Resource distribution unifies optimal offspring size and bacterial aging

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How should a parent optimally distribute limited resources among its offspring? This question is as relevant to a mother bird deciding how to allocate food among her chicks as it is to a bacterium dividing high-quality organelles between its daughters. Optimal offspring size theory has long explored the tradeoff between the number and size of offspring in higher organisms. Meanwhile, the emerging field of bacterial aging examines when cells evolve unequal sharing of old cellular components. Our study unifies these two disciplines through a model of resource allocation. This model highlights that the convexity of how resources affect offspring survivorship determines whether even or uneven resource distribution evolves. Based on this, we derive the optimal resource distribution strategies, show that they evolve, and characterize when these strategies are robust to fluctuating environments. These results not only agree with and strengthen existing models, but also provide an organizing framework that enables new predictions. These include the conditions which select for strategies that contain a "runt of the litter."

clutch size | bacterial senescence | asymmetric division | convex optimization | bet-hedging | runts

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1. Introduction

A newly hatched chick requires food from its parent, else it is sure to die. It cries out in hunger, but so too do the rest of its nest-mates, and the parent only has so many worms to go around. If the parent feeds the chick too little then the chick will grow weak and have a low chance of survival. Yet too much food means little is left for the other chicks and they grow weak instead. The parent faces a central question: how should she distribute the food to maximize her number of surviving offspring?

In the microscopic world a parallel story unfolds. When a bacterium replicates it must duplicate its components and distribute them between its two daughter cells. Newly created components perform better than the old ones, and so the daughter that inherits more new components grows faster and survives better. The mother could give both daughters an equal mix of old and new components. Or the mother could favor one daughter with all new components and give the leftover old components to the other daughter. Or should she choose any of the infinite strategies between these extremes? A good choice is essential; like the mother bird, our bacterium seeks a distribution strategy that maximizes the number of surviving offspring.

These two examples from two different scales ask the same question: how to distribute limited resources among offspring? This question arises whenever an organism reproduces. The resource can take many forms – food, space, time, attention, cellular components, damaged proteins – but two properties remain constant:

1. The resource is finite.
2. An offspring's probability of survival (or some other trait that affects reproductive success) depends on how many resources they receive.

A parent who distributes these resources well tends to leave more surviving offspring, and if these distribution strategies are heritable then we expect strategies which maximize the expected number of surviving offspring to evolve.

For simplicity we assume natural selection acts to maximize the expected number of surviving offspring in constant environments and the geometric mean number of surviving offspring in fluctuating environments. Deciding exactly what natural selection maximizes (if anything) is not an easy question and depends on many factors, including the genetic system, the levels of stochasticity, whether there exist transgenerational effects, and whether the population is stage-structured, spatially structured, frequency dependent, or has overlapping generations (Proulx and Adler 2010; J. M. Smith 1978; Frank 2011; Mangel et al. 1994).

In this paper we assume resources affect only offspring survival probability. This would be broken if at adulthood all organisms did not end up equal (e.g. resources affect size at maturity) or if resource distribution affected the parent (e.g. a parent starves and loses out on future reproduction if she invests too many resources into her offspring). We also assume that natural selection acts to maximize the expected number of surviving offspring and that there is enough standing variation for this to happen.

A. Optimal Offspring Size Theory

Whenever we ask how to best distribute resources among offspring we implicitly ask how many offspring

to make. In plants and animals this gives rise to the fundamental life history trade-off between offspring size and number. Limited resources mean that a mother can either make many offspring with few resources each or few offspring with many resources each. But she cannot have both and must choose.

Optimal offspring size theory studies this trade-off, and perhaps began with Lack's observation of bird clutch sizes (Lack 1954) . The Smith-Fretwell model forms the mathematical cornerstone of this theory, and predicts (1) that there exists an optimal offspring size, (2) that parents should make as many offspring of the optimal size as possible, and (3) the optimal offspring size is independent of the parent's total available resources (C. C. Smith and Fretwell 1974). In the years since, biologists have refined this model to account for allometrics (Charnov and Ernest 2006), multiple types of resources (McGinley and Charnov 1988), stage-based effects of resources (Mangel et al. 1994; Hendry et al. 2001), and variable environments (Forbes 1991; Olofsson et al. 2009; Monro et al. 2010) to name but a few extensions. The field is large and we do not try to review everything here. See Roff 1993 for a rich review of empirical and theoretical studies, including many applications and descendants of the Smith-Fretwell model. Marshall et al. 2018 offers a more modern review.

In these models resources improve offspring survivorship but have diminishing returns. This gives a survivorship function of the form in figure 1. But there are situations where we expect survivorship to have a more sigmoidal shape (Dani and Kodandaramaiah 2017), or start to decrease once an offspring is given too many resources (Hendry et al. 2001; Marshall et al. 2008).

These models typically assume a *symmetric strategy*, in which parents distribute resources equally among all offspring (Roff 1993, though exceptions exist, see Marshall et al. 2008). Nature does not always adhere to a symmetric strategy. Sometimes this is due to physiological constraints. For instance, in certain pea varieties, seeds located towards the middle of the pod tend to be larger, and a similar story can be told for many other plants. (Harper et al. 1970; McGinley et al. 1987; Roach and Wulff 1987). Within animals, the offspring's position in the ovary can affect size (Telfer and Rutberg 1960; McLaren and Michie 1960; McKeown et al. 1976). Even factors such as the number of adjacent eggs can impact the size of offspring, as observed in keelback snakes (Brown and Shine 2009).

However, it is conceivable that a non-symmetric strategy is optimal. This could appear statistically as high variance. Such variation may have also evolved as a form of bet-hedging in uncertain environments, although the evidence here is mixed (Einum and Fleming 2004; Marshall et al. 2008; Olofsson et al. 2009; Crean and Marshall 2009; Morrongiello et al. 2012; Childs et al. 2010). By assuming a symmetric strategy the existing theory precludes such situations.

Optimal offspring size models also assume that resources always help offspring, at least up to a point. But if we interpret resource as "anything which is distributed to offspring" then this misses the case where the resource only harms the offspring. For example, it is known that toxins may accumulate within the blubber of marine mammals (Muir et al. 1996; P. S. Ross et al. 2000; Boon et al. 2002; Houde et al. 2006) and mothers may vertically transfer these toxins to offspring during gestation and lactation (Aguilar and Borrell 1994; Hickie et al. 1999; Klanjscek et al. 2007; Noonburg et al. 2010).

B. Bacterial Aging

In the microbial world the question is not how many offspring to make but rather how to distribute components between two daughter cells. Before division, unicellular organisms must make a set of new components (DNA, organelles, cell membrane, etc.). As the cell divides it must partition the components between the two daughters. New components perform better than old components, increasing survival and growth rate of the cell. How then should a cell distribute these old and new components during reproduction?

Scientists have long thought that most cells distributed their components symmetrically. Each daughter was expected to receive equal proportions of old and new components, with any deviations arising due to stochasticity. Of course, some classic exceptions were known. *Saccharomyces cerevisiae* divides by budding off small cells, with the the larger cell inheriting old cytoskeleton and organelles (Herskowitz 1988; H. Gershon and D. Gershon 2000). *Caulobacter Crescentus* asymmetrically divides into swarmer and stalked cells (Ackermann et al. 2003). Diatoms do not divide evenly, giving new cell walls to their younger daughters (Laney et al. 2012; Moger-Reischer and Lennon 2019)

Knowledge and interest in asymmetric division have blossomed only in the last three decades with studies of cell polarity and the link to aging. Before, little discussion about asymmetric division appears except for the obviously visible cases where the daughter cells differ in size. This changed when researchers observed subpopulations of *Escherichia coli* age and die, even with abundant resources. When *E. coli* reproduce they expand their cell wall from one end, thus giving one daughter a new pole while the other daughter inherits the old pole. Damaged proteins segregate toward this old pole and can reduce the reproduction rate by more than thirty percent (Moger-Reischer and Lennon 2019; Stewart et al. 2005; Winkler et al. 2010; Lindner et al. 2008).

E. coli are not alone; asymmetry has evolved repeatedly (Kysela et al. 2013; Ackermann et al. 2007). Damaged proteins accumulate with age in *Sacharomyce Cerevisine* and *Schizosacheromyces Pombe* (Erjavec et al. 2008). Animal cells preferentially segregate genomic DNA, organelles, and damaged proteins to one cell (Fuentealba et al. 2008; Moore and Jessberger 2017; Ogrodnik et al. 2014; Rujano et al. 2006; Moger-Reischer and Lennon 2019). Cells also asymmetrically

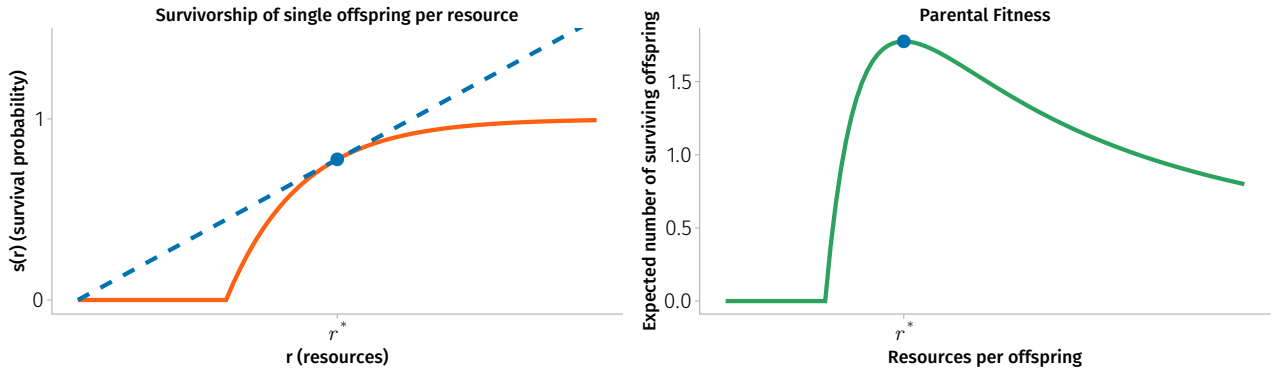

Figure 1. (Left) the survivorship function of the Smith-Fretwell model. This is a concave-increasing survivorship curve. The optimal offspring size can be found by drawing the blue dashed line from the origin so that it lays tangent to the curve. (Right) the fitness of a parent under a symmetric strategy where the parent makes as many offspring of size all offspring receive the same amount of resources.

segregate RNA, histomes, chromatids, mitochondria, and other organelles (Shlyakhtina et al. 2019). Polarization of the cell may be the mechanism that allows differential inheritance of such a variety of components, and polarity itself may have arose as a general strategy to restrict senescence to one daughter (Sunchu and Cabernard 2020; Macara and Mili 2008).

The disadvantage of asymmetric distribution is aging. The daughter, given old components, will in turn pass on its old components to its own daughter. Those components are now even older and when this daughter divides it will pass these older components to its own daughters. This continues until one daughter cell, many generations down the line, finds their components so old and worn that they no longer support the functions of life. This unlucky daughter dies, as if from old age. If the bacteria instead distributed old and new components symmetrically among the two daughters then the bacteria would never senesce. Every daughter, grand daughter, and so on would always receive half new components, enough to live, and thus the lineage would be "immortal."

Why, then, would a cell adopt an asymmetric distribution strategy in the first place? To do so treats one lineage as a "garbage dump" for damaged components (Stephens 2005) and, as damaged components are repeatedly sequestered into that lineage, dooms it to death by senescence (Proenca et al. 2018). By symmetrically distributing damage all lineages could potentially remain immortal as lineages would stabilize to half new and half old components.

Empirical evidence suggests a reason: the asymmetric strategy increases the population growth rate (Winkler et al. 2010). Many propose that, in certain species of bacteria, selection has cast aside the immortality in favor of the increased growth lineage growth rate of asymmetric division (Stephens 2005; Kysela et al. 2013; Moger-Reischer and Lennon 2019) .

Models from the last two decades also suggest that the asymmetric strategy, under certain conditions, can increase growth rate or fitness. In 2006, Watv demonstrated the evolution of asymmetry through a Leslie matrix stage structured model (Watve et al. 2006). Then in 2007 Evens applied a diffusion approach (Evans and Steinsaltz 2007). Also in 2007 Ackerman modeled this by tracking an abstract unit of damage that accumulates and passes on to offspring, with a cell's phenotype deciding what proportion of damage to give to each daughter. Damage decreased cell survival in a concave, convex, or linear way (Ackermann et al. 2007). Future models became more explicit in the mechanisms. In a model by Erjavec et al. cells must accumulate a protein to a threshold to reproduce, but these proteins can degrade to damaged ones, slowing this process (Erjavec et al. 2008). Chao created a similar model, but where damage linearly reduced the rate of accumulation (Chao 2010). Lin et al. tracked cell volume growth rate as a Hill-type function of protein concentration of a key protein, and found a phase transition from symmetric to asymmetric strategies as the protein uptake rate changed (Lin et al. 2019).

C. Unifying optimal offspring size theory and bacterial aging theory

Both the mother bird and the bacteria share the same underlying problem: how to distribute resources (food, new cellular components) or refuse (toxins, damaged proteins, old cellular components) among offspring to maximize fitness. Optimal offspring size models allow multiple offspring; however, they restrictively assume that resources are distributed equally. Bacterial aging models, on the other hand, allow only two offspring but do not assume an equal distribution of resources. Both models differ in how resources affect offspring survival.

In this paper we present a generalized resource distribution model that unifies these two fields. This model accommodates:

1. A range of distribution strategies, from symmetric and asymmetric to anything in between.

2. Any integer number of offspring.

3. Arbitrary concave or convex survivorship functions.

We then prove that concave survivorship selects for symmetric strategies while convex survivorship selects for asymmetric strategies. This allows us to derive the optimal strategies for the specific survivorship function shapes shown in figure 4. Tables 2 and 3 summarize these results.

In the subsequent section, we expand these results to fluctuating environments. If, in all environments, (1) resources start and stop affecting offspring at the same threshold amounts and (2) all survivorship functions are concave, then the symmetric strategy is optimal and evolves. If the first of these conditions does not hold, then the fitness landscape resembles a rugged mountain range, made up of many concave sections. If neither of these conditions hold then symmetric strategies are generally local extrema, even though the landscape may be highly rugged and complex. We also investigate stage-structured populations and show that, provided a constant environment and the ability to choose a distribution strategy for each stage, populations evolve the optimal strategy for each stage.

These results (1) agree with and strengthen existing models, (2) organize existing models into a unifying framework, (3) make new predictions, and (4) reveal universal properties of resource distribution models. By virtue of being an optimization model, these results extend beyond the original scope and apply to any system with the correct mathematical setup. Optimal Foraging Theory is one such example (Charnov 1976), but the applications need not be biological.

2. Constant Environment Model

A. Background: The Smith-Fretwell Model

We review the classic Smith-Fretwell model, which serves as the foundation of our model. The Smith-Fretwell model assumes the following.

1. Parents have a fixed amount of resources R to invest in reproduction.
2. Parents can choose the number of offspring n they produce.
3. The parent distributes resources equally among the offspring so that each receives R/n resources.
4. An offspring's survival probability increases as it is given more resources. This happens in a concave fashion with diminishing returns, similar to a type II functional response. The survival probability of an offspring given r resources is $s(r)$.
5. Offspring require some minimum number of resources r_{low} to have any chance of survival.
6. Once an individual reaches maturity, its survival and reproduction are independent of the resource allocation they received as a juvenile.

Smith and Fretwell showed that there exists an optimal amount of resources r^* to give each offspring. This amount maximizes fitness per unit resource. The parent's optimal strategy is to birth as many offspring of size r^* as possible. This optimal size is independent of R meaning that parents, when given additional resources, should create more offspring of size r^* rather than larger offspring. Note that this is an instance of the marginal value theorem (Charnov 1976).

