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E-Article

Time and Chance: Using Age Partitioning to Understand How Luck Drives Variation in Reproductive Success

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ABSTRACT: Over the course of individual lifetimes, luck usually explains a large fraction of the between-individual variation in life span or lifetime reproductive output (LRO) within a population, while variation in individual traits or "quality" explains much less. To understand how, where in the life cycle, and through which demographic processes luck trumps trait variation, we show how to partition by age the contributions of luck and trait variation to LRO variance and how to quantify three distinct components of luck. We apply these tools to several empirical case studies. We find that luck swamps effects of trait variation at all ages, primarily because of randomness in individual state dynamics ("state trajectory luck"). Luck early in life is most important. Very early state trajectory luck generally determines whether an individual ever breeds, likely by ensuring that they are not dead or doomed quickly. Less early luck drives variation in success among those breeding at least once. Consequently, the importance of luck often has a sharp peak early in life or it has two peaks. We suggest that ages or stages where the importance luck peaks are potential targets for interventions to benefit a population of concern, different from those identified by eigenvalue elasticity analysis.

Keywords: reproductive skew, lifetime reproductive success, trait variation, individual stochasticity, *Rissa tridactyla*, *Artemisia tridentata*.

Introduction

Over the course of an individual's lifetime, luck often explains a large fraction of the between-individual variation in life span or lifetime reproductive output (LRO) within a population, often contributing much more to LRO variation than variation in individual traits or "quality" (e.g., Tuljapurkar et al. 2009; Steiner et al. 2010; Caswell 2011; Steiner and Tuljapurkar 2012; van Daalen and Caswell 2017; Hartemink and Caswell 2018; Jenouvrier et al. 2018; Snyder and Ellner 2018). Here, "traits" are individual attributes that remain fixed for life, such as genotype, birth date, spatial location of a sessile organism, or some measure of individual quality inferred from repeated observations of individual performance (Cam et al. 2016). By "luck" we mean what Caswell and collaborators call "individual stochasticity"—random variation in outcomes among individuals having identical demographic rates, for example, identical age- or size-specific survival probability and distributions of growth and clutch size.

While good traits may be necessary for exceptional success, they have not been sufficient in the cases we have considered: you also need to be lucky (Snyder and Ellner 2018). Exceptional success is, by definition, very unlikely. The least unlikely route to high LRO is to be above average (but not exceptional) in traits or quality and to get lucky. This is true for empirical case studies (cited above) in a wide range of taxa and for stage- or size-structured theoretical models incorporating empirical estimates for the extent of trait and fitness variation in natural populations (Snyder and Ellner 2018).

The importance of luck for LRO may seem at odds with the considerable and growing evidence that selection can be strong in natural populations, causing rapid evolutionary change.[1] But luck at the individual level averages out—nobody escapes the strong law of large numbers—and genes that improve expected fitness still tend to increase (Snyder and Ellner 2018, "Selection" section; app. S2 [apps. S1–S7 are available online])). Indeed, whenever reproduction is dominated by a few individuals ("reproductive skew"), selection will quickly eliminate any genotype conferring no

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[1] LRO is not equivalent to fitness, but in many situations the evolutionarily stable strategy life history is characterized by maximization either of LRO or of population intrinsic growth rate (Mylius and Diekmann 1995; Metz et al. 2008); moreover, traits that increase LRO without increasing generation time will generally increase intrinsic population growth rate.

chance of being one of those few, leaving a population where luck is important because everyone has some chance to "win the lottery." For example, Chen et al. (2019) found "huge variation in individual fitness" (p. 2161) in a fully pedigreed population of Florida scrub jays (see their fig. S1; the top five females fledged more total offspring than the bottom 250), but their analysis of genomic data revealed that "drift is the predominant force driving allele frequency change over time" (p. 2161).

But when luck overwhelms the effects of trait variation, as it often does, why and how does it do so? Is it because some individuals enjoy long lives with many years in high-fecundity states while others' lives are "nasty, brutish, and short" (Hobbes 1651)? Because some have large clutches or frequent high breeding success, by chance? Because some were lucky to be large at birth, or born at the right time of year or in a good location? Is luck mostly about getting past some risky phase of life, or is risk spread more evenly? To answer questions like these, we need to think about the various sources of luck, and we need to understand how the relative contributions of luck and traits play out over the course of an individual's life. Is one kind of luck especially important? Is it always more important to be lucky than good, or are there ages or stages when good traits are the key to success?

In the process, we will gain a deeper understanding of how influential luck is at different ages. Some states play a key role in luck—what happens immediately after leaving that state weighs heavily on success. If the importance of luck peaks sharply at one point in life, that indicates an age when an individual is very likely to be at one of these critical stages. These states—and the ages at which they are typically reached—may be targets for management interventions to benefit a population of concern. By contrast, if luck is broadly distributed over the life span, then there is no period of life in which luck is decisive. Either no states are especially fraught or the timing of reaching such a state is spread out.

In this article, we present new tools for partitioning the contributions of luck and traits at different ages to the variance of LRO. We further break down luck into contributions from prenatal luck, state trajectory luck, and fecundity luck and show how to partition them into contributions from different ages or different states. Figures 1 and S1 (figs. S1–S4 are available online) are conceptual summaries of these different kinds of luck. Prenatal luck shows how random variation in initial state (size at birth, for many of our examples) affects variance in LRO. State trajectory luck is about an individual's course through life. If we think of life as a series of random transitions, state trajectory luck is about how the transition made at a given age (does the individual shrink? grow? die?) affects variance in LRO. Fecundity luck summarizes how random variation in the number of offspring at a given age affects variance in LRO. State trajectory luck and fecundity luck can also be written as a sum of contributions at different states rather than at different ages. Finally, we partition these three forms of luck, plus the age-specific contributions of trait variation, into variance generated by whether an individual ever breeds during its life, versus variance in LRO among individuals that breed at least once.

The power of the new tools is illustrated by a set of animal and plant case studies using published models. In particular, we return to the sagebrush steppe perennial plants that we previously analyzed (Snyder and Ellner 2018). We knew that a favorable competitive environment at birth (a trait, in our sense) is key to survival in this community, yet our analysis showed that its impact is swamped by luck. What kind of luck and when? The techniques in Snyder and Ellner (2018) only allowed us to measure the lifetime total effects of luck and trait variation. Our new tools have shown us that state trajectory luck in the first 10 years of life, especially the first year, drives the dominance of luck over the early competitive environment. The dominance of luck is the result of early variation in survival and growth, unrelated to competitive environment. Conveniently, the new methods are computationally simpler than the previous ones that provided less information. Our empirical case studies mostly focus on LRO, but our methods all also apply to life span, simply by modifying the model so that each living individual has exactly one offspring each year, and LRO then equals life span.

In most cases, we find that luck swamps the effects of trait variation, because state trajectory luck is the dominant component at all ages, and that luck early in life (but not at birth or immediately afterward) is most important. Very early state trajectory luck determines whether an individual ever breeds, likely by ensuring that an individual is not dead or doomed (by being in a very bad state) early in life. Less early luck drives variation in success among those who breed at least once. As a result, the importance of luck often has a sharp peak early in life. We suggest that ages or stages where the importance of luck peaks are a potential target for management interventions to benefit a population of concern. In situations with a constant cost per individual of intervention rather than a constant cost per fractional change in a state- or age-specific vital rate, a "management for luck" criterion may be more appropriate than standard eigenvalue elasticity analysis.

This article is long because we give an integrated presentation of methods and applications—but it is shorter, in total, than if we had made it two articles with much unavoidable overlap. It is therefore structured and signposted so that readers who choose to can focus on the

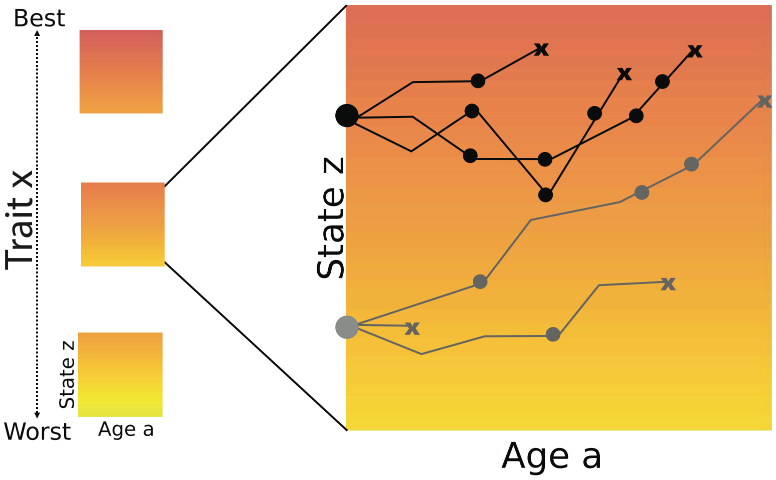

Figure 1: Conceptual figure showing the sources of variation in lifetime reproductive output (LRO): trait variation, prenatal luck, state trajectory luck, and fecundity luck. Trait x is fixed at birth and could entail, for example, higher survival and/or higher breeding probability. State z (e.g., body size) changes across life and affects immediate reproductive output. The color in the heat map is expected total reproduction from current age until death (which depends on state but not on age); darker/redder colors represent higher expected total reproduction. Note that expected reproduction is influenced by state (the heat map gets redder as z increases) and by trait (better traits mean that more of the heat map is red). The black and gray lines are potential trajectories through life, with an X mark indicating death. In this example, the number of offspring at each age is either 0 or 1, with 1 more likely in redder areas. Where an offspring was produced, there is a black circle. The number of circles on a trajectory thus represents LRO. Pluck is the variation in LRO that comes from an individual's trait: which heat map are they born on? Prenatal luck is the variation that comes from their initial state: does their trajectory start in a red area or a yellow area (black lines vs. gray lines)? State trajectory luck is the variation that comes from the path they take through life (variation among black or gray lines), which can be short or long and can wander through redder and less red areas. Finally, fecundity luck is the variation that comes from whether they produce 0 or 1 offspring at each age (circle or no circle).

central concepts, empirical applications, and practical implications rather than the technical derivations.

Background and Assumptions

The underlying model is an integral projection model (IPM) or matrix projection model (MPM) satisfying the assumptions of chapter 3 of Ellner et al. (2016). The most important assumption is that the kernel or matrix is power positive (some iterate of the kernel/matrix is positive on the entire state space); the others are satisfied by any MPM and by IPMs with bounded state distributions and continuous or piecewise continuous kernels. We use the notation of size-structured IPMs, but the results apply to any continuous individual-level state variable, a multidimensional state variable (size and age, size and quality, etc.), or an MPM if integrals are interpreted as sums. We assume that the maximum survival across states, $s_{\max}$, is <1. This implies that the survival-growth kernel on living states, P, has dominant eigenvalue $\leq s_{\max} < 1$ and that maximum survival to age a has an asymptotic exponential decrease proportional to $s_{\max}^{a}$. Unlike van Daalen and Caswell (2017), we consider only models where the distribution of immediate fecundity (i.e., offspring censused as new recruits next year) is determined by the current state rather than the current and subsequent state.

We consider only time-invariant models. However, this includes "megamatrix" models (e.g., Tuljapurkar and Horvitz 2006; Metcalf et al. 2009) for species in a time-varying Markovian random environment, where each individual experiences its own independent realization of the environment variable(s) affecting vital rates (e.g., each tree in a forest experiences a time-varying light environment, determined by events in its immediate neighborhood). One of our case studies (the bunch grass *Psuedoroegneria spicata*) is of this type, where the environmental variable is total competitive pressure from neighbors. That case study also illustrates that the individual-level models we analyze here are agnostic about density dependence at the population level. The individual-level models are Markov chains that act linearly on state probability distributions, but that is true whether the population-level IPM or MPM is itself linear (i.e., density independent) or instead represents a density-regulated population at equilibrium or stochastic steady state.

Our notation is defined in table 1 as well as in the text. RO denotes reproductive output, the offspring produced

Table 1: Notation and definitions

Notation	Formula and/or meaning
R	Lifetime reproductive output (LRO; random variable)
z, z_a	Possible value of individual state or state at age a
ω	Dead; an absorbing state (the dead stay dead) with zero fecundity
$\mathbf{z}$, $\mathbf{z}_a$	Individual state (or state at age a) considered as a random variable
$y_{j:k}$	The vector $(y_j, y_{j+1}, \ldots, y_k)$; for example, $\mathbf{z}_{0:a}$ is an individual's history of states from ages 0 to a, considered as a random vector
$\bar{\beta}(z)$	$\mathbb{E}$[immediate RO] for state z individual, $\bar{\beta}(z) = \int F(z', z)\, dz'$
$\sigma_b^2(z)$	Var(immediate RO) for state z individual (formula is model dependent)
$\bar{\beta}_2(z)$	$\mathbb{E}$[(immediate RO)^2] for state z individual, $\bar{\beta}_2(z) = \bar{\beta}(z)^2 + \sigma_b^2(z)$
$\rho_1(z)$	$\mathbb{E}$[immediate and future RO] for state z individual
$V(z)$	Variance over next year's state of $\rho_1(z)$
$\rho_2(z)$	$\mathbb{E}$[(immediate and future RO)^2] for state z individual
$c_0(z)$, $c_0(z, x)$	Probability distribution of state (or state and trait) at birth, $c_0(\omega) = c_0(\omega, \bullet) = 0$; individuals are age 0 at birth
$p_0(x)$	Marginal distribution of trait at birth
$\circ$	Hadamard product, $(f \circ g)(z) = f(z)g(z)$
$\tilde{\bullet}$	Restriction of $\bullet$ to states $z \neq \omega$; for example, $\tilde{c}_0$, $\tilde{W}$, $\tilde{\rho}_1$
$\mathbf{e}$	Vector of all 1s (MPM) or function $\mathbf{e}(z) \equiv 1$ (IPM); in both cases, $\mathbf{e}^{\mathsf{T}} P =$ state-specific survival probability
F	Fecundity kernel
P	Survival-growth kernel or matrix without an absorbing state for death; thus, $\mathbf{e}^{\mathsf{T}} P = s(z)$, state-dependent survival
P_+	Survival-growth kernel or matrix with an absorbing state for death; thus, $\mathbf{e}^{\mathsf{T}} P_+ \equiv \mathbf{e}$ because the columns of P_+ sum to 1
N	Fundamental matrix for P: $N = (I - P)^{-1}$
$p_b(z)$	Probability of attempting to breed
π_b, π_0	Survival-growth kernels for breeders and nonbreeders, respectively
$\sigma_+^2(z)$	Variance in per capita number of new recruits produced in the current year by a breeder
$p_d(z)$	Probability of producing at least one new recruit in the current year
$\bar{\beta}_d(z), \sigma_d^2(z)$	Mean and variance in per capita number of new recruits produced in the current year, conditional on producing at least one

Note: P and P_+ here correspond to $\mathbf{U}$ and $\mathbf{P}$ in van Daalen and Caswell (2017). ρ_1 and ρ_2 here correspond to $\bar{r}$ and $\bar{r}_2$ in Ellner et al. (2016). IPM = integral projection model; MPM = matrix projection model; RO = reproductive output.

by an individual. LRO denotes lifetime reproductive output, the total RO over an individual's lifetime. Our notation is largely consistent with chapter 3 of Ellner et al. (2016) but deviates somewhat to be consistent with van Daalen and Caswell (2017). We assume that expected immediate and future RO ρ_1 and expected squared immediate and future RO ρ_2 (called $\bar{r}$ and $\bar{r}_2$ in chap. 3 of Ellner et al. 2016) have been calculated for the model at hand, using the appropriate method from Ellner et al. (2016) or van Daalen and Caswell (2017). (See the tutorial code that accompanies app. S5 if you are unsure how to do this; all code can be found in the Dryad Digital Repository [https://doi.org/10.5061/dryad.1g1jwstt5; Snyder et al. 2020].) Note that $\mathbf{z}_a$ is the state at age a considered as a random variable, while z_a, z, and so on denote possible values of $\mathbf{z}_a$ and one possible state is dead, $z = \omega$. Although functions do not have a transpose, we often write v^{T} where a row vector would occur in a matrix model calculation. Be warned, however, that this notation hides bin width (h) factors that are typically present in continuous-state IPM calculations, such as h∗sum(v∗c0) for calculating $v^{\mathsf{T}} c_0$ by midpoint rule in R.

We need to use an expanded kernel (or transition matrix) $P_+(z', z)$ that includes ω as an absorbing state, $P_+(\omega, \omega) = 1$. The dead are assumed to have zero fecundity, so $\rho_1(\omega) = \rho_2(\omega) = 0$. If the underlying model is an IPM, then P_+ operates on a hybrid state space, where state of the living is continuous and ω is a discrete point. The term P_+ is constructed for numerical calculations by taking the iteration matrix for P, adding an extra row at the bottom consisting of the size-dependent probability of death, adding an extra column of zeros on the right, and putting 1 in the bottom right corner.

Partitioning without Trait Variation: Theory

Overview

Age partitions of luck can help us identify critical periods of life in which luck has a large influence on LRO. In the following subsections, we define the three forms of luck discussed in the introduction—prenatal luck, state trajectory luck, and fecundity luck—and show how to partition them into contributions from different ages or different states. We can also ask how much of the variance in LRO is about getting to breed at all versus never breeding and how much of it is about how many offspring you leave, given that you leave some. We go on to partition state trajectory luck into these two components: breeding or not, and LRO variance among breeders.

In the rest of this section, we give the mathematical definitions of the luck components and derive the partitionings by age, state, and breeding or not. If that is not what you are here for, you can skip to “Partitioning without Trait Variation: Case Studies,” where we apply the results in empirical case studies.

Partitioning Luck by Age

For now, all individuals have the same trait values, so variance in LRO is entirely due to luck. The goal in this section is to partition the total among-individual variance in LRO into contributions at each age. Explicitly age-structured models are a special case (app. S3), but our main interest is in models where individuals of a given age can be in multiple states.

The idea behind the calculations in this section is to first condition the variance in LRO on state at age 0 and then to condition that result on state at age 1 and so forth, applying the law of total variance over and over. However, conditioning a variance on multiple variables is mathematically treacherous. Therefore, we turn to a general variance decomposition derived by Bowsher and Swain (2012). In appendix S2, we give a self-contained statement and proof of this decomposition (eq. [S8]).

