

Distributions of LRS in varying environments

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Abstract

The lifetime reproductive success (LRS) of individuals is affected by random events such as death, realized growth, or realized reproduction, and the outcomes of these events can differ even when individuals have identical probabilities. Another source of randomness arises when these probabilities also change over time in variable environments. For structured populations in stochastic environments, we extend our recent method to determine how birth environment and birth stage determine the random distribution of the LRS. Our results provide a null model that quantifies effects on LRS of just the birth size or stage. Using Roe deer *Capreolus capreolus* as a case study, we show that the effect of an individual's birth environment on LRS varies with the frequency of environments and their temporal autocorrelation, and that lifetime performance is affected by changes in the pattern of environmental states expected as a result of climate change.

1 Introduction

Individual lifetime reproductive success (LRS) is often measured in vertebrate populations monitored in the wild (see Clutton-Brock (1988) and Newton (1989) for a compilation of case studies). LRS is a commonly used surrogate measure of fitness in short- and long-lived species (Brommer et al. 2004), and is most appropriate when comparing the performance of individ-

47 uals within a cohort. More generally, LRS is simply a component of fitness
 48 since it does not include the timing of reproduction. Previous work has estab-
 49 lished that individual LRS is significantly affected by random events governed
 50 by probabilities that an individual will change stage/size, make a certain
 51 number of offspring, or die (Tuljapurkar et al. 2009; Caswell 2011; Steiner
 52 and Tuljapurkar 2012; Snyder and Ellner 2018; van Daalen and Caswell 2017;
 53 Tuljapurkar et al. 2020). As a result, the analysis of the distribution of LRS
 54 has become essential to identify whether or not it is necessary to search for
 55 intrinsic trait differences among individuals. Many studies have reported
 56 that several early-life conditions or traits positively influence individual fit-
 57 ness (Lindström 1999). Individuals born early in the season (Plard et al.
 58 2015a), heavy (Kruuk et al. 1999), at low density (Nussey et al. 2007) or
 59 growing fast early in life (Vasilieva and Tchabovsky 2020) produce on aver-
 60 age more offspring throughout their lifespan than individuals with contrary
 61 traits. However, we do not yet know whether these carry-over effects (sensu
 62 Harrison et al. (2011)) are caused by heritable maternal effects and generate
 63 adaptive changes in traits (e.g. Lea and Rosebaum (2020)) or simply cor-
 64 respond to silver spoon effects (sensu Grafen (1988)) due to environmental
 65 conditions at birth. To date, we lack a model that quantifies the long-lasting
 66 influence of early-life conditions on LRS to assess whether additional effects
 67 of maternal traits are detectable. In such a model, birth conditions do not
 68 affect the subsequent single-period transition probabilities of environments
 69 or the corresponding single-period probabilities of events such as survival or

70 reproduction. In this non-adaptive scenario, birth conditions simply fix the
 71 start of all possible lifetime sequences of events, and in this way do affect the
 72 distribution of the LRS. To quantify this effect, we developed the methods
 73 presented here.

74 We assume that individuals are observed at discrete times t (such as an
 75 annual census), and that each individual is in a discrete phenotypic stage, say
 76 j (which may be a combination, e.g., of age, developmental stage, and size).
 77 In the time interval from t to $t + 1$, the environment is also observed to be
 78 in a discrete state, say β (which may also be a combination, e.g, of tempera-
 79 ture and precipitation). Between times t and $(t + 1)$, an individual may die,
 80 or transition to another (or the same) phenotypic stage, with probabilities
 81 that depend on the starting environment β and phenotype j . And over the
 82 same interval, the environment transitions from state β to a new state, say
 83 α , with probabilities that depend on β . These rates can be used to project
 84 individuals or populations over time, as in a stochastic IPM (integral projec-
 85 tion model) (Ellner et al. 2016). Thus, individuals born with any specified
 86 phenotype (say i_1) in any specified birth environment (say α_1), will follow
 87 stochastic (and likely distinct) trajectories over time, each with a realized
 88 value of the LRS. The analysis here provides the probability distribution of
 89 this realized LRS (including all possible trajectories). Consequently we can
 90 compare the distribution of LRS for individuals who are born with the same
 91 birth phenotype but into different birth environments, and thus quantify the
 92 impact of a silver spoon effect (Grafen 1988). Alternatively, we can com-

93 pare the distribution of LRS for individuals who are born in the same birth
94 environment but in different phenotypic stages, and thus quantify the effect
95 of being born, say, large or heavy. Our method also has applications in the
96 analysis of adaptive responses, as we discuss later.

97 Here we extend our previous analysis (Tuljapurkar et al. 2020) to the dis-
98 tribution of LRS in our random environment model. Our results show how
99 the distribution of LRS is affected by birth environment, birth phenotype
100 (birth size in the Roe deer example), environmental variability, and random-
101 ness of life events. Our work here extends formulas for the moments (mean,
102 variance, and so on) of LRS using a method for Markovian environments in-
103 troduced by Caswell (2011) and applied in a recent paper by van Daalen and
104 Caswell (2020). The latter method starts with the event of death and works
105 “backward” to birth; in contrast, we use a “forward” method that analyt-
106 ically follows the probabilities of all possible individual and environmental
107 trajectories starting at birth.

108 The following section outlines our method. We aim at making our gen-
109 eral method accessible, using Tables 1 and 2 to list the key steps. Supporting
110 detail is in the Appendix. We then apply our new methods using age+stage
111 vital rates for Roe deer (*Capreolus capreolus*) studied under distinct environ-
112 mental conditions (Gaillard et al. 2013). We show that our method yields
113 unique insights into the effects of an individual’s birth environment, as well
114 as of environmental pattern (variability and serial autocorrelation). The
115 subsequent section discusses these findings in the context of silver spoon ef-

fects, intraspecific competition, and shifts in environmental pattern driven by climate change. We indicate how our results illuminate other questions, including the interactive effects of survival and reproduction on LRS, and the hypothesis of a Predictive Adaptive Response (Gluckman et al. 2008). We close with some directions for future explorations.