To calculate the optimal size, one can find the value r which maximizes $s(r)/r$. This is equivalent to finding the point where a line drawn from the origin is tangent to the curve of $s(r)$ (C. C. Smith and Fretwell 1974). The optimal number of offspring in then R/r^*. If this is not an integer, one simply compares the fitness of the two nearest integers and chooses the higher (Charnov et al. 1995).

B. Model Setup

Our model generalizes the Smith-Fretwell model in two ways. First is that we no longer assume that all offspring receive equal amounts of resources; rather we allow any possible distribution resources among offspring. Second is that we allow a wider range survivorship functions, including those where resources may harm the offspring.

For clarity we call anything the parent distributes *resources*, regardless of whether they are good or bad for the offspring. (Mnemonically, one could think of r as standing for *refuse* when resources are bad.) We sometimes say that an offspring with r resources is *size* r. The *survivorship function* s determines how resources affect offspring. An individual offspring given r resources has $s(r)$ *survival probability*. This is the only way resources affect offspring; future performance is independent of how resources an offspring started with. We can think of survival probability as measuring the fitness contribution of a single offspring to the parent. In general, the model works for any trait we expect natural selection to maximize, not just survival.

For simplicity our model assumes resources affect only offspring survival and that natural selection acts to maximize expected number of surviving offspring. We ignore any evolution on the total amount of resources R. If instead R changes as the parent ages, as expected in many organisms (Roff 1993), then the analysis still holds in that the overall form of the strategy remains optimal (see table 2 and 3) rather than the specific strategy itself (which depends on the exact R value).

B.1. Asymmetric Distribution. Parents in our model can control two aspects of their strategy: the number of offspring n, and how they distribute their R total resources among those offspring. We can encode this information into the vector $\mathbf{r} = (r_1, r_2, \ldots, r_n)$, where offspring i receives r_i resources. Here the length of the vector tells us the number of offspring and the values tell us how the resources are partitioned. We call $\mathbf{r}$ the parent's

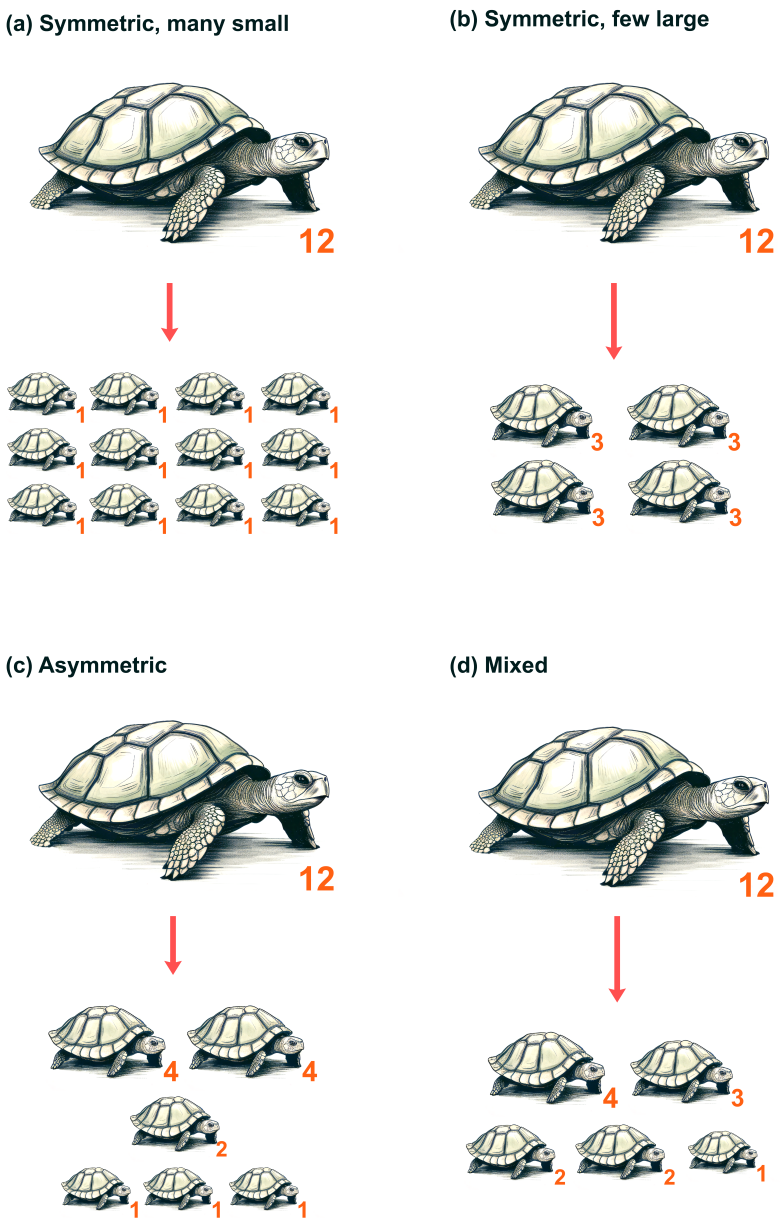

Figure 2. Four example strategies for distributing twelve resources when $r_{low} = 1$ and $r_{high} = 4$. The top row illustrates the extremes that a symmetric strategy can take. In (a), all offspring are size one or zero, while in (b), all offspring are size four or zero. Figure (c) depicts an asymmetric strategy, in which there are many offspring of sizes r_{low} and r_{high} but only one of an intermediate size. Figure (d) demonstrates a mixed strategy, which is neither symmetric nor asymmetric.

distribution strategy.

The parent's fitness (expected number of surviving offspring) for a particular strategy can then be written as

$$w(\mathbf{r}) = \sum_{i=1}^{n} s(r_i). \tag{1}$$

where $s(r)$ is the survival probability of an offspring receiving r resources. We will consider this function to take on one of the six possible shapes shown in figure 4. The above equation is a natural formulation of the resource distribution problem, though as far as we know it has been analyzed only in (Marshall et al. 2008). An optimal strategy is an $\mathbf{r}$ which maximizes $w(\mathbf{r})$ under one of the following constraints.

$$\sum_{i=1}^{n} r_i = R \quad \text{(if parents must distribute all resources)} \tag{2}$$

$$\sum_{i=1}^{n} r_i \leq R \quad \text{(if parents may withhold resources)} \tag{3}$$

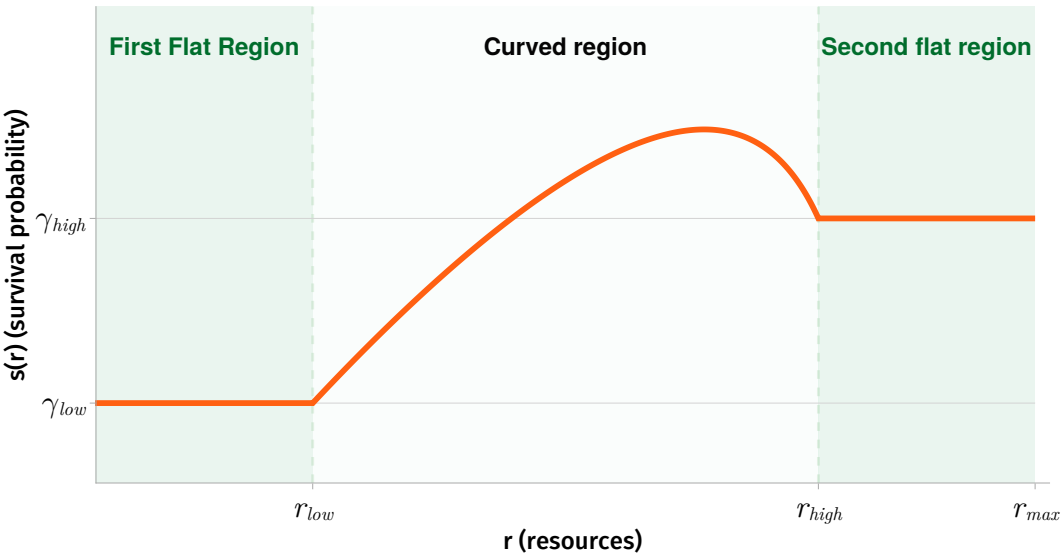

Figure 3. Anatomy of the survivorship function s. This function takes in a resource value between zero and r_{max} and outputs a survival probability. Note that r_{low} may be zero and r_{max} or r_{high} may be infinite. The constants γ_{low} and γ_{high} can take any value between zero and one.

Which constraint we choose depends on the biology of the system. The first appears when the parent must use *all* R of their resources, such as when a bacteria distributes components. Multicellular organisms fall under this first constraint if the "resource" is some kind of toxin that the parent must offload onto the offspring, or something similar to space which offspring expand to fill, or if resources are always beneficial and the parent evolved to distribute all of them. The second constraint occurs when the parent can distribute *up to* R resources, but not necessarily all. Examples of this are when the resource is food, attention, uterine capacity, or any case where the parent may wish to reserve some resources for the future.

We limit the maximum size of each offspring to r_{max}. Such a constraint could exist for many reasons: if an offspring is too large the mother or baby may die during birth, or if a baby bird is too large it may be too heavy to fly and thus always die. If such size limit exists we set r_{max} to equal R as no offspring can receive more than the total amount of resources. The total number of offspring may also be constrained due to physiological and mechanical reasons (Roff 1993). For example, carrying too many offspring could effect a fly's ability to fly (Berrigan 1991) and a snakes ability to move (Crews et al. 1988). In lizards it effects ability to climb (Andrews and Rand 1974), to hide in crevices (Vitt 1981), and to run (Garland Jr 1985; Van Damme et al. 1989). However, for this model it is enough to fix the number of offspring at exactly n. Once we derive the form of the optimal strategy for any n it is a simple matter to scan through all biologically reasonable values of n and pick the one that gives greatest fitness.

To summarize, for a given number of offspring n we wish to find the distribution strategy $(\mathbf{r})$ which maximizes parental fitness (equation 1) while using up exactly all (constraint 2), or no more than all (constraint 3), total resources (R). During this the parent cannot make offspring larger than r_{max}. Stated this way our model is a non-linear optimization problem and the solutions are our optimal strategies.

B.2. Convexity of survivorship functions. Our model allows for a wider range of survival functions s than previous models in the literature. Rather than restricting s to a functional form, we allow s to be an arbitrary continuous piecewise function made up of a curved region and two flat regions.

$$s(r) = \begin{cases} \gamma_{low} & \text{if } r < r_{low} \quad \text{(first flat region)}, \\ s_c(r) & \text{if } r_{low} \leq r \leq r_{high} \quad \text{(curved region)}, \\ \gamma_{high} & \text{if } r_{high} < r < r_{max} \quad \text{(second flat region)}. \end{cases} \tag{4}$$

The six general shapes s can take are shown in figure 4. Figure 3 contains a diagram of all the parameters and parts.

The centerpiece, both in location and importance, is the curved region given by s_c. This is a concave or convex function which is continuous and twice differentiable everywhere except at the boundaries where it touches the flat regions. In the analysis section we will discover that the concavity of s_c is the main factor in determining the optimal strategy.

The first flat region of s tells us what happens when resources are below the threshold r_{low}. For example, r_{low} may represent the minimum amount of resources that an offspring needs for life; less than this and they are guaranteed to starve and die (C. C. Smith and Fretwell 1974). Alternatively, if resources are damaged cellular components (as in bacteria), enough might need to accumulate before they begin harming the offspring. An offspring which receives below r_{low} resources has γ_{low} survivorship. Similarly r_{high} is the

threshold after which resources saturate and no longer have an effect. Offspring between this value and the maximum size r_{max} have γ_{high} survivorship.
These flat regions are not required. One can effectively remove the first flat region by setting r_{low} equal to zero. Likewise one can remove the second flat region by setting r_{high} equal to r_{max}. This does not change any of the following analysis, and the formula we derive are still valid.

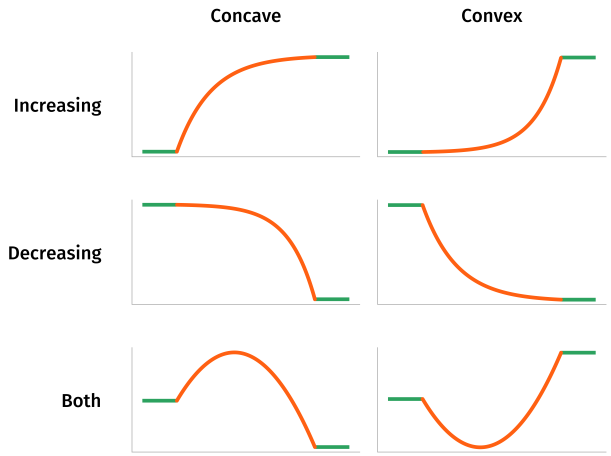

Figure 4. The six forms the survivorship function s can take, named according to the shape of their curved region (orange): concave-increasing, concave-decreasing, concave-increasing-decreasing, convex-increasing, convex-decreasing, convex-decreasing-increasing.

B.3. Six classes of survivorship functions. We show that the convexity and whether or not the function is increasing or decreasing determines the qualitative outcome. This leads to six possible descriptions of the survivorship function's curved region: concave-increasing, concave-decreasing, concave-increasing-decreasing, convex-increasing, convex-decreasing, and convex-decreasing-increasing. (For concision we will call the survivorship functions as a whole by these names, even if the convexity and derivative only refer to the curved region technically.)
The concave-increasing survivorship functions captures the diminishing returns of investment in offspring and thus is common in the optimal offspring size literature. When r_{high} and r_{max} are infinite then s is the same as a classic Smith-Fretwell survival function.
The concave-increasing-decreasing functions are seen in stage structured populations. Sockeye salmon offspring have two developmental stages: egg and fry. The egg stage follows a concave-decreasing function because more resources mean larger egg size. But large egg size decreases survivorship as they require a large surface area to volume ratio to supply oxygen. Too large and the embryo asphyxiates and dies. But the opposite is true during the post hatching stage; larger egg size correlates with higher suvivorship in a concave-increasing way. When combined these two facts give a concave-increasing-decreasing survivorship function (Hendry et al. 2001 but see Hendry and Day 2003).
The concave-decreasing and convex-decreasing functions are both seen in bacterial aging. These decrease because the mother distributes a waste product to offspring. These could be toxins or damaged proteins in the cell, but more often are old cellular components.
It is trickier to find firm examples for convex-increasing survivorship. We speculate that these apply to survivorship functions that follow a sigmoidal curve where r_{max} is less than the inflection point. For example, say puppy birth size is in reality associated with a sigmoidal survivorship curve. But what if the inflection point, where survivorship switches from convex to concave, is the size of a teenage dog? The mother can never birth a teenage-sized puppy, so from her point of view the survivorship curve is convex. Following this same logic, another example might be the time spent teaching and passing knowledge to offspring.
Convex-decreasing-increasing survivorship is the most difficult to conceive examples for. If we think it terms of nutrients then it is associated with something that is beneficial in high and low dosages, but detrimental in medium dosages – a difficult thing to find. Mutagens could be an example, and having enough of them increases the probability that the offspring gains a difficult to acquire but very beneficial mutation, but a medium amount likely sends them into a fitness valley (Shlyakhtina et al. 2019; L. Ross et al. 2022). More satisfying examples arise if we interpret convex-decreasing-increasing as the environment selecting for specialization. For example, perhaps it is good to be either small or large. Small enough and you can hide from predators. Large enough and you can fight them off. But a medium size leaves the offspring no options but to hope the predator already had dinner.

3. Constant Environments

We have two central questions: what strategies are optimal, and will organisms evolve towards these optimal strategies? To answer these, we first study concave and convex survivorship functions in general without reference to whether they are increasing or decreasing.
To streamline the presentation we focus on the case where the curved region s_c is *strictly* concave or convex. This ensures that the optima we derive are unique. The same analysis works for the non-strict case but the optima need not be unique or strict. Natural selection may become stuck at different optima or neutrally drift around flat regions.

A. Optimal strategies for concave survival functions

Say s is a concave-increasing function. Consider an optimal distribution strategy $\mathbf{r}^* = (r_1, \ldots, r_n)$. The offspring must fall into one of three categories:

1. offspring on the first flat region of s (whom receive $0 \leq r < r_{low}$ resources)

Table 1. Table of terms and symbols for the constant environment model.