Let $\mathbf{z}_{0:k}$ denote an individual’s state history from ages 0 to k. The general variance decomposition says that for any upper age A,

$$\begin{aligned}\operatorname{Var}(R) = {} & \underbrace{\operatorname{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{z}_0)]}_{\text{prenatal luck}} \\ & + \underbrace{\sum_{a=0}^{A-1} \mathbb{E}_{\mathbf{z}_{0:\alpha}} \operatorname{Var}_{\mathbf{z}_{a+1}|\mathbf{z}_{0:a}}[\mathbb{E}(R|\mathbf{z}_{0:a+1})]}_{\text{state trajectory luck}} \\ & + \underbrace{\mathbb{E}_{\mathbf{z}_{0:A}} \operatorname{Var}[R|\mathbf{z}_{0:A}]}_{\text{fecundity luck}}.\end{aligned} \tag{1}$$

The first line in equation (1) can be interpreted as prenatal luck, being in a good or less good state at birth. This will be zero in any model where all newborns have the same state. The second line adds up how luck in state transitions at different ages contributes to LRO variance through its effect on the individual’s state the following year. If we think of an individual’s life as a route through a garden of forking paths, state trajectory luck quantifies how much each state transition between one census and the next affects future expected LRO. We will see that the final line adds the effect of luck in the reproductive output at each age given the individual’s state trajectory: how many offspring did that individual have this year?

In the rest of this section we will derive analytic, easily computed formulas for each term in equation (1); those will imply that we can let $A \rightarrow \infty$ to get a partitioning of luck across all ages. The final result is equation (7); you can skip directly there if you are willing take it on trust.

Starting with prenatal luck (the first term of eq. [1]), we have

$$\mathbb{E}(R|\mathbf{z}_0 = z) = \rho_1(z) = \mathbf{e}^{\mathsf{T}} F N, \tag{2}$$

where F is the fecundity kernel and $N = (I - P)^{-1}$ is the fundamental matrix for P. If F and P are matrices, then $\mathbf{e}$ is a vector of all 1s, while if they are continuous kernels, then $\mathbf{e}$ is a function $\mathbf{e}(z) \equiv 1$. At age 0 there has not been any mortality, so the variance of R across living states $z \neq \omega$ includes the entire population. Using $\tilde{\bullet}$ to denote restriction of $\bullet$ to living states, if $c_0(z)$ is the initial state distribution, then prenatal luck is

$$\begin{aligned}\operatorname{Var}\rho_1(\mathbf{z}_0) &= \int \tilde{c}_0(z)\tilde{\rho}_1(z)^2\,dz - \left(\int \tilde{c}_0(z)\tilde{\rho}_1(z)\,dz\right)^2 \\ &= \tilde{c}_0^{\mathsf{T}}\tilde{\rho}_1^2 - (\tilde{c}_0^{\mathsf{T}}\tilde{\rho}_1)^2.\end{aligned} \tag{3}$$

Turning to state trajectory luck (the second term of eq. [1]), we can break R into two parts for each value of a: total reproduction up though age a, and reproduction at ages $a + 1$ and beyond. Conditional on $\mathbf{z}_{0:a}$, reproduction through age a does not depend on the value of $\mathbf{z}_{a+1}$. Thus, the Var in state trajectory luck is just the variance of the expected value of reproduction at ages $a + 1$ and beyond, as a function of the value of $\mathbf{z}_{a+1}$. But because state transition probabilities do not depend on age in addition to state (this is true even in models with age structure, because then age is a component of state), expected total reproduction at $a + 1$ and beyond (as a function of state at age $a + 1$) is calculated the same way as expected total reproduction from birth as a function of state at birth. The Var in state trajectory luck is thus the variance with respect to the conditional distribution of $\mathbf{z}_{a+1}$ of

$$\mathbb{E}(R|\mathbf{z}_0 = z_{a+1}) = \rho_1(z_{a+1}). \tag{4}$$

The Markov property now comes in handy. The distribution of $\mathbf{z}_{a+1}$ conditional on $\mathbf{z}_{0:a}$ is the distribution conditional on $\mathbf{z}_a$ (including the possibility of being dead at a), which is $P_+(z, \mathbf{z}_a)$. Conditional on $\mathbf{z}_a = z$, the variance of equation (4) is given by

$$\begin{aligned} V(z) &= \int \rho_1(z')^2 P_+(z', z)\, dz' - \left(\int \rho_1(z') P_+(z', z)\, dz' \right)^2 \\ &= \rho_1^2 P_+ - (\rho_1 P_+)^2, \end{aligned} \tag{5}$$

with the integrals running over all states, including ω.

The final step for state trajectory luck is to average V over the distribution of $\mathbf{z}_a$. As $V(\omega) = 0$ (the dead stay dead and have zero future RO), this average only involves the distribution omitting ω. State trajectory luck is therefore

$$\sum_{a=0}^{A-1} \tilde{V}^{\mathsf{T}} P^a \tilde{c}_0. \tag{6}$$

Note that the same formula with P_+ in place of P and tildes omitted is also valid because $V(\omega) = c_0(\omega) = 0$.

As $a \to \infty$ the age a terms exhibit an asymptotic exponential decrease because the dominant eigenvalue of P is at most the maximum size-dependent survival $s_{\max}$, which is <1 by assumption. Let $V_{\max}$ denote the largest value of $V(z)$. Then the ath term is at most $s_{\max}^a V_{\max}(a)$, and the sum of all terms from the ath on is at most $V_{\max}(a) = s_{\max}^a/(1 - s_{\max})$. The sum in state trajectory luck is therefore convergent as $A \to \infty$. In practice, for a sufficiently large, the upper bound will be much smaller than the sum of the first $a - 1$ terms, and calculation of further terms is not needed.

For fecundity luck (the third term of eq. [1]), we can divide R into total reproduction at ages 0 to A, plus total reproduction after age A. Because reproductive output in different years is conditionally independent given the state in that year, the variance in total reproduction at ages 0 to A, conditional on $\mathbf{z}_{0:A}$, is the sum of annual state-dependent conditional variances in immediate RO, $\sum_{a=0}^{A} \sigma_b^2(\mathbf{z}_a)$. Because the chance of survival past age A decreases geometrically with age, reproduction after age A decreases at least that fast. Fecundity luck is therefore $\sum_{a=0}^{A} \mathbb{E}\sigma_b^2(\mathbf{z}_a)$, plus a term that decreases geometrically in A or faster. This sum includes only the living because $\sigma_b^2(\omega) = 0$. Therefore, $\mathbb{E}\sigma_b^2(\mathbf{z}_a) = (\tilde{\sigma}_b^2)^{\mathsf{T}} P^a \tilde{c}_0$. This has an asymptotic geometric decrease with age because $\Pr(\mathbf{z}_a \neq \omega)$ has an asymptotic geometric decrease and $\sigma_b^2(\omega) = 0$. We can therefore let $A \to \infty$ in fecundity luck.

Combining these calculations and letting $A \to \infty$, we get a decomposition of Var(R) into prenatal luck, plus the contributions at each age from randomness in state trajectories and from randomness in realized fecundity conditional on the state trajectory:

$$\begin{aligned} \mathrm{Var}(R) = {} & \underbrace{\tilde{c}_0^{\mathsf{T}} \tilde{\rho}_1^2 - (\tilde{c}_0^{\mathsf{T}} \tilde{\rho}_1)^2}_{\text{prenatal}} + \underbrace{\sum_{a=0}^{\infty} \tilde{V}^{\mathsf{T}} P^a \tilde{c}_0}_{\text{state trajectory}} \\ & + \underbrace{\sum_{a=0}^{\infty} (\tilde{\sigma}_b^2)^{\mathsf{T}} P^a \tilde{c}_0}_{\text{fecundity}} . \end{aligned} \tag{7}$$

The terms in equation (7) include the effects of variation in initial state, when it exists. Alternatively, it may be of interest to see how initial state affects the partition by age, by doing decomposition for different initial distributions c_0 having only one possible state at birth.

Readers who would like to see the formulas in equation (7) implemented in R may wish to examine the code that generates figure S4, a partitioning of the toy model in appendix S5.

Luck by Age: Another Interpretation

The age-specific terms in equation (7) have an intuitive interpretation, which becomes essential for dealing with trait variation below. Specifically, the age a terms in state trajectory luck and fecundity luck are the additional variance in total LRO that results from letting luck happen up to age a (but not past that age), compared with having it happen only up to age $a - 1$.

To see why that is true, consider a modified life history in which individuals live a normal, stochastic life up to age $D \geq 0$ and then live deterministically. To implement this, we let individuals have state transitions up to age $D \geq 0$ according to the transition kernel P and then die (if not already dead). At ages 0 to $D - 1$ they follow the "normal" state-dependent fecundity distribution, but their fecundity at age D is $(\mathbf{e}^{\mathsf{T}} F N c_0)(z_D)$, their expected total immediate and future RO conditional on their state at age D in the original model without extermination at age D (this is zero if they are already dead). State-dependent fecundity followed by certain death is just a mathematical device for eliminating variance in LRO while preserving the mean. It is equivalent to letting RO at all subsequent ages equal its expected value conditional on z_D, but instead we give it as a "lump-sum" payment followed by death.

This modified life history has exactly the same expected LRO as the original, namely, their expected fecundity at ages $0, 1, 2, \ldots, D - 1$ plus their expected fecundity at all later ages. As this is true for any initial state, we have (using a superscript (D) to denote the modified life history)

$$\mathbb{E}^{(D)}(R|z) = \mathbb{E}(R|z) \tag{8}$$

for the original model. However, the modified life history has a lower variance in LRO because luck past age D has been replaced with everyone getting their expected future payoff. As $D \to \infty$, this reduction in LRO variance converges to zero because expected and actual future RO both equal zero once the individual dies.

When we apply equation (1) to the modified model, only a finite number of terms are nonzero because of certain death at D. Prenatal luck is unchanged. In the state trajectory luck term, because $\mathbf{z}_{D+1} = \mathbf{z}_{D+2} = \cdots = \omega$, $\mathbf{z}_{a+1}$ has zero variance for $a \geq D$ and therefore

$$\mathrm{Var}_{\mathbf{z}_{a+1}|\mathbf{z}_{0:a}}[\mathbb{E}(R|\mathbf{z}_{0:a+1})] = 0, \quad a \geq D. \tag{9}$$

The expectation of the expression in equation (9) is therefore zero for $a \geq D$, so the infinite sums in the state trajectory luck terms of equations (1) and (7) are actually sums up to age $D - 1$ in the modified model. Similarly, in the fecundity luck term, the conditional variance of R is fully determined by the states at ages 0 to $D - 1$ because the only subsequent payoff (at age D) is fully determined by z_D, so the sum only runs up to $D - 1$.

Because the imposed extinction between ages D and $D + 1$ does not modify either the state trajectory distribution or the state-dependent expected future RO prior to the imposed extinction, all of the nonzero terms in equation (7) for the modified model are identical to those for the original model. Deferring extinction by one year adds one more term to each sum in equation (7)—so as claimed, each age-specific term in equation (7) is the marginal effect of letting luck operate for one more year before ending.

Partitioning Luck by State

The Markov property implies that an individual's trajectory and fecundity variance at each age only depend on the individual's state at that age. It therefore makes sense to associate age-specific luck with the individual's state at the time and thus partition luck by state.

Before doing that, recall that prenatal luck is different from the others in that it does not involve the "forking paths" of individual stochasticity in state trajectories. It results from differences in state at birth, which is not determined by the model's state transition probabilities. This prenatal stochasticity does not occur at any of the possible states for living individuals. It can be made a stand-alone term or just omitted from a partitioning by state. Either way, our goal here is to reexpress the state trajectory and fecundity luck terms of equation (7), in the limit $A \to \infty$, as two integrals or sums over possible states for living individuals.

For state trajectory luck (second term of eq. [7]), the sum from ages $a = 0$ to infinity is

$$\tilde{V}^{\mathsf{T}}(I + P + P^2 + P^3 + \cdots)\tilde{c}_0 = \tilde{V}^{\mathsf{T}}\tilde{N}\tilde{c}_0. \tag{10}$$

The right-hand side of the equation is the integral (or sum) over z of the function $\tilde{V}\circ(\tilde{N}\tilde{c}_0)$. Thus, the total LRO variance from state trajectory variance is expressed as an integral or sum over states z.

Doing the same for fecundity luck (third term of eq. [7]), the sum over all ages is the integral with respect to z of $\sigma_b^2\circ(\tilde{N}\tilde{c}_0)$, again a sum of contributions from different states (which in retrospect is obviously the correct formula).

Subpartitioning: Breeders versus Nonbreeders

One source of LRO variation is that some individuals breed before dying while others do not; the other source is variance in LRO among breeders. Here we explain how each age-specific contribution to LRO variance can be subdivided into these two components. Separating those components turns out to be informative because it helps to explain the pattern of age-specific contributions. In particular, bimodal patterns (where the importance of luck peaks, declines, and peaks again with increasing age) can result from the two components peaking at different ages.

As all nonbreeders have $R = 0$, conditioning on $M =$ (1 for breeders, 0 for nonbreeders) and defining $p_M = \Pr(M = 1)$, we have

$$\begin{aligned}\mathrm{Var}(R) &= \mathbb{E}_M\mathrm{Var}(R|M) + \mathrm{Var}_M\mathbb{E}(R|M)\\ &= \underbrace{p_M\mathrm{Var}(R|M = 1)}_{\text{among breeders}} + \underbrace{p_M(1 - p_M)E(R|M = 1)^2}_{\text{breed or not}}.\end{aligned} \tag{11}$$

We show how to calculate $\mathbb{E}(R)$ and $\mathrm{Var}(R)$ conditional on breeding in appendix S4. In principle, the two terms in equation (11) may vary differently by age or state. Luck at some times may be important for whether an individual breeds at least once; luck at other times or states may mainly affect whether a breeder has many offspring or few.

The breeding probability p_M and a transition kernel P_M conditional on becoming a breeder can be calculated using standard Markov chain methods (Caswell 2001, sec. 5.2; Kemeny and Snell 1960), in ways similar to Snyder and Ellner (2016, pp. E30–E31). The calculations are detailed in appendix S4, and a worked example is provided in appendix S5 and in the code that generates figure S4.

We can then partition the among-breeders component into the contributions of prenatal, state trajectory, and fecundity luck by age or by stage by applying equations (7) and (10) using the conditional kernel P_M. The corresponding partition for the breed-or-not term is then obtained as term-by-term differences between the among-breeders partition and the total variance partition. If individuals vary in state at birth, the calculations for breeders need to take that into account by using the distribution of initial state conditional on breeding (eq. [S23]) along with the conditional kernel.

Exactly how a breeder is defined is in part a matter of choice, but it is constrained by how much detail the model provides about among-individual variability in annual reproductive success. The results in appendix S4 cover the following options.

Definition 1. Any model we can consider must specify the state-dependent mean and variance of immediate RO. Lacking any additional information, we can define a breeder to be an individual that reaches a state z with positive mean immediate RO (i.e., $\bar{\beta}(z) > 0$).

Definition 2. In a model that also includes a state-dependent probability of attempting breeding $p_b(z)$ and the mean and variance of immediate RO conditional on breeding, we can define a breeder to be an individual that attempts to breed at least once before dying.

Definition 3. In a model that includes the full state-dependent offspring distribution, we can define a breeder to be an individual that produces at least one offspring before dying.

These are not exclusive cases. If a model includes the information needed for definition 3, then any of the three definitions can be used. Moreover, in some models $p_b(z)$ takes only the values 0 or 1, in which case definition 2 can be implemented using the simpler definition 1 methods, defining an individual to be a breeder if they reach a state z where $p_b(z) = 1$. Similarly, if the state-dependent probability of producing one or more offspring is either 0 or 1, definition 3 can be implemented using the definition 1 methods.

Partitioning without Trait Variation: Case Studies

In this section we explore how and why luck is distributed over the course of an individual's life in three empirical case studies. We also ask what form of luck is dominant, overall and at different ages: is it the luck of getting to breed at all or the luck of being one of the most successful breeders?

*Eastern Hemlock (*Tsuga canadensis*)*

Lamar and McGraw (2005) developed projection matrices for eastern hemlock (*T. canadensis*) on the basis of studies in a mixed hardwood/hemlock forest in Shenandoah National Park. We used the average of the two estimated annual transition matrices, obtained from the COMPADRE database (Salguero-Gomez et al. 2015):

$$\mathbf{A} := \mathbf{F} + \mathbf{P} = \begin{bmatrix} 0.9030 & 0 & 0.29900 & 0.77415 & 1.95735 & 6.0251 \\ 0.0038 & 0.96070 & 0 & 0 & 0 & 0 \\ 0 & 0.01225 & 0.96545 & 0 & 0 & 0 \\ 0 & 0 & 0.01735 & 0.97595 & 0 & 0 \\ 0 & 0 & 0 & 0.01205 & 0.96335 & 0 \\ 0 & 0 & 0 & 0 & 0.01835 & 0.9903 \end{bmatrix}. \tag{12}$$

The six "stages" are diameter at breast height (dbh) size classes. Diagonal entries (including the top left entry) are the probability of surviving and remaining in the same size class, subdiagonal entries are probabilities of surviving and entering the next-larger size class, and the other top row entries are per capita average seedling production. The probabilities of death are 1 minus the sums of the transition probabilities (1 minus the column sums). See appendix S7 for details. Van Daalen and Caswell (2017) presented a sensitivity analysis of the mean and variance of LRO for this model with respect to stage-specific survival, growth, and fecundity. We confirmed that our scripts replicated the moments of LRO reported in their table 3. We partitioned between breeders and nonbreeders using definition 1, as there is no information on stage-specific flowering probability: a breeder is an individual that survives to enter stage 3.

The partitioning of LRO variance by age (fig. 2*A*, 2*B*) aligns with previous case studies where luck when small and vulnerable is most important (Snyder and Ellner 2016); the largest contributions occur at ages 0–100, during which most individuals are in the first three size classes (fig. 2*D*). Nearly all LRO variance is due to state trajectory variation (fig. 2*B*), and most of the variance (about 95% of the total) is variance among breeders, individuals that survive to reach stage 3 (fig. 2*C*). Variance that results from breeding versus not breeding occurs very early in life. A newborn has a roughly 1% chance of surviving to stage 3 (the first with positive fecundity), while a stage 2 individual has a 31% chance. Luck later in life mostly results from variance among breeders. Stage 3, 4, and 5 individuals each have roughly 50∶50 odds of surviving to reach the next stage, and those that reach stage 6 can expect to live 100 years on average and produce more than 600 recruits before death. The overall importance of luck peaks at around age 100, when individuals are spread among stages 2, 3, and 4 and the outcome of stage transitions determines whether they make it into the later, high-fecundity stages.

