Evidence of reduced individual heterogeneity in adult survival of long-lived species

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The canalization hypothesis postulates that the rate at which trait variation generates variation in the average individual fitness in a population determines how buffered traits are against environmental and genetic factors. The ranking of a species on the slow-fast continuum – the covariation among life-history traits describing species-specific life cycles along a gradient going from a long life, slow maturity, and low annual reproductive output, to a short life, fast maturity, and high annual reproductive output – strongly correlates with the relative fitness impact of a given amount of variation in adult survival. Under the canalization hypothesis, long-lived species are thus expected to display less individual heterogeneity in survival at the onset of adulthood, when reproductive values peak, than short-lived species. We tested this life-history prediction by analysing long-term time series of individual-based data in nine species of birds and mammals using capture-recapture models. We found that individual heterogeneity in survival was higher in species with short-generation time (< 3 years) than in species with long generation time (> 4 years). Our findings provide the first piece of empirical evidence for the canalization hypothesis at the individual level from the wild.

Life-history traits such as lifespan and reproductive rates are well known to covary, forming life-history strategies (Stearns 1976). In particular, a recurring pattern in cross-species comparative demography is the existence of a slow-fast continuum of life histories going from long-lived, late-maturing, and slow-reproducing species to short-lived, early-maturing, and highly fecund species (see Gaillard et al. 2016 for a recent review). The continuum is in part linked to variation in body mass, temperature, and development time (Harvey and Zammuto 1985; Gillooly et al. 2001) but still occurs when allometric relationships linking life-history traits and body mass or size have been accounted for (Stearns 1983; Brown and West 2000; Gaillard et al. 2016), leading to the idea that the slow-fast continuum of life histories reflects constraints or opportunities afforded by particular lifestyles (Brown and Sibly 2006), in relation to or independently of energy allocation trade-offs (Kirkwood and Holliday 1979). Irrespective of the mechanism(s) underlying this slow-fast continuum of life histories, the ranking of a species along the continuum is known to correlate with the rate at which given amounts of variation in life-history traits generates variation in population growth rate (Pfister 1998). In species close to the slow end of the continuum, called long-lived species in the following, variation in adult survival gives rise to the most variation in population growth rate (Caswell 2001). As population growth rate represents the average fitness of the population (Fisher 1930), individuals of long-lived species are therefore expected to display risk spreading and risk avoidance tactics, both part of a bet-hedging strategy aimed at maximizing survival probability (Gaillard and Yoccoz 2003; Koons et al. 2009; Nevoux et al. 2010). These are in turn expected to buffer phenotypes against perturbations caused by genetic (Stearns and Kawecki 1994) or environmental (Gaillard and Yoccoz 2003) factors. Such a buffer effect is usually called a canalization process (sensu Waddington 1953). We therefore predict adults in populations of long-lived species to have more similar survival probabilities than adults in populations of short-lived species. A few previous studies have focused on the magnitude of temporal variation in demographic rates in relation to their demographic impact (following Pfister's (1998) pioneer analysis). However, we are not aware of any study linking the demographic impact of traits to between-individual variance, except studies of *Drosophila melanogaster* in the lab (Stearns and Kawecki 1994). We took advantage of available long-term time series of demographic data in the wild and of modern statistical methods to test for the canalization of adult survival at the individual level in the wild. Under the canalization hypothesis, we expected between-individual variance in adult survival to decrease from short- to long-lived species.

Material and Methods
DATASETS
We studied nine species including four mammalian large herbivores—roe deer (*Capreolus capreolus*; two populations), chamois (*Rupicapra rupicapra*), Alpine ibex (*Capra ibex*), and greater kudu (*Tragelaphus strepsiceros*; two populations)—and five birds—black-headed gull (*Chroicocephalus ridibundus*), blue tit (*Cyanistes caeruleus*), white-throated dipper (*Cinclus cinclus*), snow petrel (*Pagodroma nivea*), and black-browed albatross (*Thalassarche melanophris*). All were subjected to detailed long-term monitoring at the individual level (Table S1 in Supplementary material A). Individuals were uniquely marked at first capture and physically recaptured or resighted later in life. Imperfect detection was accommodated using capture-recapture (CR) models (Lebreton et al. 1992).

