

# 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.



**KEY WORDS:** Capture-recapture, comparative analyses, individual differences, life-history evolution, mixture models, random-effect models, vertebrates.

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

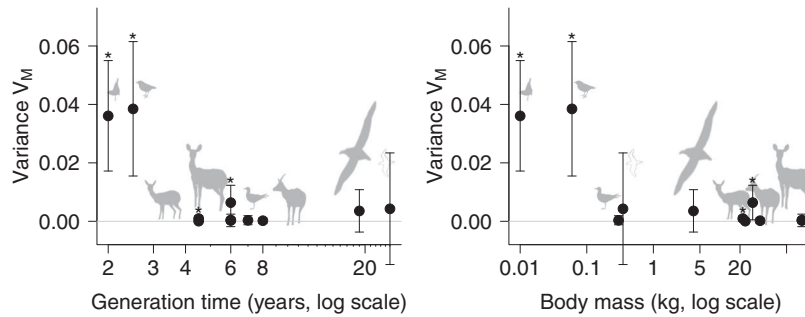
### DATASETS

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)	$V_M$	$V_R$	$s_1$	$s_2$	$\pi$
Blue tit	2	0.500	0.01	<b>0.0361 (<math>\pm 0.0189</math>)</b>	0.0097 ( $\pm 0.0064$ )	0.29	0.83	0.31
White-throated dipper	2.5	0.400	0.06	<b>0.0385 (<math>\pm 0.0230</math>)</b>	<b>0.0382 (<math>\pm 0.0043</math>)</b>	0.34	0.84	0.70
Roe deer (CH)	4.5	0.222	22	<b><math>9.60 \times 10^{-4}</math> (<math>\pm 8.69 \times 10^{-4}</math>)</b>	$1.46 \times 10^{-11}$ ( $\pm 3.46 \times 10^{-6}$ )	0.93	1.00	0.33
Roe deer (3F)	4.5	0.222	24	$7.10 \times 10^{-5}$ ( $\pm 2.17 \times 10^{-4}$ )	$1.97 \times 10^{-10}$ ( $\pm 2.96 \times 10^{-7}$ )	0.97	0.97	1.00
Chamois	6	0.167	31	<b>0.0064 (<math>\pm 0.0059</math>)</b>	$1.37 \times 10^{-22}$ ( $\pm 4.72 \times 10^{-20}$ )	0.88	0.99	0.10
Greater Kudu (TSH)	6	0.167	170	$3.04 \times 10^{-4}$ ( $\pm 2.14 \times 10^{-3}$ )	$8.07 \times 10^{-8}$ ( $\pm 6.55 \times 10^{-6}$ )	0.99	0.99	0.50
Greater Kudu (PK)	6	0.167	170	$4.29 \times 10^{-4}$ ( $\pm 9.23 \times 10^{-4}$ )	$1.40 \times 10^{-7}$ ( $\pm 4.65 \times 10^{-5}$ )	0.95	0.95	0.50
Black-headed gull	7	0.143	0.30	$3.63 \times 10^{-4}$ ( $\pm 1.55 \times 10^{-3}$ )	$1.59 \times 10^{-5}$ ( $\pm 2.43 \times 10^{-4}$ )	0.84	0.86	0.69
Alpine ibex	8	0.125	40	$2.30 \times 10^{-4}$ ( $\pm 8.79 \times 10^{-4}$ )	$1.21 \times 10^{-4}$ ( $\pm 3.85 \times 10^{-5}$ )	0.99	0.99	0.54
Black-browed albatross	19	0.053	4	0.0036 ( $\pm 0.0073$ )	$1.47 \times 10^{-6}$ ( $\pm 4.25 \times 10^{-5}$ )	0.90	0.95	0.13
Snow petrel	25	0.040	0.35	0.0043 ( $\pm 0.0191$ )	$4.00 \times 10^{-9}$ ( $\pm 2.00 \times 10^{-6}$ )	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.  $s_1$ ,  $s_2$ , and  $\pi$  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:  $-2.20 \pm$  bootstrap SE 0.90; correlation coefficient:  $-0.22 \pm 0.16$ ) and with increasing body mass (Fig. 1; log-log regression slope:  $-1.06 \pm$  bootstrap SE 0.45; correlation coefficient:  $-0.21 \pm 0.15$ ). 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.

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#### DATA ARCHIVING

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*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.



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## Appendix A: Material and Methods complements

### Part 1: Analytical demonstration of the direct link between age-specific survival probability and lifespan

That there is a link between age-specific survival rates and lifespan is intuitive, but the actual shape of that link is not trivial and has been the topic of a rich literature (Vaupel 1986; Olcay 1995; Finkelstein 2002).

The following material is not new but has to our knowledge rarely if ever been presented in a step by step way for a non-demographer audience, despite its importance for evolutionary biology.

