history tactics within a population, and when there is, they provide an objective classification of subjects into clusters, each representing a typological tactic within a population. Importantly, cluster classification is not fixed. The classification uncertainty is accounted for when estimating the parameters describing each cluster, thereby providing a more objective quantification of each tactic.

Here, using mixture models allowed determining the best level of clustering between a single cluster (population level) and a separate cluster for each cohort (cohort level), thereby identifying typological differences among cohorts. This is a major advantage in a comparative analysis of studies with different durations because the greater the number of cohorts included, the more environmental variation is likely to be encountered by cohorts. By focusing on the higher level of variation rather than on the specificity of each cohort, mixture models allowed quantifying a standardized variance among cohort clusters controlling for the different number of cohorts monitored among populations (Table 1), and hence providing reliable comparisons among species. After having assessed the presence of cohort clusters with mixture models, we used these cohort clusters to estimate cluster-specific trajectories of body size with age, and evaluated whether the cohort clusters displayed different growth trajectories later in life. Furthermore, we used these growth trajectories to determine whether body size variation among cohort clusters increased (cumulative effect) or decreased (compensatory effect) with increasing age. As we found compensatory effects to be predominant, we accounted for the disappearance of individuals with age to separate the influence of viability selection from that of compensatory/catch-up growth. To contrast results among species and between sexes, we developed standardized estimates to test whether generation time, a reliable measure of the pace of life across mammals (Gaillard et al. 2005), and sex, affected the amount of cohort variation and how this variation changed with age.

## METHODS

### Study populations

We compared body size of individuals in 11 populations of eight species of large herbivores, intensively monitored from birth to death for 13–41 yr (Table 1). Using generation time to assess the relative position of a given population on the slow-fast continuum (see Gaillard et al. [2005] for a justification and, e.g., Jones et al. [2008] or Sæther et al. [2013] for applications), these populations displayed a fivefold variation in the pace of life, from about 4 years in mouflon (*Ovis gmelini*) to about 20 years in African elephant (*Loxodonta africana*; Table 1). Generation time ( $T_b$ , sensu Leslie 1966) was calculated as the inverse of the sum of the elasticities of the recruitment parameters (i.e., the elements of the first row of a pre-breeding census Leslie matrix based on female demography and calculated over all available years; Caswell 2001), according to Lebreton (2005). Body size was measured as body mass, with the exception of elephants for which shoulder height was used because individual masses were not recorded. Skeletal measures including shoulder height strongly correlate with body mass in adult elephants ( $r > 0.9$ ; Laws et al. 1975, Christiansen 2004), and provide a reliable measure of variation in mass in this species. Data were collected on a yearly basis for both sexes, except for the two reindeer (*Rangifer tarandus*) populations for which only females were sampled. Mass was measured at the same period of the year in each population, and when needed, it was adjusted to a specific date to control for seasonal changes (see, e.g., Hamel et al. 2010). For elephants, shoulder height was measured throughout the year. Details on study areas and populations have been published elsewhere (Sources in Table 1).

To assess cohort variation in body size and its changes with increasing age, the analyses followed six steps (Table 2, Fig. 2).

#### Step 1: Selecting the number of cohort clusters

For each population, we first ran a mixture model to identify clusters of cohorts based on body size, i.e., using individual initial body size as the response variable. Mixture models classify observations into clusters based on the probability of belonging to a given cluster, where each cluster is defined by a separate set of regression parameters (McLachlan and Peel 2000). For data like body size, which follows a Gaussian distribution  $N$  with a cluster-specific mean  $\mu_k(x) = \beta_k x$  (where  $\beta_k$  is the vector of coefficients for the effects of  $x$  specific to each cluster  $k$ , and  $x$  is a vector of predictor variables) and a variance  $\sigma_k^2$ , a mixture model with  $K$  clusters takes the following form:

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

TABLE 2. 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	“cohort clusters”
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)	“body size”
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)	“relative difference”
	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)	“range of relative differences”
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)	“paired relative differences”
	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”

where  $y$  is a vector of individual initial body sizes with a conditional density  $h$  depending on  $x$  (see below for covariate predictors included for each species) and  $\psi$ , a vector of all 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 prior probabilities  $\pi_1, \dots, \pi_K$  are the proportions of each cluster  $k$  in the mixture, where  $\sum_{k=1}^K \pi_k = 1$  and  $\pi_k > 0$ . We refer to Hamel et al. (2016) for a detailed review of the use of mixture models to separate individuals in clusters that present different life-history tactics within a population.

For each population, we ran a mixture model including only the first body size measurements collected (see “age at first measurement” in Table 1) to represent cohort measurements early in life. In some populations, the first measurements were collected during the first summer of life,

referred to as age 0, whereas in other populations the first measurements were available after the first year of life, referred to as age 1 (Table 1). Therefore, the first body size measurement was collected during or just after the first year of life, which corresponds to the inter-birth interval (IBI = 1 yr) in species with annual reproduction. For African elephants at Amboseli, however, the IBI is approximately 4.5 yr (Moss et al. 2011). To be comparable with the other species, we used measurements between ages 0 and 4.5 to assess differences in body size among cohorts, using a single measure per offspring and “age at first measurement” as a covariate to account for growth between ages 0 and 4.5. This was also necessary because young elephants were measured throughout the year. For each population, the model included measurements of both males

and females because we sought to pool cohorts that experienced similar environmental conditions and not to segregate cohorts differently for each sex. We therefore included “sex” as a covariate to account for sexual size dimorphism in the first year of life, except for reindeer for which we only had data on females. In addition, we also included covariates known to influence offspring size in some species when these variables were available. Thus, for Soay sheep (*Ovis aries*), we included the covariate “twin” (born as a twin vs. as a singleton) because twins are born lighter and have slower early growth than singletons (Robertson et al. 1992, Clutton-Brock et al. 1996). For elephants, we included the covariate “primiparity of the mother” (primiparous vs. multiparous) because primiparous mothers produce smaller offspring than multiparous mothers (Lee et al. 2013a).

We used the R package FlexMix with the FLXMRglmfix driver (Grün and Leisch 2008) to run a mixture model on each population. We thus fitted a linear mixture model using “individual body size at first measurement” as the dependent variable and including as a fixed covariate “sex” (all species except reindeer), “twin” (Soay sheep), “primiparity of the mother” (elephants), and “age at first measurement” (elephants). We included “cohort” as the latent clustering variable to segregate cohorts in distinct clusters. For each run, we used a minimum of five repetitions with random initializations to avoid reaching a local maximum (Grün and Leisch 2008). We used the stepFlexmix function, which fits a model with increasing number of clusters ( $K$ ) sequentially. We then evaluated the best  $K$  based on different selection criteria. Indeed, numerous criteria have been proposed to select  $K$  in finite mixture models, but there is no agreement yet on the most appropriate statistical method because different selection criteria sometimes result in different  $K$  being selected, with some criteria performing better than others in some situations and vice versa (McLachlan and Peel 2000, Aitkin et al. 2009, Everitt et al. 2011, Stahl and Sallis 2012, Melnykov 2013, McLachlan and Rathnayake 2014). Therefore, it has been recommended to consider multiple criteria together with theoretical and practical considerations, because results from a single criterion could be misleading (Everitt et al. 2011, Stahl and Sallis 2012, see also Hamel et al. [2016] for a review). Thereby, the  $K$ s selected with different criteria represent plausible alternative typologies in a data set. These alternatives can be compared a posteriori to select the best one according to the research objectives, for example by examining the amount of overlap between clusters to limit cases where some criteria appear to overestimate  $K$  (Hamel et al. 2016). Accordingly, we compared four criteria: the bootstrap criterion provided in the package FlexMix (Grün and Leisch 2008) and three of the most commonly used criteria (Everitt et al. 2011, Stahl and Sallis 2012), i.e., the Akaike Information Criterion (AIC; using  $AIC_c$  [which is corrected for sample size] led to the same results), the Bayesian Information Criterion (BIC), and the bootstrap criterion based on the likelihood ratio test statistic (McLachlan 1987). Each of these four criteria has different merits for

selecting  $K$  (McLachlan and Peel 2000, Brame et al. 2006, Aitkin et al. 2009, Everitt et al. 2011, Cubaynes et al. 2012, Stahl and Sallis 2012, and see Hamel et al. [2016] for a demonstration). Therefore, for each  $K$  selected by a given criterion, we obtained the predictions and 95% confidence intervals (CI) for each cluster. We then selected  $K$  as the highest plausible number of clusters with no overlap among the 95% CI of body size (see Fig. 2). The left panels of Fig. 2 illustrate the plausible  $K$ s found for two populations:  $K = 2, 3$ , or 4 for bighorn sheep at Ram Mountain, and  $K = 4$  or 6 for Soay sheep at St Kilda. In bighorn sheep, two clusters have overlapping 95% CI for  $K = 4$ , but all clusters are distinct for  $K = 3$ , and so  $K = 3$  was selected. Similarly,  $K = 4$  was selected for Soay sheep because the alternative with six clusters showed overlap among clusters. We selected  $K$  accordingly for all populations. In FlexMix, a cluster needs to include a minimum of 5% of observations to be identified. The minimum value for a cluster was 8% in mountain goats. The number of individuals in a cluster only affects the uncertainty around the estimates computed for each cluster, not the mean, and these uncertainties are represented by the 95% CI in the figures. To evaluate whether the magnitude in the structure of cohort variation at the initial age varied across species along the slow-fast continuum, we determined the Pearson correlation coefficient (with its 95% CI) between the number of cohort clusters selected and generation time (on a log-scale).