2 Model description: LRS in a Markovian Environment

Individuals in a structured population are followed in discrete time. At any time, individuals are in one of S stages, labeled with indices i, j, \dots , that may be a composite of age and variables such as size. Every individual begins life in a particular stage and environment. For example some individuals may be born small while others may be born large. Some may be born in a warm year and others in a cold year.

2.1 A fixed environment

In a fixed environment, individuals can differ only by their birth phenotype, call it i . Every individual then makes random transitions each interval between phenotypes until death. The one-period transition probabilities between phenotypes are the vital rates: $u(i, j)$ is the probability of a transition $i \leftarrow j$; these probabilities make a matrix \mathbf{U} . One-period survival rates for

135 stages $j = 1, 2, \dots$ are the column sums of \mathbf{U} ; death rates by stages are
 136 $(1 - (\text{survival rate}))$. One-period reproduction is described by probabilities
 137 $\Pr[n|i]$ that an individual in stages i has $n = 0, 1, \dots$ offspring.

138 The LRS is the random total of all offspring produced during an entire
 139 lifetime, and Tuljapurkar et al. (2020) shows how to compute the probability
 140 distribution $\mathbf{\Gamma} = \{\gamma(m)\}$ whose elements are the probabilities

$$\gamma(m|i) = \Pr[\text{LRS} = m | \text{initial stage is } i].$$

141 Tuljapurkar et al. (2020) uses four main points. First, every individual has
 142 a particular age of death; the probability distribution of the age at death for
 143 a cohort born into a given stage which can be determined by analyzing the
 144 survivorship curve where survivorship to each age is obtained by raising the
 145 transition matrix \mathbf{U} to successive powers; second, at each age before death,
 146 there is a probability distribution for the number of offspring produced at
 147 that age which is $\Pr[n]$; third, convolution of these age-specific distributions
 148 yields the distribution of LRS for those individuals that die at a given age;
 149 and fourth, weighted appropriately by mortality, these distributions add to
 150 yield the distribution of LRS, $\gamma(m)$.

151 **2.2 A variable Markovian environment**

152 Now suppose that there is temporal variation in vital rates produced by a
 153 variable environment. We suppose there are K environmental states (α, β, \dots)

154 that follow a Markov chain with transition probabilities $\mathbf{P} = \{p(\alpha, \beta) =$
155 $\Pr[\alpha \leftarrow \beta]\}$. An environmental state at t , call it β , applies between t and
156 $t+1$, and the environmental transition probabilities determine the next envi-
157 ronmental state, say α at $t+1$, applying between $t+1$ and $t+2$. We assume
158 that this Markov chain is irreducible, aperiodic and has an equilibrium state
159 in which the frequency of environment α is some $\pi_\alpha > 0$.

160 The environmental state α at time t determines every individual's one-
161 period stage-transition probabilities and reproduction between t and $t+1$.
162 Individual stage-transition probabilities depend on the environment and we
163 write them as $\mathbf{U}_\alpha = \{U_\alpha(i, j) = \Pr[i \leftarrow j | \text{environment is } \alpha]\}$. Reproduction
164 by an individual in phenotypic stage i at t , in the interval t to $t+1$, also
165 depends on the environmental state α , so there are probabilities $\Pr[n|i\alpha]$ that
166 such an individual makes n offspring.

167 Recall that individual's birth "state" is a combination $(i\alpha)$ of stage i and
168 environment α .

169 2.3 Distribution of LRS

170 When the environment is fixed, individuals begin life in a particular stage
171 and, as they age, at each time-step they may stay in the same stage and
172 remain alive, transition to another stage and remain alive, or die, accord-
173 ing to the stage transition probabilities of that fixed environment. Also at
174 each time-step, they may make a certain number of offspring, according to a
175 probability distribution for reproduction by individuals of that stage in that

176 fixed environment. Each life path is a sequence of stages, the length of which
 177 varies since individuals vary in their age at death. We have recently shown
 178 that by analytically combining these probabilities across the life cycle, we
 179 can obtain the exact distribution of LRS for individuals born into a given
 180 stage (Tuljapurkar et al. 2020). When the environment varies, we have to
 181 consider not only the birth stage but also the birth environment; an indi-
 182 vidual begins life with some birth stage i_1 and some birth environment α_1 .
 183 The subsequent life path includes both a sequence of environmental states,
 184 $\alpha_1, \alpha_2, \dots, \alpha_t, \dots$, determined by environmental transition probabilities, and
 185 a sequence of individual phenotypes $i_1, i_2, \dots, i_t, \dots$, determined by pheno-
 186 type transition probabilities – but in every time interval t the phenotype
 187 transition probabilities depend on the environment α_t . So we can think of a
 188 life path as a sequence of pairs, $(i_1, \alpha_1), (i_2, \alpha_2), \dots, (i_t, \alpha_t), \dots$

189 Every life path ends because an individual must eventually die. Given a
 190 sequence of pairs, e.g., $x = (i\alpha)$ at time t followed by $y = (j\beta)$ at time $t + 1$
 191 and so on, we are in the same setting as in Tuljapurkar et al. (2020) albeit
 192 with an expanded state space. To use the results in Tuljapurkar et al. (2020),
 193 we only require the transition probabilities $\Pr[x \leftarrow y] = \Pr[i\alpha \leftarrow j\beta]$, so
 194 we can use these transition probabilities to describe the stochastic sequences
 195 of events “forward” from birth to death. We do not simulate the life paths;
 196 we obtain the results analytically. These probabilities can, in fact, be com-
 197 puted directly by using a block matrix introduced by Tuljapurkar and Horvitz
 198 (2006) to study life expectancy (age at death) in Markovian environments.