The framework is built upon the Gompertz model of ageing, which is the reference in human demography. This model assumes an exponential rate of ageing:  $x$  years after the onset of senescence, the mortality hazard rate is modeled as:

$$(1) \quad \mu(x) = a_0 e^{bx}$$

The probability for an individual to reach age  $x$ , usually called the survival function, is defined as:

$$(2) \quad l(x) = \exp\left(-\int_0^x \mu(v) dv\right)$$

Importantly, the survival function is different from age-specific survival probability, which is, with  $x$  in years:

$$(2bis) \quad s(x) = \frac{l(x+1)}{l(x)}$$

Life expectancy at the onset of senescence is in turn defined as:

$$(3) \quad e(0) = \int_0^{\infty} l(v) dv$$

Combining (1) and (2) we get:

$$(4) \quad l(v) = \exp\left(\frac{a_0}{b}\right) \exp\left(-\frac{a_0}{b} \exp(-bv)\right)$$

Making the variable change  $u = \frac{a_0}{b} \exp(-bv)$  and substituting (4) into (3), we get:

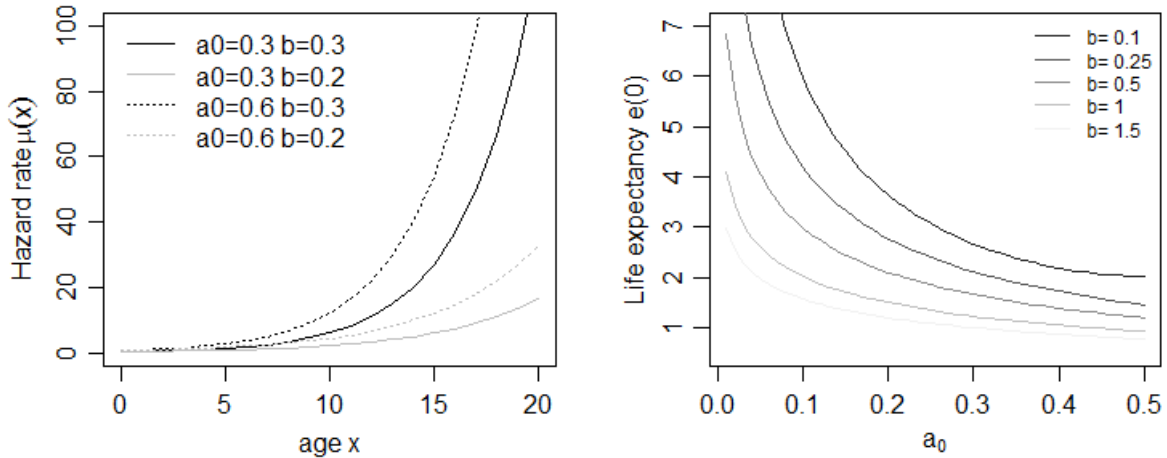
$$(5) \quad e(0) = \exp\left(\frac{a_0}{b}\right) \frac{1}{b} \int_{\frac{a_0}{b}}^{\infty} \frac{\exp(-u)}{u} du$$

The integral in (5) is convertible into a computable series expansion (Abramowitz and Stegun. 1965, p.229)

$$(6) \quad E_1(z) = \int_z^{\infty} \frac{\exp(-u)}{u} du = -\gamma - \ln(z) - \sum_{n=1}^{\infty} \frac{(-z)^n}{n \cdot n!}$$

where  $\gamma \approx 0.577$  is Euler's constant (from number theory).

It derives from (5) that life expectancy at the onset of senescence decreases with both baseline mortality and the rate of senescence.



In our study the Gompertz model is replaced by the logit-linear model which is more convenient in capture-recapture analyses. This model is defined in discrete time ( $x = 1, 2, 3 \dots$ ) by the following equation describing the annual survival probability:

