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

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

42 **KEYWORDS**

43 capture-recapture; comparative analyses; individual differences; life history evolution;
44 mixture models; random-effect models; vertebrates.

45 Life history traits such as lifespan and reproductive rates are well known to co-vary, forming
46 life history strategies (Stearns 1976). In particular, a recurring pattern in cross-species
47 comparative demography is the existence of a slow-fast continuum of life histories going from
48 long-lived, late-maturing and slow-reproducing species to short-lived, early-maturing and
49 highly fecund species (see Gaillard et al. 2016 for a recent review). The continuum is in part
50 linked to variation in body mass, temperature, and development time (Harvey and Zammuto
51 1985; Gillooly et al. 2001) but still occurs when allometric relationships linking life history
52 traits and body mass or size have been accounted for (Stearns 1983; Brown and West 2000;
53 Gaillard et al. 2016), leading to the idea that the slow-fast continuum of life histories reflects
54 constraints or opportunities afforded by particular lifestyles (Brown and Sibly 2006), in
55 relation to or independently of energy allocation trade-offs (Kirkwood and Holliday 1979).
56 Irrespective of the mechanism(s) underlying this slow-fast continuum of life histories, the
57 ranking of a species along the continuum is known to correlate with the rate at which given
58 amounts of variation in life history traits generates variation in population growth rate (Pfister
59 1998). In species close to the slow end of the continuum, called long-lived species in the
60 following, variation in adult survival gives rise to the most variation in population growth rate
61 (Caswell 2001). As population growth rate represents the average fitness of the population
62 (Fisher 1930), individuals of long-lived species are therefore expected to display risk
63 spreading and risk avoidance tactics, both part of a bet-hedging strategy aimed at maximizing
64 survival probability (Gaillard and Yoccoz 2003; Koons et al. 2009; Nevoux et al. 2010).
65 These are in turn expected to buffer phenotypes against perturbations caused by genetic
66 (Stearns and Kawecki 1994) or environmental (Gaillard and Yoccoz 2003) factors. Such a
67 buffer effect is usually called a canalization process (*sensu* Waddington 1953). We therefore
68 predict adults in populations of long-lived species to have more similar survival probabilities
69 than adults in populations of short-lived species. A few previous studies have focused on the

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70 magnitude of temporal variation in demographic rates in relation to their demographic impact
71 (following Pfister's (1998) pioneer analysis). However, we are not aware of any study linking
72 the demographic impact of traits to between-individual variance, except studies of *Drosophila*
73 *melanogaster* in the lab (Stearns and Kawecki 1994). We took advantage of available long-
74 term time series of demographic data in the wild and of modern statistical methods to test for
75 the canalization of adult survival at the individual level in the wild. Under the canalization
76 hypothesis, we expected between-individual variance in adult survival to decrease from short-
77 to long-lived species.

78 *Material and methods*

79 **DATA SETS**

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

89 **INDIVIDUAL VARIATION IN SURVIVAL PROBABILITY**

90 We aim at comparing, across species, the within-species, between-individual variance in adult
91 survival. To do that we use the concept of frailty (*sensu* Vaupel et al. 1979). Frailty
92 corresponds to the mortality risk of a given individual at a given age relative to the population
93 average. In this study we measure frailty via the variation among individuals in the intercept

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94 of the age-survival curve, i.e., the variance in the survival probability at the onset of adulthood
95 (the age at maturity when reproductive values peak). In other words, a frailty value is assigned
96 to each individual at the onset of adulthood and is conserved throughout the lifetime
97 (supplementary material A, part 3).

98 There is a direct, formal link between age-specific survival probabilities and lifespan
99 (Supplementary material A, part 1). For this reason, between-individual variation in survival
100 probability, which we study here, is fundamentally equivalent to between-individual variation
101 in lifespan, to which evolutionary biologists are more accustomed, but to which we do not
102 have direct access in our study populations. The between-individual heterogeneity in survival
103 probability that we quantify in this study does give rise to viability selection a.k.a. selective
104 disappearance: within the population, the proportion of frail individuals decreases with age.
105 This mechanism is, however, by construct accounted for in the estimation method (see below
106 and supplementary material A, part 3) and therefore does not bias our estimates.