Term	Definition
Resource	Something that is distributed among offspring which affects the offspring survival probability. Despite the positive connotation of the word, resources do not always improve offspring survival probability.
Fitness	A parent's expected number of surviving offspring.
Survivorship	The probability that an offspring will survive to reproductive age.
Strategy	How a parent distributes resources among their offspring. Represented by the vector $\mathbf{r}$.
Offspring on the curved region	An offspring who receives $r_{low} \leq r \leq r_{high}$ resources.
Symmetric Strategy	A distribution strategy that equally distributes resources among offspring in the curved region.
Asymmetric Strategy	A distribution strategy where all offspring on the curved region have either r_{low} or r_{high} resources, with at most one offspring receiving an amount r_r between these two.
r_i	The resources the ith offspring receives. Also called the offspring's size.
$\mathbf{r}$	The resource distribution strategy. This is a vector of resource amounts $(r_1, r_2, \ldots, r_n)$ where ith offspring receives r_i resources (or, depending on context, r_i resources above r_{low}.)
$s(r)$	The survivorship function. Outputs the survival probability of an offspring given r resources.
$s_c(r)$	The curved region of s. This is the function s restricted with offspring with size r restricted to $r_{low} \leq r \leq r_{high}$.
R	The total amount of resources the parent has available to distribute.
r_{low}	The minimum threshold, after which resources begin affecting survivorship. The lower border of the curved region. Must be greater than or equal to zero.
r_{high}	The maximum threshold, after which resources stop affecting survivorship. The upper border of the curved region. Must be greater than r_{low} but can be infinite.
r_{max}	The maximum amount of resource an offspring can receive.
γ_{low}	The survival probability of offspring with r_{low} or less resources.
γ_{high}	The survival probability of offspring with r_{high} or more resources.
n	The length of $\mathbf{r}$. Can be interpreted either as the number of offspring or the *maximum* number of offspring. In the latter case we interpret offspring with size r_{low} or less as offspring that are not born.
$w(\mathbf{r})$	The fitness of distribution strategy $\mathbf{r}$. The expected number of surviving offspring in a constant environment.

2. offspring on the curved region s_c (whom receive $r_{low} \leq r \leq r_{high}$ resources)
3. offspring on the second flat region of s (whom receive $r_{high} < r \leq r_{max}$ resources).

If we break down the fitness contribution into three terms, one for each of these groups, the parental fitness (equation1) becomes

$$w(\mathbf{r}^*) = \sum_{i=1}^{n_c} s_c(r_i) + \sum_{i=1}^{n_{low}} \gamma_{low} + \sum_{i=1}^{n_{high}} \gamma_{high} \quad \textbf{(5)}$$

where n_c, n_{low} and n_{high} are the number of offspring on the curved, first flat, and second flat regions respectively. As all offspring on the flat regions have the same survival probability this simplifies to

$$w(\mathbf{r}^*) = \sum_{i=1}^{n_c} s_c(r_i) + n_{low}\gamma_{low} + n_{high}\gamma_{high}. \quad \textbf{(6)}$$

Focus now on the summation term $\sum_{i=1}^{n_c} s_c(r_i)$. Because $s_c(r)$ is a strictly concave function Jensen's inequality says that

$$\sum_{i=1}^{n_c} s(r_i) < n_c s\left(\frac{\sum_{i=1}^{n_c} r_i}{n_c}\right).$$

Then, defining R_c as the total amount of resources invested in the curved region offspring, we can rewrite this as

$$\sum_{i=1}^{n_c} s(r_i) < n_c s\left(\frac{R_c}{n_c}\right) \quad \textbf{(7)}$$

which implies that any optimal strategy will ensure curved region offspring receive the R_c resources in *equal* amounts. We call such a strategy that equally distributes resources among curved region offspring a *symmetric strategy* and the form looks like

$$\mathbf{r_c^*} = \begin{pmatrix} R_c/n_c \\ \vdots \\ R_c/n_c \\ R_c/n_c \end{pmatrix}$$

where $\mathbf{r_c}^*$ denotes the optimal strategy for offspring on the curved region.

In this case a symmetric strategy is the unique and strict global optima when considering only the offspring on the curved region. (Why? Because if a multivariate function is strictly concave, and if the collection of feasible strategies lies on a convex set, then there is a single extrema which is strict. Our constraints are linear, and so the feasible strategies lie on a linear set which is by definition convex. If the curved region is instead *non-strictly* concave then the inequality signs become "$\leq$" signs. This means the symmetric strategy remains a global optima but it is no longer unique or strict. As an extreme example, if s_c is linear so that $s_c(r) = r$, then all ways of distributing the offspring on the curved region do equally well (Hillier and Lieberman 2010).)

The fact that there is only one optima under strict concavity hints that the fitness landscape is a simple, "Mt. Fuji"-style one. This would imply our population evolves towards the optima from any starting point. We show that this is indeed the case in appendix A. For fixed R_c and n_c, mutations that move the curved region's offspring towards the symmetric distribution are beneficial. These mutations do not have to be small – a large mutation is beneficial as long as it makes the distribution more symmetric. (Or, if s_c is non-strictly concave, such mutations are at worst neutral.)

Note that we have not yet shown what values of R_c and n_c give the optimal strategy. All we know is that, given a R_c and n_c, the optimal strategy is symmetric.

B. Optimal strategies for convex survival functions

For strictly convex survival functions we mimic the argument for the concave case. Split the offspring into three types: those on the two flat regions and those on the curved region. Consider only those on the curved region and again apply Jensen's inequality. Because s_c is strictly convex the inequality sign is reversed and we conclude that

$$\sum_{i=1}^{n_c} s_c(r_i) < n_c s_c\left(\frac{R_c}{n_c}\right)$$

which is to say that the symmetric strategy is worse than all other strategies. Furthermore, it is strict and is the unique global minima. (Why? Because if a multivariate function is strictly convex and the collection of feasible strategies lies on a concave set then there is a single extrema, and it is strict (Hillier and Lieberman 2010; S. P. Boyd and Vandenberghe 2004).).

This is the opposite of the concave case. Mutations that make the resource distribution more *asymmetric* for the offspring in the curved region have higher fitness. That is to say, mutations which move the strategy *away* from symmetry are selected for. (Or, if s_c is non-strictly convex, such mutations are at worst neutral.)

If we climb the fitness landscape through a series of small mutations we will end up at a distribution such that the curved region's strategy looks like

$$\mathbf{r_c^*} = \begin{pmatrix} r_{high} \\ \vdots \\ r_{high} \\ r_r \\ r_{low} \\ \vdots \\ r_{low} \end{pmatrix}$$

Table 2. Forms of optimal strategies when the parent *is not* required to distribute all resources. For the example forms the number of offspring is $n = 6$.

s_c	**Optimal Strategy (may withhold resources)**	**Example strategy vector**
Concave-increasing	Calculate the optimal offspring number as in the Smith-Fretwell model. Distribute all resources equally among these offspring. Give all remaining offspring zero resources.	$(r^*, r^*, r^*, r^*, 0, 0)$
Concave-decreasing	Give each offspring no more than r_{low} resources.	$(0, 0, 0, 0, 0, 0)$
Concave-increasing-decreasing	Same strategy as concave-increasing, except never give an offspring enough resources to enter the decreasing part of the curve.	$(r^*, r^*, r^*, r^*, 0, 0)$
Convex-increasing	Create as many offspring with r_{max} resources as possible. Put all remaining resources into a single offspring.	$(r_{max}, r_{max}, r_{max}, r_r, 0, 0)$
Convex-decreasing	Give each offspring no more than r_{low} resources.	$(0, 0, 0, 0, 0, 0)$
Convex-decreasing-increasing	If $\gamma_{low} \geq \gamma_{high}$ then give each offspring no more than r_{low} resources. Otherwise the optimal depends on the details of s and R.	*Multiple Forms*

where $r_{low} \leq r_r \leq r_{high}$. We can such a strategy an *asymmetric strategy*. We can produce this strategy with a simple algorithm: give all offspring r_{low} resources, then sequentially make as many r_{high} sized offspring as possible, then finally give any remaining resources r_r to a single offspring.
This strategy is a strict global optima, is unique (up to reorderings), and we expect it to evolve. The proof is tedious and can be found in appendix section B. Also as in the concave case this only tells us the form of the optima – to find the exact optima we require more details.

C. Optimal strategy for specific cases

The convexity of the survivorship function tells whether resources for offspring on the curved region should be distributed symmetrically or asymmetrically. But we do not know how many offspring or resources should be placed on the curved region to begin with, nor how the offspring on the flat regions of play into the optima. To understand this we must consider each of the cases in figure 4 separately. Generally the optima we find is unique for non-extreme values of R. (At extreme values all offspring may land on the lower or upper flat regions, and many distributions of resources among these offspring are equivalent.)

C.1. Concave-increasing. Concave-increasing functions are common in optimal offspring size theory. The classic Smith-Fretwell survivorship function is one of these for the special case where r_{max} equals R. They model resources which are always helpful or neutral, such as food.

Because more resources never harm the offspring any proposed optimal strategy that uses less than R resources could be improved, or at least not made worse, by distributing all R resources. Thus we can focus on only the strategies which use all R resources because we know the globally optimal strategy exists among those.

Any strategy partitions the offspring into one of the three regions: the first flat region, those on the curved region, and those on the second flat region. If R is so high that we can distribute the resources so that all n offspring have r_{high} or greater resources then any such distribution is an optimal strategy and we are done. Otherwise focus on the first flat region. An offspring there with size above zero is wasting resources – we could make that offspring size exactly zero without decreasing its survivorship and use those resources somewhere else. Likewise it never helps to give an offspring more than r_{high} resources because the resources above r_{high} could be given and elsewhere without decreasing fitness. Said another way, if we have a strategy that gives offspring i a resource value $0 < r_i \leq r_{low}$ or $r_i > r_{high}$ then we can replace r_i with zero or r_{high} respectively, place the remaining resources someplace else, and obtain a strategy with the same or better fitness.

This implies that an optimal strategy lies among those

Table 3. Forms of optimal strategies when the parent *is* required to distribute all resources. For the example forms the number of offspring is $n = 6$.

s_c	**Optimal Strategy (must distribute all resources)**	**Example strategy vector**
Concave-increasing	Same as when not required to distribute all resources.	$(r^*, r^*, r^*, r^*, 0, 0)$
Concave-decreasing	Find the optimal anti-resource offspring size $\bar{r}$. Make as many offspring of size $r_{max} - \bar{r}$ as possible. All other offspring will be size r_{max}.	$(r_{max}, r_{max}, r_{max}, r_{max}, r_{max} - \bar{r}, r_{max} - \bar{r})$
Concave-increasing-decreasing	Same as the concave decreasing case but with a different way of calculating the optimal anti-resource offspring size $(\bar{r}')$.	$(r_{max}, r_{max}, r_{max}, r_{max}, r_{max} - \bar{r}', r_{max} - \bar{r}')$
Convex-increasing	Same as when not required to distribute all resources.	$(r_{max}, r_{max}, r_{max}, r_r, 0, 0)$
Convex-decreasing	Create as many offspring with r_{low} resources as possible. For any remaining resources, sequentially take each offspring and fill them up to r_{max}, or as high as possible. Place all remaining resources in a r_r sized offspring.	$(r_{max}, r_{max}, r_r, r_{low}, r_{low}, r_{low})$
Convex-decreasing-increasing	Same as either the concave-increasing or concave-decreasing case if in the optimal there exists an offspring with size between r_{low} and r_{high}. Open problem otherwise.	*Multiple Forms*

strategies where the offspring in the first flat region are all exactly size zero and and offspring in the second flat region are all exactly size r_{high}. Except offspring of size r_{high} are technically not part of the flat region, but are (just barely) on the curved region and thus the second flat region has no offspring.

From our concave result we already know that an optimal strategy distribute resources among curved region offspring symmetrically. This means at least one optimal strategy has only zero sized offspring on the first flat region, no offspring on the second flat region, and offspring on the curved region of all the same size. Call such a strategy $\mathbf{r}^*$. From equation 6 the fitness of this strategy is

$$w(\mathbf{r}^*) = n_c s_c \left(\frac{R}{n_c}\right) + C$$

where $C = (n - m - 1)\gamma_{low}$ is the fitness given by all the zero resource offspring.

As a technical point it never a bad idea for a parent to make $\mathbf{r}$ as long as possible because $\gamma_{low} \geq 0$. But biologically speaking γ_{low} is usually zero as zero resource offspring have no chance of survival. In this case, regardless of the length of $\mathbf{r}$, we would say n_c is the actual number of offspring made by the parent. This means we wish to find the n_c which maximizes $n_c s_c(R/n_c)$. But this is the exact problem that the original Smith-Fretwell model solves. The optimal resources r^* to give each offspring should satisfy

$$\frac{ds(r^*)}{dr^*} = \frac{s(r^*)}{r^*}.$$

An easy way to find this r^* is to graph $s(r)$ and find the unique line that intersects the origin and a *single* point of the curved region of $s(r)$. The r coordinate of the point where the line intersects the curve is r^*.

Once we know r^* we can calculate that $n_c = R/r^*$. If n_c happens to be a non-integer number then we compare the two closest integers and pick the one which gives highest fitness (Charnov et al. 1995).

It may it first seem we've just repeated the original result of Smith and Fretwell. But because of the generality of our setup we have shown that even with the flexibility of distributing unequally, or if n is fixed, or if all of R must be used, the Smith-Fretwell strategy remains the best. The algorithm for finding this optimal is

1. Find the r^* which solves $ds(r^*)/dr^* = s(r^*)/r^*$.
2. If r^* is not an integer then look at the two near-

est integers and pick the one which gives highest fitness.

The form of the optimal is

$$\begin{pmatrix} r^* \\ \vdots \\ r^* \\ 0 \\ \vdots \\ 0 \end{pmatrix}.$$

C.2. Concave-decreasing. Concave-decreasing functions (and decreasing functions in general) are meant to model detrimental proteins or damaged cellular components (Moger-Reischer and Lennon 2019). It could also model toxins which multicellular animals pass onto their offspring Klanjscek et al. 2007; Noonburg et al. 2010; Paula et al. 2014, or perhaps even heavy metals which accumulate in fish eggs (Jezierska et al. 2009) and cross the placental barrier in mammals (Caserta et al. 2013).
Because resources never help the offspring if the parent has the option to withhold resources then any strategy which distributes no more than r_{low} resources to each offspring is optimal.
If the parent instead *must* distribute all their resources then the situation is more complex. To find an optima we will transform this problem into one of finding a concave-increasing optima – a problem which we know already how to solve by the previous section. This transformation consists of mirroring s across a vertical line at r_{max} to get

$$\bar{s}(\bar{r}) = s(r_{max} - \bar{r})$$

which is a concave-increasing function. The function $\bar{s}$ takes in how many resources away from r_{max} an offspring is and returns its survival probability. If we previously measured survival in units of food a chick received we now measure it in units of food that the chick *didn't* receive, relative to the maximum.
We have written the system in units of "anti-resource," which we denote as $\bar{r}$. This means $\bar{r}$ anti-resources corresponds to $r = r_{max} - \bar{r}$ resources and distributing R resources now corresponds to distributing $\bar{R} = nr_{max} - R$ anti-resources. The expected number of surviving offspring is the sum $\sum_{i=1}^{n} \bar{s}(\bar{r}_i)$.
Now that our optimization problem is in concave-increasing form we can apply the results from the previous section: there exists an optimal anti-resource amount $\bar{r}^*$ and the parent should make as many offspring of this size as possible. An optimal strategy is then

$$\bar{\mathbf{r}}^* = (\bar{r}^*, \ldots, \bar{r}^*, 0, \ldots, 0).$$

If we use $r = r_{max} - \bar{r}$ to convert anti-resources back into resources we get

$$\mathbf{r}^* = \begin{pmatrix} r_{max} - \bar{r}^* \\ \vdots \\ r_{max} - \bar{r}^* \\ r_{max} \\ \vdots \\ r_{max} \end{pmatrix}$$

as a solution. The algorithm for finding this optimal is then

1. Convert the problem into one of anti-resources.
2. Find the anti-resource optima as we would in the concave-increasing case.
   - Begin all offspring with zero anti-resources.
   - Find the Smith-Fretwell optimal anti-resource amount either by finding the tangent point or by solving $\bar{s}'(\bar{r}) = \bar{s}(\bar{r})/\bar{r}$.
   - Sequentially make as many offspring as possible with the optimal anti-resource amount.
   - Distribute any remaining anti-resources equally among the $\bar{r}_{sf}$ sized offspring. Call this offspring size $\bar{r}^*$.
3. Convert the optima back into resources.