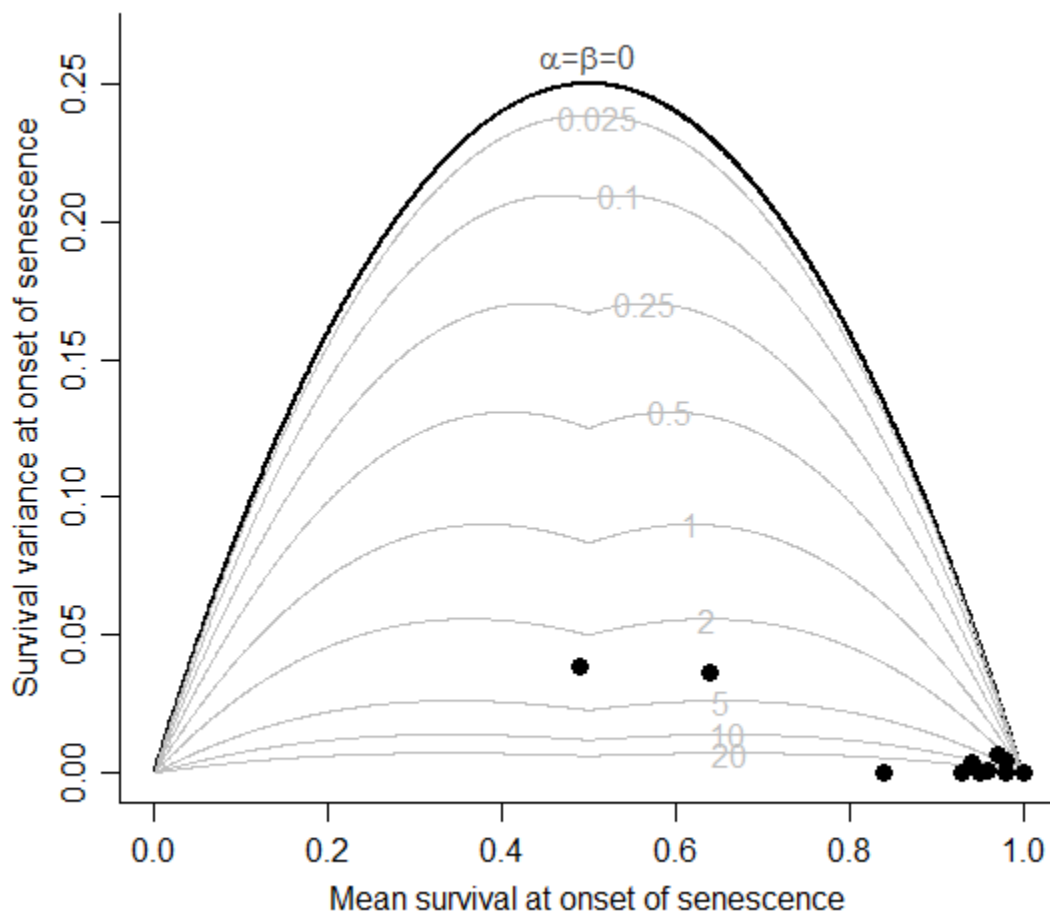
$$(7) \quad s(x) = \frac{l(x+1)}{l(x)} = \frac{1}{1 + \exp(-(\alpha + \beta x))}$$

The logit-linear model is a close approximation of the Gompertz model, meaning that for most sets of values  $(a_0; b)$  there is a set  $(\alpha; \beta)$  that yields a reasonably close fit of (7) to the Gompertz curve. In other words,  $1 - \alpha$  and  $-\beta$  are functional equivalent to the mathematically better-characterized  $a_0$  and  $b$ .



## Part 2: On the variance of a probability

Probabilities vary between 0 and 1, and this mechanistically creates a cap to what their variance can be. The closer to boundaries 0 or 1, the less variable a probability can be. In **Fig. A2** below, we represent the maximum possible variance (black line), as well as the maximum variance for a Beta distribution with various  $\alpha$  parameters, as a function of the distribution mean value. The black circles indicate the estimate for our 11 study population, showing that all but 1 (Alpine ibex, which has a survival probability of one at the onset of senescence) are well below the maximum possible variance. This confirms that the canalisation process we report is not due to the mechanistic link between average survival probability and the maximum variance in survival probability.



### Part 3: Datasets and analysis details

#### Dataset presentation

**Table A1:** Information about the long-term datasets used in this study. “Spl. size” corresponds to the number of known-age adults that were monitored since their first occurrence as mature adults in the study area. “Max. age” is the maximum age recorded for the species in its study area. “Gen. time” is the mean age of females when giving birth (computed using age at first reproduction and baseline survival rate). “Ref.” is the article(s) in which data collection is described.

Abbr.			Study area	Spl. size	Max age	Gen. time	Ref.
<b>Mammals (ungulates)</b>							
<b>GK-TSH</b>	Greater Kudu	<i>Tragelaphus strepsiceros</i>	Tshokwane, Kruger N.P., South Africa	118	15	6	(Owen-smith 1990)
<b>GK- PKP</b>	Greater Kudu	<i>Tragelaphus strepsiceros</i>	Pretorius Kop, Kruger N.P., South Africa	188	15	6	
<b>RD-CH</b>	Roe Deer	<i>Capreolus capreolus</i>	Chizé, France	1200	16	4.5	(Gaillard et al. 1993)
<b>RD-3F</b>	Roe Deer	<i>Capreolus capreolus</i>	Trois-Fontaine, France	1402	17	4.5	
<b>CH</b>	Chamois	<i>Rupicapra rupicapra</i>	Bauges, France	313	22	6	(Loison et al. 1999)
<b>AI</b>	Alpine ibex	<i>Capra ibex</i>	Belledonne, France	432	20	8	(Toïgo et al. 2007)
<b>Birds</b>							
<b>BT</b>	Blue Tit	<i>Cyanistes caeruleus</i>	Pirio, Corsica	1225	9	2	(Blondel et al. 2006)
<b>WTD</b>	White-throated Dipper	<i>Cinclus cinclus</i>	Northeastern France	1047	9	2.5	(Marzolin et al. 2011)
<b>BHG</b>	Black-headed Gull	<i>Chroicocephalus ridibundus</i>	La Ronze pond, France	1556	30	7	(Lebreton 1987; Péron et al. 2010)
<b>BBA</b>	Black-browed Albatross	<i>Thalassarche melanophrys</i>	Kerguelen Island	476	40	19	(Nevoux et al. 2010)
<b>SP</b>	Snow Petrel	<i>Pagodroma nivea</i>	Terre Adélie, Antarctica	188	47	25	(Barbraud et al. 2000)