In this first step, males and females of each population were included in the same mixture model because our aim was first to pool cohorts that experienced similar environmental conditions, to later assess whether the same environmental conditions affected the variance of males and females differently. Separate analyses for each sex could have resulted in a cohort year being included in a different cluster for each sex, so that the variance among clusters would be based on different environmental conditions for each sex and would not be comparable. After the clustering, we modeled growth trajectories separately for males and females. Therefore, each population was described by a certain number of cohort clusters, with each cluster including both males and females born the same years, while the difference in size between sexes was accounted for by using sex as a covariate in the model. In the next five steps, we used the cohort classification provided by the clusters of the mixture models in step 1 to determine the growth trajectory specific to each cohort cluster, and this separately for each sex because growth trajectories vary between sexes. Therefore, for each population, cohort years in each cluster were extracted from the mixture model (e.g., cluster 1 = 1995, 1999, ..., 2005; cluster 2 = 1990, 1998, ..., 2010; etc.). Then, all individuals born in the years included in a cluster were assigned the same cluster number. To analyze the sex-specific growth trajectory of each cohort cluster (Steps 2–6), we used the data set including all body size measurements of individuals throughout their lifetime and assigned all measurements for a given individual to its respective cluster number.

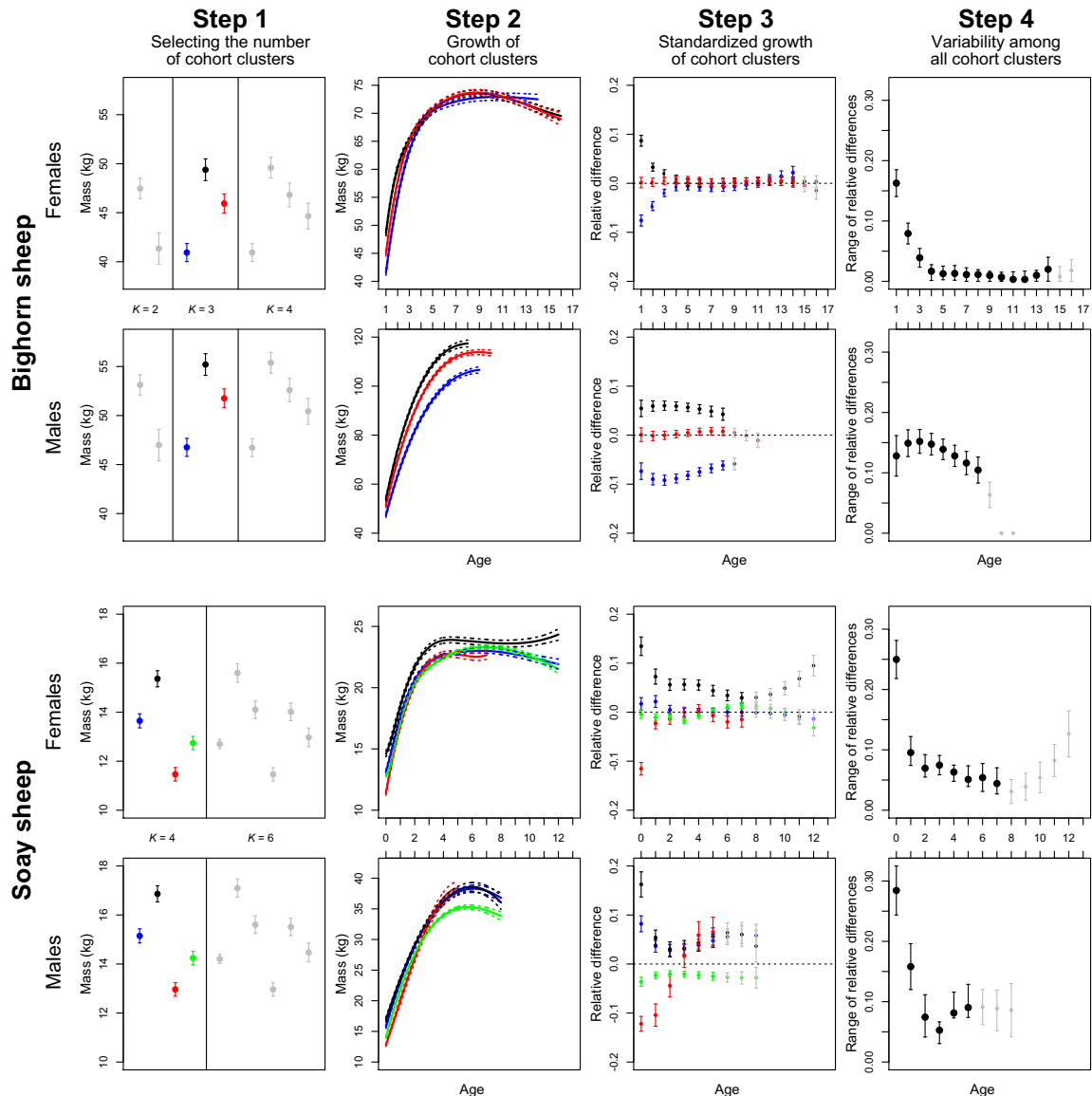


FIG. 2. Summary of the six steps to analyze cohort variation and its change throughout lifetime, illustrating two contrasting examples: bighorn sheep in the top two rows and Soay sheep in the bottom two rows. In Step 1, the number of clusters is selected based on a mixture model including body size measures 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. Gray 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 gray 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.



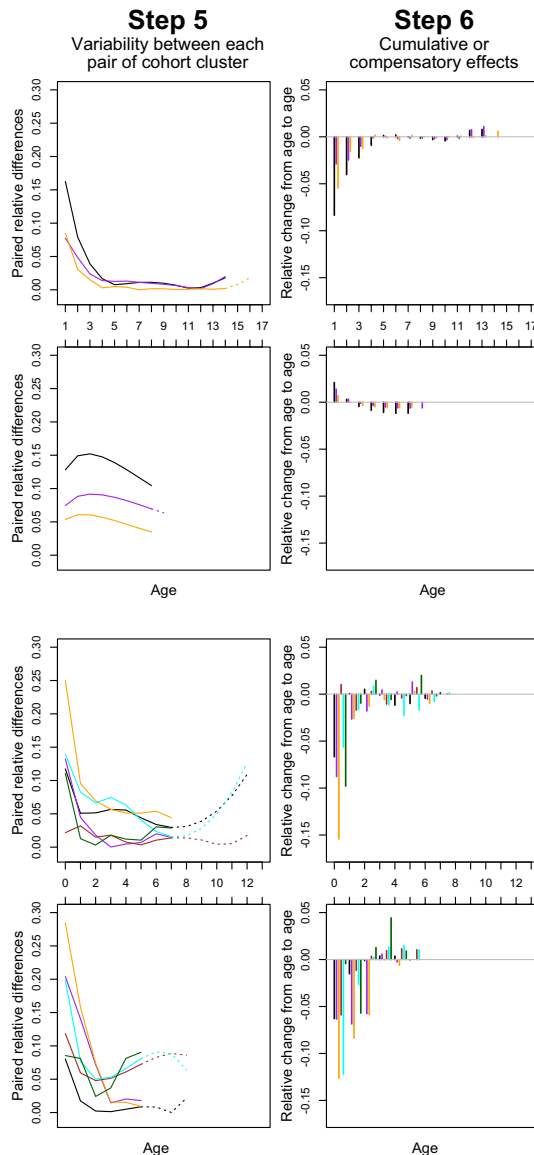


FIG. 2. (Continued)

### Step 2: Assessing growth trajectories of cohort clusters

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

linear mixed models (LMMs) using the R function `lmer` of the `lme4` package (Bates et al. 2014), including body size as the dependent variable, and including both year and individual identity as random intercepts to account for annual variation and the repeated measures of individuals with age. For the selection of fixed effects, 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 used likelihood ratio test based on the `anova` function in `lme4` to select the best model, which was appropriate since we compared nested models with the same random effects. Age was fitted with a B-spline (package `splines` in R), using likelihood ratio tests to determine the best polynomial degree of the spline function. We used this method throughout the analyses whenever we included a spline effect of age. Furthermore, we pooled data from older ages so that the oldest age examined always included at least five individuals. In addition to age and cohort cluster as fixed effects, we included all the factors reported or expected to affect body mass and for which we had data in each species. We did not systematically look for effects of these variables when there was no biological reason to do so. We included the covariate “reproductive status” for the LMMs on female mass, to account for the influence of producing an offspring on female annual mass in capital breeders. Female body mass in roe deer (*Capreolus capreolus*) is not affected by reproduction because they are income breeders (sensu Jönsson 1997) that do not rely on body reserves for gestation and lactation, as previously documented empirically in the two roe deer populations included in this study (Andersen et al. 2000, Plard et al. 2014b). Reproductive status was thus not included in the roe deer models. Furthermore, we could not include reproductive status for Wind Cave bison (*Bison bison*) and mouflon because the data were not available, and for Svalbard reindeer because reproductive status during the previous summer was uncertain for most females. Finally, we included the covariate “twin” and “primiparity of the mother” as a fixed effect in Soay sheep and elephants, respectively. We evaluated model fit by looking at diagnostic plots of residuals. On two occasions a data point seemed to be an outlier, but analyses with and without these points led to similar results. We also performed a visual assessment of parameter estimations by looking at the shapes of the deviance profiles (Bates et al. 2015).