The trend in stage-dependent contributions (fig. 2*E*, 2*F*) is opposite of the age-dependent trend: larger stages, reached later in life, make the largest contribution. The stage-specific contribution of stage 6 is largest, even though the chance of survival to stage 6 is below 0.2%, because a year spent in stage 6 contributes a lot compared with other stages and because individuals reaching stage 6 have a high mean (≈103 years) and very high variance (≈11,000) of remaining life span. The low age-specific contributions at high ages, when most survivors are in later stages, result from the fact that time in later stages (if it happens) is spread out over many ages.

Across a wide taxonomic gulf, we found similar patterns in a matrix model (Altwegg et al. 2014) for an urban

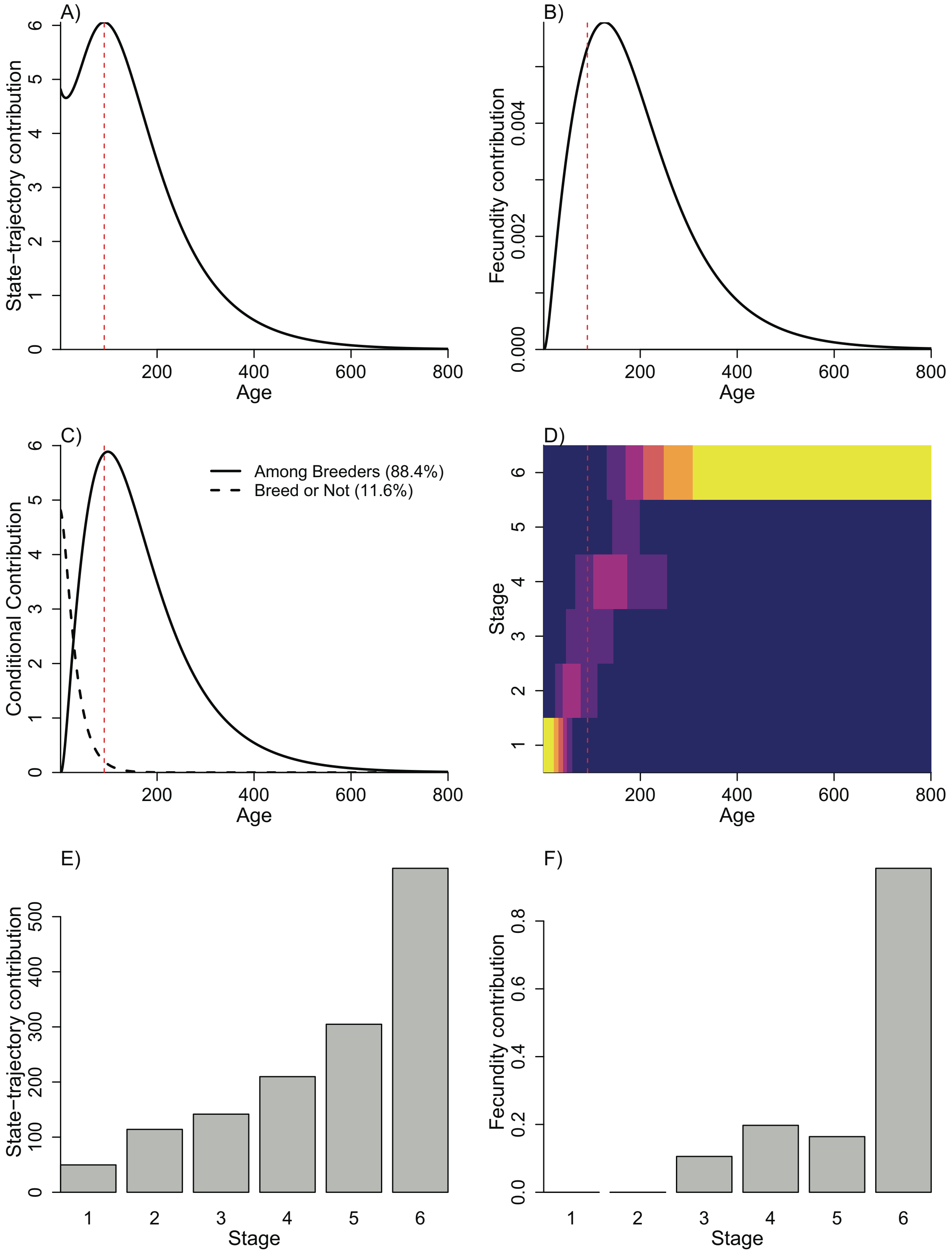

Figure 2: Partitioning of lifetime reproductive output (LRO) variance into age- and stage-specific contributions for the size class–structured *Tsuga* matrix model. *A*, *B*, Partitioning by age of the state trajectory and fecundity contributions to Var(LRO). Note the much smaller *Y*-axis scales. The dashed red vertical line shows the age that makes the largest total contribution. *C*, Subpartitioning luck into variance among breeders and variance due to breeding versus not ever breeding. *D*, Image plot of the age-dependent stage distribution of survivors, with lighter colors indicating higher values. *E*, *F*, Partitioning by state of the state trajectory and fecundity contributions to Var(LRO). Figure produced by the script TsugaPartitioning.R.

peregrine falcon population (fig. S2; the model and analysis are described in app. S6). Early luck is most important; the very earliest luck is about becoming a breeder or not, and later luck determines variation among breeders. In contrast to *Tsuga*, the luck by stage partitioning is bimodal (fig. S2*D*), because the higher early-stage mortality in falcons increases the impact of early-stage luck.

Dacrydium elatum

Zuidema et al. (2010) developed an integral projection model for the tropical rainforest tree *D. elatum*, which we have used previously as a case study (Snyder and Ellner 2016). The model has four discrete stages for seedlings (<1 cm dbh) classified by height and a continuous size range for saplings and adults classified by diameter at breast height. We partitioned between breeders and nonbreeders using definition 2, as the model includes a size-dependent flowering probability based on direct observations. There are no observations on variation in flower or recruit numbers conditional on flowering, so as with *Tsuga* we posited a Poisson distribution resulting from many seeds with low recruitment probability.

Figure 3 shows the partitioning of LRO variance by age and size (for plotting, the four seedling stages have been assigned fictitious sizes of −3,−2,−1, and 0, while the continuous size range is 0–100 cm dbh). As with *Tsuga*, state trajectory luck dominates fecundity luck by orders of magnitude. (Hence, we are not especially concerned about whether the Poisson assumption is very accurate.) As with *Tsuga*, early state trajectory luck is driven by variance in breeding versus not breeding, while later luck mostly results from variance among breeders. Because growth is nearly deterministic (age predicts size well and vice versa; fig. 3*F*), the age- and size-dependent decompositions (fig. 3*A*–3*D*) show very similar trends. All vital rates are size dependent, so the age-dependent partitioning is a smoothed version of the size-dependent partitioning resulting from the multiple ages at which individuals achieve a given size. The small kink at 50 cm dbh (fig. 3*C*) corresponds to a peak in the stable size (not shown) and size at death distributions (Snyder and Ellner 2016, fig. 10*A*), resulting from deceleration in growth that creates a pileup of individuals at ≈50 cm dbh.

The contrast between the *Tsuga* pattern (largest stage is most important) and the *Dacrydium* pattern (intermediate sizes are most important) results from the fact that the largest stage in the *Tsuga* model includes all individuals above a certain size, so individuals reaching that stage stay there for a long time on average (fig. 2*D*). In the *Dacrydium* model, large individuals never stop growing, so they do not spend a long time in any particular portion of the size range (fig. 3*F*).

The *Tsuga* pattern is thus an inevitable outcome of the model structure. It might also represent biological reality if the trees truly have determinate growth such that all older, maximally fecund individuals are fairly similar in size.

Partitioning with Trait Variation: Theory

Pluck versus Luck

Having seen how we can identify multiple kinds of luck and partition them by age, we now expand our model to include persistent trait variation among individuals and investigate the relative contributions of luck and trait variation across ages. We use the term "trait" to indicate an attribute that does not change over an individual's lifetime (which others have called "individual heterogeneity"). Possible examples are the individual's genotype at some locus or loci, their breeding value for a quantitative heritable trait, their location at birth or as sedentary adults, or their mother's age or condition when they were born. This contrasts with state variables, which are attributes that change over time in a partially stochastic manner described by a survival/growth kernel or matrix. Individual attributes that change over time in a totally deterministic manner are currently beyond the scope of our theory (see Ellner et al. 2016, chap. 3, sec. 10.4).

Equation (13) divides the total variance in LRO into a luck term, which involves the variance of LRO given a trait value, and a pluck term, which involves the expected value of LRO given a trait value. The following subsections are important for understanding how to calculate the partitions of each term by age and how to further partition these into breed-or-not and among-breeder components, but no new conceptual material is introduced. Readers who are willing to take these results on trust can skip to the case studies in "Partitioning with Trait Variation: Case Studies."

Let x denote the individual trait affecting demographic rates; state variables are still denoted z. Because x is static, we can regard it as being assigned at birth. We let $c_0(z, x)$ be the joint probability distribution of state and trait at birth and $p_0(x) = \int c_0(z, x)\, dz$ the marginal distribution of the trait at birth.

The starting point is a decomposition of total LRO variance using the law of total variance:

$$\mathrm{Var}(R) = \underbrace{\mathbb{E}_x(\mathrm{Var}(R|x))}_{\text{luck}} + \underbrace{\mathrm{Var}_x(\mathbb{E}(R|x))}_{\text{pluck}} . \tag{13}$$

Caswell (2009) used this approach to quantify the contribution of variation in initial environment state in a model with time-varying environment, and it has since been applied to other kinds of traits, as we do here (e.g., Hartemink

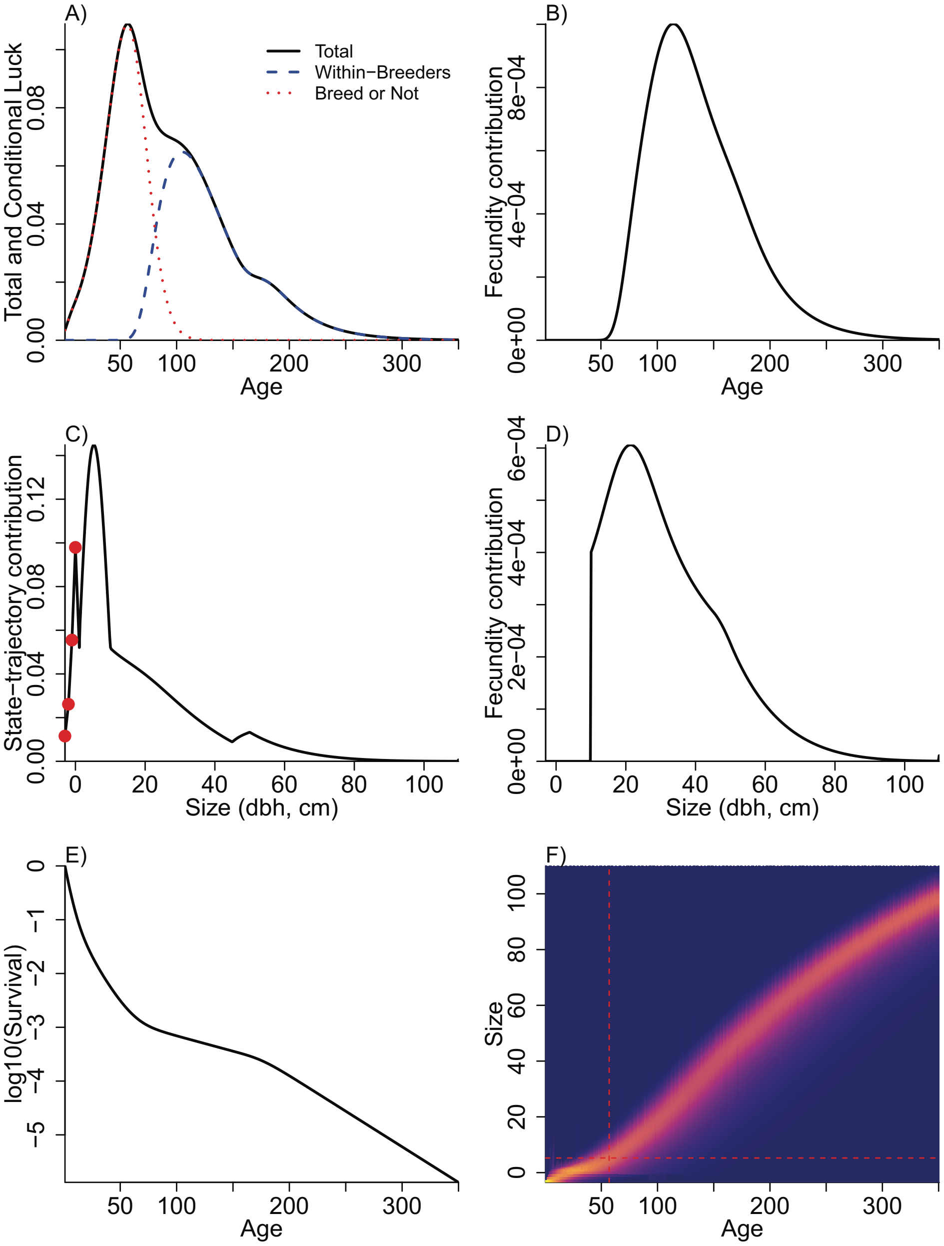

Figure 3: Partitions of lifetime reproductive output variance into age- and size-specific contributions for the *Dacrydium elatum* integral projection model of Zuidema et al. (2010). For plotting, the four seedling stages have been assigned fictitious sizes of −3, −2, −1, and 0 (red solid circles in *C*), while the continuous size range runs from 1 to 110 cm dbh. *E* shows survival to age *a*, and *F* is an image plot of the age-dependent size distribution of survivors, with lighter colors indicating higher values. Note the much smaller *Y*-axis scales for fecundity luck. Figure produced by the script DacrydiumPartitioning.R.

and Caswell 2018; Jenouvrier et al. 2018; Snyder and Ellner 2018). It is equivalent to a one-way ANOVA, in which the pluck term is variance due to the main effect of the trait.

An important feature of equation (13) for subsequent steps is the absence of any interaction terms. Luck (e.g., randomness in state transitions) affects $\mathbb{E}(R|x)$, but this interaction is subsumed into the pluck term. Similarly, trait values affect the trajectory an individual takes through life (e.g., those with higher survival will have longer trajectories on average), but because luck is a population-wide average of $\mathrm{Var}(R|x)$, this interaction is subsumed into the luck term. Consequently, finer partitioning of $\mathrm{Var}(R)$ may be possible, leading to finer cross partitions by age and/or state. Here we use the established definition in equation (13), and our goal is to partition each term as we did above for luck in the absence of trait variation.

Partitioning Luck with Trait Variation

Partitioning Luck by Age. To partition the luck term in equation (13) by age, we can apply equation (7) to each possible value of x and then average over the distribution of x. The result is

$$\begin{aligned}\underbrace{\mathbb{E}_x(\mathrm{Var}(R|x))}_{\text{luck}} &= \underbrace{\mathbb{E}_x[\tilde{c}_{0,x}^{\mathsf{T}}\tilde{\rho}_{1,x}^2 - (\tilde{c}_{0,x}^{\mathsf{T}}\tilde{\rho}_{1,x})^2]}_{\text{prenatal}} \\ &+ \underbrace{\sum_{a=0}^{\infty}\mathbb{E}_x[\tilde{V}_x^{\mathsf{T}}P_x^a\tilde{c}_{0,x}]}_{\text{state trajectory}} \\ &+ \underbrace{\sum_{a=0}^{\infty}\mathbb{E}_x[(\tilde{\sigma}_{b,x}^2)\mathsf{T}P_x^a\tilde{c}_{0,x}]}_{\text{fecundity}},\end{aligned} \tag{14}$$

with the x subscripts indicating that V, σ_b^2, P, and c_0 can in general all depend on x. Note that ρ_1 in the formula for V_x (eq. [5]) will depend on x as well.

If the trait distribution is discrete, each $\mathbb{E}_x$ is just a weighted average of (x, a)-dependent terms with respect to the distribution of x. For continuous trait distributions, each term is computed for a set of quadrature points (e.g., evenly spaced mesh points for midpoint rule), and the expectation is done by numerical integration with respect to the assumed distribution of x.

Partitioning Luck by State. As in the section without trait variation, we omit prenatal luck when partitioning luck by state, as it does not occur at any living state. The infinite sums in the other two terms in equation (14) are the integrals with respect to state z of

$$\mathbb{E}_x[\tilde{V}_x^{\mathsf{T}}\circ(\tilde{N}_x\tilde{c}_{0,x})] \quad \text{and} \quad \mathbb{E}_x[(\tilde{\sigma}_{b,x}^2)^{\mathsf{T}}\circ(\tilde{N}_x\tilde{c}_{0,x})], \tag{15}$$

respectively, thinking of the expressions in brackets as functions of z for each x.

Partitioning Pluck

Partitioning Pluck by Age. The goal is to partition $\mathrm{Var}_x\mathbb{E}(R|x)$ into contributions from trait variation at each age. The general variance decomposition (eq. [S8]) can again be applied, but in this case it involves conditional distributions that we do not know how to compute. We therefore use the alternative approach based on a modified life cycle (see "Luck by Age: Another Interpretation"), in this case one where trait variation is absent beyond a certain age.

Specifically, let $\vec{x} = (x_0, x_1, x_2, \ldots)$ be a vector of the individual's trait at all ages (up to this point in the article, all $x_j = x$), and let x^* denote a trait value such that individuals with trait x^* have the average P and F kernels across the trait distribution. Typically no actual trait value will have this property, so x^* is a discrete point added to the trait space. Define

$$\begin{aligned}\nu_{-1} &= \mathrm{Var}_x\mathbb{E}(R|\vec{x} = (x^*, x^*, x^*, \ldots)) = 0, \\ \nu_0 &= \mathrm{Var}_x\mathbb{E}(R|\vec{x} = (x, x^*, x^*, \ldots)), \\ \nu_1 &= \mathrm{Var}_x\mathbb{E}(R|\vec{x} = (x, x, x^*, \ldots)),\end{aligned} \tag{16}$$

and so on. In ν_a, each individual has its actual trait x up to age a and after that has trait x^*. The pluck-by-age decomposition is

$$\text{pluck} = (\nu_0 - \nu_{-1}) + (\nu_1 - \nu_0) + (\nu_2 - \nu_1) + \cdots. \tag{17}$$

Each difference $(\nu_a - \nu_{a-1})$ is the marginal increase in $\mathrm{Var}_x\mathbb{E}(R)$ from having trait value x and the corresponding kernels for one more year, given that you had trait value x at all previous ages.