## ***Data selection***

We restricted our analyses to known-age individuals that were either marked soon after birth, or for which age at marking could be reliably estimated using plumage features or horn growth annuli. For large mammals, white-throated dipper, and blue tit, we only used data from the females that are readily separated from male from phenotype. In others (black-headed gull, snow petrel, and black-browed albatross), we used all available individual data. This could have led to increased individual heterogeneity in survival probability, but 1) in weakly dimorphic species (black-headed gull, black-browed albatross) the difference in survival probability among sexes is expected to be low and 2) for snow petrel, earlier studies found no differences in survival between sexes (Barbraud et al. 2000). Lastly, although individuals of many species were marked at, or close to, birth, the dataset was restricted to include only the data from individuals of breeding age. We did this because we wished to standardize our datasets and methodology across species, and immature black-browed albatrosses, snow petrels, and black-headed gulls were not available for recapture.

## ***Model of age-specific survival***

Age-specific survival probability  $\varphi_a$  was modelled using the logit-linear model, which provides a close approximation to the Gompertz model often used to model actuarial senescence in vertebrate populations (Loison et al. 1999; Marzolin et al. 2011; Bouwhuis et al. 2012):

$$\log\left(\frac{\varphi_a}{1-\varphi_a}\right) = \text{logit}(\varphi_a) = \alpha + \beta \cdot a \quad \text{Eq. S1}$$

where  $\alpha$  is the intercept and  $\beta$  the slope of the age effect on the logit scale. We used  $\alpha$  as our metric for baseline mortality and  $\beta$  as our metric for the rate of actuarial senescence (note that  $\beta$  is negative when senescence occurs). A particular methodological point is that the age at first occurrence in the dataset varied among individuals within a species. We corrected for this using the methods described in Appendix 1 in (Péron et al. 2010). The statistical significance of individual heterogeneity and senescence was, however, assessed using the standard errors of their respective estimates in one-sided z-tests (rather than Akaike Information Criterion, see below). We used program E-SURGE (Choquet et al. 2009a) to build and fit CR models to the data.

## ***Computation of between-individual variance from CR mixture model parameters***

In CR mixture models, between-individual variance was estimated as a derived quantity by adapting the between-sample variance formula of Cochran (p.68) (Cochran 1977):

$$V_M = \frac{1}{C} \sum_{c=1}^C \pi_c (\varphi_c - \bar{\varphi})^2 \quad \text{Eq. S2}$$

where  $C$  is the number of heterogeneity classes (here  $C = 2$ ),  $\pi_c$  is the proportion of individuals in class  $c$  at their first capture,  $\varphi_c$  is the survival of individuals in class  $c$  at the median age at first reproduction and  $\bar{\varphi}$  is the average survival at the median age at first reproduction across heterogeneity classes (weighted by  $\pi_c$ ).

For the chamois and white-throated dipper, the selected model included age- and time-effects on  $\pi$ , so the variance estimate corresponded to the average over years for individuals at the median age at first reproduction. For all other datasets the selected model had constant  $\pi$ .

### *Other modelling choices*

In addition to the above, some further modelling choices had to be made to reflect both the previous knowledge acquired on each species and field procedures, as well as to reduce the number of models that we fit to the data. First, based on previous CR analyses, authors contributing datasets provided an appropriate model structure for recapture probabilities and for survival during the first years of adult life. Then, we tested the goodness-of-fit (GOF) of the time-dependent CR model (Cormack-Jolly-Seber model). Lack of fit could originate from transience (i.e., excess of individuals that were never seen again after their first encounter; (Pradel et al. 1997)) or trap-dependence (i.e., excess or lack of individuals seen at time  $t$ ; (Pradel 1993)). Depending on the results pertaining to each GOF test, the starting model included a trap-dependence effect, a transience effect, and/or individual heterogeneity in detection probability. The latter was considered when both sources of lack-of-fit were detected and field experience suggested this was occurring (e.g., (Péron et al. 2010)). All GOF tests were conducted using U-CARE (Choquet et al. 2009b).

We then went on selecting the structure of the  $\pi$ -parameters (proportion of the different heterogeneity classes at first capture). Originally, when Pledger et al. (Pledger et al. 2003) introduced mixture models to reduce the variance-bias trade-off in the estimation of a parameter of biological interest,  $\pi$ -parameters were interpreted as “nuisance parameters”. However, under our working hypothesis that the frequency of high survival individuals increases with age within a cohort, we cannot ignore the biological meaning of the  $\pi$ -parameters:  $\pi$  is expected to vary with age as viability selection operates within each cohort. In addition, cohort effects (i.e., long-lasting effects of conditions encountered during early life; (Albon et al. 1987)) could lead  $\pi$  to vary among years. We thus fitted models including either age- or time-dependence of the frequency distribution of individual heterogeneity at the first capture. The preferred structure for  $\pi$  was selected using AIC (corrected for small sample size). For each dataset we present results from the model with no heterogeneity, from the mixture model with preferred structure for  $\pi$ , and for the random effect model.