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

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

We standardized the predictions and 95% CI found at Step 2 to contrast cluster-specific growth trajectories and evaluate how they differed among populations and sexes. A large variation in body size occurred among species, such that a 1-kg difference in female Soay sheep that average 13 kg at the end of their first summer corresponds to a much larger size variation than a 1-kg difference in female bison weighing on average 140 kg at the same age. Therefore, we scaled the difference among cohort clusters in a given sex of a given population as the relative difference from the mean population value  $m$  at each age  $a$ . For each sex in each population, we used a LMM including measurements from all cohort clusters but excluding the cluster effect from the model, and then extracted for each age the arithmetic mean prediction,  $\beta_{ma}$ , and its 95% CI. We then computed the relative difference at each age as  $(\beta_{ka} - \beta_{ma})/\beta_{ma}$ , such that a cohort cluster had a value of 0 if it did not differ from the mean, and had either a positive or negative value if it was higher or lower than the mean (see Step 3 in Fig. 2). These values were relative to the mean body size of a specific sex in a given population (referred to as “relative difference,” see Table 2) and could thus be compared among species and between sexes. Performing all analyses based on scaled absolute differences instead of relative differences led to similar results.

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

To evaluate how the magnitude of cohort variation changed with age, we used the relative differences obtained from Step 3 and calculated the range among all cohort clusters at each age, i.e., the difference between the maximum and the minimum value, hereafter called “range of relative differences” (see Step 4 in Fig. 2, Table 2). We did this using all age-specific size data from the age at first measurement up to the last age when all clusters were measured (black dots in Step 4 of Fig. 2). When at least one cohort cluster was missing at a given age, all data from this age onward were excluded from analyses (gray dots in Step 4 of Fig. 2). We then evaluated whether the range of relative differences varied between sexes and along the slow-fast continuum using a linear model (LM) with a spline effect of age, sex as a factor, a linear effect of generation time, and two-way interactions between age and sex and between age and generation time (using the product for the latter). The data have a hierarchical structure, with population nested in species, and sex crossed with population. However, accounting for this structure using a nested random intercept of population within species did not capture more variability (random effect variance of population within species estimated close to zero), reflecting that populations within species were not strongly dependent, and that variation among populations associated with generation time accounted for much of the variability. We log-transformed

the range of relative differences to normalize the residuals, adding 0.1 because some relative differences were null. We also standardized age to account for differences in the length of the time series between sexes and among species generated by differences in lifespan. Because there was only a single cohort cluster in elephants, we replicated the analysis by including and then excluding this population. Although the influence of generation time was slightly more pronounced when elephants were included, the results were overall similar. We therefore only report the conservative results from analyses excluding elephants. In addition, the range of relative differences was influenced by the number of clusters and the age at first measurement, but including or excluding these covariates in the analysis led to qualitatively similar results.

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

In Step 4, we computed the range in relative differences among all cohort clusters for a given sex and population. In the fifth step, we calculated the difference in relative differences between each pair of cohort clusters, referred to as “paired relative differences” (see Step 5 in Fig. 2, Table 2). This paired analysis better captured the patterns of changes in cohort variation over age within a sex in a given population, illustrating whether different patterns occurred among pairs of cohorts (e.g., differences between cohort clusters 1 and 2 might compensate with age, whereas those between cohort clusters 1 and 3 might cumulate with age). Again, we used all age-specific size measurements from the age at first measurement up to the last age when all clusters were measured (solid lines in Step 5 of Fig. 2).

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

To determine whether relative cohort variation in size remained constant throughout life, increased (size divergence), or decreased (size compensation), we computed the relative change in paired relative differences between cohort clusters from age  $x$  to age  $x + 1$  (hereafter referred to as “relative change from age to age,” Table 2), using the paired relative differences calculated at Step 5 (illustrated in Fig. 4 with their 95% CI). A positive value indicated an increase in the difference between a pair of cohort clusters with age, and therefore cumulative effects with age. On the other hand, a negative value indicated reduced differences between pairs of cohort clusters with age, and thus compensatory effects. A value of 0 indicated no change in cohort variation in size with age between a pair of cohort clusters. We then evaluated whether the relative change from age to age varied between sexes and along the slow-fast continuum using a LMM including a spline effect of age, sex as a factor, a linear effect of generation time, and two two-way interactions between age and sex and between age and generation time (using the product for the latter). We included

population as a random intercept because we had repeated values. Repetitions were more numerous for populations with more cohort clusters because these populations included a greater number of paired clusters (Fig. 6). Again, adding a nested random intercept of population within species did not capture more variability (random effect variance of population within species estimated close to zero). According to the profile log-likelihood for the parameter of the Box-Cox transformation (package MASS in R; Venables and Ripley 2002), we transformed the relative change from age to age to the power 7.5 to normalize the residuals, adding 0.5 to shift the distribution above zero (Appendix S1: Fig. S2). As in Step 4, we standardized age to account for differences in the length of the time series between sexes and among species, due to differences in lifespan. We also repeated this analysis with elephants included and excluded. Again, results were similar but with a more pronounced influence of generation time when elephants, the species with the longest generation time, were included. We only report the conservative results from analyses excluding elephants. Also, including or excluding age at first measurement as a covariate in the analysis led to qualitatively similar results.

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

We sought to remove the influence of viability selection from that of differences in growth to assess the specific influence of compensatory/catch-up growth on patterns of cohort variation with age. We did this by rerunning Steps 2–6 while accounting for the disappearance of individuals (mostly through mortality because emigration was limited or absent in most populations), thereby modeling differences among cohort clusters due only to differences in growth. First, we added the age at last measurement of each individual as a covariate in each LMM run to estimate the growth of a cohort cluster (Step 2). We fitted a LMM according to Eq. 1 in van de Pol and Verhulst (2006), using the age at last measurement to reflect the timing of disappearance (i.e., parameter  $\alpha_i$  in van de Pol and Verhulst's [2006] equation). We tested for both a linear and a quadratic effect of age at last measurement and retained the best model based on a likelihood ratio test. Then, we extracted the predicted trajectories of expected body size with age ( $\beta_{ka}$ ) from these LMMs that included age at last measurement. As these LMMs provided a measure of within-cohort cluster change in body size that was independent of viability selection (i.e., parameter  $\beta_w$  in van de Pol and Verhulst's [2006] equation), we will refer to these parameters as  $\beta W_{ka}$ , for “within change in  $\beta_{ka}$ ”. The influence of age at last measurement could differ among cohort clusters of a given sex and population because each cluster was modeled using a different LMM. To obtain the  $\beta W_{ka}$  predictions, however, we used the same age at last measurement for all cohort clusters of the same sex and population, using the mean age at disappearance for that

sex and population, thereby controlling for the variation in age at disappearance among cohort clusters. Using these growth trajectories adjusted for disappearance, we then computed the standardized growth trajectory for each cohort cluster (Step 3). As the standardized growth trajectories in Step 3 provided a measure of relative difference among cohort clusters calculated as  $(\beta_{ka} - \beta_{ma})/\beta_{ma}$ , we used  $(\beta W_{ka} - \beta W_{ma})/\beta W_{ma}$ , where  $\beta W_{ma}$  was obtained from a LMM similar as that for  $\beta_{ma}$  in Step 3, but again including age at last measurement as a covariate, with either a linear or quadratic effect. We extracted  $\beta W_{ma}$  predictions for the mean age at disappearance for each sex and population. Therefore, the relative difference calculated accounted for the selective disappearance of individuals and allowed us to calculate the relative change from age to age in cohort variation (Step 6) that was only due to differences in growth. Next, we evaluated whether sex and generation time affected the relative change from age to age that was only due to differences in growth. We did this similarly to Step 6, except that we replaced the response variable “relative change from age to age due to both viability selection and growth” with the “relative change from age to age due only to differences in growth”. We could then compare the results for the relative change from age to age that represented both viability selection and compensatory/catch-up growth with those only due to differences in growth. Finally, to evaluate the importance of viability selection, we used likelihood ratio tests to determine whether the LMM including age at last measurement as a covariate received greater support than the same model without this covariate (i.e., LMMs in Step 2 with and without age at last measurement). We did this separately for each cohort cluster of a given sex in a given population. Note that for the bison population at Konza, disappearance was mostly the result of culling.

## RESULTS

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

We found statistical evidence for distinct cohort clusters in almost all populations, with up to five clusters in the Wind Cave bison population (Table 1). Only the Amboseli elephants, the species with the longest generation time, did not exhibit detectable cohort variation in size. In the species with the second longest generation time, the mountain goat (*Oreamnos americanus*), we found two cohort clusters, but one cluster only included two of 25 cohorts, suggesting no structure or low cohort variation in this species. The trend for the number of clusters to decrease with generation time (Table 1) was not statistically significant ( $r$  [95% CI] =  $-0.33$  [ $-0.78$ ,  $0.33$ ],  $P = 0.3$ ). The data on bison at Konza were characterized by four cohort clusters, but one cluster only included recent cohorts, and thus we could not examine growth trajectories in this cohort cluster because no individual was monitored past age 4. For bison at Wind