107 Another major issue which we account for in our framework is that, at the population scale,
108 senescence-related declines in survival probability and between-individual heterogeneity can
109 fully or partially compensate each other (Vaupel et al. 1979; Service 2000; our supplementary
110 material A, part 4). So, ignoring senescence or relying on information theory to decide on the
111 occurrence of frailty and/or senescence can lead to downward-biased estimates of individual
112 variance (supplementary material A, part 4). We systematically accounted for senescence in
113 our estimation framework in order to remove this bias. We used the logit-linear model of
114 ageing, which is often applied to vertebrate populations (Loison et al. 1999; Bouwhuis et al.
115 2012).

116 CAPTURE-RECAPTURE MODELS TO ESTIMATE INDIVIDUAL HETEROGENEITY IN SURVIVAL

117 The estimation of frailty in the wild has been the topic of intense methodological innovation
118 in recent years, all pivoting around improvements to the Cormack-Jolly-Seber capture-
119 recapture (CR) model (Pledger et al. 2003; Royle 2008; Pradel 2009; Gimenez and Choquet
120 2010). We resorted to two now well-established methods to estimate individual heterogeneity
121 of unspecified origin in survival probability: CR models with individual random effects
122 (Gimenez and Choquet 2010), and CR models with finite mixtures (Pledger et al. 2003).
123 Briefly, CR random-effect models are based on the assumption that individual heterogeneity
124 in survival follows a Gaussian distribution on the logit scale (logit-normal), being thereby
125 analogue to widely used generalized linear mixed models. CR mixture models are based on
126 the assumption that individuals can be categorized into a finite number of heterogeneity
127 classes (hidden states), i.e., the underlying distribution of frailty is approximated by a
128 “histogram-like”, categorical distribution. The CR mixture models that we implemented had
129 two components: low and high survival. Both methods (i.e., mixture and random effect
130 models) allow separating process (individual) variance from sampling variance in survival
131 probability. In CR random-effect models, we used the delta method to re-scale the logit-scale
132 of between-individual variance onto the identity scale. We denoted the resulting metric V_R . In
133 CR mixture models, we used a stratified sampling formula (Eq. S2 in supplementary material
134 A). We denoted the resulting metric V_M . The two metrics V_R and V_M measure the same
135 quantity (individual heterogeneity in survival probability at the onset of adulthood) but use
136 different underlying models and so are expected to differ, depending on the relative fit of the
137 two models. The relative performance of the two methods (random and mixture models) was
138 assessed using model deviances and further investigated with extensive simulations
139 (supplementary material A, part 5).

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

156 **INTERSPECIFIC COMPARISON**

157 After obtaining estimates of between-individual variance in survival at the onset of adulthood
158 for all of our eleven study populations, we regressed species-specific variance estimates
159 against the position of the species on the slow-fast life-history continuum, in order to support
160 or infirm the canalization hypothesis. We used generation time, the weighted mean age of
161 females when they give birth, to rank species on the continuum (Gaillard et al. 2005).
162 Generation time presents the interesting property that it is directly linked to the elasticities of
163 demographic traits, i.e., the relative impact of a proportional change in trait values on the
164 population growth rate (Charlesworth 2000; Lebreton 2005). In addition, given the crucial

165 role of allometric relationships in shaping the ranking of species along the slow-fast
166 continuum of life histories, we replicated the same regression but including the average
167 female body mass of our study populations as predictor.

168 To estimate the standard error of the regression parameters, we performed a parametric
169 bootstrap by resampling 1,000 times in the approximate multivariate normal distribution of
170 the species-specific CR models, i.e., taking the sampling variance and covariance of the
171 population-specific vital rates estimates into account (this was also used to compute standard
172 error on V_M and V_R estimates). Due to the relatively small number of species, we did not
173 consider phylogenetic inertia (Sæther et al. 2013). However, we incorporated a fixed class
174 effect (bird/mammal) in the above regression. These analyses were performed with R.