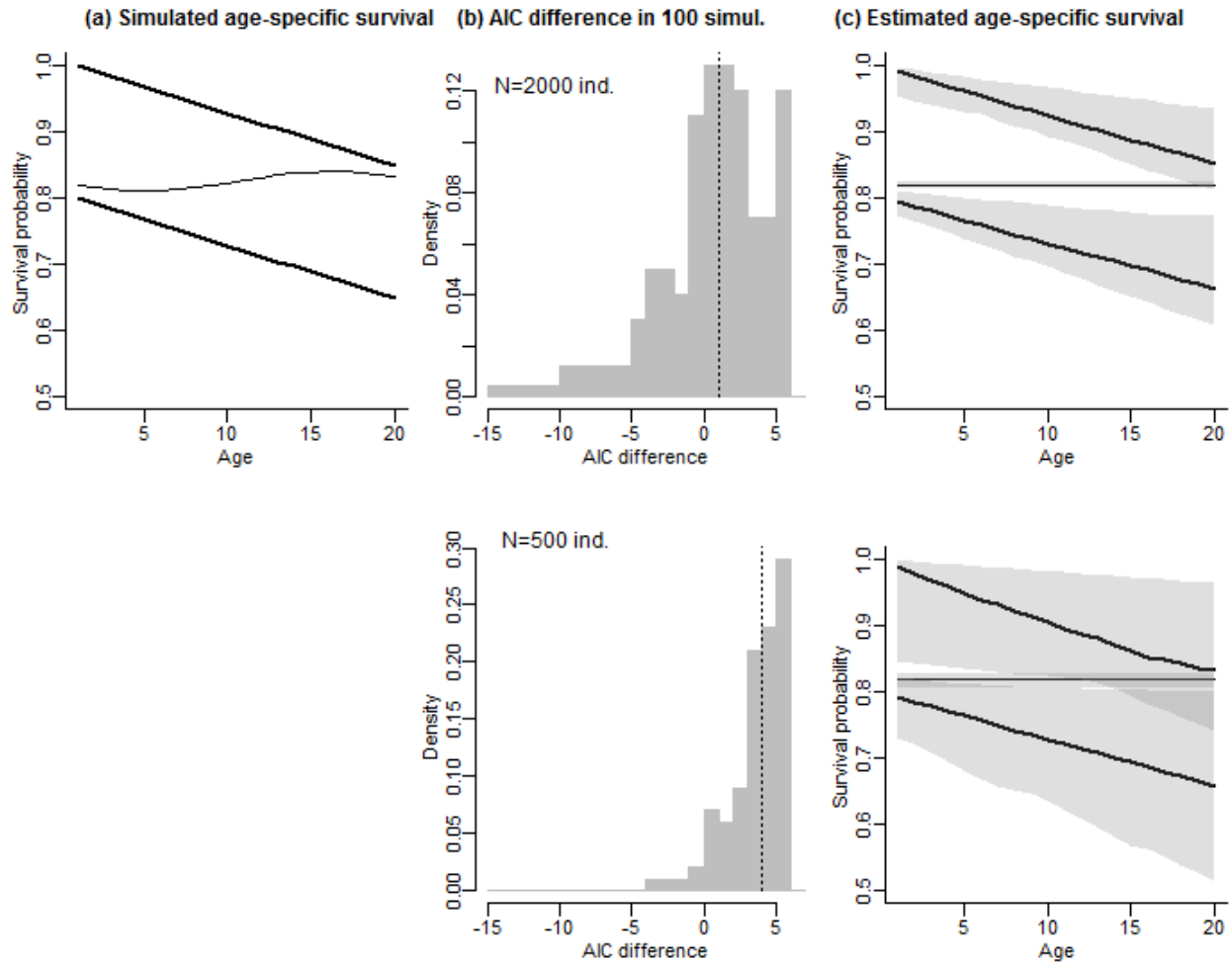
## **Part 4: Shortcomings of using the information theoretic approach to detect class heterogeneity in survival in presence of senescence**

It has been repeatedly shown that individual heterogeneity and age-related declines in survival probability (senescence) interplay at the population level (Vaupel et al. 1979; Service 2000), so that neglecting one of these biological processes when assessing the other can lead to major biases. As a preliminary analysis, we therefore performed a simulation study comparing the deviance of models with senescence only, heterogeneity only, both, or none of these features.

We ran simulations with a linear decline in survival probability within each of two classes of individuals (Fig. A3a below). Eighty per cent of individuals started with a survival probability of one declining linearly to 0.85 at age 20. The remaining 20% started with a survival probability of 0.8 declining to 0.65 at age 20. Under these conditions, a sample size of 2000 individuals guaranteed a 50% chance only that the correct model was selected; for a sample size of 500 individuals, which is still larger than most real life datasets, the wrong model was almost always selected. In other words, when the individual-level decline in survival probability with age is compensated at the population level by heterogeneity in baseline survival, then the AIC of the model with neither heterogeneity nor senescence will almost always be equivalent or lower than that of the model with both heterogeneity and senescence (Fig. A3b).