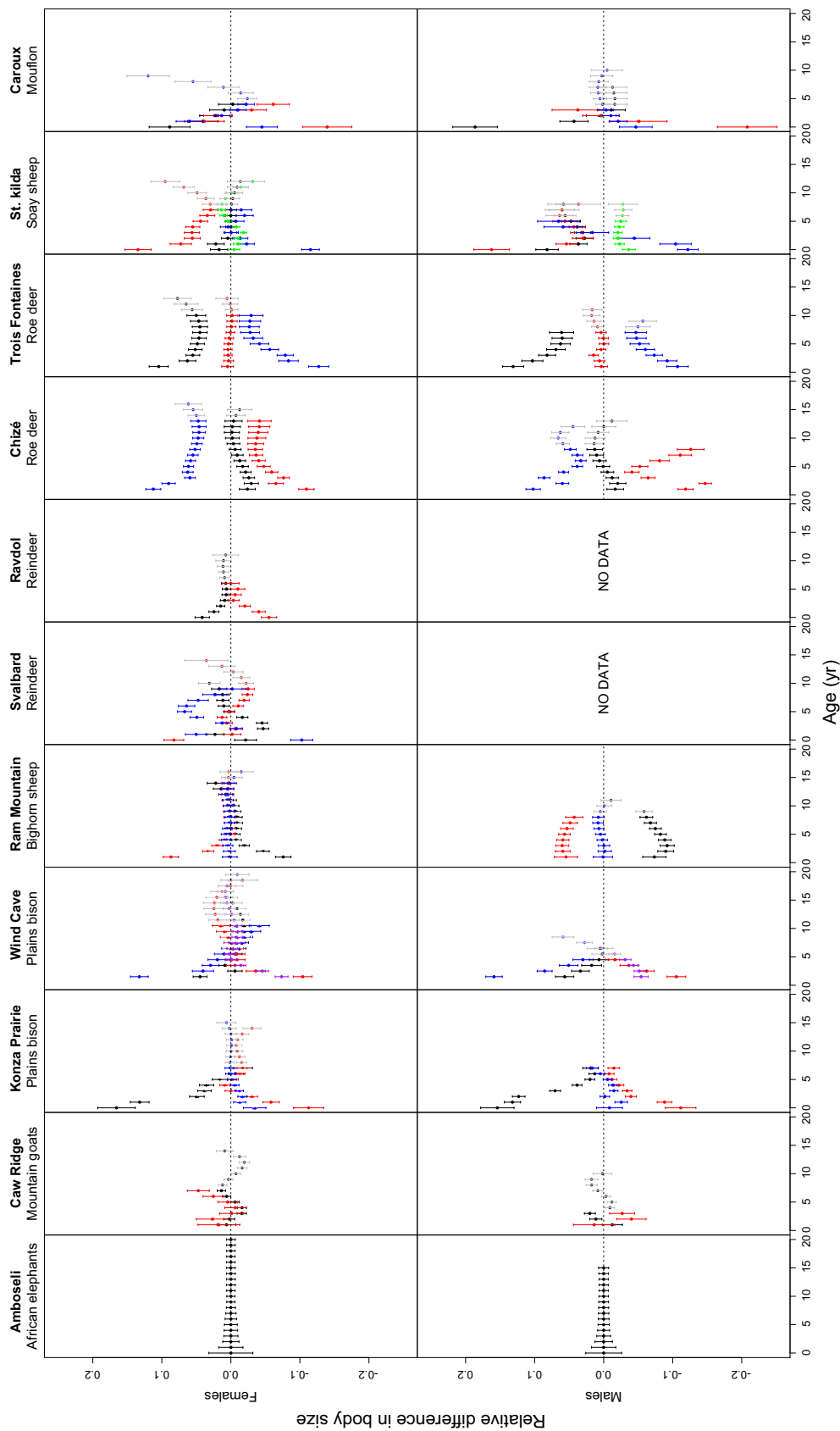


FIG. 3. The difference in the trajectory of each cohort cluster relative to the predicted mean (specific to each population and sex), illustrating the standardized growth of the different cohort clusters (Step 3) for each population (ordered from a long [left] to a short [right] generation time, corresponding 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. Gray bars correspond to ages from which at least one cohort cluster was missing.



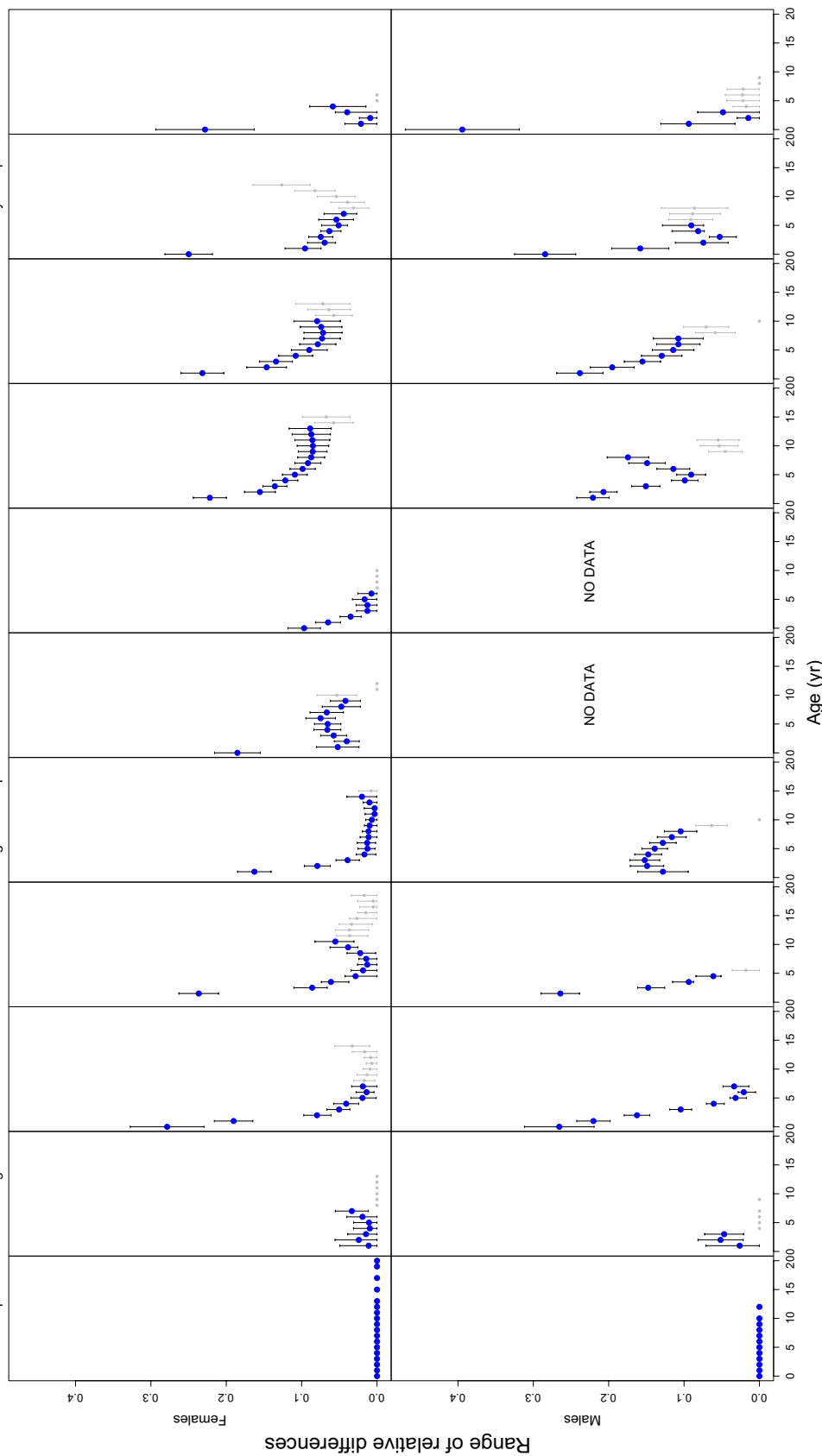


FIG. 4. The magnitude of cohort variation in size at each age (Step 4), i.e., the range of relative differences among all cohort clusters (computed from the standardized growth, Step 3; Fig. 3), for each population (ordered from a long [left] to a short [right] generation time, corresponding to the “slow-fast”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

TABLE 3. ANOVA table for the sequential† 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 Table 2), 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	P
(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 <sup>-4</sup>	0.39 <sup>-4</sup>	3	400.8	22.3	<0.001
Sex	0.10 <sup>-4</sup>	0.10 <sup>-4</sup>	1	396.3	5.9	0.02
GT	0.08 <sup>-4</sup>	0.08 <sup>-4</sup>	1	41.4	4.7	0.04
Age × Sex	0.33 <sup>-4</sup>	0.11 <sup>-4</sup>	3	400.5	6.2	<0.001
Age × GT	0.32 <sup>-4</sup>	0.11 <sup>-4</sup>	3	400.5	6.0	<0.001
(c) Relative change from age to age, differences in growth only						
Age	0.49 <sup>-4</sup>	0.16 <sup>-4</sup>	3	401.7	12.1	<0.001
Sex	0.13 <sup>-4</sup>	0.13 <sup>-4</sup>	1	397.9	9.5	0.002
GT	0.01 <sup>-4</sup>	0.01 <sup>-4</sup>	1	37.3	1.1	0.3
Age × Sex	0.30 <sup>-4</sup>	0.10 <sup>-4</sup>	3	401.2	7.2	<0.001
Age × GT	0.11 <sup>-4</sup>	0.04 <sup>-4</sup>	3	401.7	2.7	0.04

Notes: SS, sum of squares; MSS, mean sum of squares; Num df, degrees of freedom in the numerator; Den df, degrees of freedom in the denominator; GT, generation time, in years, computed as  $T_b$  according to Lebreton (2005).

†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.

Cave, one of the five clusters also had no individual monitored past age 4. Thus, for the bison populations, we performed steps 2–6, which assess growth trajectories, only for clusters with enough data later in life, i.e., three for Konza and four for Wind Cave.

#### *Growth trajectories of cohort clusters*

Models including an interactive effect between age and cluster received most support in almost all cases (likelihood ratio, all  $P < 0.1$ ; Appendix S1: Table S1), supporting that growth trajectories differed substantially among cohort clusters throughout life. The only exceptions were for roe deer males at Trois Fontaines and female mountain goats where the additive model was retained, and for male mountain goats where the selected model only included age (Appendix S1: Table S1).