C.3. Convex-increasing. In the convex-increasing case resources never harm offspring. This means, like the concave-increasing case, at least one optimal strategy uses all R resources. If $R > nr_{high}$ then any strategy that gives all offspring r_{high} or more resources is optimal. Otherwise we can show that the optimal strategy is of the form

$$\mathbf{r}^* = \begin{pmatrix} r_{high} \\ \vdots \\ r_{high} \\ r_r \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

where r_r is between 0 and r_{high}. The proof relies on the concave-increasing result of section C.1 and can be found in appendix C.
The following algorithm will bring us to one of these optima.

1. Start all offspring at zero resources.

2. Make as many offspring of size r_{high} as possible.

3. There now remains $0 \leq r_r < r_{high}$ resources. Do one of the following.

   - If all offspring are now size r_{high} then we have reached maximum fitness and it does not matter how we distribute the remaining resources.
   - Otherwise put the remaining r_r resources in a single offspring.

C.4. Convex-decreasing. In the convex-decreasing case resources never help offspring. This can be the case if resources are old components, and is possible in animals under certain conditions concerning size dependent mortality (Jørgensen et al. 2011).
If the parent may withhold resources they should make as many offspring as possible and give each no more than r_{low}. This is the optimal strategy as it ensures each offspring has the highest possible survivorship.
But say the parent must distribute all R resources and that giving each offspring r_{low} resources still leaves some resources remaining. To find the optimal strategy we mimic what we did for concave-decreasing functions. First transform the problem into one of anti-resources. The problem becomes one of optimizing a concave-increasing function where we must use exactly $\bar{R}$ anti-resources. By our previous result for the concave-increasing case we know the optima is of the form

$$(\bar{r}_{high}, \ldots, \bar{r}_{high}, \bar{r}_r, \bar{0}, \ldots, \bar{0})$$

Observing that $\bar{r}_{high} = r_{low}$ and $\bar{0} = r_{max}$ we convert from anti-resources to resources to find the optima is

$$\begin{pmatrix} r_{max} \\ \vdots \\ r_{max} \\ r_r \\ r_{low} \\ \vdots \\ r_{low} \end{pmatrix}$$

where $r_r = r_{max} - \bar{r}_r$. The following algorithm will bring us to this optima.

1. Give every offspring r_{low} resources. This uses up as many resources as possible without decreasing fitness.

2. If resources remain then sequentially bring as many offspring as possible up to size r_{max}, or as close as possible. All these offspring should land on the second flat region.

3. If after this resources still remain, then put those remaining resources all into one of the r_{low} offspring. It is now of size r_r.

C.5. Concave-increasing-decreasing. In the concave-increasing-decreasing case resources are beneficial or neutral up until a certain point. After this point which they begin decreasing survival. Let us call this threshold value, after which resources harm the offspring, r_{top}. Functions of this type have been considered in (Marshall et al. 2008; Hendry et al. 2001; Hendry and Day 2003).
Given the option the parent should never give an offspring more than r_{top} resources. Otherwise they would spend resources to decrease fitness. If the parent can withhold resources this is easy to do. Even if the parent must spend all their resources, as long as $R \leq nr_{top}$ it is still possible. In either of these cases s effectively becomes a concave-increasing function as the parent never makes an offspring that lands beyond the increasing region. The optimal strategy is then the same in the concave-increasing case; r_{top} takes the place of r_{max}. This does not hold when the parent must use up all R resources *and* R is high enough that they must give at least one offspring more than r_{top} resources. In this case the optimal strategy takes the form

$$\begin{pmatrix} r_{max} - \bar{r}'^{*} \\ \vdots \\ r_{max} - \bar{r}'^{*} \\ r_{max} \\ \vdots \\ r_{max} \end{pmatrix}$$

where $r_{max} - \bar{r}'^{*}$ is acting as the optimal offspring size and the offspring of size r_{max} are used to remove extra resources. The value of $\bar{r}'^{*}$ can be calculated as described below in the algorithm of how to find this optimal strategy.

1. If $R < nr_{top}$ then set r_{max} to r_{top}. This restricts the domain of s to between zero and r_{top}. Survivorship is now concave-increasing, so find the optima as one normally would for the concave-increasing case.

2. Otherwise give every offspring r_{top} resources. This leaves $R' = R - nr_{top}$ remaining resources to distribute.

3. Make the function s_d which gives the survivorship of an offspring with r' resources above r_{top}.

4. Notice s_d is a concave-decreasing function. Calculate how to optimally distribute the R' remaining resources under s_d by following the algorithm given in the concave-decreasing section. Call this strategy $\mathbf{r}'^{*}$.

5. Add r_{top} to each entry in $\mathbf{r}'^*$. This is a optimal strategy.

The proof that this algorithm gives a optimal strategy can be found in the appendix D.

C.6. Convex-decreasing-increasing. This case describes some resource that is beneficial at low and high levels but detrimental when given in moderation. It could also describe environments that favor specialization (ex. small offspring can hide, large offspring can fight, and medium offspring can do neither.)
When all R resources must be used, and if the optimal strategy contains a offspring with size strictly between r_{low} and r_{high}, then the optimal strategy same as either the convex-increasing or the convex-decreasing case. But which of the two it is depends on the exact survivorship function being used.
Heuristically, the convex-decreasing strategy works best when the first flat region is higher, and the convex-increasing strategy works best when the second flat region is higher. But this is only a heuristic, and counterexamples exist (appendix E.2).
When the parent need not use all R and the first flat region is higher or equal to the second flat region then the optimal strategy is to place all offspring in the first flat region. Otherwise the form of the optima is not easy to classify, and depends on the exact survivorship function.
Appendix E contains the proof of these statements, along with some discussion about the cases where the optima does not contain a runt. An easy algorithmic solution to this case remains an open problem. Unlike the other cases, this one seems to depend on the specific values of the survivorship function.

4. Fluctuating Environments

A. Model Setup

The constant environment model predicts that mixed strategies never occur; evolution prefers pure symmetric or pure asymmetric strategies. Yet nature disagrees and hosts a vast array of mixed strategies. We can explain this mismatch between theory and reality in many ways: sibling competition, spatial constraints, parasitism, differing offspring quality, or imperfect information are a few But here we focus on one of the most common explanations: diversifying bet hedging under unpredictable, fluctuating environments (Roff 1993; Crean and Marshall 2009; Olofsson et al. 2009).
If the parent's strategy is completely plastic then things are easy within our framework; the parent observes the current environment and applies the optimal strategy for it. However, if strategies are nonplastic, the parent is forced to commit to a single strategy across all environments. For example, they may produce offspring of a single size that performs decently in all environments. Or they may instead hedge their bets and make a wide diversity of offspring sizes so that that at least some subset of their children will thrive in any environment.
Mathematically, the parent chooses an $\mathbf{r}$ and n that remain constant across all environments they encounter. The optimal strategy will be the $\mathbf{r}$ which maximizes the geometric mean fitness $W(\mathbf{r})$ (Haldane and Jayakar 1963; Karlin and Liberman 1975; Proulx and Adler 2010; Frank 2011; Proulx and Teotónio 2017; Proulx et al. 2019).

$$W(\mathbf{r}) = \exp\left(\sum_{j=1}^{m} p_j \ln\left(w_j(\mathbf{r})\right)\right)$$

Here p_j is the frequency of encountering environment j out of the m possible environments, and $w_j(\mathbf{r})$ is the parental fitness of applying strategy $\mathbf{r}$ in environment j.

$$w_j(\mathbf{r}) = \sum_{i=1}^{n} s_j(r_i)$$

As before, n remains the maximum number of offspring, i indexes them, and parents cannot distribute more than their total resources. Unlike before, we may also have different total resource amounts in each environment. For example, a parent finds more food in a good year's environment than in a bad year's. But varying the values of the total resources complicates the mathematics. Instead, we can interpret r_i as the proportion of resources given to the ith offspring. This rescales the system so that parents have $R = 1$ in every environment. Then $s_j(r_i)$ gives the survival probability of an offspring in environment j which is given r_i proportion of the total resources of a parent in environment j . By re scaling we no longer need to analyze both a varying survival function and varying total resource amount, but instead can focus solely on the varying survivorship function.

Table 4. Additional terms and symbols for the fluctuating environments model. Note that j indexes the environments and m is the total number of environments while i still indexes offspring and n is the total number of offspring.

Term	Definition
$s_j(r)$	The survivorship of an offspring given r resources in environment j.
$w_j(\mathbf{r})$	The fitness of distribution strategy $\mathbf{r}$ in environment j.
$W(\mathbf{r})$	The geometric mean fitness of distribution strategy $\mathbf{r}$ across all environments.
m	The number of environments
p_j	The probability of environment j.

B. Model analysis

We analyze this model in three parts, building in complexity. First, we study the situation where (1) all the survivorship functions s_j share convexity and (2) the

curved region begins and ends at the same points (that is, they all share the same resource thresholds r_{high} and r_{low}). We then consider cases with the second restriction removed. Finally we consider the general case with neither of the restrictions.

The analysis here is informal – otherwise one requires an unenlightening mess of notation and definitions. We quarantine the formal derivation of the general case to appendix section F.

B.1. Environments share resource thresholds and convexity. Assume that the thresholds r_{low} and r_{high} remain the same across all environments. That is, the curved region for each s_j share the same domain. We can then define a curved section of the fitness landscape W by restricting all the r_i to be between r_{low} and r_{high}. This is analogous to the curved region of the survivorship function when we had a constant environment. Denote this restricted fitness landscape as W_c.

W_c must then be a concave function if all s_j are concave, as in figure 5(a). This is because W_c is the composition of the weighted geometric mean (a non-decreasing concave function) with the parental fitness for each environment w_j (a concave function on the restricted domain, as it is the sum of concave s_j).

Surprisingly, W_c is not guaranteed to be convex if each of the s_j is convex. Previously, a result for a concave function would have a corresponding dual result for a convex function. Fitness landscapes of concave survivorship systems were, in a sense, “upside down" landscapes of convex survivorship systems. This mathematical symmetry is broken once we move to fluctuating environments and we can find examples where the landscape has a sigmoidal shape. That said, in our numerical explorations such cases are subtle and appear convex to the naked eye.

As in constant environments, the convexity of W_c determines the optimal strategy; concave implies symmetric and convex implies asymmetric. To see why, assume that W_c is concave. Given any non-symmetric strategy we can make two of the offspring more symmetric without reducing fitness. By Jensen's inequality this action does not decrease each w_i and thus does not decrease W_c. A similar proof can show that an asymmetric strategy must be optimal for the convex case.

The “concave survivorship implies symmetric strategies are optimal" result thus remains robust, even in the face of fluctuating environments. Bet-hedging does not occur – the parent makes as many offspring of the optimal size as possible.

This starkly contrasts with other models of bet-hedging. The classic result is that bet-hedging evolves if s_1 and s_2 are Gaussian survivorship curves such that their peaks are at different points and they are narrow enough that they are sufficiently nonoverlapping. A symmetric strategy that puts all offspring between peaks and guarantee them low survivorship in both environments. And to put them on one peak would be to doom them when the environment switches to favor the other peak. The best strategy is to make two sets of offspring, one for each peak.

We can reconcile our result with this classic one by noticing just how immensely restrictive our two conditions are. All the s_j must have the same r_{high} and r_{low}. This would be fine should s_j be Gaussian – we could rely on the long convex tails to force sufficient non-overlap. But with the s_j concave there is always a large amount of overlap. Even should one push the peaks to opposite extremes, one at r_{low} and the other at r_{high}, the rest of the curved region would appear a straight line from the peak at r_{low} to r_{high} and visa versa giving the appearance of two mirrored right triangles. Our conditions prevent us from having two different peaks and low overlap at the same time.

These conditions are also biologically restrictive and only make sense if parents collect the same amount of resources in all environments, and resources start and stop affecting offspring at the same threshold. We explore the most interesting and biologically relevant case next, but note that once we move beyond these restrictions we no longer can say concave survivorship guarantees symmetric strategies are optimal.

B.2. Environments share convexity but not resource thresholds. Say that all the survival functions are concave, but the thresholds r_{low} and r_{high} differ as in figure 5(b). The curved regions of survival functions may overlap partially or not at all. In this case W is made up of many of concave sections.

Loosely this is because we can view each s_j as being made up of a first flat region, the curved region, and a second flat region. Consider a randomly placed $\mathbf{r}$. Each r_i is on either the curved region or one of the flat regions for each s_j. Imagine now restricting each r_i to remain in the regions it started in, for all the s_j. For example, say r_1 is in the first flat region of s_1 and the curved region of s_2. Then r_1 must remain in both those regions simultaneously. Geometrically we can visualize these regions by partitioning the line segment $[0, r_{max}]$ and laying copies of it perpendicular to create a multi-dimensional grid of regions, each which corresponds to a section of W as shown in the middle column of figure 5.

The point of cutting the domain of possible strategies into these sections is that, while the s_j are not themselves concave, they are concave under each restriction. This is because composition of concave survivorship with geometric mean fitness is concave, as discussed in the previous case (recall a constant function is both concave and convex). Metaphorically each section is a concave patch of a quilt and the fitness landscape W is the entire quilt of concave patches. The boundary region is then the stitching which holds each patch together.