We now need to compute the terms. Let $\bar{P}$ and $\bar{F}$ be the averages of the trait-dependent kernels P_x and F_x with respect to x, and let $\bar{N} = (I - \bar{P})^{-1}$. Then

$$\begin{aligned}\nu_a &= \mathrm{Var}_x(\rho_{0,a}(x)) = p_0^{\mathsf{T}}\rho_{0,a}^2 - (p_0^{\mathsf{T}}\rho_{0,a})^2, \text{where} \\ \rho_{0,a}(x) &= \mathbb{E}(R|\vec{x} = (\overbrace{x, x, \ldots, x}^{a+1 \text{ times}}, x^*, x^*, \ldots)) \\ &= \underbrace{\mathbf{e}^{\mathsf{T}}F_xc_{0,x}}_{\text{RO at age} = 0} + \underbrace{\mathbf{e}^{\mathsf{T}}F_xP_xc_{0,x}}_{\text{RO at age} = 1} + \cdots \\ &\quad + \underbrace{\mathbf{e}^{\mathsf{T}}F_xP_x^ac_{0,x}}_{\text{RO at age} = a} + \underbrace{\mathbf{e}^{\mathsf{T}}\bar{F}\bar{N}P_x^{a+1}c_{0,x}}_{\text{RO later}} \\ &= \mathbf{e}^{\mathsf{T}}F_x(I + P_x + P_x^2 + \cdots + P_x^a)c_{0,x} \\ &\quad + \mathbf{e}^{\mathsf{T}}\bar{F}\bar{N}P_x^{a+1}c_{0,x} \\ &= \mathbf{e}^{\mathsf{T}}[F_xN_x(I - P_x^{a+1}) + \bar{F}\bar{N}P_x^{a+1}]c_{0,x}.\end{aligned} \tag{18}$$

As a check on equation (18), note that when $a = 0$ the formula reduces to $\rho_{0,0}(x) = \mathbf{e}^{\mathsf{T}}[F_x + \bar{F}\bar{N}P_x]c_{0,x}$, as it ought to, because $N_x(I - P_x) = I$. Newborns with trait x have initial state distribution $c_{0,x}$ and one year with fecundity kernel F_x; total expected RO at all later ages results from the age 1 state distribution $P_xc_{0,x}$ and the average kernels.

For calculation, write

$$\begin{aligned}\rho_{0,a}(x) &= \mathbf{A}_x + \mathbf{b}_x^{\mathsf{T}}P_x^ac_{0,x}, \text{where} \\ \mathbf{A}_x &= \mathrm{e}^{\mathsf{T}}F_xN_xc_{0,x} \text{ and } \mathbf{b}_x^{\mathsf{T}} = \mathbf{e}^{\mathsf{T}}(\bar{F}\bar{N} - F_xN_x)P.\end{aligned} \tag{19}$$

For each x, $\mathbf{A}_x$ and $\mathbf{b}_x^{\mathsf{T}}$ can be computed once and for all, so computing all $\rho_{0,a}(x)$ for any one x is only as demanding as one iteration of the model up to an age at which nearly all reproduction has occurred, regardless of trait value.

Equation (19) implies that the differences $\rho_{0,a+1}(x) - \rho_{0,a}(x)$ have an asymptotically exponential decrease at a rate given by the dominant eigenvalue of P_x. The same is therefore true for the variance differences $(\nu_{a+1} - \nu_a)$, implying that the series in equation (17) is convergent with an exponentially decreasing tail.

Can We Partition Pluck by State? Can the effects of trait variation be partitioned sensibly by the individual's state when they occur, analogous to the luck-by-state decomposition (eq. [15])? We think the answer is no. This is because trait-dependent LRO variance is a comparison across groups of individuals with different state transition probabilities, which therefore spend different average amounts of time in each state. If one group is persistently fast growing and another slow growing, for example, the resulting difference between them in average LRO is due to events that happen to one group in one set of states and to the other group in another set of states. To which set of states should we credit the difference in average LRO? Some arbitrary decision could be made (e.g., using the average state distribution), but this does not seem meaningful to us, so we do not try to partition effects of trait variation by state.

Breeders versus Nonbreeders with Trait Variation

We begin with the usual luck/pluck partitioning, equation (13); total luck is $\mathbb{E}_x(\mathrm{Var}(R|x))$. Applying our earlier breeder/nonbreeder partitioning, equation (11), the among-breeders component of $\mathrm{Var}(R|x)$ is $\Pr(M = 1|x)\mathrm{Var}(R|x, M = 1)$. We can then apply our age decomposition of luck, equation (1), to $\mathrm{Var}(R|x, M = 1)$. The result is that the age partitioning for the among-breeders component of luck is given by

$$\begin{aligned}&\mathbb{E}_x\{\Pr(M = 1|x)[\mathrm{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{z}_0)]]_{x,1}\}\\ &\quad+\sum_{a=0}^{A-1}\mathbb{E}_x\{\Pr(M = 1|x)[\mathbb{E}_{\mathbf{z}_a}\mathrm{Var}_{\mathbf{z}_{a+1}|\mathbf{z}_a}[\mathbb{E}(R|\mathbf{z}_{a+1})]]_{x,1}\}\\ &\quad+\mathbb{E}_x\{\Pr(M = 1|x)[\mathbb{E}_{\mathbf{z}_{0:A}}\mathrm{Var}[R|\mathbf{z}_{0:A}]]_{x,1}\},\end{aligned} \tag{20}$$

where the subscript "x,1" indicates that the term in brackets is calculated for individuals with trait value x conditional on $M = 1$. The three lines in expression (20) are the among-breeders components of the prenatal, state trajectory, and fecundity components of total luck. Note that the outer $\mathbb{E}_x$ in each line is the unconditional trait distribution; the $\Pr(M = 1|x)$ factor does the weighting of the trait distribution based on the probability of becoming a breeder.

With the formulas in equation (7), we calculate expression (20) in the limit $A \to \infty$ as

$$\begin{aligned}&\mathbb{E}_x\{\Pr(M = 1|x)[\tilde{c}_{0,x}^{\mathsf{T}}\tilde{\rho}_{1,x}^2 - (\tilde{c}_{0,x}^{\mathsf{T}}\tilde{\rho}_{1,x})^2]_1\}\\ &\quad+\sum_{a=0}^{\infty}\mathbb{E}_x\{\Pr(M = 1|x)[\tilde{V}_x^{\mathsf{T}}P_x^a\tilde{c}_{0,x}]_1\}\\ &\quad+\sum_{a=0}^{\infty}\mathbb{E}_x\{\Pr(M = 1|x)[(\tilde{\sigma}_{b,x}^2)^{\mathsf{T}}P_x^a\tilde{c}_{0,x}]_1\},\end{aligned} \tag{21}$$

where the subscript 1 again indicates that the term is calculated conditional on $M = 1$.

$\Pr(M = 1|x, z)$ is calculated by methods described in appendix S4, where it is denoted $B(z)$, using the kernels/matrices for trait value x. The conditioning of bracketed terms in expression (21) on $M = 1$ is done as follows. First, appendix S4 explains how to compute the conditional P kernel/matrix and fecundity moments for each of the three definitions of becoming a breeder. These can be used to compute $\tilde{V}$ and $\tilde{\rho}_1$ conditional on $M = 1$ for each value of x (or for a grid of x mesh points if x is continuous). Second, individuals destined to become breeders have a different distribution of birth states. For individuals with trait value x, the birth-state distribution (without any conditioning on M) is

$$c_{0,x}(z) = \frac{c_0(z,x)}{\int c_0(u,x)\,du}. \tag{22}$$

To compute the corresponding distribution conditional on $M = 1$, we imagine that all individuals with trait x are born into state z with probability $c_{0,x}(z)$. The distribution of z at birth conditional on $M = 1$ for individuals with trait value x is then (by Bayes theorem)

$$c_{0,x,1}(z) = \frac{c_{0,x}(z)\Pr(M = 1|z,x)}{\Pr(M = 1|x)}. \tag{23}$$

Appending probability zero of birth at ω gives the conditional $\tilde{c}_{0,x}$ function used in expression (21).

With these ingredients, all terms in expression (21) can be computed and averaged across the trait distribution. The breed-or-not portion of luck is then partitioned by doing term-by-term subtraction of the among-breeder partition (21) from the total luck partition (14). For example, the breed-or-not portion of age 1 fecundity luck is

$$\mathbb{E}_x[(\tilde{\sigma}_{b,x}^2)^{\mathsf{T}}P_x\tilde{c}_{0,x}] - \mathbb{E}_x\{\Pr(M = 1|x)[(\tilde{\sigma}_{b,x}^2)^{\mathsf{T}}P_x\tilde{c}_{0,x}]_1\}. \tag{24}$$

Next, we aim to partition by age the contribution of trait variation to variation in R among breeders. From equation (11) the among-breeder variance in R is $\mathbb{E}_M(\mathrm{Var}(R|M) = p_M\mathrm{Var}(R|M = 1)$. We can partition that as follows, using the fact that $R = 0$ if $M = 0$:

$$\begin{aligned}\mathbb{E}_M(\mathrm{Var}(R|M) &= \mathbb{E}_M[\mathbb{E}_{x|M}(\mathrm{Var}(R|M,x))]\\ &\quad + \mathbb{E}_M[\mathrm{Var}_{x|M}(\mathbb{E}(R|M,x))]\\ &= \underbrace{p_M\mathbb{E}_{x|M=1}[\mathrm{Var}(R|M=1,x)]}_{\text{luck}}\\ &\quad + \underbrace{p_M\mathrm{Var}_{x|M=1}[\mathbb{E}(R|M=1,x)]}_{\text{pluck}}.\end{aligned} \tag{25}$$

The luck term above is already dealt with (eq. [21]). What remains is to age partition $\mathrm{Var}_{x|M=1}[\mathbb{E}(R|M=1,x)]$ and multiply each term by p_M. We already know how to do the age partitioning—it is the same as what we have already done to age partition pluck, except that we condition on $M = 1$ at two stages: computing $\rho_{0,a}(x)$, and computing the variance over trait values x. Specifically, define

$$\rho_{0,a,1}(x) = \mathbf{A}_{x,1} + \mathbf{b}_{x,1}^{\mathsf{T}} P_{x,1}^{a} c_{0,x,1}, \tag{26}$$

where

$$\begin{aligned}\mathbf{A}_{x,1} &= \mathbf{e}^{\mathsf{T}} F_{x,1} N_{x,1},\\ \mathbf{b}_{x,1}^{\mathsf{T}} &= \mathbf{e}^{\mathsf{T}}(\bar{F}_1 \bar{N}_1 - F_{x,1}N_{x,1})P_{x,1},\end{aligned} \tag{27}$$

and as in expression (20), the "x,1" subscript indicates that the item is calculated for individuals with trait value x conditional on $M = 1$. Then calculate

$$v_{a,1} = \mathrm{Var}_{x|M=1}\rho_{0,a,1}(x) = p_{0,1}^{\mathsf{T}}\rho_{0,a,1}^{2} - (p_{0,1}^{\mathsf{T}}\rho_{0,a,1})^{2}, \tag{28}$$

where $p_{0,1}$ is the trait distribution conditional on $M = 1$, $p_{0,1}(x) = p_0(x)\Pr(M = 1|x)/p_M$. As before, the among-breeder pluck at age a is $v_{a,1} - v_{a-1,1}$.

Partitioning with Trait Variation: Case Studies

Sagebrush Steppe Perennial Plants

The new results here let us complete our analysis of luck across the life span in Idaho sagebrush steppe perennial plants. Competition with conspecific neighbors has a large effect on seeding survival. We had hypothesized that the "happy few" seedlings that established and grew to be large and fecund adults were individuals that had relatively little competition as seedlings and therefore thrived in their early years of life (Snyder and Ellner 2018). We developed IPMs for the shrub *Artemisia tripartita* (threetip sagebrush) and the perennial grass *Pseudoroegneria spicata* (bluebunch wheatgrass) with individuals cross classified by size and the strength of competition from neighboring plants. To our surprise, we found that variation in first-year competition neighborhood accounted for under 1% of Var(LRO) in both species. Luck in the first transition (size and competitive neighborhood change between ages 0 and 1) was much more important, but these two annual contributions (the only ones we could compute then) contributed under 15% of the total variance in both species—other forms of luck made up the rest of the variance.

Here we use the theory developed above to present a complete partitioning of LRO variance by age, which clarifies how later-in-life luck can dominate the very visible impacts of early luck. In this analysis, the effect of initial competitive neighborhood is the prenatal luck term because that is the only way in which one seedling differs from another. The trait in the analysis is spatial location, to account for spatial variation in demographic rates. Data analyses (described in Snyder and Ellner 2018) reveal that survival of both seedlings and larger plants (but not growth) vary among spatially clustered groups of permanent quadrats. However, the limitations of our previous methods forced us to model a typical location.

Because data on individual seed production is sparse and year-to-year variation in recruitment is very large, we consider variance in life span rather than LRO. Life span is an effective indicator for the highly productive in this species because growth is nearly deterministic (Snyder and Ellner 2018, figs. 5, 6) and older plants are all large and fecund. As we noted above, our methods for LRO apply to life span simply by giving each individual exactly one fictional offspring in each year of life.

For both species, pluck (the effect of spatial variation) is swamped by luck, which accounted for more than 99.5% of the variance in life span in both species. As we previously found, prenatal luck (i.e., your competition neighborhood when first censused) contributes very little in both species (fig. 4). The year between first and second census makes the largest single contribution to luck, but later transitions in size and competitive neighborhood together account for most of the total (71% in *Artemisia*, 77% in *Pseudoroegneria*). Because age-specific luck declines rapidly with age, most of the total variance is the result of luck in the first 10 years of life (67% in *Artemisia*, 63% in *Pseudoroegneria*).

Kittiwakes

The kittiwake (*Rissa tridactyla*) remains at the center of debates about the magnitude and ecological significance of within-population heterogeneity (Steiner et al. 2010; Steiner and Tuljapurkar 2012; Cam et al. 2013, 2016; Authier et al. 2017). Decades-long study of marked individuals has revealed persistent individual differences that manifest as correlated variation in age-dependent survival and breeding probabilities (Cam et al. 2002, 2013). Because the traits underlying this variation are unknown, they are collectively referred to as "quality." We previously concluded (Snyder and Ellner 2018) that individual quality was only very weakly predictive of LRO, based

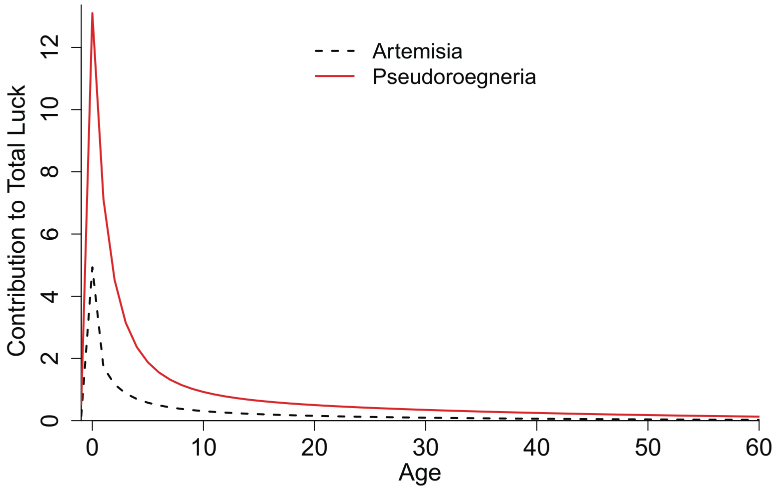

Figure 4: Partitions of life span variance into age-specific contributions for *Artemisia tripartita* and *Pseudoroegneria spicata*. For plotting, prenatal luck has been assigned to age −1. Figure produced by the scripts IdahoPartitioning.R and IdahoPartitioning-Plots.R.

on extending the Steiner and Tuljapurkar (2012) model to incorporate the quality variation estimated by Cam et al. (2002). The Steiner and Tuljapurkar (2012) model has some imperfections: it was parameterized in ways that might exaggerate the importance of luck (Authier et al. 2017); breeding success may depend less on age (as the model assumes) than on experience (Desprez et al. 2011), which the model omits; and we find that it predicts steady-state breeding probabilities lower than those reported by Cam et al. (2002). Nonetheless, the extensiveness of the empirical data and the effort that has gone into analyzing the data still make it one of the best available animal examples for our purposes.

The effects of luck and quality peak early in life (fig. 5). Effects of quality probably peak early because quality includes survival, and the key to having many offspring is not dying young. Quality becomes more important relative to luck as age increases, finally exceeding the contributions of luck at advanced ages. However, the high effect of trait variation at such advanced ages may be an artifact of the infinite tails in the fitted model's quality distribution (Gaussian, on the scale of the linear predictor in logistic regression). The trait variation that becomes dominant at advanced ages is mostly the difference between the living and the dead. But the average life span of an average quality individual is just over 8 years, so living to age 51 (where the contributions of quality exceed those of luck) is possible only for birds very far out in the tails of the quality distribution (fig. 5*C*).

In the first few years, about half of luck contributions and a quarter of quality contributions determine whether an individual gets to breed at all. Birds who have survived longer than this are likely to have bred, so the contributions of luck and quality determine how often and how successfully they bred.

Management for Luck

When eigenvalue elasticity analysis is used to guide management decisions, we are tacitly assuming that the cost of a certain percentage increase in a vital rate is the same for all vital rates, regardless of how many individuals are affected by changing a particular vital rate. High elasticity results, in part, when many individuals are affected by a particular transition. But if there is, instead, a constant cost of shepherding one well-chosen individual through a particularly important transition, then elasticity analysis would be misleading. Using the new results in this article to "manage for luck," as we now describe, might then be a useful alternative.

In populations where state trajectory luck dominates LRO variance, we might want to intervene at a key point in a life's trajectory. State trajectory luck is most decisive for individuals in the state with the highest value of V, the variance, over possible transitions from that state, of expected LRO from that point onward (see eqq. [5], [6]). From that state, we would like to facilitate the possible transition yielding the highest expected LRO and prevent the possible transition yielding the lowest expected LRO (usually death).

For example, consider a population of kittiwakes with widely varying quality. In our model, the highest V occurs for 5-year-old or older failed breeders of the highest quality.