#### *Magnitude of cohort variation in body size*

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

and sex, and by an additive effect of generation time (Table 3a). Differences among cohort clusters decreased markedly with increasing age, in both sexes and for any generation time (Fig. 5). Males, however, showed about 7% greater cohort variation in early life than females, while both sexes displayed similar magnitude of cohort variation in size at the end of life. The decrease in the magnitude of cohort variation in size with increasing age was more progressive and extended for a greater part of life in males than in females, for which cohort variation stabilized just before mid-life (Fig. 5). The strength of the decrease in cohort variation with increasing age was independent of generation time (Table 3a). Nevertheless, populations with a short generation time exhibited more cohort variation in size throughout their entire life than populations with a long generation time (Fig. 5).

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

The curves of paired relative differences (Step 5; Fig. 6) were generally similar within a sex in a given population. From these curves, we computed the relative change from age to age in the magnitude of cohort variation in size between paired cohorts (Step 6; Fig. 7). The relative change from age to age was influenced by interactive effects between age and sex and between age and generation time (Table 3b). Early in life, the relative change from age to age

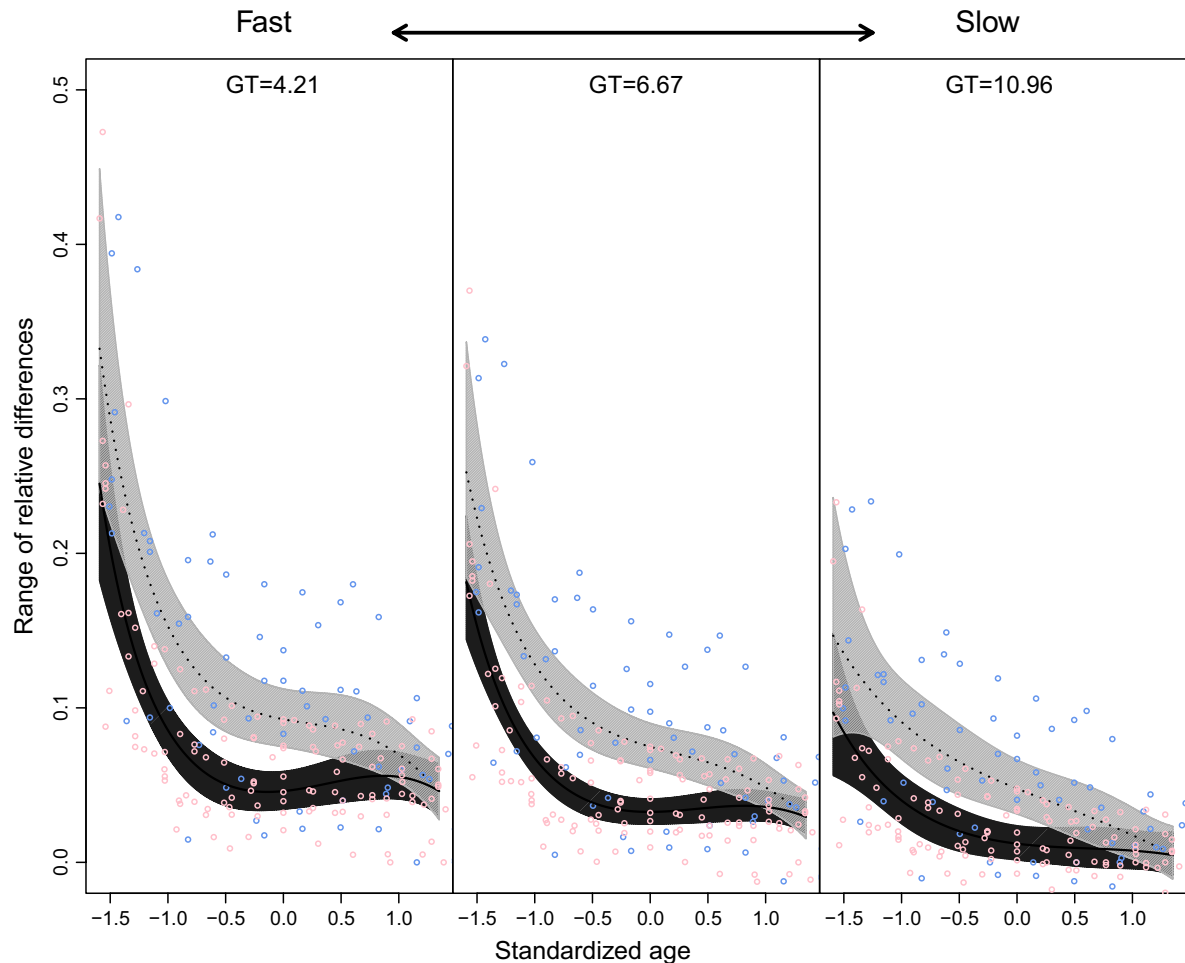


FIG. 5. Change with age in the range of relative differences in size (Step 4) in relation to sex (males, dotted lines, light gray zones, blue dots; females, solid lines, dark gray zones, pink dots) and generation time (GT). The lines are the mean predictions and the zones are the 95% confidence intervals. 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.

was negative, corresponding to compensatory effects (Fig. 8). In general, these compensatory effects rapidly decreased with age (sharp increase in the curves in Fig. 8) and stopped just before mid-life (stabilizing around zero, implying neither cumulative nor compensatory effects; Fig. 8). In males, however, compensatory effects were weaker early in life compared with females, but continued throughout the lifetime, decreasing only progressively with age (Fig. 8). Compensatory effects were stronger in early life in species with a short generation time. In contrast, species with a long generation time had a relative change from age to age that stabilized more rapidly, reaching a plateau close to zero at an earlier age relative to their lifetime (Fig. 8). Comparing Figs. 6 and 7 reveals that the stabilization in species with a long generation time is mainly the result of a dissipation of cohort variation in size with increasing age, whereas cohort variation in size in species with a short generation time stabilized but was still present from mid-age to late life.

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

With the exception of mountain goats and reindeer, likelihood ratio tests revealed viability selection in all species, but not necessarily in both sexes or in all cohort clusters (Table 4). Overall, about half of the cohort clusters (Table 4) for both males (50%, 13 of 26 cases) and females (52%, 16 of 31 cases) showed evidence for viability selection. With the exception of Wind Cave bison, the coefficient for the effect of age at last measurement on body size (i.e., Step 2 including age at last measurement) was consistently positive, suggesting disappearance of lighter individuals with increasing age (e.g., males in Chizé, Fig. 9). Nevertheless, the relative change from age to age in the magnitude of cohort variation that was only due to differences in growth did not differ much from that due to both viability selection and growth (range of differences from 0% to 17.1% in the relative change from age

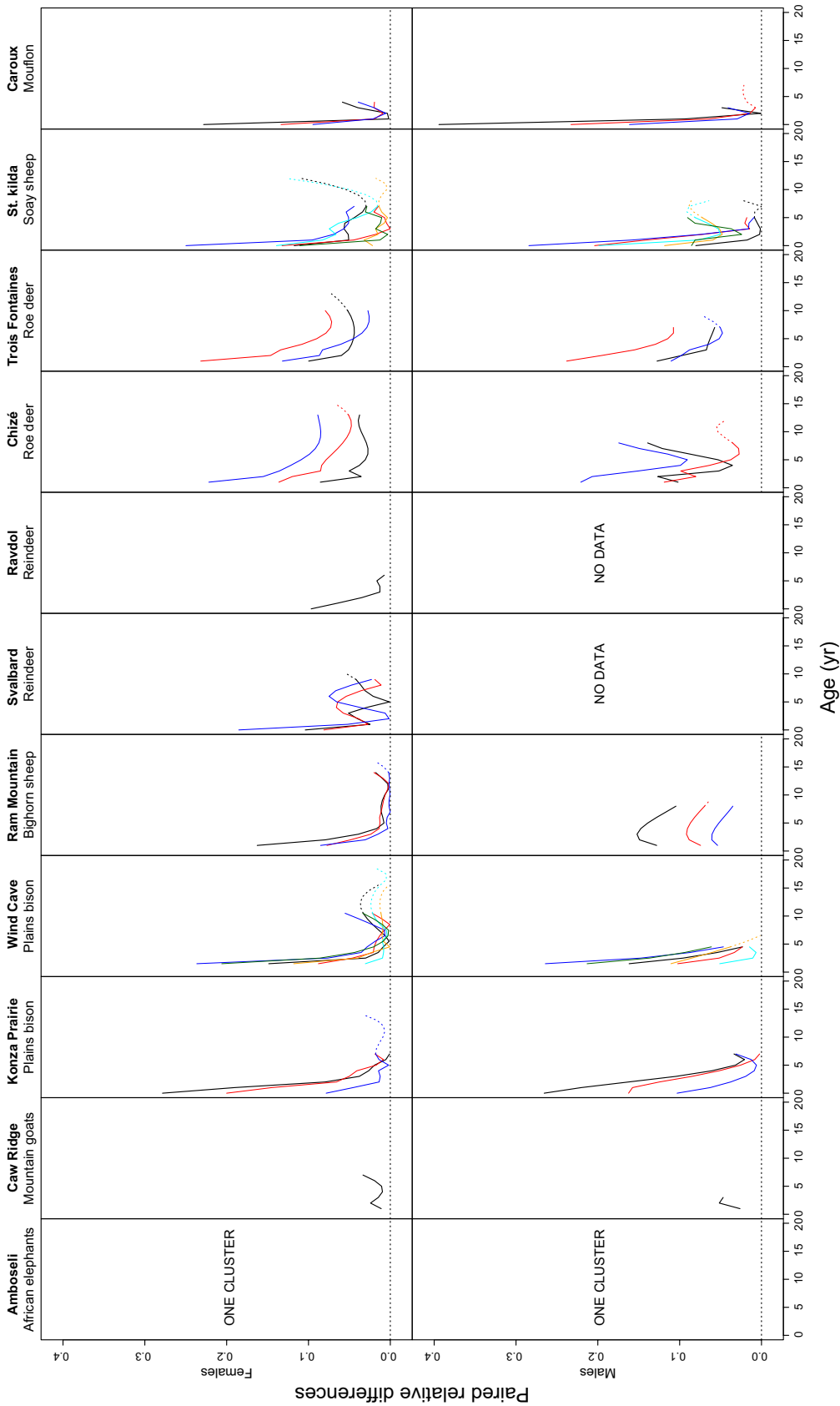


FIG. 6. The paired relative differences in size between cohort clusters (Step 5) in relation to age (computed from the standardized growth trajectories, Step 3; Fig. 3), for each population (ordered from a long [left] to a short [right] generation time, corresponding to the "slow-fast" continuum of life 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.