In conclusion, we recommend to a priori include individual heterogeneity in survival probability in all attempts to estimate individual heterogeneity in survival or survival senescence or both, rather than relying on AIC to decide on the presence of heterogeneity (Vaida and Blanchard 2005). The use of AIC to select other features than heterogeneity or senescence is still supported and was used as usual in this study.

We also noted that in c.10% of simulations, even the model with heterogeneity failed to capture the correct values of between-individual variance and rate of senescence. In these cases, the model converged towards a solution close to the model with neither heterogeneity nor senescence (i.e., with a rate of senescence close to zero and almost no difference among heterogeneity classes). This illustrates the challenge of making inference about senescence in small datasets where few individuals reach senescent ages. This is reflected in the 95% confidence intervals of Fig. A3c.



**Fig. A3:** (a) Simulated scenario with 80% high and 20% low baseline survival (bold lines), and senescence. The thin line represents the average survival probability at the population level as a function of age. (b) AIC difference between the model with neither heterogeneity nor senescence and the model including both. Positive values indicate replicates where the wrong model (no heterogeneity and no senescence) would have been selected. The dotted line represents the median AIC difference. (c) Median and 95% confidence interval (shaded areas) of the estimated age-specific survival from 100 replicates. Bold line: estimates from the model matching the way data were simulated. Thin lines: estimates from the model with neither heterogeneity nor senescence. Upper panels: scenario with 2000 individuals sampled. Lower panels: scenario with 500 individuals sampled.

## Part 5: Shortcomings of using the logit normal random effect model

We aim here to challenge the logit-normal random effect model by fitting it to a dataset with a strongly multimodal distribution of individual differences.

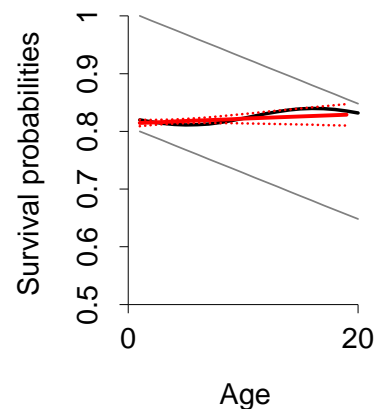
We fitted a random effect model to the same simulated datasets as above, which had been simulated using a mixture model (two classes of individuals with low or high survival). Random effect models were fitted using the Gauss-Hermite quadrature with 10 nodes, and the linear effect of age on survival was modelled on the logit scale (while when simulating data, the decrease in survival with age was linear on the natural scale).

The estimated slope of senescence and between-individual variance estimated from the random effect model were consistently near zero (average estimate slope on the logit scale:  $-0.006$ ; average estimated variance on the logit scale:  $2.7E-0.5$ ).

This indicated that the random effect model failed to detect senescence and heterogeneity, although the model used to simulate the data had both features.

Fig. A4 further illustrates the fact that under the scenario we simulated, the random effect model only captured the population-average survival probability, but not the underlying heterogeneity and ageing processes.

**Fig. A4:** Actual values of age-specific survival probability (grey lines: in the two mixture levels; black line: population average) and values estimated from the random effect model with logit-linear effect of survival (red line; dotted lines are the one standard deviation confidence interval over 100 replicates).





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***Evidence of reduced individual heterogeneity in adult survival of long-lived species*** by Guillaume Péron, Jean-Michel Gaillard, Christophe Barbraud, Christophe Bonenfant, Anne Charmantier, Rémi Choquet, Tim Coulson, Vladimir Grosbois, Anne Loison, Gilbert Marzolin, Norman Owen-Smith, Déborah Pardo, Floriane Plard, Roger Pradel, Carole Toïgo, Olivier Gimenez

## Appendix B

### Model selection in each of the study populations

H denotes the presence of survival heterogeneity,  $a_1$  denotes the logit-linear effect of age,  $a_c$  denotes the full age effect (one parameter per age-class), t denotes the effect of year, + and \* denotes additive and interacting effects, and a dot denotes that survival is independent of age. np denotes the number of model parameters, Dev is the deviance, pi denotes the  $\pi$ -parameters (the proportion of each heterogeneity class at first capture), and  $\Delta AICc$  is the difference in information criterion between the focal and preferred model.

The difference in the number of model parameters depends on the number of age-classes (duration of the study), how variable was age at first entry in the dataset, the existence of transience, the parameterization of detection probability (time-effect, trap-dependence), and the age at the onset of senescence.

In the particular case of the BHG dataset we also incorporated individual heterogeneity in detection and emigration probability because heterogeneity in these parameters had been shown to prevent the detection of senescence.