This paints W as a rugged landscape, but one with predictable regularity. If the s_j are concave each section is a hill, and a $\mathbf{r}$ starting within a section is expected to stay in that section, evolving towards the peak of it. Sections

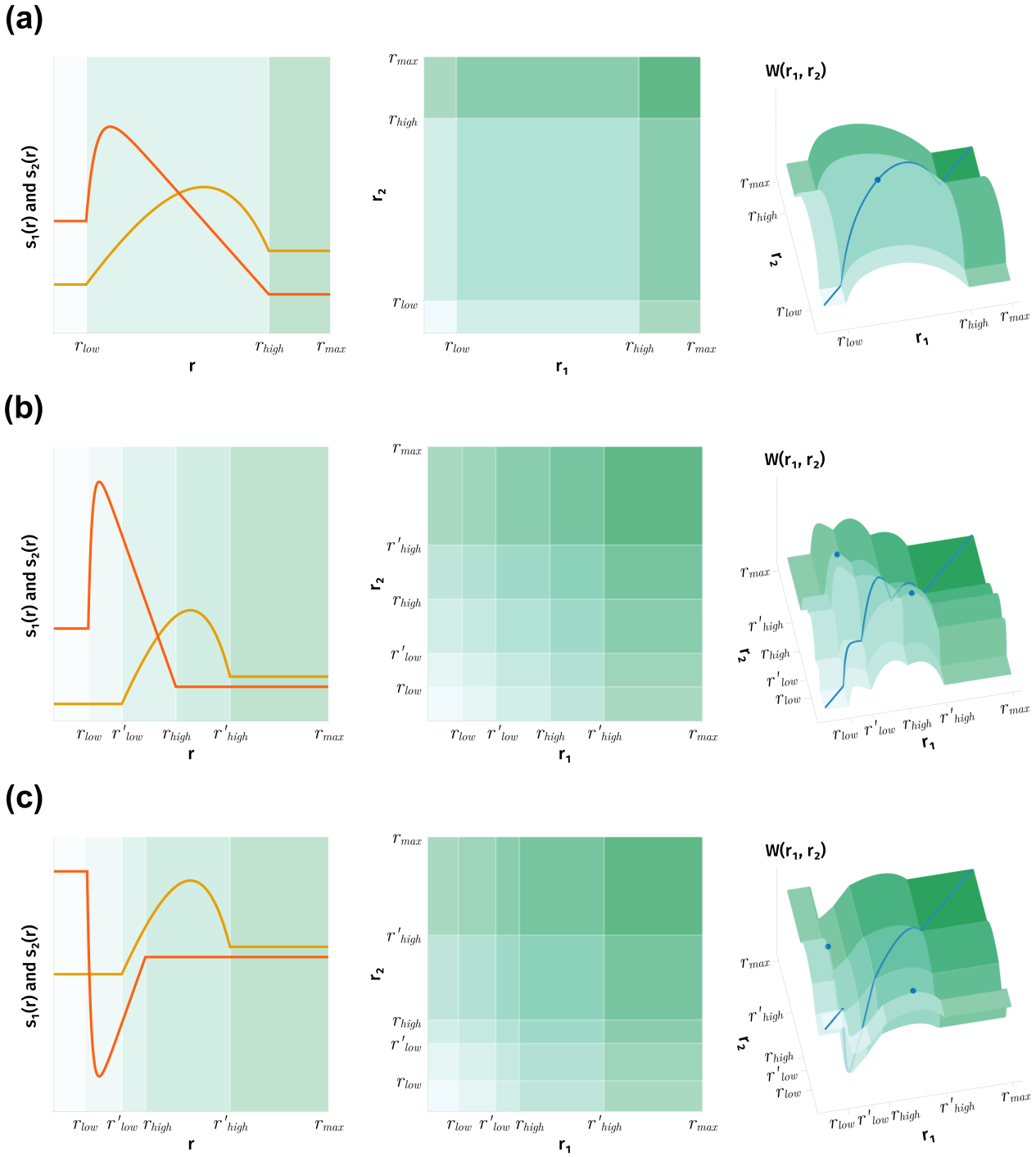

Figure 5. Each row shows a system with two offspring and two equally occurring environments. The dark orange survivorship curve corresponds to the first environment and the light orange survivorship curve to the second. Along the axes the ticks of the second environment are denoted by primes. In (a) the survivorship functions are both concave and share resource thresholds – that is, boundaries of their curved regions (r_{low} and r_{high}). In (b) they are both concave but do not share boundaries. In (c) they do not share convexity nor boundaries. The first column illustrates how the "corners" at $r_{low}, r'_{low}, r_{high}, r'_{high}$ define regions. The second column shows how these regions divide up the space of possible strategies – in the case of two offspring this is a two dimensional grid. For example, the cell in the upper left corner of each grid represents all strategies where the first offspring has less than r_{low} resources and the second offspring has more than r'_{high} or r_{high}. The third column shows the fitness landscape W. Here (a) and (b) demonstrate how these cells map exactly onto concave regions when both the survivorship functions are concave. The blue dots are the global optima. The blue line gives all symmetric strategies. Each point of this line is always a local optima when restricted to the slice of the landscape which uses the same amount of resources.

are evolutionary basins of attraction. There are between 1 and at most $(2m+1)^n$ of these sections.
If the s_j are instead convex then *typically* the sections are fitness valleys and basins of repulsion. The strategy is then expected to evolve to the border of the sections and move along it. But this is not always true as it is not guaranteed that the sections are convex. Many open questions remain for this case.

B.3. Environments share neither resource thresholds nor convexity. In the final case we might have a mix of concave and convex s_j and no shared thresholds, as in figure 5(c). The patchwork strategy above still partially applies in that we can split each s_j into flat and curved regions and restrict the strategy to form patches. But the convexity can differ, meaning sections are not always concave.
This landscape is complex. If the previous landscape was a mountain range then this is a world of mountains and valleys and rolling sigmoidal hills. Understanding the course of evolution here is difficult enough warrant its own paper. Yet despite this complexity we observe that symmetric strategies are always extrema when restricted to the set of strategies that use the same total amount of resources. The symmetric strategies may change from being a minima to a saddle point to a maxima, but they always remain local extrema.
This is due to the *Purkiss Principle*, which loosely states that symmetric problems have symmetric solutions. Below is the principle as written in Waterhouse 1983. (The source contains far stronger and more general versions of this theorem, but we only require the basic one.)

Purkiss Principle. *Let $f(\mathbf{r})$ and $g(\mathbf{r})$ be symmetric functions (i.e. the order of r_i does not matter) and consider some vector $\mathbf{r}^* = (r^*, r^*, \ldots, r^*)$ with all entries equal. Say that f and g both have continuous second derivatives in the neighborhood $\mathbf{r}^*$. Then, when constrained to vectors $\mathbf{r}$ such that $g(\mathbf{r}) = g(\mathbf{r}^*)$, the function $f(\mathbf{r})$ will have a local maximum or minimum at $\mathbf{r}^*$ as long as*

1. $\nabla g(\mathbf{r}^*) \neq 0$.
2. *All second order terms of $f - \lambda g$, are non-zero in directions perpendicular to $\nabla g(\mathbf{r}^*)$, for all constants λ.*

For us f represents geometric mean fitness W and $g(\mathbf{r}) = \sum_{i=1}^{n} r_i$ represents our resource constraint. These are both symmetric functions that meet the conditions above, thus the Purkiss Principle applies. By limiting n to be the number of non-zero sized offspring this further shows that any symmetric strategy is an local extrema when restricted to non-zero sized offspring.
Note that the constraint on $\mathbf{r}$ tells us that symmetric strategies are extrema when we restrict ourselves to strategies that use the same number of resources – that is, strategies where parents must use up all of their total resources R. They are not generally extrema if we allow strategies where parents use less than or equal to R resources.

5. Stage Structure

Adding age or stage structure can often modify a model's predictions (Caswell 2006). However, our predictions still follow those of tables 2 and 3, provided that the parent has the flexibility to decide on a different distribution strategy for each stage.
Consider a stage structure defined by the following Leslie matrix, under a constant environment.

$$\begin{pmatrix} w_1(\mathbf{r}_1) & w_2(\mathbf{r}_2) & w_3(\mathbf{r}_3) & \cdots & w_k(\mathbf{r}_k) \\ \alpha_2 & \beta_2 & 0 & \cdots & 0 \\ \alpha_3 & 0 & \beta_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_k & 0 & 0 & \cdots & \beta_k \end{pmatrix}$$

Subscript index the lifestages. Here α_i and β_i are the probabilities of respectively surviving to or staying in the ith stage. The $w_i(\mathbf{r}_i)$ captures the expected number of surviving offspring from a stage i individual adopting strategy $\mathbf{r}_i$. The fitness w_i is subscripted because each stage may have a different fitness landscape, may have a different amount of available resources, or for physiological reasons may have resources affect offspring differently.
We must be careful about what "surviving offspring" means here; they are offspring which survive to the first reproductive stage, stage one. There is implicitly a zeroth juvenile stage through which the offspring immediately pass, and only $w_i(\mathbf{r})$ of them survive. Alternatively one could explicitly adds this juvenile stage and change the interpretation of "surviving offspring" to "offspring that survive the process of birth."
The eigenvalue of this matrix will give the long-term population growth rate. Because each stage's strategy is independent it is best to adopt the optimal strategy for each stage. This maximizes each $w_i(\mathbf{r}_i)$ element in the matrix, and it is well known that increasing an individual element of a matrix does not decrease the lead eigenvalue (Berman and Plemmons 1994). The parent's overall strategy is then simple: look at the lifestage you are in, how many resources you have, and the fitness landscape w_i of your lifestage. Then perform the optimal strategy for that situation as per tables 2 and 3. Furthermore, such a strategy can evolve by small mutations as each of the $w_i(\mathbf{r}_i)$ can evolve the optimal strategy, and the evolution of each of the $\mathbf{r_i}$ are independent.
This all of course presupposes that the $\mathbf{r}_i$ are independent, a reasonable assumption under predictable environments. All the organism requires is a way to measure

which lifestage they are in along with the genetic flexibility to encode and trigger a different distribution strategy for each lifestage.
Fluctuating environments complicate this story. Say each environment is independently distributed with probability p_j. We can imagine that each timestep we select a Leslie matrix L_j, corresponding to the current environment, to update the population with.

$$L_j = \begin{pmatrix} w_{1,j}(\mathbf{r}_1) & w_{2,j}(\mathbf{r}_2) & w_{3,j}(\mathbf{r}_3) & \cdots & w_{k,j}(\mathbf{r}_k) \\ \alpha_{2,j} & \beta_{2,j} & 0 & \cdots & 0 \\ \alpha_{3,j} & 0 & \beta_{3,j} & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{k,j} & 0 & 0 & \cdots & \beta_{k,j} \end{pmatrix}$$

Here the Leslie matrix is the same as in the constant environment case, except the j subscript communicate that parameters and fitness landscapes may change across environments. The strategy for each lifestage remain fixed across environments, modeling an organism which can genetically encode its distribution strategy for each lifestage but cannot predict the environment. We cannot easily analyze this as the matrix elements are no longer independent – choosing the best $\mathbf{r_i}$ for one environment may reduce fitness in another environment.
We expect the population to evolve the $\mathbf{r_i}$ which maximize the average-of-growth-rates. Imagine replicating the evolution of the system many times from a given initial condition. For each replicate we can calculate the growth rate. Take the average of all these growth rates and you find the average-of-growth rates

$$\ln \lambda_s = \lim_{t\to\infty} E[\ln N(t)].$$

This is the parallel to geometric mean fitness for stage structure in that it is what natural selection optimizes (Caswell 2006) since almost all populations grow at the rate $\ln \lambda$. Exact calculation of $\ln \lambda$ is difficult but approximations exist (Cohen 1977; S. D. Tuljapurkar 1982a; S. D. Tuljapurkar 1982b; Caswell 2006; S. Tuljapurkar 2013). If we calculate the related average-population-size growth rate we discover that each $\mathbf{r_i}$ independently evolves over a landscape similar to those found in fluctuating environments without stage structure (appendix I). It would be a nice parallel if the maximization of the average-of-growth-rates is equivalent to independently maximizing the geometric mean fitness of each lifestage, but whether this is true we leave as an open question.

6. Discussion

Optimal offspring size and bacterial aging both study the same problem of resource distribution. Despite this their literature rarely intersects. This is unsurprising as they deal with biologically deal with vastly different scales of life and mathematically make distinct assumptions about the shape of the survival function and the number of offspring allowed.
Here we have stripped away the system specifics to reveal a more general and unifying resource distribution model which

1. agrees with and strengthens predictions of existing models.
2. organizes existing models into a unifying framework.
3. makes new predictions.
4. reveals universal patterns in resource distribution models.

The Smith-Fretwell model and its descendants assume that resources affect offspring in a concave increasing manner and are distributed *equally* among n offspring. This later assumption is often implicit, and perhaps reflects mathematical convenience rather than biological reality. In contrast, bacterial aging models allow for unequal distribution, but between only two offspring and generally under convex survivorship. However, concave survivorship is also possible and not all bacteria make only two daughters (Angert 2005).
Our model fills these gaps by allowing arbitrarily many offspring with any distribution strategy and concave or convex functions. Even in this more general framework the Smith-Fretwell model's prediction that a symmetric strategy is optimal remains robust, provided that the survivorship function remains concave. For bacterial aging, we can characterize that asymmetric strategies exactly when the survivorship function is convex. This avoids requiring damage accumulation across generations (which these models often rely on), and applies to microbes that do not reproduce by binary fission (Angert 2005).
Furthermore, prove that any mutation which places the strategy closer to optimal is selected for. This implies not only that optimal strategies evolve via small mutations (something not always explicitly shown) but that they can also evolve by large mutation or recombination. It also suggests that evolution will follow the optimal strategy evolution will get as close as possible, even in face of reproductive constraints. (E.g. the pelvic width in some turtles limits the size of eggs (Tucker et al. 1978; Congdon et al. 1983; Congdon and Gibbons 1987).
We then show these results remain robust under stage structure, provided the parent can change distribution strategies under each lifestage. The results also hold under fluctuating environments, provided that the survivorship functions are all concave that the resource thresholds r_{low} and r_{high} do not change between environments. When the thresholds do change, the symmetric strategy is a local maximum but not necessarily a global one.
All these results support and strengthen previous theory. But our model also sets up a framework where the

shape of the survivorship function is the organizing principle. Convexity is key. It not only determines the optimal strategy but also whether symmetric or asymmetric mutations are favored.

Counter-intuitively, whether resources help or harm the offspring matters less than whether they affect the offspring in a concave or convex manner. Concave implies symmetric strategies evolve and convex implies asymmetric strategies evolve. For example, any concave survivorship function gives a qualitatively similar result as the Smith-Fretwell model: create as many optimally sized offspring as possible and make the rest of a different size. It does not matter whether survivorship is increasing or decreasing with resources – the symmetric strategy is optimal just by virtue of survivorship being concave.

Symmetric and asymmetric strategies stand at the extremes of fitness. If one is the best strategy while the other must be the worst (appendix section G). This shifts the biological focus. The subtle mechanisms, physiology, and detail that switch a function from convex to concave matter at least as much as the easier question of whether resources help or harm. This is bad news; modelers must work harder to justify the convexity of the survivorship function, and experimentalists must work harder to collect data with enough resolution to see the convexity.

The upside is a powerful tactic: ignore all strategies except these two extremes. Since we expect populations will evolve to the optimal it is enough to compare the symmetric and asymmetric strategies and determine which is superior. We can extend this tactic further for convex-increasing and convex-decreasing functions. To decide the optimal form we only require r_{low}, r_{high}, and r_{max}. The rest of the survival function is irrelevant. When gathering data one can then focus on determining these three values rather than the entire survivorship function. The only information that the rest of the survivorship function gives us is the fitness of the single runt, and when there are many offspring the fitness contribution of the runt will be minimal and they can be ignored. That said, the exact form of a survivorship function matters when gauging the strength of selection. Flatter areas on the fitness landscape lead to weaker selection and allow drift to take over. We expect there exists effective values of r_{low} and r_{high} where selection selection can overpower drift.

By abstracting to a convexity based framework we can also make now predictions. One concerns runts: a single, significantly smaller, offspring appearing in a litters. A dog's“runt of the litter," is the popular culture version, and the frequency of runts has been studied in pigs (van der Lende et al. 1990). Yet the literature on runts is sparse, and we can find no literature proposing an adaptive reason why a single runt would evolve.

We can now give a reason: runts maximize expected fitness under convex-increasing survival functions. Convex survivorship causes offspring to segregate into large and small offspring, with at most one middle-sized offspring. In particular, under convex-increasing survivorship the optimal strategy is to create as many r_{high} size offspring as possible, put all remaining resources r_r in one last offspring, and leave the rest size r_{min}. Under the classic optimal offspring size interpretation, r_{low} is zero and those offspring are never born. Then if the r_r offspring happens to receive significantly less resources we would see multiple large offspring and a single small runt.

Where might we find such convex survivorship functions? The start of a sigmoidal function is convex-increasing, and such sigmoidal functions arise when we allow for sibling rivalry and parent preference for the larger offspring (Dani and Kodandaramaiah 2017; Jørgensen et al. 2011). If the mother cannot create any offspring that can reach the concave region, then the mother is effectively working under a convex-increasing survivorship function. In this case we further predict that increasing total resources will create a “phase shift," where the mother abruptly switches from an asymmetric strategy to a symmetric one.

Another prediction concerns when animals vertically transmit toxins to their offspring. Assuming toxins induce a concave-decreasing survivorship function then we predict there are always two classes of offspring – those with large amounts of toxins and those with few toxins. This pattern can be seen in a dynamic energy budget model of the North Atlantic right whale (Klanjscek et al. 2007).

Moving our discussion from whales to bacteria, we predict that that convexity alone is enough to evolve bacterial asymmetric reproduction. We do not need to follow the age of the components or the accumulation of damage over multiple generations. Local information about survival after one generation is enough.