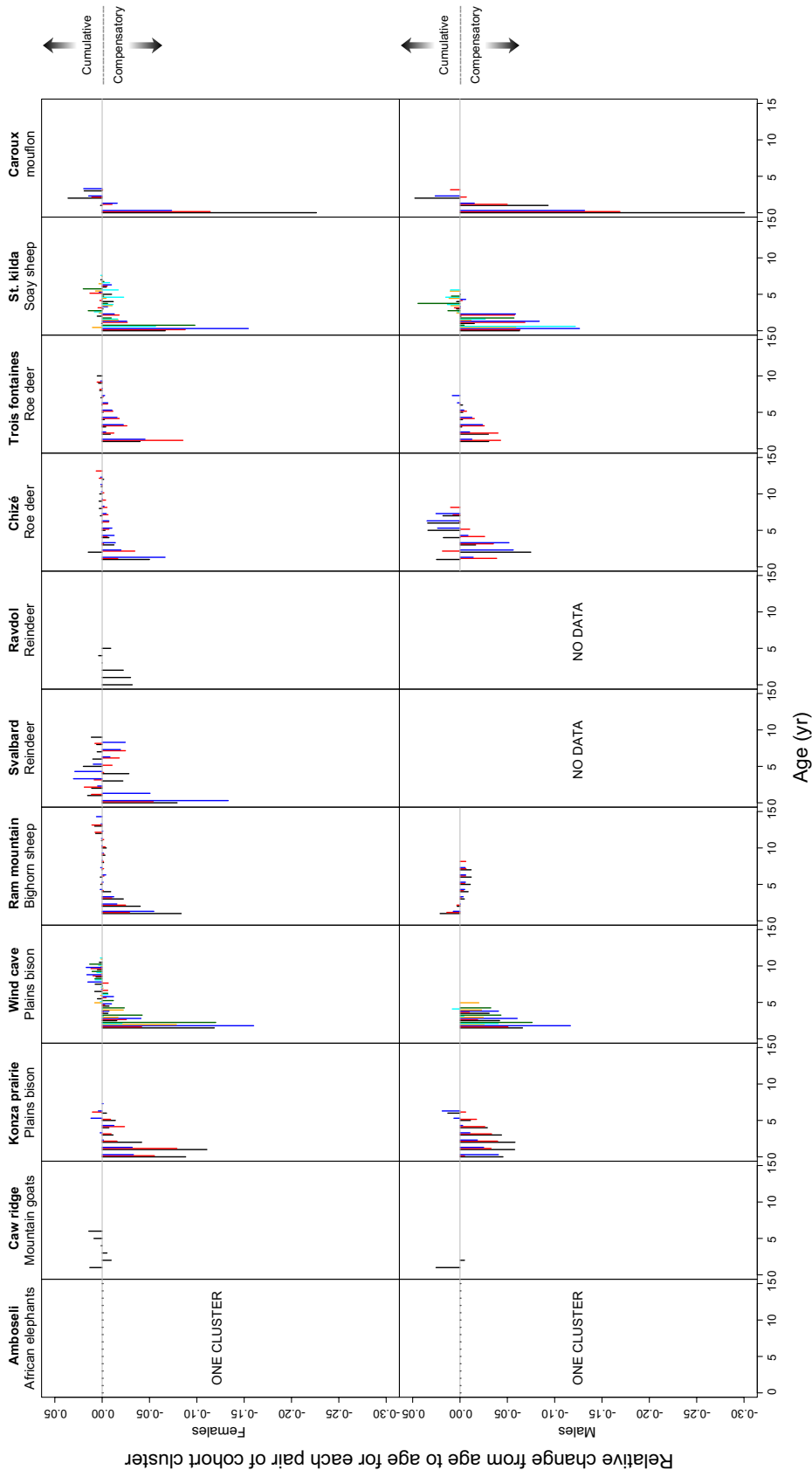


FIG. 7. The relative change from age to age in cohort variation in size between each pair of cohort clusters (Step 6) in relation to age (computed from the values compiled at Step 5; Fig. 6), for each population (ordered from a long [left] to a short [right] generation time, corresponding to the “slow-fast” 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.

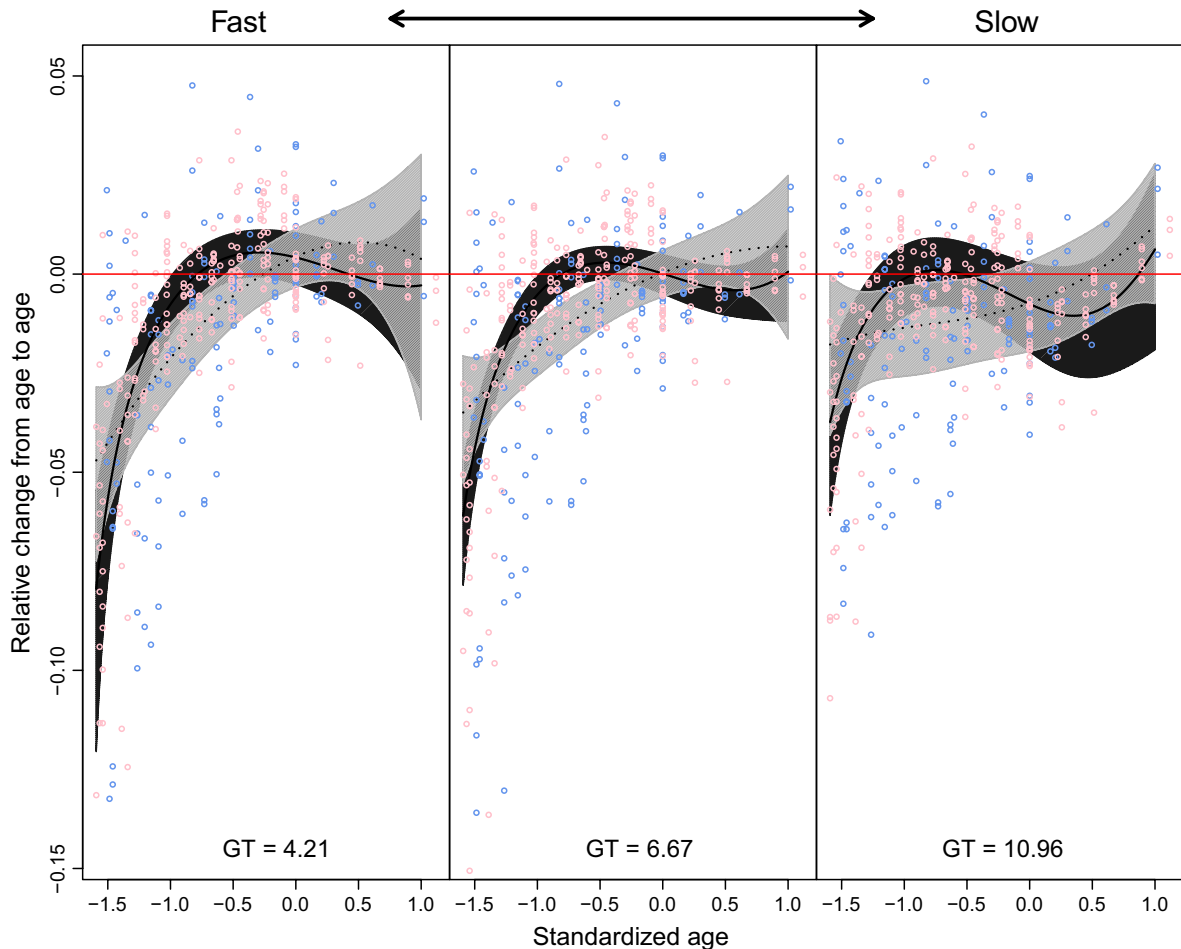


FIG. 8. Variation in the relative change from age to age (Step 6) in relation to sex (males, dotted lines, light gray zones, blue dots; females, solid lines, dark gray zones, pink dots) and generation time (GT). The lines are the mean predictions and the zones are the 95% confidence intervals. The dots 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.

to age after accounting for viability selection; Fig. 10). Overall, the change from age to age only due to differences in growth was influenced by the same variables as when including viability selection (Table 3b, c, Fig. 10), with the influence of age, sex and generation time showing very similar patterns (compare Figs. 8 and 10, which are on the same scale). The main difference was early in life, when the relative change from age to age only due to differences in growth was less than when the data included both viability selection and growth, particularly for short-lived species (blue and pink lines in Fig. 10). This effect was slightly stronger in males than in females (Fig. 10).