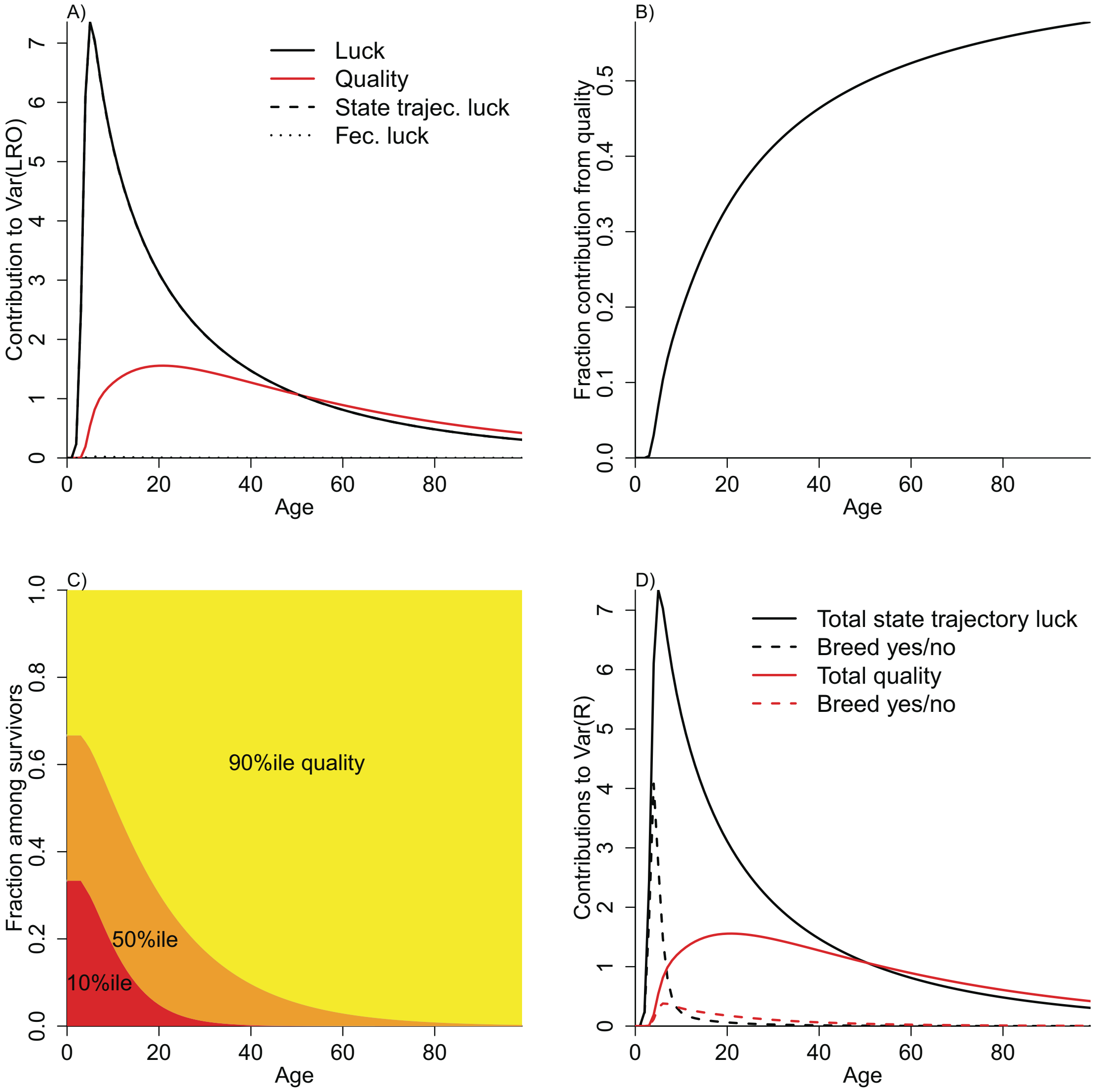

Figure 5: Partitions of lifetime reproductive output (LRO) variance into age-specific contributions for kittiwake (*Rissa tridactyla*). *A*, Age-specific contributions of luck (solid black line) and quality (solid red line). Luck is further broken down into state trajectory luck (dashed line, nearly coincident with the solid black line) and fecundity luck (dotted line, nearly coincident with the abscissa). All chicks are born into the same state, so there is no prenatal luck. *B*, Fraction of LRO variance coming from quality variation as a function of age. *C*, Change in quality distribution as a function of age—very old birds are all very high-quality birds. *D*, Total contribution of state trajectory luck (essentially total luck) and quality (solid red and black lines) and within each, the variance due to breeding versus never breeding. Figure produced by the script KittiwakePartitioningNewLuckPluck13.R.

From that state, birds can die or become either nonbreeders, failed breeders, parents of one chick, or parents of two or three chicks. At this quality level, the living states have expected LRO varying from 62 to 68. The most important thing, then, is to help these older, high-quality failed breeders to survive (death has an LRO of zero) and, to a lesser degree, to become successful parents (LRO of 68 instead of 62). Exactly what help to provide depends on what limits survival. If energy stores are limiting, we could supplement food. If predators are a problem, we could install predator-excluding barriers.

In contrast, the highest elasticity for the kittiwake model is the transition from age 5 or older highest-quality parents of one chick to having one chick again the following year. This is due in part to there being more one-chick parents than failed breeders at steady state.

We see similar results for our other models. For *Tsuga*, luck peaks (V is largest) in size classes 5 and 6, and the most important thing is to help these individuals survive and, to a lesser extent, to help size class 5 individuals to grow. However, eigenvalue elasticity says that survival of stage 6 is by far the most important. This reflects the fact that in the steady-state distribution, size class 6 is substantially more abundant than size class 5. For the peregrine falcons, managing for luck means helping age 1 nonbreeders to survive and ideally breed the next year. In contrast, the highest elasticity is for survival of breeders, again because of the high abundance of breeders at steady state. For *Dacrydium*, management for luck tells us to enhance the survival of trees with the highest expectation of future reproduction given their current size (about 25 cm dbh), while elasticity analysis says to help the small (either the largest of the four sapling stages or the smallest postsapling individuals, depending on whether we include the sapling stages), in large part because of their higher abundance. Roe deer (app. S6) tell a similar story. Managing for luck means aiding the survival of adults with the highest expected LRO—those with the earliest birthday and the highest body mass—while elasticity is highest for the most abundant adults, which are those with intermediate body mass and birth timing.

Discussion

Using the age partitioning we have presented here, we can see how the balance of luck and trait variation plays out over an individual's life. For some organisms luck peaks sharply early in life (e.g., peregrine falcon, *Pseudoroegneria spicata*, *Artemisia tripartita*). This indicates a period of high risk, after which individuals are relatively safe. For other organisms, luck still peaks early but it declines more gradually: the first step in leaving many offspring is always to avoid dying young, but events later in life still have substantial influence over reproductive success (e.g., *Tsuga canadensis*, *Dacrydium elatum*, kittiwakes, roe deer).

In general, it is better to be lucky than good at all ages. Our earlier work showed theoretically that good traits are often necessary but not sufficient for exceptional reproductive success (Snyder and Ellner 2018). The age partitioning presented here shows that the contributions of luck to LRO variance outweigh those of trait variation at all ages in our case studies. The relative importance of traits may peak earlier or later in life, depending on the traits that vary between individuals, but luck trumps pluck.

Luck comes from different sources. We find that having lucky state transitions (in particular, not dying) is especially influential. The right change in state at the right age can have an outsize influence on LRO. Random variation in the number of offspring is the second most influential form of luck, and random variation in birth state can also contribute. Liu et al. (2019) provide some empirical support for the importance of state trajectory luck. For caged *Drosophila* populations, maximum likelihood estimates of drift were well above those predicted by a Wright-Fisher model, which includes fecundity luck but not state trajectory luck. (Specifically, the drift-effective population size for a Wright-Fisher model [their table 1] was far below actual population sizes [their fig. 1].) The evolutionary models underlying genomic data analysis typically do not include population structure, which amounts to assuming that state trajectory luck has no effect. Our findings about state trajectory luck suggest that models without population structure will typically underestimate substantially the random component of genetic change. This does not stop natural selection from acting, as we noted in the introduction, because effects of luck still average out in large enough populations. More precisely, luck adds a correction term to the strength of selection, which scales as the inverse of population size but vanishes more slowly when the random variation in LRO is larger (Snyder and Ellner 2018).

We further partition the age-specific contributions of luck and traits into contributions toward whether an individual breeds at all versus how many offspring they have, given that they breed. These contributions explain the double-peaked age distribution of luck that we see in organisms with long reproductive spans, such as trees. Very early luck in state transitions—probably ensuring that the individual does not die young—contributes to whether that individual ever breeds, while less early luck in state transitions drives variation in the LRO of individuals who breed at least once.

We have proposed that the partitioning of LRO variance presented here may offer new insights for population management. Eigenvalue elasticities are useful when one intervention affects all members of a stage (e.g., protecting adult sea turtles by adding turtle excluder devices to fishing nets). However, the cost of some interventions is likely to scale with the number of individuals helped. In those cases, we may wish to "manage for luck" and help well-chosen individuals at life stages where the outcome of their next transition has a large effect. This often produces different answers than elasticity analysis, in which benefits are weighted by the abundance of individuals in a given stage. In many cases, managing for luck leads to a simple principle: help individuals with the highest expected total reproductive output over the remainder of their life.

We believe that luck will always peak early in life because if you die young, it does not matter how lucky you would have been once you got older. We further suggest that state trajectory luck will be increasingly dominant as life span increases—the longer your life, the greater the number of paths through it. Playing with a model with a flexible life history (the toy model in app. S5) suggests contingent effects of juvenile maturation rate and juvenile and adult mortality. More work is needed on the effects of life history.

Here we have used variance as a measure of variability in LRO, but higher moments may be important. Tuljapurkar et al. (2020) show how to calculate the full distribution of LRO and, among other case studies, show that the LRO distribution for *T. canadensis* is highly skewed while that of *C. capreolus* is multimodal. These distributions cannot be characterized simply by mean and variance. However, we know of no good way to partition a full distribution. The law of total cumulance shows how to partition higher moments, but anything above variance quickly becomes unwieldy. We advise readers interested in characterizing the full range of variation in LRO to use the techniques in Tuljapurkar et al. (2020) and to consider the techniques here for exploring some of the reasons that variation comes about.

Writing this article brought home to us the paucity of empirical data on distributions of annual reproductive output. We are prepared to accept Poisson distributions for plants (many seeds, low survival, no parental care, lottery for survival) or zero-inflated Poisson when there is information on flowering probability. But for animals this assumption is dubious. Information on variation in clutch sizes is even a potential data item in COMADRE. We encourage adding this information, when available, to collections like COMADRE, and we encourage efforts to gather the data in empirical studies. While only the mean age- or state-specific fecundity matters for deterministic population projections using a matrix or IPM, because these do not account for demographic stochasticity, the full distribution matters when analyzing individual life trajectories. Tools to do that are now available and rapidly growing (Caswell 2012, 2019; Steiner et al. 2012; van Raalte and Caswell 2013; van Daalen and Caswell 2015, 2017; Roth and Caswell 2018; Tuljapurkar et al. 2020).

More generally, we are taking models constructed for one purpose, population projection, and using them for another. We have mentioned some potential issues in the *Tsuga* and kittiwake models. But using old models for new purposes is generally problematic because model selection is always selection for some purpose (Tredennick et al. 2021). We do not know how to select the best model complexity or structure for inferring life cycle variability and its origins, as in this article (how many ages/stages in a matrix model, degree of smoothing in demographic rates for IPMs, etc.), or for the many other analyses that are possible (e.g., Caswell 2019). Our ability to extract information from population models is running ahead of our ability to construct those models.

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Statement of Authorship

R.E.S. and S.P.E. shared responsibility for conceptualization, coding, and writing. Mathematical development was led by R.E.S. and S.P.E. with contributions from G.H.

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Supplemental information for "Time and chance: using age partitioning to understand how luck drives variation in reproductive success," *the American Naturalist*

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Appendices

S1 A supplementary figure for understanding different kinds of luck

To make the luck and pluck calculations more concrete, fig. S1 gives some sample life trajectories for the kittiwake model with average and below-average traits. Trajectories are different between the trait clusters — most of the average quality individuals live longer and have more offspring than the below-average quality individuals. This is the way that trait variation contributes to variance in LRO. However, there is also considerable variability within each cluster — this is the contribution of luck. It is also worth noting that because of luck, the LRO distributions of average and low-quality individuals overlap: some average quality individuals live shorter lives and have fewer offspring than some of the below-average quality individuals. State trajectory luck is the contribution of path length and route to lifetime reproductive output — the more time spent in states 4 and 5, the more offspring an individual has. Fecundity luck is the contribution of clutch size variation — here, whether a state 5 individual has two or three offspring. There is no pre-natal luck, as all individuals begin in state 1.

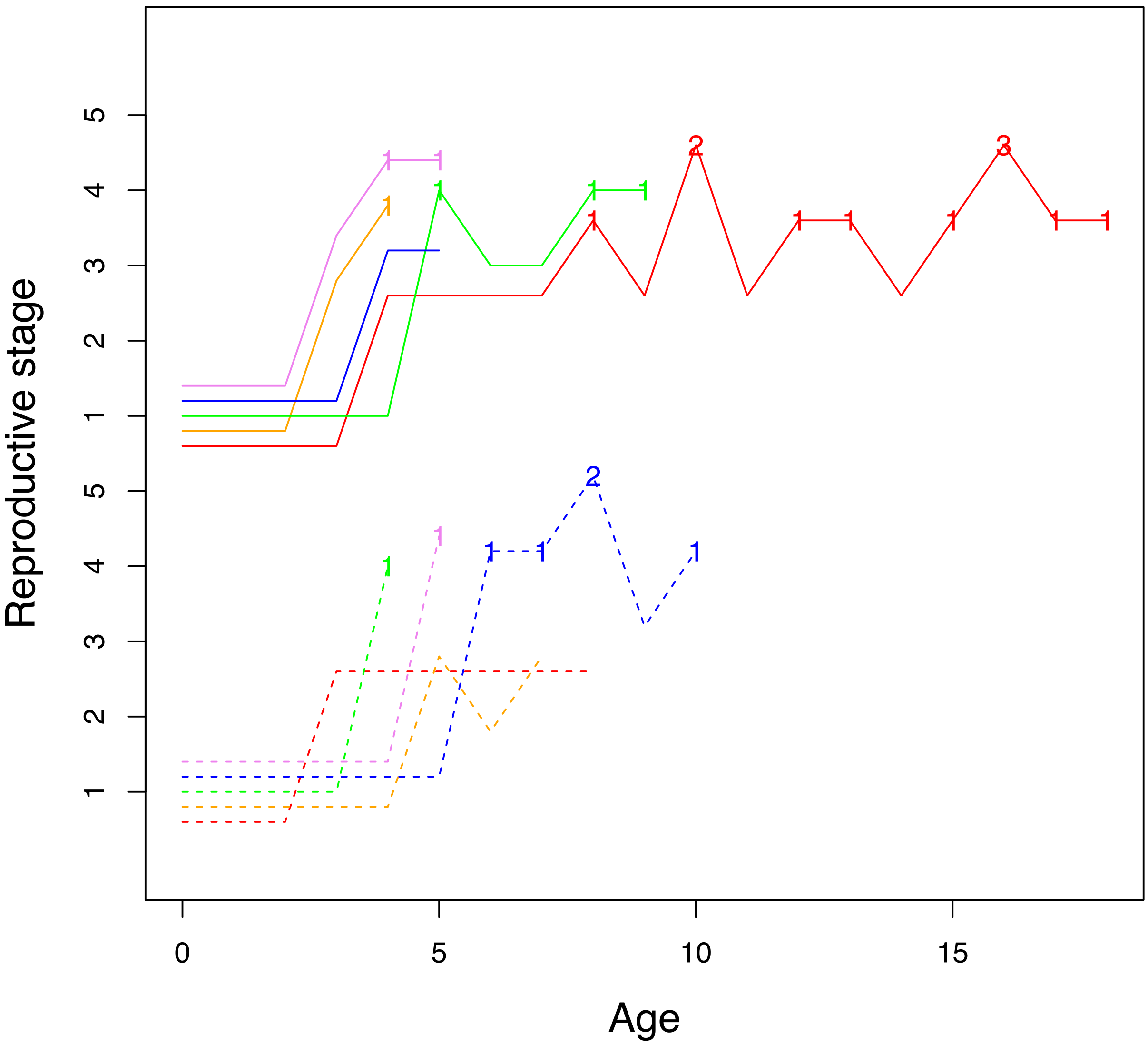

Figure S1: Life trajectories for average and below-average quality kittiwakes. Each colored line represents a life simulated from the kittiwake model and ends with death. The upper cluster of lines is for average quality individuals and the lower cluster of lines is for below-average quality individuals — reduced adult survival and breeding probability. Y-values represent reproductive states (pre-reproductive, failed reproduction, one chick, two or three chicks) and are offset slightly for visibility. Each time an individual has offspring, the number of offspring is marked on the line. Figure produced by script `KittiwakeLifeTrajecPlot.R`.

S2 The Bowsher and Swain (2012) general variance decomposition

The goal of this Appendix is to state the Bowsher and Swain (2012) variance decomposition for stochastic dynamic systems and give a self-contained proof, in the case where information about system dynamics is represented by a sequence of real-valued random variables. Bowsher and Swain (2012) consider the more general case where the information is a sequence of σ-fields. But conditional expectations, variances, etc. with respect to σ-fields are not familiar to most ecologists, and for this paper we only need the random-variable case.

We use more explicit notation than Bowsher and Swain (2012) for conditional expectations and variances. Specifically, $\mathbb{E}_{X|Y}, Var_{X|Y}$ denote expectation and variance in the conditional distribution of X given Y. Expectations without a subscript are unconditional, $\mathbb{E}\,X = \int_\Omega X(u) d\mathcal{P}(u)$ where $(\Omega, \mathcal{F}, \mathcal{P})$ is the underlying probability space, and $Var\,X = \mathbb{E}\,X^2 - (\mathbb{E}\,X)^2$.