Each element of the matrix is the product of a stage-transition probability with an environmental-transition probability (see Table 1 for the structure). This matrix is similar (but not identical) to the population projection block matrix called the megamatrix (Cohen 1977; Tuljapurkar 1982; Pascarella and Horvitz 1998; Tuljapurkar et al. 2003); unlike the megamatrix, the block matrix here has no rows for fertility.

To keep matters simple and usable, Table 1 enumerates the steps needed to compute exactly the distribution of the LRS in a random Markovian environment. The various transition probabilities and an appropriate block transition matrix are also defined in Table 1. The final result is the exact, complete probability distribution $\mathbf{\Gamma} = \gamma(m|i\alpha)$ of the probabilities that an individual produces $m \geq 0$ offspring during its life, conditional on starting with $(i\alpha)$: birth phenotype i and birth environment α . The example in the next section shows how the model is used in a realistic case. Mathematical details are in the Appendix.

2.4 Probability of reproductive failure

There is a direct way of finding the probability that a start in $i\alpha$ results in reproductive failure, which is given by $\gamma(0|i\alpha) = \Pr[\text{LRS} = 0|i\alpha]$. In an age-structured population, this probability is close to the probability of juvenile death, except e.g., for humans practicing contraception, or species with social rank that affects reproduction. In many species where reproduction depends only on size or stage, but not age, there is sometimes no obvious analog

221 for juvenile death. Hence it would be useful to compute $\gamma(0)$ directly, and
222 we can do this by a considerable simplification of the above procedure; the
223 simplified method is detailed in steps in Table 2.

224 **3 Application: Effects of spring onset on Roe** 225 **Deer**

226 Climate change is characterized by warmer mean annual temperatures in
227 many locations and earlier springs in temperate zones (Schwartz et al. 2006).
228 Earlier warmer springs result in a change in plant phenology with leaves
229 flushing out earlier in the year, which markedly influences the population
230 dynamics of herbivores such as Roe deer. Here we distinguish two environ-
231 mental states based on the timing of spring onset, "normal" vs. "early." Vital
232 rates for a normal spring were used to construct an age+size model using data
233 reported in Plard et al. (2015a). The environment was treated as a constant
234 or fixed environment in Tuljapurkar et al. (2020) to find the distribution of
235 the LRS. However, in years with early springs Gaillard et al. (2013) found
236 that survival of young Roe deer females (from 1 to 7 years of age) was only
237 90% of the survival rates seen in "normal" springs. Thus, we consider "nor-
238 mal spring" years vs. "early spring" years to represent "good" and "poor"
239 years, respectively (all vital rates and environment effects are given in Ap-
240 pendix). Here we create a model which allows transitions back and forth
241 between good and poor years. Despite a secular trend from good to poor

environments for the particular subset of years over which the current data were collected, other studies have found that good and poor demographic conditions alternate over time; an alternance between good and poor cohorts show up in each of the three decades during which Roe deer populations were monitored (Gaillard et al. 1997). Thus, we explore the LRS distribution in the context of random environmental variation; specifically how it is influenced by changes in both the relative frequencies of environmental states and the temporal autocorrelation between them. We also explore how these responses are affected by birth stage.

The phenotypes for Roe deer are defined by a combination of one of 12 age classes – yearlings, prime-aged adults (2-7 years old), old adults (8-11 years old) and senescent adults (> 11 years) – with one of 200 size classes (200 equal body mass intervals from 1 to 44 kg). Yearlings can be in any of several size classes. The typical range of birth (ie., yearling) weight is 11.6 to 20.2 kg (classes 50 to 90); here we ignore twinning (Plard et al. 2015a). Yearlings are typically censused after they have had several months to grow (about 8 at first winter capture), so the term “birth weight” rather means the weight of yearlings.

Our previous work (Tuljapurkar et al. 2020) on the distribution of LRS for this species focused on fixed conditions, one environmental state fixed for all time, either a “normal” spring (births into size class 75 which is about 16 kg, Fig. 1, left panel, blue solid line), or an “early” spring (same size at birth, Fig. 1, right panel, red solid line). In fixed environments, a cohort born in

265 a “good” year (a “normal” spring) would stay in that environmental state
266 for the rest of its life. So would a cohort born in a “poor” year (an “early”
267 spring).

268 Here, by contrast, we allow environmental states to change over time,
269 so cohorts do not spend their whole lives in the environmental state into
270 which they are born. To characterize the dynamics of Markovian environ-
271 mental transitions between two environments, we use two parameters. One
272 is the equilibrium (average, long-run) frequency π_1 of environment 1 which
273 is a good year; the equilibrium frequency of a poor year, environment 2, is
274 $\pi_2 = 1 - \pi_1$. The second parameter is the serial autocorrelation, ρ , with
275 value between -1 and $+1$. ρ describes the degree to which environments at
276 subsequent time steps are the similar or alternating. Thus, $\rho = 0$ means that
277 the random environment is independent of the past (i.e., the probability that
278 next year’s environment is 1 or 2 is independent of the environment in this
279 year), positive ρ means that the environment is “sticky” and environment
280 next year is likely to be the same as this year’s, and of course, negative ρ
281 means that environments are likely to alternate.