#### DISCUSSION

Based on an exceptional set of long-term data collected in 11 populations of large herbivores, we quantified cohort variation and assessed how it changed throughout

life, demonstrating that this fundamental biological process varied both across species in relation to their pace of life and between sexes. Variation in size peaked at the start of life, then quickly decreased with increasing age in all species and stabilized around mid-life. Even after accounting for viability selection, compensatory/catch-up growth was still a major process explaining the decrease in the amount of cohort variation with increasing age. Among-cohort variation was lower in species with a slower than a faster pace of life throughout the lifetime, and vanished at prime ages in the species with the slowest paces of life. Females showed less phenotypic variability and stronger compensatory/catch-up growth than males early in life, whereas males showed more progressive changes throughout life. This resulted in old males having the same low level of cohort variation as old females. Our findings concern mainly body mass variation because mass was used to describe body size in all except one species.

TABLE 4. Likelihood ratio tests for each cohort cluster (Gr) 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.

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

Notes: 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 boldface italic type, we highlight support or a tendency to support the model including age at last measurement, and thereby the presence of viability selection. Dashes indicate no data.

We found large variation in body size among cohorts in all species except the slowest species along the slow-fast continuum of life histories included in this study. Mixture models (McLachlan and Peel 2000), an innovative method to assess individual differences in life-history traits (Hamel et al. 2016), identified clusters of cohorts sharing similar body size at the start of life. We showed that cohort variation was structured, as opposed to the unstructured variation (i.e., uniform distribution) usually assumed when studying cohort effects with mixed models. This structured variation led to distinct growth trajectories throughout life among clusters of cohorts sharing similar initial size, in all species and most often in both sexes, thereby showing that early body size is a key driver of the growth trajectory later in life. Disentangling

whether cohort-specific growth trajectories results from early or late environmental conditions is difficult without an experimental approach because individuals of the same cohort can experience the same environmental conditions throughout their entire lifetime (Metcalf and Monaghan 2003). In this regard, one major novelty in our study is that we showed that environmental conditions experienced early in life per se, not just the cohort year modeled as a random effect term, typically have long-term consequences irrespective of late-life conditions. Indeed, cohort clusters with similar body size at the start of life included cohorts born in different years, and hence individuals included in the same cluster experienced different environmental conditions later in life. In many species, clusters included cohorts that were more

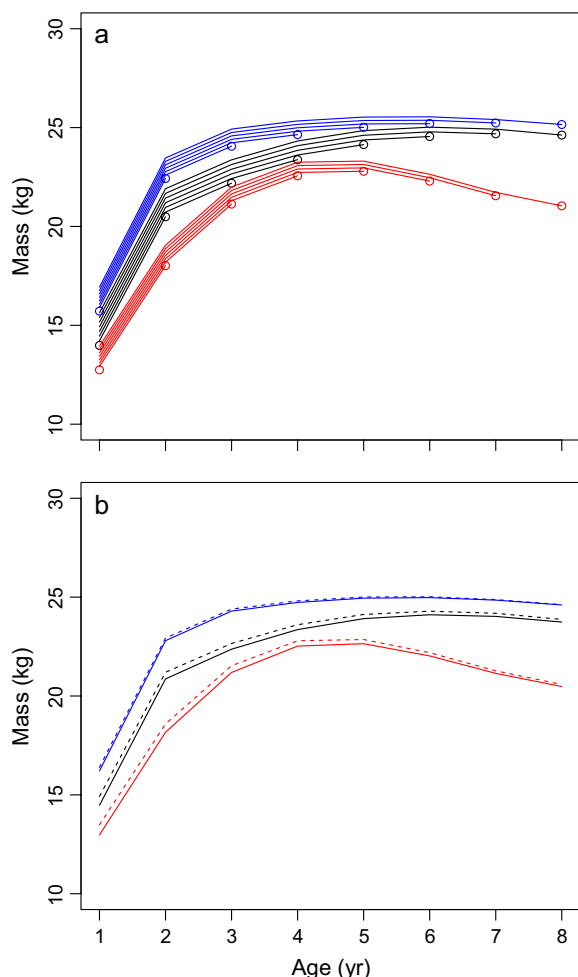


FIG. 9. Effect of viability selection on growth trajectories in three cohort clusters of male roe deer at Chizé. Each color represents a different cohort cluster. (a) Trajectories with the same colors represent mean growth predictions for individuals of the same cohort cluster but with different ages 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).

than 20 years apart. Still, cohort clusters characterized by different initial body sizes displayed different growth trajectories throughout life, supporting the hypothesis that individual growth trajectories in large herbivores are considerably affected by early development. Of course, cohort variation does not account for all observed variation among body mass trajectories in a given population. The specific early mass of an individual, for instance, should markedly influence its future age-specific mass, as often reported for large herbivores (Clutton-Brock and Pemberton 2004, Douhard et al. 2013). Here, because individuals were not measured every year in several populations, we did not assess the contribution of individual variation in early mass to observed variation in age-specific mass later in life.

The greatest cohort variation in size occurs at the start of life, with on average a 20% (up to 40%) difference between cohort clusters. Cohort variation in size, however, decreased relatively rapidly with increasing age in all species. Our results indicate much potential for compensation in the magnitude of cohort variation in large herbivores despite limited time to compensate due to growth cessation at maturity. Nevertheless, the meta-analysis by Hector and Nakagawa (2012) pointed out that mammals and birds allocate more to accelerating growth after food restriction compared to fish and arthropods, possibly because species with determinate growth gain more benefits by compensating early, before growth ceases (Metcalf and Monaghan 2003). The decreasing cohort variation with increasing age was a consequence of both higher survival of larger individuals, and compensatory/catch-up growth, which allowed some cohorts to partly make up for a poor start. Our results demonstrate that viability selection resulting from the positive influence of large size on individual survival is common in natural populations of large herbivores (Nussey et al. 2011). Nevertheless, although viability selection was detectable in almost all species and both sexes, it only explained a small fraction of the compensation in the magnitude of cohort variation, affecting mostly shorter-lived species. Viability selection is likely to peak during the neonatal stage in large herbivores, when survival is low and most variable (Gaillard et al. 2000b), and for many of our study populations it had likely already taken place when body size was first measured (Table 1). Consequently, our results imply that viability selection is influential, but that compensatory/catch-up growth is the main factor explaining the decrease in cohort variation with increasing age after the neonatal stage.

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



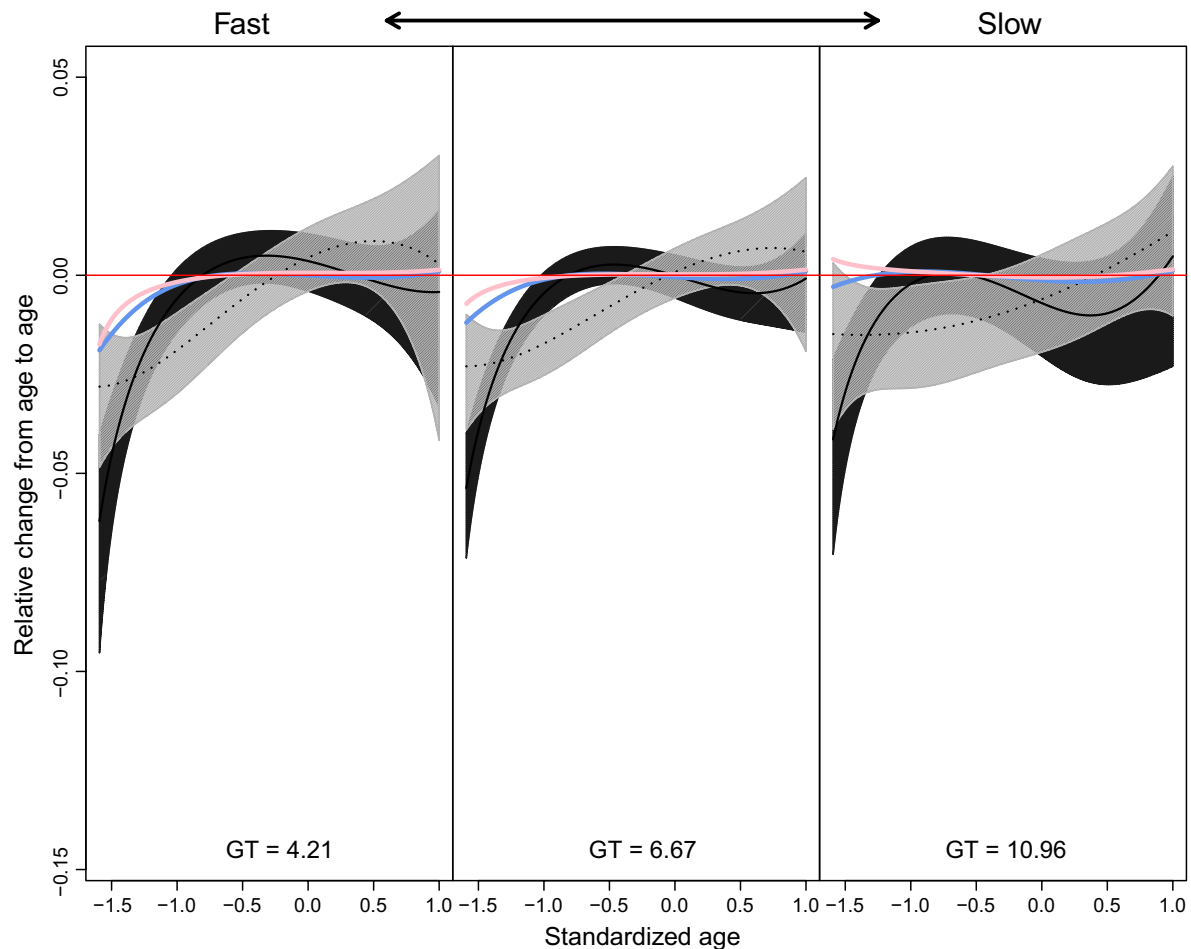


FIG. 10. Variation in the relative change from age to age only due to differences in growth, in relation to sex (males, black dotted lines, light gray zones; females, black solid lines, dark gray zones) and generation time (GT). The black lines are the mean predictions and the zones are the 95% confidence 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.