Conditional Law of Total Variance

Our first aim is to prove the Conditional Law of Total Variance, stated without proof as eqn. [15] in Bowsher and Swain (2012),

$$Var(Z|G_1) = \mathbb{E}_{G_2|G_1}(Var(Z|G_1, G_2)) + Var_{G_2|G_1}(\mathbb{E}(Z|G_1, G_2)). \tag{S1}$$

Here Z, G_1, G_2 are three random variables defined on the same probability space; either or both of the G_i may be a vector of random variables. Conditional variance is defined as

$$Var(Z|X) = \mathbb{E}(Z^2|X) - \mathbb{E}(Z|X)^2, \tag{S2}$$

where X is any random variable, vector of random variables, or σ-field on the same probability space as Z.

A crucial property for the proof is the following general property of conditional expectations:

$$\mathbb{E}(Z|\mathcal{H}_1) = \mathbb{E}(\mathbb{E}(Z|\mathcal{H}_1, \mathcal{H}_2)), \tag{S3}$$

where $\mathcal{H}_1, \mathcal{H}_2$ are any two σ-fields in the probability space where Z is defined. For the case of σ-fields defined by random variables, eqn. (S3) is

$$\mathbb{E}(Z|G_1) = \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z|G_1, G_2)). \tag{S4}$$

Here G_1 and/or G_2 can again be vectors of random variables. In (S4) both sides of the equation are random variables. If G_1 has a density, the meaning of (S4) is that for all g_1 where the density is positive,

$$\mathbb{E}(Z|G_1 = g_1) = \mathbb{E}_{G_2|G_1=g_1}(\mathbb{E}(Z|G_1 = g_1, G_2)). \tag{S5}$$

Eqn. (S4) is just like nested integrals. If all random variables (or random vectors) have densities (using $f(z, g_1, g_2)$,$f(g_1, g_2)$ and $f(g_1)$ as the density over the arguments)

$$\begin{aligned}
\mathbb{E}_{G_2|G_1=g_1}(\mathbb{E}(Z|G_1 = g_1, G_2)) &= \int\int z\frac{f(z,g_1,g_2)}{f(g_1,g_2)}dy\frac{f(g_1,g_2)}{f(g_1)}dg_2 \\
&= \int z\frac{f(y,g_1,g_2)}{f(g_1)}\,dz\,dg_2 \\
&= \int z\frac{f(y,g_1)}{f(g_1)}\,dz = \mathbb{E}(Z|G_1 = g_1),
\end{aligned} \tag{S6}$$

which is exactly the meaning of (S4) for this case. Note, however, that (S3) implies that (S4) also applies when G_1 and G_2 are vectors of random variables.

We can now derive the Conditional Law of Total Variance. A square outside the brackets following an expectation, e.g. $\mathbb{E}(Z)^2$, means to take the expectation first and then square: $(\mathbb{E}(Z))^2$. Starting with the definition of conditional variance,

$$\begin{aligned}
Var(Z|G_1) &= \mathbb{E}(Z^2|G_1) - \mathbb{E}(Z|G_1)^2 \\
&= \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z^2|G_1,G_2)) - \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z|G_1,G_2))^2 \\
&\qquad \text{(sequentially unconditioning, eqn. (S4))} \\
&= \mathbb{E}_{G_2|G_1}(Var(Z|G_1,G_2) + \mathbb{E}(Z|G_1,G_2)^2) - \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z|G_1,G_2))^2 \\
&\qquad \text{(because } Var(Z|G_1,G_2) = \mathbb{E}(Z^2|G_1,G_2) - \mathbb{E}(Z|G_1,G_2)^2\text{)} \\
&= \mathbb{E}_{G_2|G_1}(Var(Z|G_1,G_2)) + \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z|G_1,G_2)^2) - \mathbb{E}_{G_2|G_1}(\mathbb{E}(Z|G_1,G_2))^2 \\
&\qquad \text{(first expectation is additive, just broke it apart)} \\
&= \mathbb{E}_{G_2|G_1}(Var(Z|G_1,G_2)) + Var_{G_2|G_1}(\mathbb{E}(Z|G_1,G_2)). \\
&\qquad \text{(definition of variance applied to } Y = \mathbb{E}(Z|G_1,G_2)\text{)}
\end{aligned} \tag{S7}$$

Our eqns. (S1) and (S7) seems to differ from eqn. [15] in Bowsher and Swain (2012), in which both terms on the right-hand side are conditional on G_1, but this is just a matter of notation. Bowsher and Swain (2012) denote conditioning with $Z|X$ notation, and it is tacitly understood that you take the expectation over everything else. Thus $V[\mathbb{E}(Z|X,Y)|X]$ in their notation is interpreted as *Evaluate the expectation of Z as a function of the values of X and Y, and then take the variance of that quantity conditional on X, i.e. with respect to the distribution of* $Y|X$. Technically, conditioning on X twice is redundant, but they use it to signify the distribution over which the expectation is to be taken. To accomplish the same thing, we write $Var_{Y|X}[\mathbb{E}(Z|X,Y)]$, to be explicit that the variance is with respect to the conditional distribution of Y given X. It helps us stay out of trouble.

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The general variance decomposition

Let Z be a random variable with finite variance, and $H_1, H_2, \cdots$ a set of random variables defined on the same probability space as Z. Define $H_{1:m} = (H_1, \cdots, H_m)$. We aim to prove that for any $k > 0$

$$\begin{aligned} Var[Z] &= Var\,\mathbb{E}(Z|H_1) \\ &+ \sum_{j=2}^{k} \mathbb{E}\left\{ Var_{H_j|H_{1:j-1}}[\mathbb{E}(Z|H_{1:j})] \right\} \\ &+ \mathbb{E}\,Var[Z|H_{1:k}]. \end{aligned} \tag{S8}$$

This is eqn. [13] in Bowsher and Swain (2012) written in our notation with conditioning with respect to random variables, rather with respect to σ-fields. Note that here (in contrast with the main text) following Bowsher and Swain (2012) we start the time index at 1 rather than 0 so that our derivation more closely parallels theirs.

First, note that the following identity is true because terms on the right-hand side cancel to leave the identity $Var[Z] = \mathbb{E}\,Var[Z]$:

$$\begin{aligned} Var[Z] &= \mathbb{E}\{-\,Var[Z|H_1] + Var[Z]\} \\ &+ \sum_{j=2}^{k} \{ -\,\mathbb{E}\,Var[Z|H_{1:j}] + \mathbb{E}\,Var[Z|H_{1:j-1}] \} \\ &+ \mathbb{E}\,Var[Z|H_{1:k}]. \end{aligned} \tag{S9}$$

The proof consists of showing that (S9) and (S8) are equal line-by-line. The third lines of (S8) and (S9) are exactly the same. Using the (unconditional) Law of Total Variance to write

$$\mathbb{E}\,Var[Z] = Var[Z] = \mathbb{E}\,Var[Z|H_1] + Var\,\mathbb{E}(Z|H_1),$$

we see that the first lines of (S8) and (S9) are the same. For the second line, we apply the Conditional Law of Total Variance (S1) with $G_1 = H_{1:j-1}$ and $G_2 = H_j$ so that $(G_1, G_2) = H_{1:j}$:

$$Var[Z|H_{1:j-1}] = \mathbb{E}_{H_j|H_{1:j-1}}\,Var(Z|H_{1:j}) + Var_{H_j|H_{1:j-1}}\,\mathbb{E}(Z|H_{1:j}). \tag{S10}$$

Taking expectations of both sides,

$$\begin{aligned} \mathbb{E}\,Var[Z|H_{1:j-1}] &= \mathbb{E}\,\mathbb{E}_{H_j|H_{1:j-1}}\,Var(Z|H_{1:j}) + \mathbb{E}\,Var_{H_j|H_{1:j-1}}\,\mathbb{E}(Z|H_{1:j}) \\ &= \mathbb{E}\,Var(Z|H_{1:j}) + \mathbb{E}\,Var_{H_j|H_{1:j-1}}\,\mathbb{E}(Z|H_{1:j}). \end{aligned} \tag{S11}$$

The second line of (S9) is therefore

$$\sum_{j=2}^{k} \mathbb{E}\, Var_{H_j|H_{1:j-1}}\, \mathbb{E}(Z|H_{1:j}), \tag{S12}$$

identical to the second line of (S8), completing the proof.

Why can't we use this to partition pluck?

In theory, we can. The previous derivations still work if "random variable" is replaced by "random vector," so we could define $H_j = (x_j, z_j)$ in (S8) and apply the partition. The result is mathematically correct. However, to use the formulas in practice we need to calculate (among other things) the variance of future LRO over the distribution of H_{a+1} conditional on past values of H — i.e., a variance over size and trait value at some age conditioned on past sizes and traits. We have not found any effective way of finding the distribution of trait value conditional on past sizes. Bayes Theorem gives us a formula for that conditional distribution, but as it involves high-dimensional integrals over past states and trait values, in practice it is computationally infeasible.

S3 Purely age-structured models

Consider now a model where vital rates depend only on age $a = 0, 1, 2, \cdots$; in particular there is no trait variation. Let p_a denote survival from a to $a+1$, l_a survival to age a (with $l_0 = 1$), and f_a the offspring production at age a.

For an age-structured model $P^a \tilde{c}_0$ is a vector of all zeros except for l_a as its $a+1$ entry. The age-a contribution from variation in realized fecundity in eqn. (7) is therefore $l_a \sigma_b^2(a)$, and the contribution from state-trajectory variation (eqn. 6) is $l_a V(a)$. $V(a)$ is the variance (over possible states at age $(a+1)$ of expected future RO conditional on state at age $a+1$, $V(a) = p_a(1-p_a)\rho_1(a+1)^2$, where

$$\rho_1(a+1) = f_{a+1} + (l_{a+2}/l_{a+1})f_{a+2} + (l_{a+3}/l_{a+1})f_{a+3} + \cdots = \frac{1}{l_{a+1}}\left(R_0 - \sum_{k=0}^{a} l_a f_a\right), \tag{S13}$$

where $R_0 = \sum\limits_{k=0}^{\infty} l_a f_a$ is expected LRO. The age-a contribution from state-trajectory variation is therefore

$$\frac{p_a(1-p_a)}{l_{a+1}}\left(R_0 - \sum_{k=0}^{a} l_a f_a\right)^2. \tag{S14}$$

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S4 Conditioning on reaching maturity, attempting breeding, or producing an offspring

Here we detail the calculations for computing the LRO variance among breeders. The general methods are the same as Snyder and Ellner (2016, p. E30 - E31), which was based on Kemeny and Snell (1960, Chapter III) via Caswell (2001, sec. 5.2). We assume that you have read at least one of these. The new complication is that here we want to consider several different definitions of "breeder" to accommodate models with different amounts of information about state-dependent immediate RO. In particular, we want the following options for how "breeder" is defined:

1. Any model we can consider must specify the state-dependent mean and variance of immediate RO. Without any additional information we can define a breeder to be an individual that attains a state with positive mean immediate RO before dying.
2. In a model that also includes a state-dependent probability of attempting breeding, and the mean and variance of immediate RO conditional on breeding, we can define a breeder to be an individual that attempts breeding at least once before dying.
3. In a model that includes the full state-dependent offspring distribution, we can define a breeder to be an individual that produces at least one offspring before dying.

These are not exclusive cases. If a model includes the probability of attempting to breed, and the distribution of immediate RO conditional on making the attempt, any of the three definitions can be used.

In each case, our goal is to derive a model conditional on becoming a breeder before death with all the necessary components for partitioning LRO variance by age: state distribution at birth, state-transition kernel, and the state-dependent mean and variance of immediate RO.

Breeder definition 1

For definition 1, let **S** be the set of immature "small" states with zero fecundity ($\bar{\beta}(z) = 0$), and **M** the set of "mature" states with positive mean fecundity. Once an individual has entered **M**, conditioning on entering **M** has no further effect on their transition probabilities. We therefore need to distinguish between individuals with state in **S** who have entered **M** and returned to **S**, and those who never entered **M**. To do this, following Snyder and Ellner (2016, pp. E30-E31), we expand the state space so that this information is contained in individuals' state. Specifically, we

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expand the state space to from $\mathbf{Z}$ to $\hat{\mathbf{Z}} = \mathbf{Z}_1 \cup \mathbf{Z}_2$ where

$$\begin{cases} \mathbf{Z}_1 = \{(z,1), z \in \mathbf{S}\} & \text{Has never had state in } \mathbf{M} \text{ including the current year} \\ \mathbf{Z}_2 = \{(z,2), z \in \mathbf{Z}\} & \text{Is in } \mathbf{M} \text{ now, or was in some past year} \end{cases}. \tag{S15}$$

The second coordinate (1 or 2) of a point $\hat{z} \in \hat{\mathbf{Z}}$ is just a label for which part of $\hat{\mathbf{Z}}$ the individual is in, e.g. $\hat{z} = (3,1)$ is a state-3 individual in $\mathbf{Z}_1$, $\hat{z} = (3,2)$ is a state-3 individual in $\mathbf{Z}_2$.

Let $1_A(z)$ be the function that is 1 if $z \in A$ and 0 otherwise. States $\hat{z} = (z,1)$ or $(z,2)$ will denote elements of the expanded state space. We can then define a transition kernel on $\hat{\mathbf{Z}}$ so that a breeder is an individual whose state at death is in $\mathbf{Z}_2$, as follows:

$$\mathbf{P} = \begin{array}{c} \\ \\ \end{array} \begin{array}{ccc} \text{from } \mathbf{Z}_1 & \text{from } \mathbf{Z}_2 & \\ P(z',z) & \mathbf{0} & \text{to } \mathbf{Z}_1 \\ 1_{\mathbf{M}}(z')P(z',z) & P(z',z) & \text{to } \mathbf{Z}_2 \end{array}, \tag{S16}$$

where $1_{\mathbf{M}}(z')P(z',z)$ represents ordinary multiplication of the scalars $1_{\mathbf{M}}(z')$ and $P(z',z)$, with the interpretation that

$$\begin{pmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} P_{11}n_1 + P_{12}n_2 \\ P_{21}n_1 + P_{22}n_2 \end{pmatrix}. \tag{S17}$$

$\mathbf{P}$ says that reaching a state $z \in \mathbf{M}$ puts you in $\mathbf{Z}_2$ for life, even if your state is again in $\mathbf{S}$ at some subsequent time.

Let Q_1 be the kernel $\mathbf{P}$ restricted to $\mathbf{Z}_1$, and $N_1 = (I - Q_1)^{-1}$. For an individual in $\mathbf{Z}_1$, the probability of entering $\mathbf{Z}_2$ in one step is

$$a_M(z) = \int_{\mathbb{M}} P(z',z)\, dz' \; z \in \mathbf{S}. \tag{S18}$$

The probability of reaching $\mathbf{Z}_2$ before death, starting from state $\hat{z} \in \hat{\mathbf{Z}}$, is given by

$$B(\hat{z}) = (a_M N_1; \mathbf{e}) = \begin{cases} a_M N_1(z) & \hat{z} = (z,1) \in \mathbf{Z}_1 \\ 1 & \hat{z} = (z,2) \in \mathbf{Z}_2 \end{cases}. \tag{S19}$$

(Note: here and below we use semi-colons to separate the components of a state-distribution vector on different components of an expanded state space.) On the expanded state space, the state distribution at birth is

$$\hat{c}_0(\hat{z}) = \left(c_0(z); c_0(z)1_{\mathbf{M}}(z)\right) = \begin{cases} c_0(z) & \hat{z} = (z,1) \in \mathbf{Z}_1 \\ c_0(z)1_{\mathbf{M}}(z) & \hat{z} = (z,2) \in \mathbf{Z}_2 \end{cases}. \tag{S20}$$

Averaging across newborn states, the average probability of a newborn reaching $\mathbf{Z}_2$ before death is

$$p_M = \hat{c}_0^{\mathsf{T}} B. \tag{S21}$$

The state-transition kernel conditional on entering $\mathbf{Z}_2$ before death is

$$\mathbf{P}_B(\hat{z}', \hat{z}) = B(\hat{z}')\mathbf{P}(\hat{z}', \hat{z}) / B(\hat{z}). \tag{S22}$$

Note that if $B(\hat{z}) = 1$ and $\mathbf{P}(\hat{z}', \hat{z}) > 0$ it must be the case that $B(\hat{z}') = 1$, so the conditioning does not affect the transition probabilities of an individual in $\mathbf{Z}_2$. Additionally, if $B(\hat{z}) = 0$ then the chain conditional on breeding must have zero probability of ever reaching $\hat{z}$, so $\mathbf{P}_B(\hat{z}', \hat{z})$ can be defined arbitrarily. In particular, the conditional transition chain can be defined so that anyone reaching a state where $B = 0$ is killed.

When individuals vary in initial state $\mathbf{z}_0$, conditioning on breeding also affects the distribution of initial state. The conditional distribution follows from (S22) by imagining that individuals all have pre-natal state α and transition to state at birth $\hat{z}$ with probability $\hat{c}_0(\hat{z})$. Then $B(\alpha) = p_M$ and the conditional state at birth is

$$\hat{c}_{0,B}(\hat{z}) = B(\hat{z}) c_0(\hat{z}) / p_M. \tag{S23}$$

The state-dependent mean and variance of immediate RO are the those of the original model, applying on both $\mathbf{Z}_1$ and $\mathbf{Z}_2$.

If individuals entering $\mathbf{M}$ can never return to $\mathbf{S}$, we can instead take $\mathbf{Z}_1 = \mathbf{S}$, $\mathbf{Z}_2 = \mathbf{M}$. This situation is identical to Snyder and Ellner (2016, p. E30), but for completeness we repeat it here. Let Q be P restricted to $\mathbf{S}$ and $N_S = (I - Q)^{-1}$. For an individual of state $z \in \mathbf{S}$, the probability of entering $\mathbf{M}$ in one step is

$$a_M(z) = \int_{\mathbb{M}} P(z', z)\, dz',\ z \in \mathbf{S}. \tag{S24}$$

The probability of reaching $\mathbf{M}$ before death, starting from state z is given by

$$B(z) = (a_M N_S; \mathbf{e}) = \begin{cases} a_M N_S(z) & z \in \mathbf{S} \\ 1 & z \in \mathbf{M} \end{cases}. \tag{S25}$$

Equations (S21), (S22), and (S23) hold with the carets ˆ omitted.

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Breeder definition 2

In definition 2, a breeder is defined as an individual who has attempted breeding at least once. Individuals attempt breeding with probability $p_b(z)$, and have transition kernels π_b, π_0, respectively, for those who do and do not attempt breeding in the current year. The overall transition kernel is $P(z', z) = p_b(z)\pi_b(z', z) + (1 - p_b(z))\pi_0(z', z)$.