#### Kudu TSH

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta AICc$
1	.		14	1348.89	1377.79	20.51
2	$a_c$		28	1308.56	1366.59	9.31
<b>3</b>	<b><math>a_1</math></b>		<b>15</b>	<b>1326.69</b>	<b>1357.28</b>	<b>0</b>
4	H	.	14	1352.9	1381.42	24.14
5	H+ $a_c$	.	30	1299.97	1362.3	5.02

#### Black-headed gull

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta AICc$
<b>1</b>	.		<b>36</b>	<b>7799.44</b>	<b>7871.44</b>	<b>0</b>
2	$a_c$		63	7785.36	7911.36	39.92
3	$a_1$		44	7795.47	7883.47	12.03
4	H	.	45	7790.32	7880.32	8.88
5	H+ $a_c$	.	67	7764.40	7898.40	26.96

6	H+a <sub>l</sub>	.	17	1326.69	1361.45	4.17	<b>6</b>	<b>H+a<sub>l</sub></b>	.	<b>47</b>	<b>7781.31</b>	<b>7875.31</b>	<b>3.87</b>
7	H+a <sub>l</sub>	a <sub>c</sub>	25	1319.10	1370.72	13.44	7	H+a <sub>l</sub>	a <sub>c</sub>	83	7753.60	7926.09	54.65
8	H+a <sub>l</sub>	a <sub>c</sub> +t	34	1307.62	1378.61	21.33	8	H+a <sub>l</sub>	a <sub>c</sub> +t	13 2	7656.30	7937.01	65.57
9	H+a <sub>l</sub>	T	26	1309.70	1363.46	6.18	9	H+a <sub>l</sub>	t	93	7744.08	7938.25	66.81
10	R+a <sub>l</sub>		16	1326.69	1359.36	2.08	10	R+a <sub>l</sub>		42	7797.90	7881.90	10.46

### Kudu PKP

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		14	2014.92	2043.26	26.87
2	a <sub>c</sub>		28	1964.75	2022.08	5.69
<b>3</b>	<b>a<sub>l</sub></b>		<b>15</b>	<b>1986.00</b>	<b>2016.39</b>	<b>0</b>
4	H	.	16	2014.92	2048.34	31.95
5	H+a <sub>c</sub>	.	30	1964.75	2026.27	9.88
6	H+a <sub>l</sub>	.	17	1986.00	2020.50	4.11
7	H+a <sub>l</sub>	a <sub>c</sub>	25	1969.33	2020.39	4.00
8	H+a <sub>l</sub>	a <sub>c</sub> +t	34	1954.37	2024.32	7.93
9	H+a <sub>l</sub>	T	26	1977.65	2030.79	14.40
10	R+a <sub>l</sub>		16	1986.00	2018.44	2.05

### Roe deer Chizé

### Blue tit

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		33	1836.89	1902.89	10.70
2	a <sub>c</sub>		67	1818.92	1952.92	60.73
3	a <sub>l</sub>		34	1826.93	1894.93	2.73
4	H	.	5	1899.11	1909.11	16.92
5	H+a <sub>c</sub>	.	69	1816.54	1954.54	62.34
<b>6</b>	<b>H+a<sub>l</sub></b>	.	<b>36</b>	<b>1820.20</b>	<b>1892.20</b>	<b>0</b>
7	H+a <sub>l</sub>	a <sub>c</sub>	37	1820.53	1896.96	4.76
8	H+a <sub>l</sub>	a <sub>c</sub> +t	64	1773.05	1908.41	16.22
9	H+a <sub>l</sub>	t	60	1777.30	1903.75	11.55
10	R+a <sub>l</sub>		35	1826.93	1896.93	4.73

### Black-browed albatross

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		58	4255.59	4375.64	103.87
2	a <sub>c</sub>		89	4123.18	4310.83	39.07
<b>3</b>	<b>a<sub>l</sub></b>		61	4149.26	4275.74	3.98
4	H	.	60	4255.59	4379.93	108.16
5	H+a <sub>c</sub>	.	91	4117.37	4309.48	37.71
<b>6</b>	<b>H+a<sub>l</sub></b>	.	<b>63</b>	<b>4140.98</b>	<b>4271.77</b>	<b>0</b>
7	H+a <sub>l</sub>	a <sub>c</sub>	65	4149.25	4284.35	12.59
8	H+a <sub>l</sub>	a <sub>c</sub> +t	96	4083.11	4286.38	14.62
9	H+a <sub>l</sub>	t	95	4085.49	4286.53	14.76
10	R+a <sub>l</sub>		62	4149.26	4277.89	6.13

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
<b>1</b>	.		<b>30</b>	<b>3710.16</b>	<b>3771.03</b>	<b>1.81</b>
2	a <sub>c</sub>		66	3673.94	3810.17	40.95
<b>3</b>	<b>a<sub>l</sub></b>		<b>31</b>	<b>3706.29</b>	<b>3769.22</b>	<b>0</b>
4	H	.	32	3710.16	3775.15	5.93
5	H+a <sub>c</sub>	.	68	3673.96	3814.45	45.23
6	H+a <sub>l</sub>	.	33	3706.29	3773.34	4.12
7	H+a <sub>l</sub>	a <sub>c</sub>	43	3690.49	3778.27	9.06
8	H+a <sub>l</sub>	a <sub>c</sub> +t	67	3637.68	3776.04	6.82
9	H+a <sub>l</sub>	t	57	3669.23	3786.38	17.16
10	R+a <sub>l</sub>		32	3709.17	3774.16	4.95