282 To begin, suppose that good and poor year are equally likely ($\pi_1 = \pi_2 =$
283 0.5). Applying the method in Table 1, we ask: how does the distribution of
284 LRS differ between birth environments (1 or 2), and how it is influenced by
285 autocorrelation? Recall that for fixed environments, the LRS distributions
286 (for the same size at birth) are shown by solid lines in Fig. 1. Even with no
287 change in the long-run frequency, the LRS distribution for either birth envi-

288 ronment changes markedly with autocorrelation. Consider individuals born
 289 into environment 1 (left panel): as ρ ranges from -0.8 (environments tend to
 290 cycle) to +0.8 (environments tend to persist), the most probable non-zero
 291 LRS for these individuals changes from near 1 to near 3. By contrast, birth
 292 into environment 2 means (right panel) that most individuals do not repro-
 293 duce (the most likely LRS equals zero) regardless of environmental pattern;
 294 however the shape of the distribution changes noticeably. Clearly birth en-
 295 vironment matters to individual life cycles. There are two extreme cases of
 296 autocorrelation ($\rho = -1$ and 1). When $\rho = 1$, only one environment (the
 297 initial one) occurs during life so we have a fixed environment (blue and red
 298 solid lines in Fig. 1). When $\rho = -1$, those two environments switch every
 299 year. In both extreme cases, the environment changes deterministically.

300 Suppose now that we change both π_1 (the long-run frequency of a good
 301 year) and the autocorrelation ρ . For the same size at birth but different
 302 birth environments, our methods yield corresponding distributions of the
 303 LRS. From these distributions we computed the average and the variance
 304 of the LRS, and the probability of reproductive failure. The averages and
 305 variances are plotted in the upper and lower panel of Fig. 2 respectively, with
 306 blue circles for birth environment 1 and red crosses for birth environment
 307 2. In each vertical segment the value of π_1 is indicated at the top of the
 308 figure, increasing from 0.2 to 0.8. Within every vertical segment (so for a
 309 fixed π_1), birth into a good year results in an average LRS that increases
 310 with autocorrelation ρ . In contrast, birth into a poor year results in an

311 average LRS that decreases with autocorrelation ρ . Thus the difference in
 312 the averages increases dramatically with autocorrelation ρ , regardless of the
 313 long-run frequency. Not surprisingly, increases in the probability π_1 of a good
 314 year result in increases in the average LRS for either birth environment and a
 315 fixed autocorrelation. In contrast to this pattern of differences, the variances
 316 change less than the averages within every vertical segment (for a fixed π_1 ,
 317 changing ρ), but do increase with increases in the long-run frequency π_1 .

318 We found a large difference in $\Pr[LRS = 0]$ for birth into a good year
 319 (environment 1) versus a poor year (environment 2) (Fig. 3). This finding
 320 was unexpected because the birth size is the same in each birth environment,
 321 and previous work (e.g., Plard et al. (2015a)) suggested that birth size was
 322 key. But apparently the birth environment strongly affects juvenile survival
 323 for individuals born with typical sizes. The difference we show here decreases
 324 for much smaller birth sizes (Fig. A.1), at which juvenile survival is already
 325 so low that the added effect of birth environment is modest.

326 4 Discussion

327 Our new approach makes it possible to quantify the impact of early-life envi-
 328 ronmental conditions, and weight in the first year of life, on the distribution
 329 of LRS in the context of temporally variable environments. The variability
 330 among individuals in LRS that we quantify arises from stochastic variation
 331 among their life paths. Here, stochastic variation in the sequence of environ-

332 mental states is governed by probabilities that are identical for all individuals
333 (i.e. without any maternal effects). And given the environment, stochastic
334 variation among individuals depends on probabilities determined only by the
335 stages (e.g., age and size). Our analysis does not include the effects of un-
336 observed trait variation, and thus provides a null model against which an
337 empirically observed distribution of LRS could be compared to assess the
338 contribution of unobserved traits (e.g. maternal traits).

339 In particular, our approach directly quantifies the contribution of silver
340 spoon effects originally defined by Grafen (1988) as “positive correlations
341 between characters in the adult that are positively associated with fitness,
342 brought about by the common underlying cause of favorable or unfavorable
343 environmental events during development.” As rightly pointed out by Grafen
344 (1988) a positive covariation generally occurs among good environmental
345 conditions during early life, high intensity of maternal care, high phenotypic
346 quality, and high fitness, thus making cumbersome the assessment of the role
347 of simply being lucky by being born in a good year independently of other
348 factors (Table 3). We are able to separate the effect of birth size from the
349 effect of the birth environment; we can compare the consequences of different
350 birth sizes given the same birth environment, or vice versa. Thus we quantify
351 the role of being lucky to be born in a good environment separately from
352 the role of size at birth. Although many empirical case studies (reviewed
353 in Table 3) have reported evidence of silver spoon effects on demographic
354 performance (e.g. Reid et al. (2003) and van de Pol and Verhulst (2006)),

on habitat selection (Stamps 2006), and on phenotypic traits (e.g. Minias et al. (2015)), no study to the best of our knowledge has ever quantified the LRS impacts of early environments independently of maternal influences or offspring attributes in animals. It is worth noting that the effects of birth environment on LRS found here were echoed in earlier work on life expectancy in plants in Markovian environments by Tuljapurkar and Horvitz (2006) and Metcalf et al. (2009).