INDIVIDUAL VARIATION IN SURVIVAL PROBABILITY
We aim at comparing, across species, the within-species, between-individual variance in adult survival. To do that we use the concept of frailty (sensu Vaupel et al. 1979). Frailty corresponds to the mortality risk of a given individual at a given age relative to the population average. In this study, we measure frailty via the variation among individuals in the intercept of the age-survival curve, that is the variance in the survival probability at the onset of adulthood (the age at maturity when reproductive values peak). In other words, a frailty value is assigned to each individual at the onset of adulthood and is conserved throughout the lifetime (Supplementary material A, part 3).

There is a direct, formal link between age-specific survival probabilities and lifespan (Supplementary material A, part 1). For this reason, between-individual variation in survival probability, which we study here, is fundamentally equivalent to between-individual variation in lifespan, to which evolutionary biologists are more accustomed, but to which we do not have direct access in our study populations. The between-individual heterogeneity in survival probability that we quantify in this study does give rise to viability selection a.k.a. selective disappearance: within the population, the proportion of frail individuals decreases with age. This mechanism is, however, by construct accounted for in the estimation method (see below and Supplementary material A, part 3) and therefore does not bias our estimates.
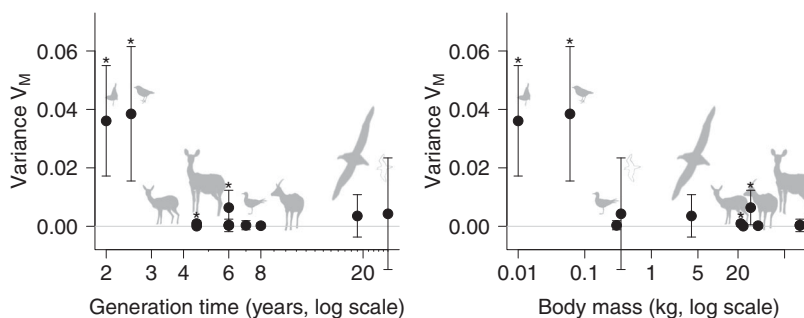
Figure 1. Between-individual variance estimate V_M plotted against generation time (left panel) and body mass (right panel). One-standard deviation confidence intervals are from a parametric bootstrap with 1000 replicates. Asterisks indicate statistically significant likelihood-ratio tests ($P < 0.05$).

Table 1. Individual heterogeneity in survival probability of our study populations.

	T (year)	e	m (kg)	V_M	V_R	s_1	s_2	π
Blue tit	2	0.500	0.01	**0.0361 (±0.0189)**	0.0097 (±0.0064)	0.29	0.83	0.31
White-throated dipper	2.5	0.400	0.06	**0.0385 (±0.0230)**	**0.0382 (±0.0043)**	0.34	0.84	0.70
Roe deer (CH)	4.5	0.222	22	**9.60×10^{-4} (±8.69×10^{-4})**	1.46×10^{-11} (±3.46×10^{-6})	0.93	1.00	0.33
Roe deer (3F)	4.5	0.222	24	7.10×10^{-5} (±2.17×10^{-4})	1.97×10^{-10} (±2.96×10^{-7})	0.97	0.97	1.00
Chamois	6	0.167	31	**0.0064 (±0.0059)**	1.37×10^{-22} (±4.72×10^{-20})	0.88	0.99	0.10
Greater Kudu (TSH)	6	0.167	170	3.04×10^{-4} (±2.14×10^{-3})	8.07×10^{-8} (±6.55×10^{-6})	0.99	0.99	0.50
Greater Kudu (PK)	6	0.167	170	4.29×10^{-4} (±9.23×10^{-4})	1.40×10^{-7} (±4.65×10^{-5})	0.95	0.95	0.50
Black-headed gull	7	0.143	0.30	3.63×10^{-4} (±1.55×10^{-3})	1.59×10^{-5} (±2.43×10^{-4})	0.84	0.86	0.69
Alpine ibex	8	0.125	40	2.30×10^{-4} (±8.79×10^{-4})	1.21×10^{-4} (±3.85×10^{-5})	0.99	0.99	0.54
Black-browed albatross	19	0.053	4	0.0036 (±0.0073)	1.47×10^{-6} (±4.25×10^{-5})	0.90	0.95	0.13
Snow petrel	25	0.040	0.35	0.0043 (±0.0191)	4.00×10^{-9} (±2.00×10^{-6})	0.98	0.99	0.76