The Markov Chain theory that we are exploiting tells us how to condition on reaching a particular set of states before death. To make use of it, we need to expand the state space such that one can tell retrospectively whether a just-deceased individual was a breeder or a non-breeder just by looking at their lifetime state trajectory. Otherwise, conditioning on breeding would also affect the state-dependent fecundity distribution, making the calculations much more challenging. In addition, the mean and variance of immediate RO must be functions only of the individual's expanded state.

For breeder definition 2, we can expand the state space so that individual state is defined jointly by state z from the original model and by attempted breeding history:

$$\begin{cases} \mathbf{Z}_1 = \{(z,1), z \in \mathbf{Z}\} & \text{Never attempted breeding, and does not in the current year} \\ \mathbf{Z}_2 = \{(z,2), z \in \mathbf{Z}\} & \text{Attempts breeding for the first time in the current year} \\ \mathbf{Z}_3 = \{(z,3), z \in \mathbf{Z}\} & \text{Has attempted breeding in some past year} \end{cases} . \tag{S26}$$

A breeder, then, is an individual who enters $\mathbf{Z}_2$, and then moves to $\mathbf{Z}_3$ if they survive to the next year.

The initial state distribution on this expanded state space is

$$\hat{c}_0 = (c_0(z)(1 - p_b)(z); c_0(z)p_b(z); \mathbf{0}). \tag{S27}$$

The transition kernel/matrix is

$$\mathbf{P} = \begin{array}{c} \\ \\ \\ \end{array}\left(\begin{array}{ccc} \text{from } \mathbf{Z}_1 & \text{from } \mathbf{Z}_2 & \text{from } \mathbf{Z}_3 \\ (1 - p_b(z'))\pi_0(z', z) & \mathbf{0} & \mathbf{0} \\ p_b(z')\pi_0(z', z) & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \pi_b(z', z) & P(z', z) \end{array}\right) \begin{array}{l} \\ \text{to } \mathbf{Z}_1 \\ \text{to } \mathbf{Z}_2 \\ \text{to } \mathbf{Z}_3 \end{array} . \tag{S28}$$

which can be understood as follows:

- Individuals in $\mathbf{Z}_1$ are by definition not attempting to breed this year, so their state transition kernel/matrix is π_0. Whether they are in $\mathbf{Z}_1$ or $\mathbf{Z}_2$ next year depends on whether or not they attempt breeding at their new size, determined by the value of p_b at that size.

- Individuals in $\mathbf{Z}_2$ either move to $\mathbf{Z}_3$ or die (i.e., the "from **Z**2" portion of (S28) is 0 outside the "to $\mathbf{Z}_3$" portion). By definition they are attempting to breed this year, so their state transition kernel/matrix is π_b.
- Individuals in $\mathbf{Z}_3$ either stay in $\mathbf{Z}_3$ or die. Within $\mathbf{Z}_3$ there are no subdivisions based on breeding history, so they are governed by the overall kernel/matrix P.

Finally, the mean and variance of immediate RO on the expanded state space are given by:

$$\begin{aligned} \hat{\bar{\beta}} &= (\mathbf{0};\ \bar{\beta}_+;\ \bar{\beta}) \\ \hat{\sigma}_b^2 &= (\mathbf{0};\ \sigma_+^2;\ \sigma_b^2), \end{aligned} \tag{S29}$$

where $\bar{\beta}_+(z), \sigma_+^2(z)$ are the state-dependent mean and variance of immediate offspring number conditional on attempting to breed ($\bar{\beta}$ and σ_b^2 are the unconditional mean and variance, as usual, and we have $\bar{\beta}_+ = \bar{\beta}/p_b$).

With the model specified, the rest of dealing with breeder definition 2 is straightforward. We need to condition $\mathbf{P}$ on reaching $\mathbf{Z}_2$ before dying. Accordingly, let Q_2 be $\mathbf{P}$ restricted to $\mathbf{Z}_1$, i.e. $Q_2(z', z) = \pi_0(z', z)(1 - p_b(z'))$. The corresponding fundamental operator on $\mathbf{Z}_1$ is $N_2 = (I - Q_2)^{-1}$. For an individual in $\mathbf{Z}_1$ with state $(z, 1)$ the probability of moving to $\mathbf{Z}_2$ in one step is

$$a_M(z) = \int_{\mathbf{Z}} \pi_0(z', z) p_b(z')\, dz'\ ; \tag{S30}$$

note that $\mathbf{Z}_2$ and $\mathbf{Z}$ have the same set of z values. The probability of reaching $\mathbf{Z}_2$ before death, starting from state $\hat{z} \in \hat{\mathbf{Z}}$, is given by

$$B(\hat{z}) = (a_M N_2;\ \mathbf{e};\ \mathbf{e}) = \begin{cases} a_M N_2(z) & \hat{z} = (z, 1) \in \mathbf{Z}_1 \\ 1 & \hat{z} = (z, k) \in \mathbf{Z}_k,\ k = 2, 3 \end{cases}. \tag{S31}$$

The state transition probabilities conditional on breeding are again given by eqn. (S22) and the average probability of a newborn reaching $\mathbf{Z}_2$ before death is again given by eqn. (S21).

As with Definition 1, conditioning on breeding affects the distribution of initial state if individuals vary in initial state, and the formula for the conditional distribution, eqn. (S23), is exactly the same.

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Breeder definition 3

In definition 3, a breeder is defined as an individual who has produced at least one offspring. For this definition, the model must specify the state-dependent distribution of current offspring number, or minimally, enough information to calculate the state-dependent probability of producing at least one offspring in the current year, $p_d(z)$, and state-dependent mean and variance of total current offspring conditional on having at least one, which we denote $\bar{\beta}_d(z)$ and $\sigma_d^2(z)$.

This definition can be handled much like definition 2. We expand the state space so that individual state is defined by state z from the original model, and offspring production history:

$$\begin{cases} \mathbf{Z}_1 = \{(z,1), z \in \mathbf{Z}\} & \text{No offspring yet, including the current year} \\ \mathbf{Z}_2 = \{(z,2), z \in \mathbf{Z}\} & \text{Produces their first offspring in the current year} \\ \mathbf{Z}_3 = \{(z,3), z \in \mathbf{Z}\} & \text{Has produced at least one offspring in some past year} \end{cases} . \tag{S32}$$

As in definition 2, a breeder is an individual who enters $\mathbf{Z}_2$, and then moves to $\mathbf{Z}_3$ if they survive to the next year. The initial state distribution on this expanded state space is

$$\hat{c}_0 = (c_0(z)(1 - p_d(z));\ c_0(z)p_d(z);\ \mathbf{0}). \tag{S33}$$

The transition kernel/matrix is

$$\mathbf{P} = \begin{array}{c} \\ \\ \end{array}\!\!\begin{array}{cccc} \text{from } \mathbf{Z}_1 & \text{from } \mathbf{Z}_2 & \text{from } \mathbf{Z}_3 & \\ \left(\begin{array}{c} (1 - p_d(z'))P(z',z) \\ p_d(z')P(z',z) \\ \mathbf{0} \end{array}\right. & \begin{array}{c} \mathbf{0} \\ \mathbf{0} \\ P(z',z) \end{array} & \left.\begin{array}{c} \mathbf{0} \\ \mathbf{0} \\ P(z',z) \end{array}\right) & \begin{array}{l} \text{to } \mathbf{Z}_1 \\ \text{to } \mathbf{Z}_2 \\ \text{to } \mathbf{Z}_3 \end{array} \end{array} . \tag{S34}$$

That is, from $\mathbf{Z}_1$ you move to either $\mathbf{Z}_1$ or $\mathbf{Z}_2$ according to your reproductive outcome the following year, and from $\mathbf{Z}_2$ you die or move to $\mathbf{Z}_3$. From the definition of $\mathbf{P}$ it may appear that we don't really need both $\mathbf{Z}_2$ and $\mathbf{Z}_3$. However, the fecundity functions on $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are different, because individuals in $\mathbf{Z}_2$ are by definition certain to have at least one offspring in the current year.

The rest is almost a repeat from definition 2. The mean and variance of immediate RO on the expanded state space are given by

$$\begin{aligned} \hat{\bar{\beta}} &= (\mathbf{0};\ \bar{\beta}_d;\ \bar{\beta}) \\ \hat{\sigma}_b^2 &= (\mathbf{0};\ \sigma_d^2;\ \sigma_b^2). \end{aligned} \tag{S35}$$

Let Q_3 be $\mathbf{P}$ restricted to $\mathbf{Z}_1$, i.e. $Q_3(z',z) = P(z',z)(1 - p_d(z'))$. The corresponding fundamental operator on $\mathbf{Z}_1$ is $N_3 = (I - Q_3)^{-1}$. For an individual in $\mathbf{Z}_1$ with state $(z,1)$ the probability of moving to $\mathbf{Z}_2$ in one step is

$$a_M(z) = \int_{\mathbf{Z}} P(z', z) p_d(z')) \, dz' \, . \tag{S36}$$

The probability of reaching $\mathbf{Z}_2$ before death, starting from state $\hat{z} \in \hat{\mathbf{Z}}$, is given by

$$B(\hat{z}) = (a_M N_3; \, \mathbf{e}; \, \mathbf{e}), \tag{S37}$$

and formulas (S21), (S22), and (S23) continue to hold for this definition.

S5 A simple breed/no-breed example

To demonstrate the three methods of partitioning LRO variance conditional on becoming a breeder, we turn to a simple size-structured model for sneetches, which is analyzed in the tutorial code `SneetchCalculations3.R`. Following Geisel's classic demographic study, we classify sneetches as ***S***mall, ***M***edium, ***L***arge, and e***X***tra-large and note that only the L and X size classes are reproductive (Geisel, 1953). In the absence of a Star-On or Star-Off Machine, the presence or absence of a star on a sneetch's belly is a fixed trait, and we take this to be the trait variation of interest. Those with "stars on thars" have higher survival, likely as a result of higher social status leading to greater access to resources. Otherwise, star-belly and plain-belly sneetches are demographically identical.

State transitions. Size-class transitions, conditional on survival, can be parameterized in terms of the class-specific probability of stasis (remaining the same size). For S and X there is only one alternative to stasis; for M and L there are two, and they occur with equal probability.

Let $s(i)$ denote the size-specific survival probability for plain-belly sneetches, and $\sigma(i)$ the size-specific probability of stasis. To streamline the notation let $\tau(i) = 1 - \sigma(i)$ denote the probability of making a size-class transition. The transition matrix for plain-belly sneetches is then

$$\mathbf{U}_1 = \begin{pmatrix} s(1)\sigma(1) & s(2)\tau(2)/2 & 0 & 0 \\ s(1)\tau(1) & s(2)\sigma(2) & s(3)\tau(3)/2 & 0 \\ 0 & s(2)\tau(2)/2 & s(3)\sigma(3) & s(4)\tau(4) \\ 0 & 0 & s(3)\tau(3)/2 & s(4)\sigma(4) \end{pmatrix}. \tag{S38}$$

The transition matrix for star-belly sneetches, $\mathbf{U}_2$, is the same except that mortality in all size-classes is lower by a factor $\rho < 1$, hence

$$s^*(i) = 1 - \rho(1 - s(i)). \tag{S39}$$

Annual breeding outcomes. L and X sneetches have probabilities $p_b(3), p_b(4)$ of attempting to breed in the current year, whether starred or starless. Conditional on attempting to breed, offspring production is Poisson with means $\theta(3), \theta(4)$ respectively for both star-belly and plain-belly sneetches.

Our analyses use some moments of the breeding distribution. For size classes 1 and 2, all moments are zero because they never attempt breeding. For size classes 3 and 4, the mean and variance of immediate RO, combining those who do and do not attempt breeding that year, are

$$\bar{\beta}(j) = p_b(j)\theta(j), \qquad \sigma_b^2(j) = p_b(j)\theta(j) + p_b(j)(1 - p_b(j))\theta(j)^2. \tag{S40}$$

Conditional on attempting to breed, the mean and variance of immediate RO are

$$\bar{\beta}_+(j) = \theta(j), \qquad \sigma_+^2(j) = \theta(j). \tag{S41}$$

Conditional on producing at least one offspring, the offspring distribution is a zero-truncated Poisson. The moments are

$$\bar{\beta}_d(j) = \frac{\theta(j)}{1 - e^{-\theta(j)}}, \qquad \sigma_d^2(j) = \bar{\beta}_d(j)\big(1 + \theta(j) - \bar{\beta}_d(j)\big). \tag{S42}$$

Breeder definition 1: breeders have, or had, positive mean immediate RO. For the sneetches, $\mathbf{S} = \{1, 2\}$ and $\mathbf{M} = \{3, 4\}$. Following eq. S16, the expanded-state transition matrix is therefore

$$\mathbf{P}_1 = \left(\begin{array}{cc|c} s(1)\sigma(1) & s(2)\tau(2)/2 & \mathbf{0} \\ s(1)\tau(1) & s(2)\sigma(2) & \\ \hline 0 & 0 & \\ 0 & 0 & \mathbf{U}_1 \\ 0 & s(2)\tau(2)/2 & \\ 0 & 0 & \end{array}\right) \tag{S43}$$

for plain-belly sneetches, and the same with survival rates $s^*(i)$ for star-belly sneetches. Sneetches are born Small, thus in $\mathbf{Z}_1$. They enter $\mathbf{Z}_2$, becoming a breeder, by growing from Medium ($z = 2$) to Large ($z = 3$) unless they die first. Once in $\mathbf{Z}_2$ they remain there until death, regardless of subsequent size transitions.

The initial condition is

$$\hat{c}_0 = (1, 0; \mathbf{0}), \tag{S44}$$

and the probability of breeding is

$$\hat{p}_b = (0, 0; 0, 0, p_b(3), p_b(4)). \tag{S45}$$

The mean immediate reproductive output is

$$\hat{\hat{\beta}} = (0,0;0,0,p_b(3)\theta(3),p_b(4)\theta(4)), \tag{S46}$$

and the variance in immediate reproductive output is

$$\hat{\sigma}_b^2 = (0,0;0,0,p_b(3)\theta(3)+p_b(3)(1-p_b(3))\theta(3)^2,p_b(4)\theta(4)+p_b(4)(1-p_b(4))\theta(4)^2). \tag{S47}$$

Breeder definition 2: breeders are those who attempt breeding at least once. Breeding attempts do not affect survival or growth for sneetches, so $\pi_0 = \pi_b = P$. Recalling that the probability of breeding p_b is zero for sizes 1 and 2, we follow eqn. (S28) to find

$$\mathbf{P}_1 = \left(\begin{array}{cccc|cc}
s(1)\sigma(1) & s(2)\tau(2)/2 & 0 & 0 & \mathbf{0} & \mathbf{0} \\
s(1)\tau(1) & s(2)\sigma(2) & s(3)\tau(3)/2 & 0 & & \\
0 & s(2)\tau(2)(1-p_b(3))/2 & s(3)\sigma(3)(1-p_b(3)) & s(4)\tau(4)(1-p_b(3)) & & \\
0 & 0 & s(3)\tau(3)(1-p_b(4))/2 & s(4)\sigma(4)(1-p_b(4)) & & \\
\hline
0 & 0 & 0 & 0 & \mathbf{0} & \mathbf{0} \\
0 & 0 & 0 & 0 & & \\
0 & s(2)\tau(2)p_b(3)/2 & s(3)\sigma(3)p_b(3) & s(4)\tau(4)p_b(3) & & \\
0 & 0 & s(3)\tau(3)p_b(4)/2 & s(4)\sigma(4)p_b(4) & & \\
\hline
\multicolumn{4}{c|}{\mathbf{0}} & \mathbf{U}_1 & \mathbf{U}_1
\end{array}\right) \tag{S48}$$

for plain-belly sneetches, and the same with survival rates $s^*(i)$ for star-belly sneetches.

The initial condition is

$$\hat{c}_0 = (1,0,0,0;\mathbf{0};\mathbf{0}), \tag{S49}$$

and the probability of breeding is

$$\hat{p}_b = (\mathbf{0};\mathbf{1};0,0,p_b(3),p_b(4)). \tag{S50}$$

The mean immediate reproductive output is

$$\hat{\hat{\beta}} = (\mathbf{0},0,0,\theta(3),\theta(4),0,0,p_b(3)\theta(3),p_b(4)\theta(4)), \tag{S51}$$

and the variance in immediate reproductive output is

$$\hat{\sigma}_b^2 = (\mathbf{0},0,0,\theta(3),\theta(4),0,0,p_b(3)\theta(3)+p_b(3)(1-p_b(3))\theta(3)^2,p_b(4)\theta(4)+p_b(4)(1-p_b(4))\theta(4)^2). \tag{S52}$$

Breeder definition 3: breeders are those who produce at least one offspring.

For stages 3 and 4, the probability of producing at least one offspring in the current year is

$$p_d(j) = 1 - \exp(-\theta(j)). \tag{S53}$$

Following eq. S34, we find

$$\mathbf{P_1} = \left(\begin{array}{cccc|cc}
s(1)\sigma(1) & s(2)\tau(2)/2 & 0 & 0 & & \\
s(1)\tau(1) & s(2)\sigma(2) & s(3)\tau(3)/2 & 0 & \mathbf{0} & \mathbf{0} \\
0 & s(2)\tau(2)(1-p_d(3))/2 & s(3)\sigma(3)(1-p_d(3)) & s(4)\tau(4)(1-p_d(3)) & & \\
0 & 0 & s(3)\tau(3)(1-p_d(4))/2 & s(4)\sigma(4)(1-p_d(4)) & & \\
\hline
0 & 0 & 0 & 0 & & \\
0 & 0 & 0 & 0 & \mathbf{0} & \mathbf{0} \\
0 & s(2)\tau(2)p_d(3)/2 & s(3)\sigma(3)p_d(3) & s(4)\tau(4)p_d(3) & & \\
0 & 0 & s(3)\tau(3)p_d(4)/2 & s(4)\sigma(4)p_d(4) & & \\
\hline
 & & \mathbf{0} & & \mathbf{U}_1 & \mathbf{U}_1
\end{array} \right) \tag{S54}$$

for plain-belly sneetches, and the same with survival rates $s^*(i)$ for star-belly sneetches.