Our application to the Roe deer is useful in the current context of ecological studies that identify early-life conditions as a determinant of individual trajectories. Birth environment affected the mean, variance and other features of the LRS distribution both through effects on first year survival and growth, and also through the probabilities of all lifetime sequences of events. Cohorts born in a good environment had higher mean LRS than cohorts born in a poor environment. The probability of producing zero offspring was half that of cohorts born in a good environment. Nevertheless birth environment had little or no effect on the probability of producing many (8 or more) offspring. However, as see in Fig. 2, the variance of LRS depends strongly on the environmental autocorrelation. Lomnicki (1978) observed that individual differences in performance should increase with decreasing resource availability, but his model involved asymmetric competition among individuals in response to decreasing resources generated by increased density. In contrast our study assumes the distribution of individual body size (a proxy of individual competitive ability) to be identical in Roe deer born

378 in both good and poor environments: meaning that large individual dif-
379 ferences in LRS can result purely from stochastic differences generated by
380 environmental autocorrelation. This does not mean that individual differ-
381 ences in asymmetric competitive ability are not involved in increased vari-
382 ance in LRS when poor conditions occur, but rather that these differences
383 are not a necessary condition for observing an increased LRS variance in
384 poor conditions. Interestingly, our finding that variance in LRS increased
385 with increasing frequency of good environments indicates that the relation-
386 ship between resource availability and variance in LRS is more complex than
387 envisioned by Lomnicki (1978) (see also Uchmański (1985)). Further studies
388 could be performed using our approach to quantify the potential contribution
389 of individual competitive ability.

390 A key finding of our analysis is the large influence of environmental au-
391 tocorrelation. The effect of birth environment on the life course, i.e., on
392 all transitions until death, is affected by environmental autocorrelation and
393 the long-term frequency distribution of environments. The strength of se-
394 rial temporal autocorrelation of early-life conditions strongly affects mean
395 LRS, with opposite influences for good and poor birth environments, and
396 had a smaller but still significant effect on the variance in LRS. The effects
397 described here add to evidence that temporal autocorrelation has to be con-
398 sidered when studying demographic patterns (Tuljapurkar and Horvitz 2006)
399 and life history evolution (Paniw et al. 2018).

400 The Roe deer application only illustrated the potential of our approach

401 and did not embrace the range of questions that our approach could ad-
 402 dress. We provide three examples. First, a recent review of the influence of
 403 early-life conditions on demographic senescence in birds and mammals found
 404 pervasive effects on reproductive senescence but no detectable effect on actu-
 405 arial senescence (Cooper and Kruuk 2018). Using our analytical methods we
 406 could quantify the contribution of reproduction and survival components to
 407 LRS (e.g. using Brown and Alexander (1991)’s decomposition), and assess
 408 in a straightforward way whether the difference pointed out by Cooper and
 409 Kruuk (2018) shows up when only considering the stochastic environmen-
 410 tal variation associated with early-life conditions. Second, a large body of
 411 literature has focused on the role of the match/mismatch between early-life
 412 and adult-life environmental conditions. Thus, the hypothesis of a Predictive
 413 Adaptive Response (see e.g. Gluckman et al. (2008)) says that any fitness
 414 benefit of a birth environment is determined by the fit to adult environmental
 415 conditions. Thus, being born in poor conditions would be associated with
 416 fitness benefits compared to being born in good conditions when all adults
 417 face poor conditions. Case studies that tested this hypothesis have not, so
 418 far, found support to this hypothesis (see e.g. Hayward and Lummaa (2013)
 419 and Douhard et al. (2014)). Using our approach, one could analyze scenarios
 420 of match/mismatch between early-life and late-life environmental conditions
 421 across different life histories to assess whether being born in a poor year can
 422 be beneficial to fitness. Lastly, we assumed that being born in a good or
 423 a poor year did not influence the offspring phenotype. However, it is well-

424 established that early-life conditions also affect phenotypic traits at birth,
425 and perhaps also later in life (e.g. Barker (1995)). In the case of Roe deer,
426 the date of birth has been shown to influence strongly the fitness of individ-
427 uals, with being born earlier being always better (Plard et al. 2014, 2015b).
428 One could easily assess the contribution of such traits to variation in the
429 LRS.

Table 1: Computing the distribution of LRS

$i, j = 1, \dots, S$	Discrete individual phenotypic stages.	
$\alpha, \beta = 1, \dots, K$	Discrete environmental states.	
$i\alpha, j\beta = 1, \dots, SK$	Discrete combinations of phenotypic stages with environmental states.	
\mathbf{U}_α , with components $0 \leq u_\alpha(i, j) \leq 1$	Matrix of phenotypic stage transition probabilities, $\Pr[i \leftarrow j]$ in environment α	
\mathbf{d}_α , $d_\alpha(j) = 1 - \sum_i u_\alpha(i, j)$	Vector $S \times 1$ of probabilities that an individual dies during one time period when it is in stage j and environment α	Eq. A.7
\mathbf{P} , $0 \leq p(\alpha, \beta) \leq 1$	Matrix of environmental state transition probabilities, $\Pr[\alpha \leftarrow \beta]$	
$\mathbf{U} = \text{diag}(\mathbf{U}_\alpha)$	Block diagonal matrix $SK \times SK$ formed from K environment-specific stage transition matrices, each $S \times S$	Eq. A.1
$\tilde{\mathbf{P}} = \mathbf{P} \otimes \mathbf{I}_S = \{p(\alpha, \beta) \mathbf{I}_S\}$	Block matrix $SK \times SK$ of $K \times K$ blocks, \mathbf{I}_S is $S \times S$ identity matrix	Eq. A.3
$\mathbf{Z} = \tilde{\mathbf{P}}\mathbf{U}$, $0 \leq z(i\alpha, j\beta) \leq 1$	Block matrix $SK \times SK$ of transition probabilities for combined stage-environment states, $\Pr[i\alpha \leftarrow j\beta]$	Eq. A.4