Imagine then a bacteria which, upon being born, immediately repairs all old components given to it by its mother. The energy cost of this initial repair induces a convex survivorship function. After this initial repair it allows its components to age normally, and by the time it is ready to divide those components are old. The bacteria duplicates its components to make a set of new components, then splits and distributes them among its offspring. In this case we still predict that asymmetry evolves, even though components never grow older than one generation. This is not to say component aging and repair can be ignored, but rather that concavity alone implies a default evolutionary trajectory which these can then modify.

We may be able to select for specific strategies in real systems by manipulating the convexity of the survivorship function. For example, enforcing concave survivorship could reduce variability in farming applications, and enforcing a convex function could slow the runaway symmetric division found in stem cell cancers (Clevers 2005; Morrison and Kimble 2006; Wodarz and Gonzalez 2006; Clevers 2011; López-Lázaro 2015; López-

Lázaro 2018; Shlyakhtina et al. 2019).

Further predictions arise from more universal properties of resource distribution models. Nature does not confine itself to our six survivorship shapes of figure 4, nor does she adhere to the restrictive conditions of fluctuating environments and stage structure which we have explored. Yet even if we have complicated survivorship functions in non-independent fluctuating environments with wild stage structure we still find that symmetric strategies are often local extrema.

This reflects the deep mathematical symmetry of resource distribution models. All offspring play by the same rules and take from the same resource pool in the same manner. Mathematically, the parental fitness and resource constraint are symmetric functions. The Purkiss Principle then applies and tells us that (except in degenerate cases, and provided parents use all resources) symmetric strategies are extrema. Even if offspring mutate or migrate to different regions they share rules in how they mutate or move. Organisms following the same rules, interacting with the environment in the same way, is an almost universal simplification in evolutionary and ecological modeling. Yet this implies symmetry and hints that the generalized versions of the Purkiss Principle may apply widely, beyond optimization models.

If we combine our results of section B.2 with the Purkiss Principle find that symmetric strategies tend to be local maxima under concave survivorship functions in fluctuating environments when parents use up all their resources. Symmetric strategies then are local fitness peaks where evolution may become stuck. A bird in a constant environment might evolve to symmetrically distribute resources. If the environment later changes so that a mixed strategy is optimal the bird population will remain stuck within the local optima of symmetric distribution.

The changing of a survivorship's convexity could thus imply much about evolutionary history. It has been suggested that bacteria originally divided symmetrically and it is only with the evolution of asymmetry that the concept of "parent" emerged (Ackermann et al. 2003; Ackermann et al. 2007). But if symmetry was the historical stable state then the survivorship function must have originally been concave and symmetric division a local optima. To evolve asymmetric division by small mutations the survivorship function must have become convex. The evolution of symmetric to asymmetric division is then the evolution of a concave survivorship to convex.

While convexity unifies optimal offspring size and bacterial aging in our framework we have ignored a cornerstone of the latter: transgenerational effects. We do not track how cellular components deteriorates over generations – rather we show that such transgenerational effects are not *required*. Such effects could still reinforce or change the predicted optima (and some early pilot simulations suggest this happens in non-trivial way). Old components could even change the ability to reach the optima; aging has been shown to reduce a cell's ability to divide asymmetrically (Lai et al. 2002; Moger-Reischer and Lennon 2019).

This is a flaw, but could sometimes be a feature as is may fit certain bacterial systems better. Imagine a bacteria's survivorship depends on concentration of damaged proteins. In our model, regardless of how many damaged proteins a daughter inherits, by the time it divides (provided it survives) it has the same amount R of damaged proteins to distribute as every other bacteria. In real bacteria the amount damaged proteins may be diluted by growth, and they may be recycled or repaired. Under such conditions we expect the amount damaged proteins tend towards an equilibrium steady state (Erjavec et al. 2008). If cells then divide once they reach a certain undamaged protein threshold then at division all cells have the same steady state number R of damaged proteins.

Transgenerational effects are not limited to bacteria either. Larger offspring may mature faster and gain more resources, giving a time and resource advantage to the fitness of offspring from a large parent (Roach and Wulff 1987; Mousseau and Dingle 1991; Roff 1993; Donohue 2009). Current models of offspring size often ignore this aspect, but this could perhaps be remedied by incorporating transgenerational effects in the style of bacterial aging models.

Our model also lacks repair. As an alternative to distributing damaged components cells may repair them at the cost of energy (Ackermann et al. 2007; Watve et al. 2006; Evans and Steinsaltz 2007; Proenca et al. 2018). Adding repair allows one to map out at which energy cost the optimal strategy switches from symmetric to asymmetric. We do not consider repair in our model, again being content to show it is not required to evolve symmetry or asymmetry. But, as with transgenerational effects, repair may reinforce or modify the predicted course of evolution. Repair might also extend to optimal offspring size theory. Vertical transfer of toxins to offspring have been seen in butterflies Paula et al. 2014, minks (Janelle C. Restum John P. Giesy James A. Render Elizabeth B. Shipp David A. Verbrugge Richard J. Aulerich 1998), and marine mammals (Hickie et al. 1999; Klanjscek et al. 2007). The parent may be able to spend resources or energy to remove such toxins before they are transferred (Noonburg et al. 2010).

Understanding how transgenerational effects, repair, and other effects such as environmental stress (Vedel et al. 2016) interplay with our model would complete the unification. One possible path is to translate these mechanisms into survivorship functions and focus on when the convexity changes since that is when we expect a qualitatively different result. That said, we cannot fully divorce ourselves from mechanistic models – our approach is limited as optimization models rarely tell the full story once we add in environmental feed-backs (Parker and J. M. Smith 1990; Bernardo 1996; J. a. J.

Metz et al. 2008; J. A. J. Metz et al. 2008) .

While the elements of bacterial aging models we lack are the most pressing questions for research, Many others. One concerns stage structure in fluctuating environments. All our stage structure results assume that each life-stage is independent of the others. What happens when an organism must choose a single strategy for all lifestages? If all the survivorship functions share convexity do we still get the qualitative outcome that concave implies symmetry and convex implies asymmetry? What is the most general biological system where we find this outcome?

Another key problem is to find the optimal strategy when the survivorship function is sigmoidal, an alternative realistic scenario (Brockelman 1975; Rollinson and Hutchings 2013). Lin et al. explored Hill-type functions in a bacterial aging model and witnessed a phase-transition from asymmetric to symmetric strategies as protein accumulation rates change (Lin et al. 2019). Our own pilot simulations suggest the optimal strategies tend to have a form similar to an asymmetric strategy (see appendix section H). This hints that protein uptake rates might have a similar role to total resources values. A solution to the sigmoidal case would give us a grip fluctuating environments that mix concave and convex survivorship functions, as sections of these landscapes are can appear as multidimensional sigmoidal functions.

We can extend the sigmoidal problem to the problem of Gaussian survivorship, and the even more ambitious problem of when the survivorship function is made out of a finite number of concave and convex sections. An answer to the latter would let us approximate the optima to almost all naturally occurring survivorship functions. While problems of this sort are easy to state that does not guarantee they are easy to solve; the general resource distribution problem under arbitrary survivorship functions is equivalent to the NP-hard unbounded knapsack problem (Martello and Toth 1990; Bretthauer and Shetty 2002).

No matter how flexible we make the survivorship function our model assumes that all offspring share it. In reality, offspring may have different genotypes. Or sibling competition may create differences in offspring success. A fetus's placement in the womb, and egg's placement in a clutch, or a seed's placement in the plant can all grant different survivorship functions to each offspring (Telfer and Rutberg 1960; McLaren and Michie 1960; Harper et al. 1970; McKeown et al. 1976; Roach and Wulff 1987; Brown and Shine 2009).

If we give each offspring it's own survival function the theory of convex optimization lets us say some mathematical truths. (As long as the functions all remain concave then their sum will be concave. The set of feasible strategies will be the same as before, and this set is both concave and convex. Then any local maxima is in fact global. If parental fitness is strictly concave, which is true when each survival function is strictly concave, then such a maxima is unique. In the case where the survival functions are convex then the above also holds, expect the maxima are now minima.) Organisms will evolve towards the global optimal strategy or away from a global minima. But we cannot say what these extrema are and have no deep understanding. We cannot even invoke the Purkiss principle.

Just as offspring are not identical neither are resources. Plants require both carbon and nitrogen for their seeds and both elements affect survival in a concave-increasing manner (McGinley and Charnov 1988). In general there may be multiple resources, each with their own effect on the survivorship function. Such situations are another open problem. We expect the results to remain similar if the (now multidimensional) survivorship function remains concave or convex increasing. But the situation quickly becomes complicated with different resources affecting survivorship with different kinds of convexity. We might expect that survivorship becomes a multidimensional sigmoidal-like function, again bringing us back to question of optimizing sigmoidal functions.

7. Conclusion

We have united and expanded the theories of optimal offspring size and bacterial aging through a resource distribution framework. In constant environments we have classified the optimal distribution strategies, as shown in tables 2 and 3. We further demonstrated that populations evolve towards these optimal. These results highlight the central role of convexity; concave survivorship implies a symmetric strategy evolves while convex survivorship implies an asymmetric strategy evolves. We then extend some of these results to systems with fluctuating environments and stage structure.

There remains much to explore. We do not understand convex survivorship under fluctuating environments, nor do we understand how stage structure and fluctuating environments interplay. Identifying the optimal strategy under sigmoidal survivorship functions is another crucial open question.

Most importantly, future work should aim to incorporate the transgenerational effects, repair, and other mechanisms of bacterial aging. To do so will complete the unification of optimal offspring size and bacterial aging. This will foster the flow of ideas and insights between the two worlds, all in a framework that leverages the powerful and well developed theory of convex optimization.

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Appendix

A. Symmetric strategies evolve under concave survivorship functions

In the main paper we showed that the symmetric strategy (having all curved region offspring the same size) is an optimal strategy. Here we show that mutations towards this optimal are always neutral or beneficial (non-detrimental), implying that the fitness landscape is a simple hill and populations evolve to this optima.

Our proof strategy is to at first consider pairwise mutations: mutations which change resources between two offspring but leave the rest alone. We show that these pairwise mutations are non-detrimental only when the make the pair of offspring closer in size. We then show a mutation in a straight line towards the symmetric strategy can be made by a sequence of non-detrimental pairwise mutations, and thus itself must be non-detrimental.

Lemma 1. Say that an organism makes n offspring under survival function s. The curved region of this function, s_c, is concave, and at least two of these offspring fall on this region.

Then a pairwise mutation which transfers resources from one curved region offspring to another is either neutral or beneficial if and only if the mutation causes the two offspring to end up closer in size. If s_c is strictly concave then such a mutation is always beneficial.

Proof: Say that the strategy is not perfectly symmetric. Then at least two offspring on the curved region do not have the same amount of resources. Call these offspring one and two, and without loss of generality say that offspring one has less resources than offspring two. We write this as $r_1 < r_2$.

Consider a mutation takes ϵ resources away from offspring two and gives to offspring one. Here ϵ is small enough that this action does not move either offspring out of the curved region. We will compare the fitness of the original strategy to that of this new mutant strategy where offspring one and two are moved.

Case 1: say that the mutation does not make offspring one larger than offspring two. The mutant strategy's fitness is then

$$s_c(r_1+\epsilon)+s_c(r_2-\epsilon)+\sum_{i=3}^{n} s(r_i).$$

We put in the subscript c to emphasize that these offspring remain on the curved region of s. Because offspring three and above remain the same between the original and mutant strategies we ignore. The mutant strategy fitness is higher than the original strategy's when

$$s_c(r_1)+s_c(r_2) < s_c(r_1+\epsilon)+s_c(r_2-\epsilon).$$

If we let ϵ go to zero then this inequality is true if and only if the directional derivative of the fitness w increases in the direction of $\mathbf{r}_\mu = (\epsilon, -\epsilon, 0, \ldots, 0)$. This directional derivative can be written as

$$\frac{dw}{d\mathbf{r}_\mu} = \epsilon s_c'(r_1) - \epsilon s_c'(r_2).$$

and is either zero or positive when

$$s_c'(r_1) \geq s_c'(r_2).$$

Because s_c is concave s_c' must be monotonically decreasing. This means our assumption that r_1 is less than r_2 implies the above inequality. (If s_c is not strictly concave then equality could be possible, in which case our small mutation would be neutral.)

As the derivative in the direction of the mutation will always be non-negative we know that the full mutation for the original non-infinitesimal ϵ will be non-detrimental.

Case 2: Say the mutation transfers so many resources that offspring one ends up larger than offspring two. That is, $r_1 < r_2$ but $r_1+\epsilon > r_2-\epsilon$. Such a mutation would be equivalent to switching the offspring indices and transferring a smaller number of resources. This places us back in case one. This is illustrated in 6.

Case 3: Say a mutation causes the two offspring to have exactly equal resources. In this case $(r_1+\epsilon)$ equals $(r_2-\epsilon)$, which equals $\frac{(r_1)+(r_2)}{2}$. Jensen's inequality then tells us that this too is either neutral or an improvement.

$$2s_c\left(\frac{r_1+r_2}{2}\right) \leq s_c(r_1)+s_c(r_2).$$

■

To summarize, we've considered pairwise mutations that take two offspring and redistribute resources between them. As long as the mutation makes the offspring's resource values closer together then that mutation is non-detrimental. In the case that s_c is a strictly concave the mutation is always beneficial. On the other hand, pairwise mutations which move the strategy away from symmetry are either non-negative, and are always detrimental when s_c is strictly concave.

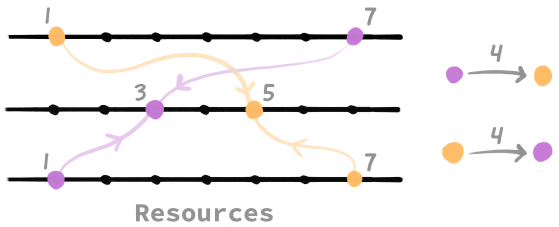

Figure 6. Here there are two offspring, orange and purple. The line is a measure of how many resources an offspring has. The transition from the top line to the middle line illustrates a mutation where the purple offspring gives the orange offspring four resources. This causes the purple offspring to become the smaller offspring as in case 2. Compare this to an equivalent transition from the bottom line to the middle line, which illustrates a mutation where the orange offspring gives four resources to the purple one. This keeps the orange offspring larger than the purple one, placing this transition in case 1. We already know a case 1 transition is non-detrimental, which means the equivalent case 2 situation is also non-detrimental.

Now let us consider mutations that affect more than a pair of offspring at a time. We can make any such mutation by composing multiple pairwise mutations together. One way to see this consider all possible strategies and realize that this space is spanned by the displacement vector of all pairwise mutations. A quick induction can also give this (the lemma proves the base case, for the induction step take the first $n-1$ elements of the strategy and make them so that a pairwise mutation between the first and nth element gives the target vector).

In particular this means that we can reach the symmetric strategy by mutating towards it a series of small pairwise mutations that approximates the path of a straight line. Each of these mutations, if small enough, can be guaranteed to be beneficial or neutral. At the limit the mutation is a straight line towards the symmetric strategy. Doing this from all possible strategies implies that the fitness landscape is a simple "Mt. Fuji" style one with a peak at the symmetric strategy.

Note that we have purposefully left the definition of "closer to the symmetric strategy" loose. Given an arbitrary mutant strategy $\mathbf{r}'$ it is difficult to say whether it is detrimental compared to the original strategy $\mathbf{r}$. If there exists a pathway of only pairwise non-detrimental mutations then it is clearly beneficial. But if there is only a pathway that makes some detrimental mutations but also some beneficial ones then the picture is less clear as detriments could outweigh benefits or visa versa.