The initial condition is

$$\hat{c}_0 = (1, 0, 0, 0, \mathbf{0}, \mathbf{0}), \tag{S55}$$

and the probability of breeding is

$$\hat{p}_b = (\mathbf{0}, \mathbf{1}, 0, 0, p_b(3), p_b(4)). \tag{S56}$$

The mean immediate reproductive output is

$$\hat{\hat{\beta}} = \left(\mathbf{0}, 0, 0, \frac{\theta(3)}{1-\exp(-\theta(3))}, \frac{\theta(4)}{1-\exp(-\theta(4))}, 0, 0, \theta(3), \theta(4) \right), \tag{S57}$$

and the variance in immediate reproductive output is

$$\hat{\sigma}_b^2 = \left(\mathbf{0}, 0, 0, \frac{\theta(3)}{1-\exp(-\theta(3))} \left(1 + \theta(3) - \frac{\theta(3)}{1-\exp(-\theta(3))} \right), \frac{\theta(4)}{1-\exp(-\theta(4))} \left(1 + \theta(4) - \frac{\theta(4)}{1-\exp(-\theta(4))} \right), 0, 0, \theta(3), \theta(4) \right). \tag{S58}$$

Fig. S4 shows within-breeder state trajectory and fecundity luck for the three breeder definitions. The figure is generated by `SneetchCalculations3.R`, which some readers may wish to use as a tutorial.

S6 Additional case studies

We present here two additional empirical case studies. Results from these studies were mentioned in the main text, without information about the study system, model, or analysis.

Peregrine falcon, Falco peregrinus

Altwegg et al. (2014) developed a stage-structured matrix model for the urban Peregrine Falcon population in Cape Town, South Africa based on studies running from 1997-2010. The stages in the model are Juvenile, Non-breeders of ages 1,2, and 3, and Breeder. We obtained the stage-transition matrix from the COMADRE database (Salguero-Gomez et al., 2016), and converted it from post-breeding to pre-breeding census (using the expressions for matrix entries in their eqn. (1)) so that only stage 5 has nonzero fecundity. The resulting matrix (slightly rounded) is

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.52 \\ 0.225 & 0 & 0 & 0 & 0 \\ 0 & 0.344 & 0 & 0 & 0 \\ 0 & 0 & 0.193 & 0 & 0 \\ 0 & 0.372 & 0.659 & 0.852 & 0.852 \end{pmatrix}. \tag{S59}$$

We assumed a Poisson offspring distribution for breeders, and partitioned between breeders and non-breeders using Definition 1, as breeding is exactly equivalent to reaching stage 5.

Roe deer

Roe deer (*Capreolus capreolus*) born early in the season have access to more nutritious food. This results in higher early survival and higher body mass as adults, which in turn leads to higher reproductive success (Plard et al., 2015). Plard et al. (2015) presents an IPM for roe deer, with individuals classified by stage (yearling or adult), body mass, and birth date. Fitness of the earliest born females, measured as reproductive value at 8 months old, is found to be 1.29 times higher than that of the latest-born females. Reproductive value is an expected value, however, something one would observe by averaging over a large population. How important is birth date at the level of an individual?

Fig. S3 shows the contributions of luck and birth date to $Var(R)$ as a function of age. Birth date has a small contribution for age 0 individuals (yearlings), presumably through its influence on early survival, and a negligible contribution for adults. While the effects of birth date will be evident for a sufficiently large population, its effects are drowned out by luck for individuals.

The effects of luck peak at age 1, and while the contribution of fecundity luck is important, the effects of state trajectory luck are roughly double in size. All mothers are assumed to bear twins in this model, so fecundity luck comes from whether or not breeding was successful.

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S7 Additional details on case study models

Tsuga canadensis

The projection matrix we analyzed is

$$\mathbf{A} := \mathbf{F} + \mathbf{P} = \begin{pmatrix} 0.9030 & 0 & 0.29900 & 0.77415 & 1.95735 & 6.0251 \\ 0.0038 & 0.96070 & 0 & 0 & 0 & 0 \\ 0 & 0.01225 & 0.96545 & 0 & 0 & 0 \\ 0 & 0 & 0.01735 & 0.97595 & 0 & 0 \\ 0 & 0 & 0 & 0.01205 & 0.96335 & 0 \\ 0 & 0 & 0 & 0 & 0.01835 & 0.9903 \end{pmatrix}. \tag{S60}$$

This is the matrix analyzed by van Daalen and Caswell (2017); the matrix as shown in eqn. (64) of their paper is rounded, but using the exact matrix above we replicate the mean and variance of LRO given in their Table 3, while the rounded matrix gives slightly different results. The "stages" in the model are size-classes based on dbh (cm): $< 5, 5-10, 10.1-17.5, 17.6-27.5, 27.6-42.5$, and > 42.5. Top-row entries other than $\mathbf{A}_{1,1}$ are indirectly estimated fecundities, based on seedling counts and the assumption that individual fecundity is proportional to dbh^2 (Lamar and McGraw, 2005). There is no data on between-individual variation in annual fecundity. Following van Daalen and Caswell (2017) we assumed a Poisson distribution with mean (and therefore variance) given by the top-row entries. We expect that the actual distribution is more dispersed, e.g., zero-inflated as a result of some individuals not flowering in a given year. This would produce a higher variance/mean ratio. However, the fecundity contributions to luck resulting from the Poisson assumption are so small, relative to the state-trajectory contribution, that even a 100-fold increase in the variance/mean ratio would not change our conclusions, so we see no point in trying to improve on the Poisson model.

Idaho sagebrush steppe

The analysis in Snyder and Ellner (2018) gave only the beginnings of an age-partitioning of luck, calculating the contributions from pre-natal luck, the first year of life, and everything else put together. In addition, it omitted one component of early-life variation among individuals which our methods then could not deal with: large-scale spatial variation in size-specific vital rates across spatially separated quadrat groups. The transition kernels used here are based on the same statistical models, regression models with quadrat group as a factor covariate. However, Snyder and Ellner (2018) set all quadrat group effects to 0, to represent a "typical" location. Here we use models that include large-scale spatial variation by using quadrat group as the trait x.

There are 6 quadrat groups, which we treat as 6 equally likely values of x. Script files mentioned below are part of the online Supplementary Material for Snyder and Ellner (2018) available at `doi.org/10.5061/dryad.pd959`.

So what does quadrat group affect?

- Seedling survival is affected by quadrat group in *Pseudoroegneria* ($P = 0.026$) but not *Artemisia* ($P = 0.6$, `Fit_Survival_Seedlings.R`). The estimated group effects in logistic GLMM for *Pseudoroegneria* seedling survival are

  ```
  0.07354396 -0.23961535 0.22278200 0.29098337 -0.05889084 -0.28880314
  ```

- Survival of older plants is affected in both species (`Fit_Survival_Older.R`). For *Artemisia* the estimated Group effects in a logistic GLMM for older plant survival are significant at $P < 0.01$,

  ```
  -0.323598954 0.163705362 -0.109165424 -0.718369219 0.989199680 -0.001771444
  ```

  For *Pseudoroegneria* the estimated group effects are marginally significant at $P = 0.091$, but AIC preferred the model with group effects to the corresponding model without group effects (ΔAIC = 5.6), so here we assumed that group affects survival of older *Pseudoroegneria*. The estimated group effects are

  ```
  -0.005277883 0.074223526 -0.132938796 -0.164246152 0.000389793 0.227849513
  ```

- Seedling growth is not affected by Group ($P > 0.45$ for both species, `Fit_Growth_Seedlings.R`).
- Growth of older plants is also not affected by Group. The model fitting in this case was Bayesian (`Fit_Growth_JAGS.R`). Samples from the posterior distributions of group effect parameters all had wide distributions straddling 0, except for one quadrat group in *Pseudoroegneria* where about 93% of samples for the group effect are negative.

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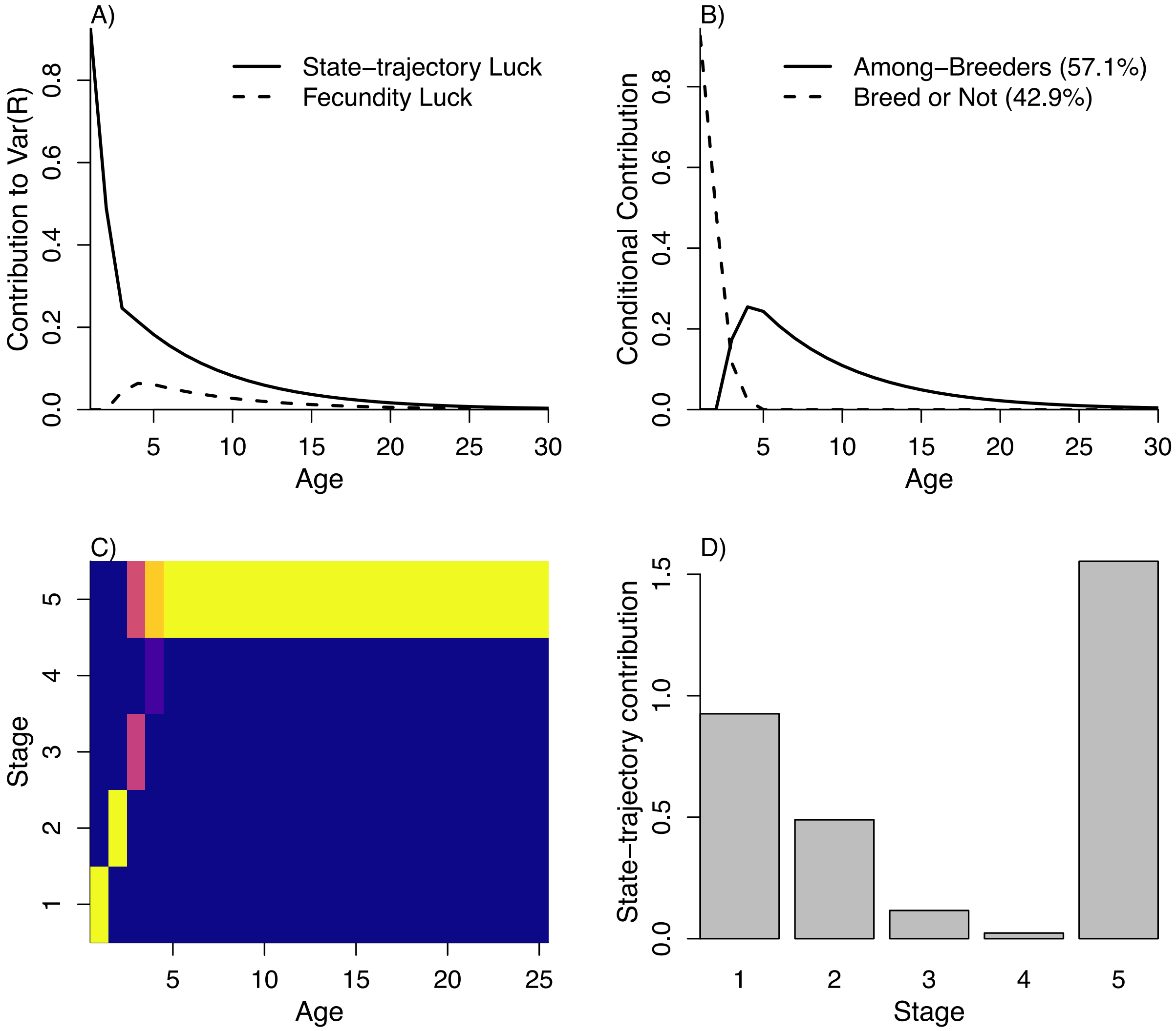

Figure S2: Partitioning of LRO variance into age-specific and stage-specific contributions for the stage-structured Peregrine Falcon matrix model. A) Partitioning by age of the state-trajectory and fecundity contributions to Var(LRO). B) Sub-partitioning luck into variance among breeders, and variance due to breeding vs. not ever breeding. C) Image plot of the age-dependent stage distribution of survivors, with lighter colors indicating higher values. D) Partitioning by stage of the state-trajectory contribution to Var(LRO). The fecundity contribution all occurs in stage 5. Figure produced by script `FalconPartitioning.R`.

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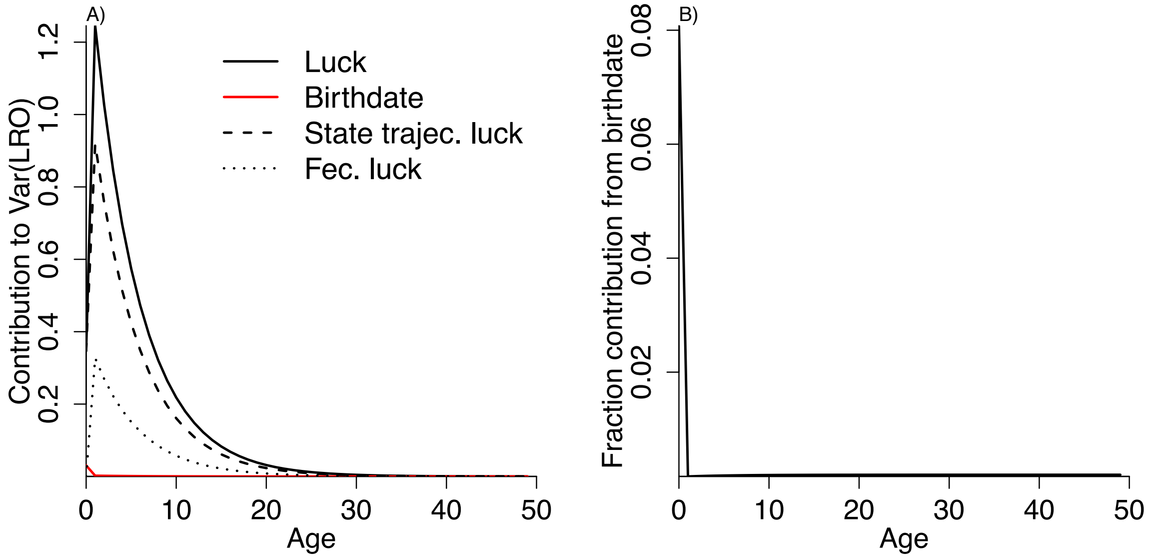

Figure S3: The partitions of LRO variance into age-specific contributions for roe deer, *Capreolus capreolus*. A) The age-specific contributions of luck (solid black line) and quality (birth date, solid red line). Luck is further broken down into state trajectory luck (dashed line) and fecundity luck (dotted line). B) Fraction of LRO variance coming from birth date variation, as a function of age. Figure produced by script `roePartitioningNewLuckPluck4.R`.

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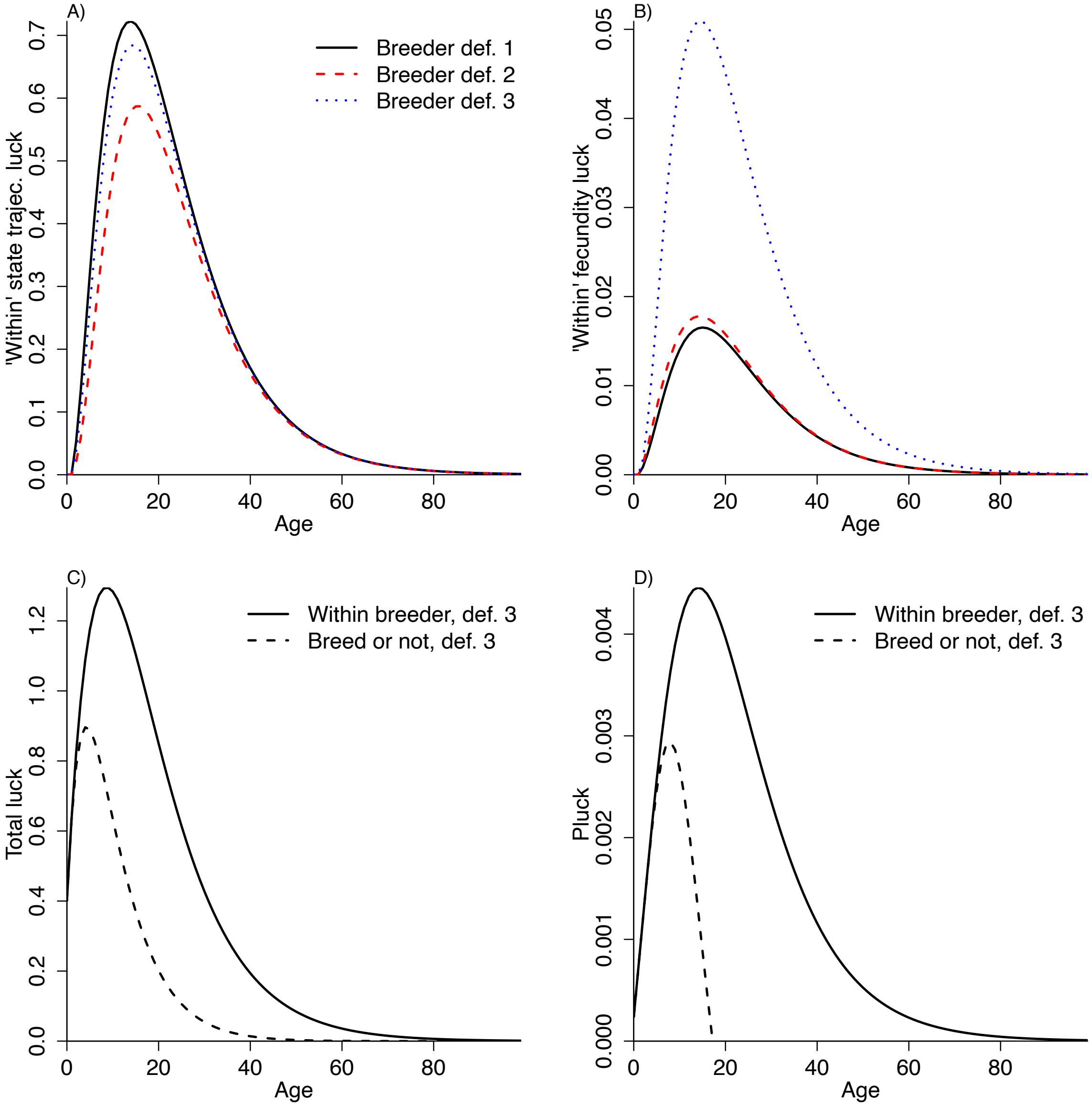

Figure S4: The partitions of state trajectory and fecundity luck into age-specific within- and between-breeder contributions for the sneetch (*Sneetch geiseli*). A) The age-specific contributions of within-breeder state trajectory luck for breeders defined as those who have or have had positive mean LRO (def. 1), those who attempt breeding at least once (def. 2), and those who have produced at least one offspring (def. 3). B) Age-specific contributions of within-breeder fecundity luck for the same definitions. C) Within-breeder and breed-or-not contributions to total luck, using definition 3. D) Within-breeder and breed-or-not contributions to pluck, using definition 3. Figure produced by script `SneetchCalculations3.R`