\mathbf{d}	Column vector $SK \times 1$ formed of K environment-specific blocks \mathbf{d}_α each $S \times 1$	Eq. A.8
$\kappa_{i\alpha}, 0 \leq \kappa_{i\alpha}(n) \leq 1, n = 0, \dots, N$	Vector $(N + 1) \times 1$ of probabilities $\Pr[n i\alpha]$ that an individual in the combined stage-environment state $i\alpha$ produces n offspring during one time period	Eq. A.9
$\widehat{\kappa}_{i\alpha} = \{\widehat{\kappa}_{i\alpha}(j)\}, j = 0, \dots, J$	Vector $(J + 1) \times 1$ of Fourier transforms for each vector $\kappa_{i\alpha}$. J is maximum number lifetime offspring. Use generating function and FFT (Fastest Fourier Transform, details see Appendix and METHODS in Tuljapurkar et al. (2020)) to calculate. For each j , $\widehat{\kappa}_{i\alpha}(j) = \sum_{n \geq 0} \kappa_{i\alpha}(n) z^n$, where the frequency $z = \theta(j) = \exp\left[\frac{-2\pi j \mathbf{i}}{J}\right]$, with $\mathbf{i} = \sqrt{-1}$.	Eq. A.10
$\widetilde{\mathbf{W}} = \text{diag}(\widehat{\kappa}_{i\alpha}(j))$	Using the preceding computation, for each life time number of offspring j , make this matrix with entries on the diagonal and zeros elsewhere, size $(SK \times SK)$	Eq. A.11
$\mathbf{V} = \widetilde{\mathbf{W}} \left(\mathbf{I} - \mathbf{Z}^T \widetilde{\mathbf{W}} \right)^{-1} \mathbf{d}$	For each life time number of offspring j , this is a vector of length SK	Eq. A.12

$\gamma_{i\alpha}(j), j = 0, 1, 2, \dots J$	For each birth state $i\alpha$, calculate inverse Fourier transform of the \mathbf{V} to obtain the life-time probability of making each number of offspring j (details see METHODS in Tuljapurkar et al. (2020))	
$\mathbf{\Gamma}_{i\alpha} = \{\gamma_{i\alpha}(j)\}$, each between 0 and 1, $j = 0, \dots, J$	Vector $(J+1) \times 1$ of probabilities that an individual produces j offspring during its lifetime given birth into state $i\alpha$	

Table 2: Computing the probability that LRS= 0

Follow line 1-9 of Table 1	
$h_\alpha(i) = 1$	For all non-reproductive individual states (e.g., juveniles, or small plants) in environment α
$h_\alpha(i) = \Pr[0 i\alpha]$	Probability that an individual produces NO offspring when in potentially reproductive states in environment α
$h_\alpha = \text{diag}(h_\alpha(i))$	A diagonal matrix for fixed α and all individual states, size $(S \times S)$
$\widetilde{\mathbf{W}}_1 = \text{diag}(h_\alpha)$	A diagonal block matrix of the preceding with $(K \times K)$ blocks
$\mathbf{v} = \widetilde{\mathbf{W}}_1 \left(\mathbf{I} - \widetilde{\mathbf{P}}^T \mathbf{U}^T \widetilde{\mathbf{W}}_1 \right)^{-1} \mathbf{d}$	This computation yields a vector of length $SK \times SK$
Births are in state $\{i\alpha\}$, where i is birth phenotype and α is birth environment	The number $v(i\alpha)$ is corresponding element of vector \mathbf{v}
For births in $\{i\alpha\}$	Probability of LRS =0, $\gamma(0)$, is given by number $v(i\alpha)$

Table 3: Empirical evidence of silver spoon effects. Interestingly, none of the studies reviewed here looked for partialing out the effects of being lucky to be born in a good year from maternal effects on individual fitness but a recent one on clownfish (Salles et al. 2020), which provided evidence for an overwhelming effect of randomness of life events over maternal effect. The approach we propose in the present work provides a reliable and general way to tease apart the influence of randomness of life events from that of maternal effects. Data collecting method is in Appendix.)

Species	Surrogate measure of fitness	Natal Environ- mental Driver	Evidence	Reference
Birds				
<i>Accipiter gentilis</i>	LBS*	Temperature in April in the year of birth	Negative effect	Herfindal et al. 2015
<i>Columba livia</i>	Reproductive success	Early-life food condition	Positive effect	Hsu et al. 2017

<i>Falco punctatus</i>	Lifespan	Anthropogenic natal habitat change	Negative effect	Cartwright et al. 2014
<i>Ficedula albicollis</i>	LRS	Competition at birth	Negative effect	Spagopoulou et al. 2020
<i>Forpus passerinus</i>	LRS	Rainfall in the year of birth	Positive or negative effects depending on population and dispersal status	Tarwater and Beissinger 2012
<i>Haematopus ostralegus</i>	LRS	Natal habitat quality	Positive effect	Van De Pol et al. 2006
<i>Nipponia nippon</i>	LRS	Hatching order	Negative effect	Song et al. 2018
<i>Parus major</i>	Lifespan & Reproductive success	Natal habitat quality	Positive effect in males	Wilkin and Sheldon 2009
<i>Pyrrhonorax pyrrhonorax</i>	LRS	Population breeding success in the year of birth	Positive effect	Reid et al. 2003

<i>Strix aluco</i>	LRS	Phase of the vole cycle when starting breeding career	Positive effect of the increase phase of the vole cycle	Millon et al. 2010
<i>Taeniopygia guttata</i>	Lifespan	Brood size at rearing	Negative effect when food availability is low	Briga et al. 2017
<i>Turdus merula</i>	LRS	Population density at birth Rainfall in the year of birth	Positive effect in males Positive effect in males	Wysocki et al. 2019
Fish				
<i>Amphiprion percula</i>	Reproductive success LRS	Site (anemone) quality Natal habitat quality	Positive effect Positive effect	Buston and Elith 2011 Salles et al. 2020
Insects				