B. Asymmetric strategies are optimal under convex survivorship, when restricted to the curved region

Consider a survival function s has a convex curved region. Then a optimal strategy for offspring *restricted to*

the curved region is of the form

$$\begin{pmatrix} r_{high} \\ \vdots \\ r_{high} \\ r_r \\ r_{low} \\ \vdots \\ r_{low} \end{pmatrix}$$

where there is at most one r_r such that $r_{low} < r_r < r_{high}$. Furthermore, if the curved region of s is strictly convex then this strategy is the strict and unique optima (up to reorderings of the offspring). Call this optimal strategy $\mathbf{r_c}$. We subscript this strategy with a c to emphasize that this is the optimal when offspring are restricted to the curved region.

Notice we do not say how many r_{high} or r_{low} there are. This can depend on the exact function. All we claim is that there is some amount (possibly zero) of these, one or zero r_r's, and nothing else.

Proof: Proceed by contradiction. Let $\mathbf{r_c}$ be the optimal strategy of the form given above. Assume there is an alternative strategy $\mathbf{r_c^*}$ of a different form but that does at least as good as $\mathbf{r_c}$ while the same amount of resources. We will let r_i^* denote the ith element in the alternative strategy and r_i the ith element in the original. We will say that two such elements with the same index *correspond* with each other.

Since $\mathbf{r_c^*}$ and $\mathbf{r_c}$ are different at least one of the elements between the two strategies must also be different. Without loss of generality let r_1 and r_1^* be these elements. Say that the difference between these elements has magnitude ϵ so that $r_1^* = r_1 \pm \epsilon$. Because r_1 is either r_{high}, r_r, or r_{low} we must be one of the four following cases.

$$\begin{aligned} r_1^* &= r_{high} - \epsilon && (r_1 = r_{high}) \\ r_1^* &= r_r - \epsilon && (r_1^* < r_1 \text{ and } r_1 = r_r) \\ r_1^* &= r_r + \epsilon && (r_1^* > r_1 \text{ and } r_1 = r_r) \\ r_1^* &= r_{low} + \epsilon && (r_1 = r_{low}) \end{aligned}$$

The cases $r_1^* = r_{high} + \epsilon$ and $r_1^* = r_{low} - \epsilon$ are not possible because we have restricted offspring to the curved region.

Focus on the case where ϵ resources have been *added* (the logic for the subtraction case is similar). The extra resources in r_1^* must of come from somewhere, as the total resources used in both strategies are the same. Without loss of generality, say that r_2^* contributed some (maybe even all) of these resources. This offspring must have $\delta \leq \epsilon$ fewer resources than it's corresponding strategy in $\mathbf{r_c^*}$. This means r_2 cannot be of value r_{low}, because then r_2^* would be outside the curved region. We thus deduce r_2^* must correspond to either r_{high} or r_r.

	$r_1^* = r_{low} + \epsilon$	$r_1^* = r_r + \epsilon$
$r_2^* = r_{high} - \delta$	Possible	Possible
$r_2^* = r_r - \delta$	Possible	Impossible

Table 5. Possible combinations of r_1^* and r_2^*. Notice that r_1 is always less than r_2.

$$\begin{aligned} r_2^* &= r_{high} - \delta \\ r_2^* &= r_r - \delta \end{aligned}$$

Recall that r_1^* can correspond to either r_r or r_{low}.

$$\begin{aligned} r_1^* &= r_r + \epsilon \\ r_1^* &= r_{low} + \epsilon. \end{aligned}$$

There are three possible combinations of values for $r_1^*$and r_2^*. These are shown in the following table. Note that both cannot correspond to r_r at the same time because there is only one r_r, so the lower right combination is impossible.

For each possible combination, r_1^* and r_2^* must be closer together than their corresponding entries in the original strategy. For example, taking the upper left possibility we have that the difference between the two entries is

$$\begin{aligned} |r_1^* - r_2^*| &= |(r_{low} + \epsilon) - (r_{high} - \delta)| \\ &= |(r_{low} - r_{high}) + (\epsilon + \delta)|. \end{aligned}$$

Here the $(r_{low} - r_{high})$ gives the difference of the two entries in the original strategy and is negative. Meanwhile the $(\epsilon + \delta)$ term is positive. But neither ϵ or δ can be more than $|r_{low} - r_{high}|$, else r_1^* would be out of bounds. At most we can have $\epsilon + \delta = 2|r_{low} - r_{high}|$. But this is impossible as it would imply the alternative strategy $\mathbf{r_c^*}$ is a swap with $r_1^* = r_{high} = r_2$ and $r_2^* = r_{low} = r_1$, meaning that $\mathbf{r_c^*}$ is just a reordering of $\mathbf{r_c}$ and thus not a different strategy.

Therefore $\epsilon + \delta < 2|r_{low} - r_{high}|$ and when we compare the original and alternative strategies we can then say

$$|r_1 - r_2| = |r_{low} - r_{high}| > |r_1^* - r_2^*|.$$

A similar calculation shows that all remaining cases move the two offspring closer together. As convex regions select for moving offspring further apart we expect we can then improve the alternative strategy $\mathbf{r_c^*}$ by moving offspring further apart.

Specifically we can move offspring one and two further apart. Consider a new strategy $\mathbf{r_c^{**}}$, which is the same as $\mathbf{r_c^*}$ except

$$r_1^{**} = r_1^* - \delta = r_1 + \epsilon - \delta$$
$$r_2^{**} = r_2^* + \delta = r_2.$$

By shuffling resources only between offspring one and two we have made their sizes more like the original strategy, which we know is further apart than those in $\mathbf{r_c^*}$.

This action of moving resources between two offspring is the pairwise mutation we considered in lemma 1. We can make a corollary to this lemma for when the survival function is convex instead of concave.

Lemma 2. Say that an organism makes n offspring under survival function s. The curved region of this function, s_c, is convex, and at least two of these offspring fall on this region.

Then a pairwise mutation which transfers resources from one curved region offspring to another is either neutral or beneficial if and only if the mutation causes the two offspring to be further apart in size. If s_c is strictly convex then such a mutation is always beneficial.

Proof: It's the same proof as for lemma 1, except we let the strategy $(r_1+\epsilon, r_2-\epsilon, r_3, \ldots, r_n)^T$ be the original strategy and $(r_1, r_2, r_3, \ldots, r_n)^T$ be the mutant strategy. Since the curved region s_c is now convex we know s_c' is monotonically increasing and we must also swap the appropriate inequalities.

■

By this lemma a pairwise mutation that moves offspring further apart must decrease fitness. Strategy $\mathbf{r_c^{**}}$ then must have higher fitness than strategy $\mathbf{r_c^*}$. But this contradicts that $\mathbf{r_c^*}$ is an optimal strategy.

■

C. Optima under convex-increasing survivorship

Consider an optimal strategy. We know by our analysis of convex functions that the offspring on the curved region must be either size r_{low} or r_{high}, with an exception of at most one offspring of some intermediate value r_r.

Say that this intermediate value offspring exists. Then there can be no offspring of size $0 < r \leq r_{low}$. This is because if such an offspring existed we could take resources away from it (which would not reduce fitness) and give those resources to the r_r sized offspring (which would increase fitness). This would give a total increase in fitness and contradict that the strategy is optimal. For the same reason no offspring can have above r_{high} resources if there is an offspring size r_r.

Thus if an intermediate size offspring exists the optimal strategy must look like

$$\begin{pmatrix} r_{high} \\ \vdots \\ r_{high} \\ r_r \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

and if there is no intermediate offspring then all offspring are either size less than r_{low} or size greater than r_{high}. These are optimal strategies for convex-increasing survival functions. The following algorithm will bring us to one of these optima.

1. Start all offspring at zero resources.
2. Make as many offspring of size r_{high} as possible.
3. There now remains $0 \leq r_r < r_{high}$ resources. Do one of the following.
   (a) If all offspring are now size r_{high} then we have reached maximum fitness and it does not matter how we distribute the remaining resources.
   (b) Otherwise put all r_r resources in a single offspring.

D. Optima under concave-increasing-decreasing survivorship

Say s is a survival function with a concave-increasing-decreasing curved region, and say the maximum of the curved region occurs at r_{top} resources. (In the case the curved-region is not strict and looks like figure x then let r_{top} be the lowest resource value which maximizes survival.) If the parent must give at least one offspring more than r_{top} resources (that is, the parent may not withhold resources and $R > nr_{top}$) then the optimal strategy is of the form

$$\begin{pmatrix} r_{max} - \bar{r}^* \\ \vdots \\ r_{max} - \bar{r}^* \\ r_{max} \\ \vdots \\ r_{max} \end{pmatrix}$$

where $r_{max} - \bar{r}^*$ is acting as the optimal offspring size and the offspring of size r_{max} are used to remove extra resources.

Before we begin the proof of this we must show the following lemma.

Lemma 3. If the parent must give at least one offspring more than r_{top} resources then they must give all offspring more than r_{top} resources in the optimal strategy.

Proof:
Proceed by contradiction. Say that $\mathbf{r}$ is an optimal strategy where one offspring is of size less than r_{top}. Call this the *small offspring*. We know there is at least one offspring with size larger than r_{top}. Call any such offspring *large offspring*. Let r_s be the size of the small offspring and r_j be the size of the jth large offspring (of which there may be more than one). We can write these resource amount in terms of how far each is from r_{top}

$$r_s = r_{top} - r'_s$$
$$r_j = r_{top} + r'_j$$

Now take the r'_j of all the large offspring and sum them up. This sum must be greater than r'_s because $R > nr_{top}$. This means we can take r'_s worth of resources from the collection of large offspring and give them to the small offspring, and do it in such a way that each large offspring never goes below r_{top} resources. Call this new strategy $\mathbf{r}^*$.
This process does not lower survival of any of the large offspring. But, because r_{top} is the lowest value where s reaches its maximum, this process must increase the survival of the small offspring. Thus $\mathbf{r}^*$ has higher fitness than $\mathbf{r}$, contradicting that $\mathbf{r}$ is an optimal strategy. ■

With this lemma we can prove the main result.

Proof: Observe that $s(r_{top})$ is the maximum possible survivorship. This means a parent who makes n offspring and has no resource constraints has a maximum fitness of $ns(r_{top})$. Call this strategy, $\mathbf{r}^{**} = (r_{top}, \ldots, r_{top})$, the *ideal strategy.*
Sadly for our parent the ideal strategy is an impossible strategy, as by assumption the parent must distribute all resources and R is high enough that least one offspring must be larger than r_{top}. The fitness of an optimal strategy then must be less than or equal to the fitness of the ideal strategy. However, the parent can seek to minimize the difference between their strategy and the ideal strategy. Call this difference Δw and see that

$$\Delta w = ns(r_{top}) - \sum_{i=1}^{n} s(r_i)$$

where the r_i are the offspring sizes in the parent's strategy. Finding an optimal strategy is equivalent to finding a strategy which minimizes Δw.
Because at least one offspring must be larger than r_{top} our lemma tells us that in an optimal strategy all offspring must be larger than r_{top}. This allows us to rewrite the above equation in terms of how far above r_{top} each offspring is.

$$\Delta w = ns(r_{top}) - \sum_{i=1}^{n} s_d(r'_i)$$

Here $r'_i = r - r_{top}$ measures how far beyond r_{top} each offspring is. Call these the *remaining-resources*. There are $R_r = R - nr_{top}$ total remaining-resources. The function s_d gives the survival probability of these offspring in terms of r'_i. That is, $s_d(r'_i) = s(r_{top} + r'_i)$.
We can now minimize Δw by maximizing the summation term. This is equivalent to the concave-decreasing problem which we already know how to solve by section C.2. Following that algorithm we transform the problem into one of anti-resources. That is, we wish to maximize $\sum_{i=1}^{n} \bar{s_d}(\bar{r'_i})$ under the constraint that $\sum_{i=1}^{n} \bar{r'_i} = \bar{R_r}$ where the over-bar signifies anti-resources as explained in section C.2. We find that the optimal distribution of remaining-anti-resources is

$$\bar{\mathbf{r}}'^* = \begin{pmatrix} \bar{r}' \\ \vdots \\ \bar{r}' \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

where $\bar{r}'$ is the optimal offspring size found by optimizing $\bar{s_d}$. Each offspring can have at most $r_{max} - r_{top}$ remaining-resources, so if we transform this strategy from units of remaining-anti-resources to units of remaining-resources we have that the optimal distribution of remaining-resources is

$$\mathbf{r}'^* = \begin{pmatrix} r_{max} - r_{top} - \bar{r}^* \\ \vdots \\ r_{max} - r_{top} - \bar{r}^* \\ r_{max} - r_{top} \\ \vdots \\ r_{max} - r_{top} \end{pmatrix}.$$

Since this strategy is written in terms of remaining-resources we must add r_{top} to each entry to get the overall optimal strategy, which is

$$\begin{pmatrix} r_{max} - \bar{r}^* \\ \vdots \\ r_{max} - \bar{r}^* \\ r_{max} \\ \vdots \\ r_{max} \end{pmatrix}.$$

■

E. Optima under convex-decreasing-increasing survivorship

When there is a runt, the the optimal strategy for the convex-decreasing-increasing survivorship case is either the optimal strategy for the convex-increasing survivorship case or the optimal strategy for the convex-decreasing survivorship case. To show this we first require a lemma.

Lemma 4. At the optimal strategy, if the runt exists the flat region's offspring must all be at either 0 and r_{high} or at r_{low} and r_{max}.

Proof: Given that we have a runt at least one other offspring must be on one of the flat regions (since we have previously proved that for convex cases there is at most one runt.)
Depending on the size of the runt it needs to either lose or gain resources to increase its fitness. Say it needs to increase its resources. If the flat region offspring are not all either at 0 or r_{high} then the runt can take a small amount of resources from one of these offspring to increase its own fitness. This will not decrease the flat region offspring's fitness long as it remains on the flat region. This increases overall fitness, contradicting that this was an optimal strategy.
The same argument works for the case where the runt requires less resources to increase its fitness. The flat region offspring must all be at r_{low} or r_{high}, else the runt could give its resources to one of the flat region offspring without decreasing its own fitness.

■

By our lemma we know there are only two possible forms for the optima.

$$\mathbf{r}^* = \begin{pmatrix} r_{high} \\ \vdots \\ r_{high} \\ r_r \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} r_{max} \\ \vdots \\ r_{max} \\ r'_r \\ r_{low} \\ \vdots \\ r_{low} \end{pmatrix}$$

where r_r and r'_r are the respective runt sizes. These forms must be unique in terms of the number of first and second flat region offspring. For the first one, creating this form in a way that uses up all R is equivalent to dividing out r_{high} from R to get the number of size r_{high} and taking the remainder to be the runt. This is exactly the same as the convex-increasing algorithm. If we convert to anti-resources the argument works for the second optima, showing that this form too is unique.

E.1. A heuristic for deciding which strategy performs better. A natural conjecture is that the increasing strategy will work when the first flat region is higher than the second, and visa versa. This is an okay heuristic, but is not true as per the convex-decreasing-increasing counterexample (next subsection).
We can derive a basic condition though. Say we run the increasing algorithm. Let n_l be the number of offspring on the first flat region and let n_h be the number in the second flat region. Let γ_{low} and γ_{high} be the fitnesses of those regions respectively. Let r_r be the remainder. Then the fitness of the increasing strategy is

$$n_l\gamma_{low} + n_h\gamma_{high} + s(r_r)$$

Now consider running the decreasing algorithm. Say that the algorithm produces Δn more offspring on the lower region. It should always be more or equal as the convex-decreasing survivorship algorithm generates more small offspring. (We have not proved this statement, but it is intuitively true and a large simulation agrees.)
The fitness for the decreasing strategy is then

$$(n_l + \Delta n)\gamma_{low} + (n_h - \Delta n)\gamma_{high} + s(r'_r)$$

Where r'_r is the size of the runt. Then a basic inequality calculates that the fitness of the decreasing strategy is higher if and only if

$$s(r_r) - s(r'_r) < \Delta n(\gamma_{low} - \gamma_{high})$$

It is possible that the runts are in one of the flat regions so we would still need to consider that.
Temporarily, let us call the very last offspring that the algorithms move the runt. This way the chosen runt is unique and there is always a runt, even if they are technically in the flat regions. This means we can keep the above inequality and simply look at all the combinations of the runt's fitness and how the inequality simplifies
These can tell us about specific cases. But note we have not proved that the increasing or decreasing strategy are optima for the runt-on-flat-region cases. This table only compares the two to say which is better. There is no guarantee of the choice being the best.