T and m are the generation time and average female body mass in the study populations. e is the inverse of T and measures the impact of a given variation in recruitment rate on average individual fitness (Charlesworth 2000; Lebreton 2005). V_M and V_R are the estimated between-individual variances from mixture and random-effect capture-recapture models, respectively, with standard error from 1000 replicates of the parametric bootstrap between parentheses. Bold font indicates P-values < 0.05 for the likelihood ratio test of individual heterogeneity. s_1, s_1, and π are parameter estimates from the CR mixture models (annual survival at the onset of adulthood for the low survival group, for the high survival group, and proportion of individuals in the low survival group at first capture).

Another major issue which we account for in our framework is that, at the population scale, senescence-related declines in survival probability and between-individual heterogeneity can fully or partially compensate each other (Vaupel et al. 1979; Service 2000; our Supplementary material A, part 4). So, ignoring senescence or relying on information theory to decide on the occurrence of frailty and/or senescence can lead to downward-biased estimates of individual variance (Supplementary material A, part 4). We systematically accounted for senescence in our estimation framework to remove this bias. We used the logit-linear model of ageing, which is often applied to vertebrate populations (Loison et al. 1999; Bouwhuis et al. 2012).

CAPTURE-RECAPTURE MODELS TO ESTIMATE INDIVIDUAL HETEROGENEITY IN SURVIVAL

The estimation of frailty in the wild has been the topic of intense methodological innovation in recent years, all pivoting around improvements to the Cormack-Jolly-Seber capture-recapture (CR) model (Pledger et al. 2003; Royle 2008; Pradel 2009;

Gimenez and Choquet 2010). We resorted to two now well-established methods to estimate individual heterogeneity of unspecified origin in survival probability: CR models with individual random effects (Gimenez and Choquet 2010), and CR models with finite mixtures (Pledger et al. 2003). Briefly, CR random-effect models are based on the assumption that individual heterogeneity in survival follows a Gaussian distribution on the logit scale (logit-normal), being thereby analogue to widely used generalized linear-mixed models. CR mixture models are based on the assumption that individuals can be categorized into a finite number of heterogeneity classes (hidden states), that is the underlying distribution of frailty is approximated by a "histogram-like," categorical distribution. The CR mixture models that we implemented had two components: low and high survival. Both methods (i.e., mixture and random effect models) allow separating process (individual) variance from sampling variance in survival probability. In CR random-effect models, we used the delta method to rescale the logit-scale of between-individual variance onto the identity scale. We denoted the resulting metric V_R. In CR mixture models,

we used a stratified sampling formula (eq. S2 in Supplementary material A). We denoted the resulting metric V_M. The two metrics V_R and V_M measure the same quantity (individual heterogeneity in survival probability at the onset of adulthood) but use different underlying models and so are expected to differ, depending on the relative fit of the two models. The relative performance of the two methods (random and mixture models) was assessed using model deviances and further investigated with extensive simulations (Supplementary material A, part 5).

All CR models were fitted using program E-SURGE (Choquet et al. 2009). Detailed accounts of the analytical protocols we used can be found in Péron et al. (2010) for CR mixture models and Gimenez and Choquet (2010) for CR random effect models. Additional elements to reproduce our CR analyses are provided in Supplementary material A (part 3). In particular, whether or not the study populations exhibited individual heterogeneity in capture probability was assessed prior to this study in each population, and the result of that assessment was carried over in our models. The statistical significance of between-individual variance was assessed using likelihood ratio tests designed to accommodate the fact that the null hypothesis "zero variance" is at the boundary of the parameter space (variance being always positive; see Gimenez and Choquet 2010 for the technical details of the test). We also assessed whether the bounded nature of survival probability itself, that is the fact that it must vary between zero and one, acted as a constraint. Under the binomial assumption, we computed the maximum variance value for mean survival probabilities varying between zero and one. We found that observed between-individual variance was always much smaller than the maximum possible variance under the binomial assumption. Therefore, the boundary constraint was unlikely to affect the results of our interspecific comparison (Supplementary material A, part 2).