<i>Drosophila melanogaster</i>	Reproductive success	Early-life diet	Positive (yeast content) and negative (sugar content) effects	Klepsatel et al. 2020
	Lifespan & Reproductive success	Early-life temperature & dietary P:C ratio	Positive (temperature) and negative (P:C) effects	Min et al. 2021
<i>Forficula auricularia</i>	Reproductive success	Early-life food availability	Positive effect	Wong and Kölliker 2014
<i>Nicrophorus vespilloides</i>	Reproductive success (contest success)	Early-life nutrition	Positive effect	Hopwood et al. 2014
<i>Phaedon cochleariae</i>	Reproductive success	Larval density	Negative effect	Müller et al. 2016
<i>Tribolium castaneum</i>	Reproductive success	Yeast-rich diet in early life	Positive effect	Scharf et al. 2015
Mammals				
<i>Capreolus capreolus</i>	Lifespan	Early survival in the year of birth	Positive effect in males	Garratt et al. 2015

<i>Homo sapiens</i>	Lifespan & Reproductive success	Crop yields at birth	Positive effects	Rickard et al. 2010 Hayward et al. 2013
<i>Leptonychotes weddellii</i>	Lifespan	Winter sea-ice extent	Positive effect	Stauffer et al. 2013
<i>Marmota marmota</i>	LRS	Number of helpers at birth	Positive effect	Berger et al. 2015
<i>Mungos mungo</i>	LRS	Variation in rainfall in the first year of life	Positive effect in males	Marshall et al. 2017
<i>Mus musculus</i>	LRS	Social group composition at birth	Positive effect of the presence of mother's sisters	König 1994
<i>Mustela erminea</i>	LRS	Food resources at birth	Negative effect (reversed silver-spoon effect)	King 2002

<i>Ovis canadensis</i>	Lifespan	Yearling body mass in the year of birth	Positive effect	Douhard et al. 2019
	Reproductive success	Population density at birth	Negative effect	Pigeon et al. 2017
	LRS	Population density at birth	Negative effect	Pigeon and Pelletier 2018
<i>Papio cynocephalus</i>	Reproductive success	Rainfall during the year of birth	Positive effect	Lea et al. (2015)Lea et al. 2015
<i>Rangifer tarandus platyrhynchus</i>	Reproductive success	8 years-old body mass in April in the year of birth	Positive effect when environmental conditions are intermediate during adulthood	Pigeon et al. 2019
<i>Spermophilus fulvus</i>	LRS	Population density at birth	Negative effect	Vasilieva and Tchabovsky 2020

<i>Tamiasciurus hudsonicus</i>	LRS	Population density at birth	Negative effect	Descamps et al. 2008
<i>Urocitellus richardsonii</i>	LRS	Year of birth	Negative effect of catastrophic climatic events	Catton and Michener 2016
<i>Ursus arctos</i>	LRS	Population density at 1 year of age	Positive effect	Zedrosser et al. 2013
Plants				
<i>Agrostemma githago</i>	Lifespan	Early-life environment (manipulated seasonal germination time)	Complex interactions with genotype and age	Goodrich and Roach 2013
Reptiles				
<i>Zootoca vivipara</i>	Reproductive success	Early-life food amount	Positive effect when females are maintained with fully fed conspecifics	Mugabo et al. 2010

*Lifetime Breeding Success (measured at offspring birth)

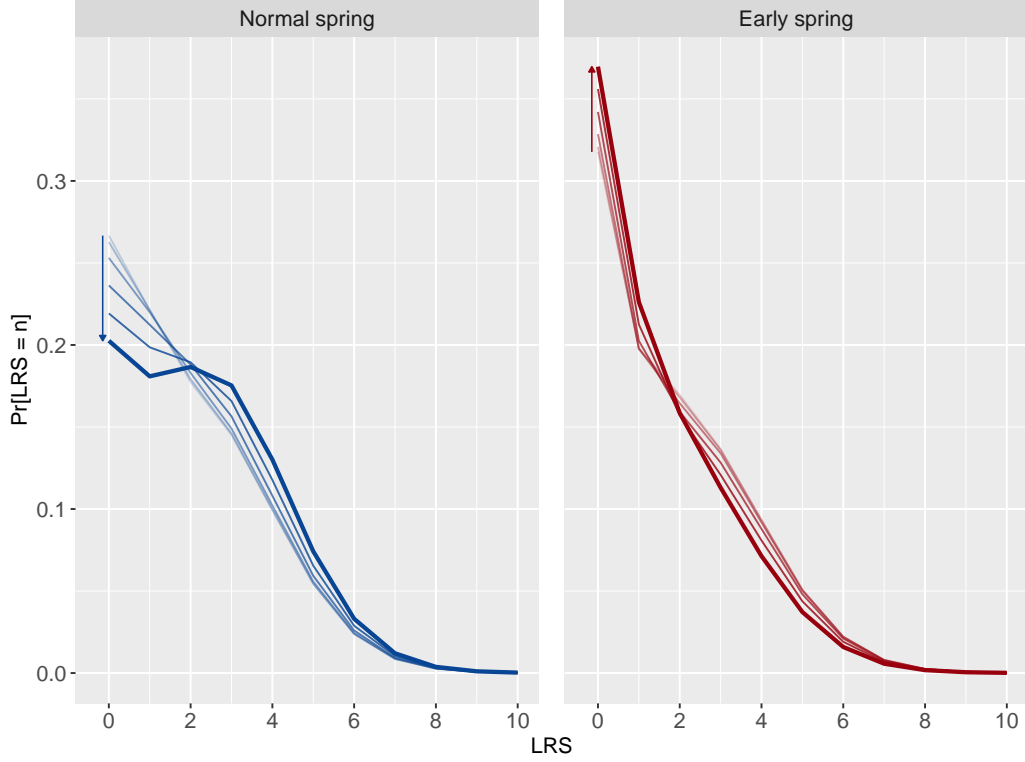


Figure 1: The probabilities of values of LRS for Roe deer born into two distinct environments (normal vs. early spring) at the same birth size (here, size class 70). The long term environmental frequency is 50% normal spring. Autocorrelations follow the arrows with $\rho = -0.8, -0.5, 0, 0.5, 0.8$ and 1 . Lines are darker with increasing autocorrelation. The left (resp., right) panels: probability distribution of LRS for individuals born in an normal spring year (resp., an early spring year). In each panel, the solid thick line indicates a fixed environment of that type. The transparency decreases with autocorrelations and the arrows also point to the direction with increasing autocorrelations.