and thereby exposure to predators (Dmitriew 2011). Faster or prolonged growth during development can also result in detectable trade-offs in other life-history traits later in life (Nussey et al. 2007, Dmitriew 2011, Douhard et al. 2014). For instance, according to the disposable soma theory (Kirkwood 1977), individuals allocating more to growth early in life are expected to pay a cost later in terms of reproduction or survival (Metcalf and Monaghan 2001, Lemaître et al. 2015). Indeed, an increase in oxidative stress and in the repair of damaged cells can affect ageing patterns and longevity (Mangel and Munch 2005, Monaghan et al. 2009, Nussey et al. 2009, Dmitriew 2011), leading to subtle costs that might appear only late in life and hence might be under lower selection pressure (e.g., Lee et al. 2013b). The long-term trade-offs associated with growth during development are a cornerstone of life-history theory (Dmitriew 2011), and hence it is

essential to assess how variation in individual growth changes with age to understand better its impact on individual fitness (Lee et al. 2013b). However, the relevance for population dynamics of subsequent changes in growth and trade-offs with life-history traits depends on the survival of individuals from different cohorts. Given the documented potential negative long-term fitness consequences of a poor start (reviewed in Metcalf and Monaghan 2001), the benefits, and thereby selection pressures, of compensating for a bad start are likely to be high. This is supported by our finding that compensatory/catch-up growth is a key process in the dissipation of cohort variation with increasing age. Hence, the benefits/costs ratio for compensatory/catch-up growth is likely high in large herbivores, with strong selection pressures for compensatory/catch-up growth in all species irrespective of their pace of life.

Although compensatory effects were detected in all species, we found important differences among species in relation to their ranking on the slow-fast continuum of life histories. Cohort variation in size in early life was greater in species with a fast than a slow pace of life. This was supported by (1) our inability to detect any cohort variation in size in the African elephant, which had the longest generation time, (2) the tendency to identify more cohort clusters in species with a fast than a slow pace of life, and (3) the greater relative differences in size among cohort clusters in species with a fast pace of life than in species with a slow pace of life. Long-lived species have evolved a slow pace of life: individuals generally show a conservative reproductive tactic that favors their own survival over that of their offspring because longevity increases fitness (Clutton-Brock 1988, Newton 1989). In these species, selection pressures have resulted in environmental canalization of adult survival, which shows lower variance than reproductive traits across a wide range of environmental conditions (Gaillard and Yoccoz 2003). Conversely, short-lived species have evolved a faster life-history strategy in which individuals allocate a high reproductive effort to each reproductive occasion, and environmental canalization has led to a lower variance in reproductive traits compared with long-lived species (Gaillard and Yoccoz 2003). The lower variance in growth at the start of life in long-lived than short-lived species suggests that initial growth is more affected by fluctuations in environmental conditions in species with a fast than a slow pace of life. This lower variance might also result from maternal effects, for example if mothers of longer-lived species provided more care to offspring, thereby buffering against environmental fluctuations. Although elephant mothers allocate to maternal care for a much longer period than any other large herbivore, the absolute time devoted to offspring by female elephant corresponds to the same allocation relative to their pace of life as other large herbivores included in our analysis (Langer 2008). Therefore, the lower variance in initial growth in long-lived species does not correspond to higher maternal investment in response to potentially higher time constraints. Moreover, maternal effects are unlikely to have a strong influence because mothers of long-lived species tend to favor their own survival at the expense of their offspring when resources are scarce (Sæther et al. 1993, Festa-Bianchet and Jorgenson 1998, Therrien et al. 2007, Martin and Festa-Bianchet 2010). Because body size is one of the main determinants of juvenile survival in most vertebrates including large herbivores (Plard et al. 2015, Théoret-Gosselin et al. 2015), our results suggest that body growth during development is likely to have been under strong selective pressures to promote survival, particularly in long-lived species.

Although cohort variation in size decreased markedly with increasing age and the strength of this decrease was similar across species, body size still varied among cohorts in short-lived species when they reached prime

ages. In long-lived species, cohort variation almost totally vanished at the same life stage. Although compensatory/catch-up growth is relatively common, it is often incomplete (Metcalf and Monaghan 2001, Dmitriew 2011). This is likely because of physiological constraints, where individuals are trapped in a developmental trajectory, or because the benefits/costs ratio is not high enough, and so growth rates are usually not maximal (Metcalf and Monaghan 2003, Dmitriew 2011). Our results further suggest that there is a limited time window for compensatory/catch-up growth before prime age in species with determinate growth. Furthermore, cohorts of species with a fast pace of life were more variable in size early in life and, as the rate of decrease in cohort variation with increasing age was similar across species, they did not fully compensate/catch up for initial size differences compared with species with a slow pace of life. With a limited time window and the costs paid later in life, the advantages of compensatory/catch-up growth should depend on its timing, with earlier compensatory/catch-up growth likely to be selected because of its direct benefits to survival and lifetime reproductive success (Dmitriew 2011).

In addition to differences in cohort variation in size across species, we highlighted between-sex differences in cohort variation of large herbivores. Cohort variation in size was higher in early life in males than in females. Although the magnitude of cohort variation stabilized at mid-life in females, it continued to decrease progressively throughout lifetime in males, reaching the same level as that of females only at the end of life. Compensatory/catch-up growth, however, was stronger early in life in females and stopped at mid-life compared with males that showed a weaker but constant compensatory/catch-up growth throughout lifetime. These results likely emerged from the contrasted sexual selection pressures in males and females in relation with sex differences in intra-sexual competition (Bonduriansky et al. 2008). Indeed, although sexual selection can be strong in females (Clutton-Brock 2007), selection for traits affecting competitive abilities is generally stronger in males than in females, especially in sexually size dimorphic and polygynous species such as large herbivores (Orlans 1969, Clutton-Brock 2007). Males and females adopt different tactics to increase their lifetime reproductive success. The reproductive success of males is often highly skewed and dependent on their ability to compete for reproductive opportunities (Orlans 1969, Trivers 1972). Thus, males often must fight to reproduce, and body size is a major determinant of fighting and reproductive success (Lidgard et al. 2005, Pelletier and Festa-Bianchet 2006, Mainguy et al. 2009). Females, on the other hand, usually compete for resources (Orlans 1969, Trivers 1972, Clutton-Brock 1991). Body size can therefore have a stronger influence on the reproductive success of males than females, as shown in red deer (*Cervus elaphus*; Kruuk et al. 1999). As a result of these differences in sexual selection, males often evolve a

“grow fast, die young” life-history strategy (Bonduriansky et al. 2008), allocating more resources to rapid growth and fewer to maintenance (see, e.g., Toïgo et al. 1999, Robinson et al. 2006). Males will therefore grow faster early in life and for longer compared with females (Garel et al. 2006), thereby requiring more nutrients than females (Michener and Locklear 1990, Landete-Castillejos et al. 2005). Consequently, males are more sensitive to food shortage during early life and often show greater juvenile mortality than females (Clutton-Brock et al. 1985). Greater vulnerability to nutritional stress in males likely explains the larger cohort variation and the slightly stronger viability selection found in males than in females. Furthermore, even though males should have a shorter catch-up time window than females because they grow faster and die younger, compensatory/catch-up growth was much weaker and slower in males than in females. This pattern seems to confirm that even though it would be beneficial for males to compensate early in life, they have a lower ability to compensate/catch up for a bad start than females (Toïgo et al. 1999, Festa-Bianchet et al. 2000, but see Solberg et al. [2008] and Rughetti and Festa-Bianchet [2010]). Perhaps the costs of compensation/catch-up growth are greater for males, or small females can allocate more resources to growth by postponing primiparity (Martin and Festa-Bianchet 2012), an option that is not available to males.

#### CONCLUSION

The role of cohort variation as a process in life-history variation has often been explored. Our study, however, provides novel results on how the magnitude of cohort variation changes over the lifespan, and how these patterns vary among species in relation to the pace of life and between sexes. These topics have been neglected in previous studies likely because the required data for a comparative analysis were lacking until recently. We found that cohort variation in size decreased markedly during the first half of life and then almost vanished, particularly in species with a slow pace of life. Both compensatory/catch-up growth and viability selection dampened cohort variation in size with ageing, but compensatory/catch-up growth was the main underlying process beyond the neonatal stage. Our findings suggest that the costs associated with compensatory/catch-up growth are not necessarily high, at least early in life and particularly in females, or that the benefits are high. It remains to be determined whether differences in growth trajectories are adaptive. For instance, no study has yet tested whether delayed costs of rapid or prolonged early growth exist in wild vertebrates (see Lemaître et al. [2015] for a review). As fitness mostly depends on survival and reproductive success, which are both linked with body size (Dmitriew 2011), it is fundamental to evaluate the degree to which body size early in life and variability in developmental patterns among cohorts influence other traits later in life.

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

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1232/supinfo>

## DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.n358r>