### Roe deer Trois-Fontaines

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		60	4513.71	4637.86	195.30
2	a <sub>c</sub>		86	4293.41	4480.65	38.08
<b>3</b>	<b>a<sub>l</sub></b>		<b>63</b>	<b>4311.98</b>	<b>4442.56</b>	<b>0</b>
4	H	.	62	4513.71	4642.15	199.58

### Snow petrel

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
<b>1</b>	.		<b>39</b>	<b>1729.15</b>	<b>1810.76</b>	<b>1.01</b>
2	a <sub>c</sub>		74	1724.94	1886.30	76.55
<b>3</b>	<b>a<sub>l</sub></b>		<b>40</b>	<b>1725.96</b>	<b>1809.75</b>	<b>0</b>
4	H	.	40	1729.09	1812.88	3.13

5	H+a <sub>c</sub>	.	10 <sub>9</sub>	4285.66	4517.65	75.09
6	H+a <sub>l</sub>	.	65	4311.98	4446.86	4.30
7	H+a <sub>l</sub>	a <sub>c</sub>	66	4311.88	4448.91	6.35
8	H+a <sub>l</sub>	a <sub>c</sub> +t	99	4243.56	4453.05	10.48
9	H+a <sub>l</sub>	t	98	4248.84	4456.09	13.53
10	R+a <sub>l</sub>		64	4311.98	4444.71	2.15

5	H+a <sub>c</sub>	.	76	1694.68	1860.80	51.05
6	H+a <sub>l</sub>	.	42	1725.88	1812.87	3.12
7	H+a <sub>l</sub>	a <sub>c</sub>	52	1776.01	1886.47	76.72
8	H+a <sub>l</sub>	a <sub>c</sub> +t	79	1709.37	1882.68	72.93
9	H+a <sub>l</sub>	t	66	1740.13	1882.68	72.93
10	R+a <sub>l</sub>		41	1725.96	1811.89	2.14

### Alpine ibex

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		24	1125.58	1175.05	31.21
2	a <sub>c</sub>		46	1062.74	1160.21	16.36
<b>3</b>	<b>a<sub>l</sub></b>		<b>26</b>	<b>1090.12</b>	<b>1143.85</b>	<b>0</b>
4	H	.	27	1121.68	1177.55	33.70
5	H+a <sub>c</sub>	.	61	1062.74	1194.49	50.64
6	H+a <sub>l</sub>	.	28	1090.12	1148.12	4.28
7	H+a <sub>l</sub>	a <sub>c</sub>	40	1067.95	1152.06	8.21
8	H+a <sub>l</sub>	a <sub>c</sub> +t	60	1048.46	1177.88	34.03
9	H+a <sub>l</sub>	t	48	1064.52	1166.48	22.64
10	R+a <sub>l</sub>		27	1090.12	1145.99	2.14

### Chamois

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		7	2368.99	2382.99	57.16
2	a <sub>c</sub>		30	2301.31	2362.81	36.98
3	a <sub>l</sub>		10	2315.21	2335.38	9.55
4	H	.	10	2359.84	2380.01	54.18
5	H+a <sub>c</sub>	.	33	2300.29	2368.10	42.27
6	H+a <sub>l</sub>	.	12	2311.91	2336.16	10.33
7	H+a <sub>l</sub>	a <sub>c</sub>	19	2308.15	2346.75	20.92
<b>8</b>	<b>H+a<sub>l</sub></b>	<b>a<sub>c</sub>+t</b>	<b>36</b>	<b>2251.67</b>	<b>2325.83</b>	<b>0</b>
<b>9</b>	<b>H+a<sub>l</sub></b>	<b>t</b>	<b>29</b>	<b>2268.34</b>	<b>2327.74</b>	<b>1.91</b>
10	R+a <sub>l</sub>		11	2314.33	2336.54	10.71

### White-throated dipper

Model #	Sub-model for survival	Sub-model for $\pi$	np	Dev	AICc	$\Delta$ AICc
1	.		33	3114.57	3182.53	26.71
2	$a_c$		42	3078.02	3165.21	9.39
3	$a_1$		34	3090.41	3160.51	4.69
4	H	.	35	3101.28	3173.49	17.67
5	H+ $a_c$	.	45	3075.15	3168.81	12.99
<b>6</b>	<b>H+<math>a_1</math></b>	.	<b>36</b>	<b>3081.4</b>	<b>3155.82</b>	<b>0</b>
<b>7</b>	<b>H+<math>a_1</math></b>	<b><math>a_c</math></b>	<b>38</b>	<b>3077.7</b>	<b>3156.38</b>	<b>0.56</b>
8	H+ $a_1$	$a_c+t$	64	3037.74	3183.23	27.41
9	H+ $a_1$	t	69	3040.46	3187.19	31.37
10	R+ $a_1$		36	3087.81	3162.14	6.32