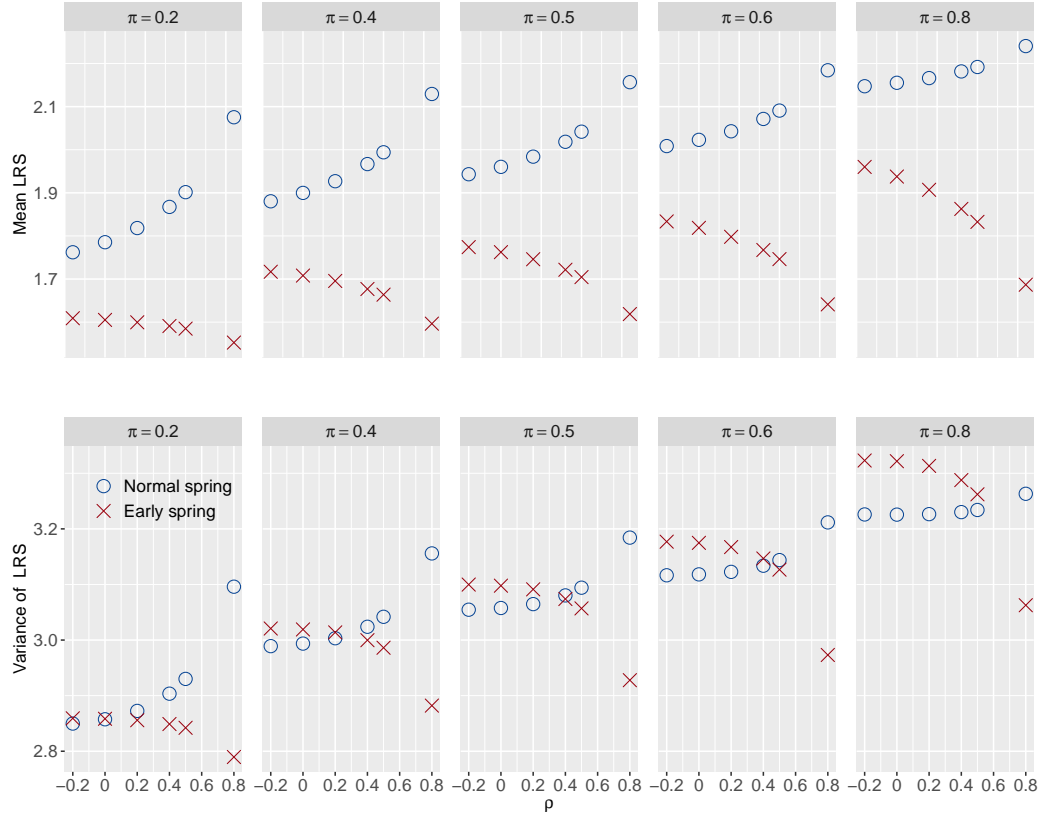


Figure 2: Mean (upper panel) and the variance (lower panel) of LRS for Roe deer born into two distinct environments (normal vs. early spring) at the same birth size (here, size class 75). Blue circles are births in a normal spring year, red crosses are births in an early spring year. In both panels, segments shown are for the π_1 marked at the top of the figure. In each segment, environmental autocorrelations are $\rho = -0.2, 0.0, 0.2, 0.4, 0.5, 0.8$.

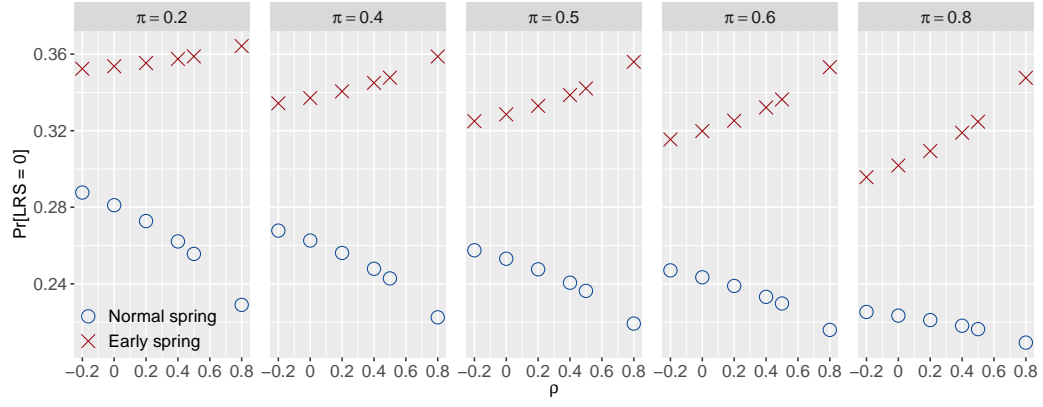


Figure 3: $\Pr[LRS = 0]$ for Roe deer born into two distinct environments (normal vs. early spring) at the same birth size (here, size class 75). Blue circles, red crosses, segments, autocorrelations as in Fig. 2.

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