175 *Results*

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

188 *Discussion*

189 Using eleven long-term time series of individual-based demographic data, we found that
190 individual heterogeneity in survival at the onset of adulthood was low and mostly
191 undetectable in long-lived species, whereas it was marked in short-lived species. In long-lived
192 species, the same variation in adult survival that we found in short-lived species would have
193 had a much greater impact on average individual fitness than in short-lived species (Pfister
194 1998). Our finding thus corroborates the hypothesis that traits whose variation has the greatest
195 potential effect on fitness are the most canalized. Reduced variation in adult survival has
196 previously been reported in large mammalian herbivores and large seabirds, but using
197 temporal, not individual, variation (Gaillard and Yoccoz 2003; Nevoux et al. 2010). Although
198 few studies have quantified individual heterogeneity in adult survival in the wild, those that
199 did so far support our findings. A bird species with a generation time of 2 years exhibited
200 detectable individual heterogeneity (Knape et al. 2011), whereas a bird species with a
201 generation time of 25 years exhibited almost none (Barbraud et al. 2013). Our result is not
202 tautological, in the sense that it is not due to the bounded space in which survival probability
203 varies between zero and one (supplementary material A, part 2), nor is it affected by the bias
204 that senescence would have generated in variance estimates if not accounted for (Service
205 2000). Rather, and even though we cannot disentangle the relative contributions of
206 environmental and genetic factors, our finding aligns with the recent analysis by Caswell
207 (2014) of the between-individual variation in lifespan. Caswell (2014) found that individual
208 heterogeneity accounted for less than 10% of the between-individual variation observed in
209 lifespan of Humans (generation time >25 years), whereas it accounted for between 46 and
210 83% of the individual variation in lifespan of short-lived laboratory-bred invertebrate species
211 with generation times shorter than a year.

212 In conclusion, we provide a first systematic assessment of individual heterogeneity in adult
213 survival along the slow-fast continuum of vertebrate life histories. That only the shortest-
214 lived species with generation times shorter than 3 years exhibited detectable and substantial
215 individual heterogeneity in survival at the onset of adulthood corroborates the canalization
216 hypothesis.

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224 *Supplementary material*

225 Supplementary material **A**: Material and method complements

226 Supplementary material **B**: Deviances and Akaike Information Criteria.

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299 *Tables*

300 **Table 1:** Individual heterogeneity in survival probability of our study populations. T and m are the generation time and average female body mass in the study
 301 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
 302 2005). V_M and V_R are the estimated between-individual variances from mixture and random-effect capture-recapture models, respectively, with standard error
 303 from 1000 replicates of the parametric bootstrap between parentheses. Bold font indicates P-values < 0.05 for the likelihood ratio test of individual
 304 heterogeneity. s_1 , s_2 , and π are parameter estimates from the CR mixture models (annual survival at the onset of adulthood for the low survival group, for the
 305 high survival group, and proportion of individuals in the low survival group at first capture).

	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	9.60E-04 ($\pm 8.69E-04$)	1.46E-11 ($\pm 3.46E-06$)	0.93	1.00	0.33
Roe deer (3F)	4.5	0.222	24	7.10E-05 ($\pm 2.17E-04$)	1.97E-10 ($\pm 2.96E-07$)	0.97	0.97	1.00
Chamois	6	0.167	31	0.0064 (± 0.0059)	1.37E-22 ($\pm 4.72E-20$)	0.88	0.99	0.10
Greater Kudu (TSH)	6	0.167	170	3.04E-04 ($\pm 2.14E-03$)	8.07E-08 ($\pm 6.55E-06$)	0.99	0.99	0.50
Greater Kudu (PK)	6	0.167	170	4.29E-04 ($\pm 9.23E-04$)	1.40E-07 ($\pm 4.65E-05$)	0.95	0.95	0.50
Black-headed gull	7	0.143	0.30	3.63E-04 ($\pm 1.55E-03$)	1.59E-05 ($\pm 2.43E-04$)	0.84	0.86	0.69
Alpine ibex	8	0.125	40	2.30E-04 ($\pm 8.79E-04$)	1.21E-04 ($\pm 3.85E-05$)	0.99	0.99	0.54
Black-browed albatross	19	0.053	4	0.0036 (± 0.0073)	1.47E-06 ($\pm 4.25E-05$)	0.90	0.95	0.13
Snow petrel	25	0.040	0.35	0.0043 (± 0.0191)	4.00E-09 ($\pm 2.00E-06$)	0.98	0.99	0.76

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306

307 *Figure legends*

308 **Figure 1:** Between-individual variance estimate V_M plotted against generation time (left
309 panel) and body mass (right panel). One-standard deviation confidence intervals are from a
310 parametric bootstrap with 1000 replicates. Asterisks indicate statistically significant
311 likelihood-ratio tests ($P < 0.05$).