INTERSPECIFIC COMPARISON

After obtaining estimates of between-individual variance in survival at the onset of adulthood for all of our eleven study populations, we regressed species-specific variance estimates against the position of the species on the slow-fast life-history continuum, to support or infirm the canalization hypothesis. We used generation time, the weighted mean age of females when they give birth, to rank species on the continuum (Gaillard et al. 2005). Generation time presents the interesting property that it is directly linked to the elasticities of demographic traits, that is the relative impact of a proportional change in trait values on the population growth rate (Charlesworth 2000; Lebreton 2005). In addition, given the crucial role of allometric relationships in shaping the ranking of species along the slow-fast continuum of life histories, we replicated the same regression but including the average female body mass of our study populations as predictor.

To estimate the standard error of the regression parameters, we performed a parametric bootstrap by resampling 1000 times in the approximate multivariate normal distribution of the species-specific CR models, that is taking the sampling variance and covariance of the population-specific vital rates estimates into account (this was also used to compute standard error on V_M and V_R estimates). Due to the relatively small number of species, we did not consider phylogenetic inertia (Sæther et al. 2013). However, we incorporated a fixed class effect (bird/mammal) in the above regression. These analyses were performed with R.

RESULTS

As a general rule, the random-effect CR model fitted data less well than the mixture CR model (deviance in Supplementary material B and simulation in Supplementary material A, part 5). The amount of individual heterogeneity in survival at the onset of adulthood decreased with increasing generation time (Fig. 1; log–log regression slope: –2.20 ± bootstrap SE 0.90; correlation coefficient: –0.22 ± 0.16) and with increasing body mass (Fig. 1; log–log regression slope: –1.06 ± bootstrap SE 0.45; correlation coefficient: –0.21 ± 0.15). However, these relationships were mostly caused by the contrast between two short-lived, small species (blue tit and white-throated dipper; Table 1) and all the other, longer lived, heavier species. Indeed, although most of the populations we studied did not exhibit any detectable individual heterogeneity in survival, our findings actually show that individual heterogeneity in survival at the onset of adulthood does decline from fast- to slow-living species, in line with the canalization hypothesis.

DISCUSSION

Using 11 long-term time series of individual-based demographic data, we found that individual heterogeneity in survival at the onset of adulthood was low and mostly undetectable in long-lived species, whereas it was marked in short-lived species. In long-lived species, the same variation in adult survival that we found in short-lived species would have had a much greater impact on average individual fitness than in short-lived species (Pfister 1998). Our finding thus corroborates the hypothesis that traits whose variation has the greatest potential effect on fitness are the most canalized. Reduced variation in adult survival has previously been reported in large mammalian herbivores and large seabirds, but using temporal, not individual, variation (Gaillard and Yoccoz 2003; Nevoux et al. 2010). Although few studies have quantified individual heterogeneity in adult survival in the wild, those that did so far support our findings. A bird species with a generation time of two years exhibited detectable individual heterogeneity (Knape et al. 2011), whereas a bird species with a generation time of

25 years exhibited almost none (Barbraud et al. 2013). Our result is not tautological, in the sense that it is not due to the bounded space in which survival probability varies between zero and one (Supplementary material A, part 2), nor is it affected by the bias that senescence would have generated in variance estimates if not accounted for (Service 2000). Rather, and even though we cannot disentangle the relative contributions of environmental and genetic factors, our finding aligns with the recent analysis by Caswell (2014) of the between-individual variation in lifespan. Caswell (2014) found that individual heterogeneity accounted for less than 10% of the between-individual variation observed in lifespan of Humans (generation time >25 years), whereas it accounted for between 46 and 83% of the individual variation in lifespan of short-lived laboratory-bred invertebrate species with generation times shorter than a year.

In conclusion, we provide a first systematic assessment of individual heterogeneity in adult survival along the slow-fast continuum of vertebrate life histories. That only the shortest lived species with generation times shorter than three years exhibited detectable and substantial individual heterogeneity in survival at the onset of adulthood corroborates the canalization hypothesis.

DATA ARCHIVING
The doi for this article is 10.5061/dryad.bd7q6.

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Associate Editor: M. Zelditch
Handling Editor: M. Noor

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supplementary material **A**: Material and method complements.
Supplementary material **B**: Deviances and Akaike Information Criteria.