E.2. Counterexample to heuristic. This is a counterexample to the conjecture that a higher first flat region implies we should use the convex-increasing survivorship optima and a higher second flat region implies we should the convex-decreasing survivorship optima.
Take a convex-decreasing-increasing survivorship function such that $n = 4$, $R = 8$, $r_l = 2$, $r_h = 5$, $r_m = 8$, and $s(3) = 0.2$. The optimal strategy from applying the convex-increasing algorithm is $(5, 3, 0, 0)$. If we instead apply the convex-decreasing algorithm the optimal strategy is $(2, 2, 2, 2)$.
Next, imagine two situations. Situation A has the left side of the survivorship function higher with $\gamma_{low} = 1$ and $\gamma_{high} = .9$. Situation B has the right side higher with the numbers swapped. We can calculate the fitnesses for both in the following table.

Table 6. The specific conditions for when following the convex-decreasing strategy gives higher fitness than following the convex-increasing strategy.

$s(r_r)$	$s(r'_r)$	**Condition for when convex-decreasing strategy is better**
$s(r_r)$	$s(r'_r)$	$s(r_r) - s(r'_r) < \Delta n(\gamma_{low} - \gamma_{high})$
$s(r_r)$	γ_{low}	$s(r_r) < \Delta n(\gamma_{low} - \gamma_{high}) + \gamma_{low}$
$s(r_r)$	γ_{high}	$s(r_r) < \Delta n(\gamma_{low} - \gamma_{high}) + \gamma_{high}$
γ_{low}	$s(r'_r)$	$-s(r'_r) < \Delta n(\gamma_{low} - \gamma_{high}) - \gamma_{low}$
γ_{high}	$s(r'_r)$	$-s(r'_r) < \Delta n(\gamma_{low} - \gamma_{high}) - \gamma_{high}$
γ_{low}	γ_{low}	$0 < \Delta n(\gamma_{low} - \gamma_{high})$
γ_{low}	γ_{high}	$0 < (\Delta n - 1)(\gamma_{low} - \gamma_{high})$
γ_{high}	γ_{low}	$0 < (\Delta n + 1)(\gamma_{low} - \gamma_{high})$
γ_{high}	γ_{high}	$0 < \Delta n(\gamma_{low} - \gamma_{high})$

Situation	Strategy	Fitness
B	Convex-increasing	3
B	Convex-decreasing	3.6
A	Convex-increasing	3.1
A	Convex-decreasing	4

We find that following the convex-decreasing strategy is always better.

F. Optima for Fluctuating Environments

Here we will prove the results of the fluctuating environments section more formally. Recall that we wish to maximize geometric mean fitness. This can be written both in exponential form and product form.

$$W(\mathbf{r}) = \exp\left(\sum_{j=1}^{m} p_j \ln\left(w_j(\mathbf{r})\right)\right) = \prod_{j=1}^{m} w_j(\mathbf{r})^{p_i}$$

Here p_i is the frequency of the ith environment and $w_j(\mathbf{r}) = \sum_{i=1}^{n} s_j(r_i)$ is the fitness of strategy $\mathbf{r}$ under environment j. For all the follows we consider only the feasible $\mathbf{r}$, i.e. those that meet our constraints that we can use no more than (or exactly) R resources.

In this fitness landscape we have an analogue of curved region of s from the constant environment case: a concave or convex function which we can apply the techniques of convex optimization to. But under fluctuating environments there may be many such curved regions, rather than one (see figure 5).

Our first task is to then craft a way to refer to regions. This will require a language to describe the s_j, as shown below.

$$s_j(r) = \begin{cases} s_j\left(r^j_{low}\right) & r < r^j_{low} \quad \text{first flat region} \\ s_j(r) & r^j_{low} \le r \le r^j_{high} \quad \text{curved region} \\ s_j\left(r^j_{high}\right) & r^j_{high} < r < r_{max} \quad \text{second flat region} \end{cases} \tag{8}$$

The j superscript on r is not a power but a indicator of environment. For example, r^j_{low} is the lower bound of the curved region of s_j. Notice that all environments must share the same r_{max}, as otherwise the geometric mean would be undefined if any offspring was larger than the minimum of the r^j_{max}.

Observe that the r^j_{low} and r^j_{high} partition the line segment $[0, r_{max}]$. Because this is equivalent to placing $2m$ points we can have up to $2m+1$ segments. As a technical detail will define each segment open, so that the points r^j_{low} and r^j_{high} along with the endpoints 0 and r_{max} are not in any of the segments. For two environments this is shown in the first column of figure 5.

Enumerate these segments such that the first is 1 and the last is q. We can then define an indicator function f that takes in a strategy $\mathbf{r}$ and, for the ith offspring, tells us which segment it is in, or if it is in one of boundary points that correspond to no segment.

$$f(\mathbf{r}) = (x_1, \ldots, x_n)^T$$

$$\text{where } x_i = \begin{cases} 0 & \text{if } r_i \text{ is in no segment} \\ 1 & \text{if } r_i \text{ is in the first segment} \\ 2 & \text{if } r_i \text{ is in the second segment} \\ \vdots & \qquad\qquad \vdots \\ q & \text{if } r_i \text{ is in the last segment} \end{cases}$$

Let $\mathbf{x}$ be such a indicator vector. Define the set

$$\mathcal{R}(\mathbf{x}) = \{\mathbf{r} \text{ such that } f(\mathbf{r}) = \mathbf{x}\}.$$

That is, $\mathcal{R}(\mathbf{x})$ is the set of all resource vectors for which the r_i are restricted to their respective segments. For

example, in a three offspring system $\mathcal{R}(1,5,5)$ gives all strategies such that the first offspring size is restricted to the first segment while the second offspring and third offspring sizes are restricted to the fifth segment. In the two environment case this is shown by the grid in the second column of 5. Each cell of the grid corresponds to a $\mathcal{R}(\mathbf{x})$. The same idea holds for more than two environments, but the grid is multidimensional.

Why do we do this? Because once a strategy $\mathbf{r}$ is restricted to a $\mathcal{R}(\mathbf{x})$ the convexity of $W(\mathbf{r})$ is guaranteed not to change provided that all the curved regions of s_j are concave (we will prove this is true in the next section). This paints a picture of W as a partition of *sections*, at most one for each the q^n possible indicator vectors $\mathbf{x}$. If the curved region of s_j is concave then each of these sections is concave, even if the entirety of W is not. There is also a region described by the boundaries of the segments, which is the union of all the $\mathcal{R}(\mathbf{x})$ where at least one element of $\mathbf{x}$ is zero. For two environments this is illustrated in the third column of figure 5.

To make an analogy, the fitness landscape W is a quilt of concave patches, and the boundary region is the stitching between each patch. In the next subsection we prove that this is true.

F.1. All the s_j are concave. Take the sections and number them arbitrarily and let W_k denote the kth section. That is, W_k is the restriction of W to $\mathcal{R}(\mathbf{x})$, where $\mathbf{x}$ is the kth indicator vector. We wish to show the following.

Theorem 1. If the curved region of all the s_j are concave, then each W_k is concave.

Our strategy is to decompose W_k into a composition of concave functions, then take advantage of the conditions where compositions of concave functions are concave. To begin, let G be the weighted geometric mean

$$G(\mathbf{y}) = \exp\left(\sum_{j=1}^{m} p_j \ln(y_j)\right) = \prod_{j=1}^{m} y_j^{p_j}.$$

We will consider G on non-negative y_j, as these will ultimately be the fitness from each environment. W can be thought of as the composition of the w_j with G. Define the function w which outputs a vector of fitnesses for each environment,

$$W(\mathbf{r}) = G(w(\mathbf{r})) = G(w_1(\mathbf{r}), \ldots, w_m(\mathbf{r})).$$

With this setup we can prove that each W_k is concave.

Lemma 5. The weighted geometric mean $G(\mathbf{x})$, for positive x_i, is a non-decreasing function. That is, if we increase any of the x_i then $G(\mathbf{x})$ does not decrease.

Proof: For positive reals exponentiation by p_i is non-decreasing and multiplication is non-decreasing. The composition must also be non-decreasing. ■

Lemma 6. The weighted geometric mean is concave.

Proof: MaoWao n.d.; S. Boyd 2023 ■

Lemma 7. Let $h : \mathbb{R}^m \to \mathbb{R}$ and $g_i : \mathbb{R}^n \to \mathbb{R}$ be twice differentiable functions. Let $f(\mathbf{x}) = h(g_1(\mathbf{x}), g_2(\mathbf{x}), \ldots, g_m(\mathbf{x}))$. Then f is concave if h is concave and nondecreasing and all the g_i are concave.

Proof: See (S. P. Boyd and Vandenberghe 2004, Chapter 3) for the proof and extensions to situations where h and g_i are not differentiable. ■

Observe that if all the s_j are concave then w_j is concave, as sums of concave functions remain concave. By remaining restricted to the domain of W_k we guarantee that the s_j are concave. The r_i in flat regions must remain in flat regions and r_i in curved regions must remain in curved regions. The above lemma then applies as W_k is the composition of the weighted geometric mean with the w_j.

$$W_k(\mathbf{r}) = G(w_1(\mathbf{r}), w_2(\mathbf{r}), \ldots, w_m(\mathbf{r}))$$

Here the w_j are restricted to the same domain as W_k. We know G is a non-decreasing concave function by lemmas 6 and 5. We also know the w_i are all concave. Lemma 7 then implies W_k is a concave function.

This tells us every extrema is a local optima – local to the section it is one. If these are global extrema is a far more difficult question. The Karush-Khun-Tucker conditions is one approach to finding these (see supplementary materials).

F.2. All the s_j are concave. One might naively expect we can mimic the above proof to show the W_k are all convex if the s_j are convex. But this does not work, as we would require that the geometric mean to be a non-*increasing* function. We can in fact find examples where W_k is not convex (see supplementary materials).

That said, in numerical simulations the W_k are often convex or almost convex (which is to say, it looks convex to the naked eye). Discovering the conditions which guarantee convexity of W_k we leave as an open problem.

G. If the symmetric strategy is best then the asymmetric strategy is worst, and visa-versa.

Imagine s is a concave function. We know the optimal strategy is symmetric. Instead of measuring offspring in terms of survival probability, let us measure them in terms of death probability. Call this function d and see that

$$d(r) = 1 - s(r).$$

The strategy that minimizes expected number of surviving offspring is the same strategy that maximizes the expected number of dying offspring. But d is a convex function with two flat regions; we already have shown in the main paper that the optimal here is an asymmetric strategy.

Thus we have shown that if s is concave, the best possible strategy is symmetric while the worst possible is asymmetric. The argument is similar for when s is convex.

H. Conjectured strategies for Sigmoidal, Gaussian-like, and other survivorship functions

Gaussian-like and Sigmoidal For sigmoidal or Guassian-like survivorship functions (that is, a convex increasing region followed by a concave increasing region followed by a concave decreasing region followed by a convex decreasing region) we conjecture another optimization algorithm. We will go through the algorithm for Gaussian-like survivorship functions. The sigmoidal function is special case where we assume that $s(r_p)$ to $s(r_{max})$ is flat.

Say that the survivorship function has a single maximum point, which we say occurs when we give r_p resources. Then the first phase of the algorithm is to give as many offspring r_p resources as possible. If the parent has enough resources to do this and does not need to distribute them all offspring are on the peak, thus have maximum value, and we are done.

Otherwise if the parent does not have enough resources to do this they will act like an asymmetric distribution strategy and create one runt. The strategy vector will have the form

$$\mathbf{r}_1 = (r_p, \ldots, r_p, r_p - \Delta r, 0, \ldots, 0)$$

where Δr is how many resources away from the peak the runt offspring is. We have labeled it 1 to denote the first case. Likewise, should we have too many resources to put each offspring at r_p but all resources must be distributed, then we can start all offspring at r_p and successively fill each offspring to the maximum number of resources until we run out of resources. Such a strategy will take the form with a "runt-like" offspring too. We will denote this strategy $\mathbf{r}_2$.

$$\mathbf{r}_2 = (r_p, \ldots, r_p, r_p + \Delta r, r_{max}, \ldots, r_{max})$$

Here now the “runt" is larger than the peak offspring, and Δr measures how much larger.

These are not the final optimized strategies but just the starting points. To further refine our optimization we will take all the offspring with r_p resources and either take or give them all the same ϵ amount of resources, and either give or take from the runt to insure the total amount of resources remain the same. Let k be the number of offspring with size r_p. Then the final optimized strategies are

$$\mathbf{r}_1 = (r_p - \epsilon, \ldots, r_p - \epsilon, r_p - \Delta r + k\epsilon, 0, \ldots, 0)$$
$$\mathbf{r}_2 = (r_p + \epsilon, \ldots, r_p + \epsilon, r_p + \Delta r - k\epsilon, r_{max}, \ldots, r_{max})$$

where the exact value of ϵ is found by starting it at 0 and continuously increasing it until the total fitness no longer increases. These two equations above are then the conjectured forms of the optimal strategies under Gaussian-like survivorhip functions.

Biologically we will have two classes of offspring, small and large, with possibly one offspring in the middle. On the first case the small offspring may not exist and we have many large offspring and one runt as in the convex-increasing case.

Some numerical simulations suggest this “sliding-ϵ" technique can be generalized to monotonically increasing then decreasing survivorship functions with an arbitrary finite number of inflection points.

Concave-convex-increasing One could also ask about sigmoidal and Gaussian-like functions where the convexities are swapped. The convexity-swapped sigmoidal function would then have an increasing concave component followed by an increasing convex component.

For these functions the optimal appears to be to give some number of offspring r_{high} resources to distribute the remaining resources equally among the other offspring.

To find the number of offspring with r_{high} resources is non-trivial. Let n be the total number of offspring and n' be the number of offspring that receive r_{high} resources. For every possible n' value calculate a corresponding r' to be the positive solution to the following equation.

$$(n - n')\frac{s(r' - n')}{n - n'} = s(1) + (n - n' - 1)s\left(\frac{r' - n' - 1}{n - n' - 1}\right)$$

Pick the largest of these r' which is smaller than R. The corresponding n' is the number of offspring that receive r_{high} resources. This latter case could explain situations where parents make some of their offspring large and some small.

Note that these two conjectures, concerning Gaussian-like and the concave-convex-increasing survivorships, are tentative. We have only numerically checked that they hold against a small handful of “reasonable" functions.

I. Stage structure in fluctuating environments

There are at least two sensible definitions for population growth rate in for matrix models under a stochastic environment. Using the notation of (Caswell 2006), let $N(t)$ be a random variable giving the population size at time t.

The growth rate discussed in the text is the average-of-growth-rates,

$$\ln \lambda_s = \lim_{t \to \infty} E[\ln N(t)].$$

Here we replicate evolution of the system many times from a given initial condition. For each replicate we calculate the growth rate. Take the average of all these growth rates to get $\ln \lambda_s$.

Compare this to the average-population-size growth rate,

$$\ln \mu = \lim_{t \to \infty} \ln E[N(t)].$$

Here at every time t we take average population size and measure how fast it grows.
If natural selection $\ln \mu$ then we have an answer similar to our constant environment case. Provided that environments are independently distributed, the average-population-size growth rate is equal to the dominant eigenvalue of $\bar{L} = \sum_{j=1}^{m} p_j L_j$, the weighted average of matrices. In particular, the elements of the first row are weighted sums. For example, the first element of the first row is

$$\bar{L}_{1,1} = \sum_{j=1}^{m} p_j w_{1,j}(\mathbf{r}_1).$$

Say that each $w_{1,j}$ is concave; that is, all of the survivorship functions that make them up are concave and the convexity does not change with environments. Then the entire weighted sum must be concave, as weighted sums preserve convexity. Or, more accurately, the sum will correspond to a fitness landscape made of concave sections, patched together under the same logic as in the non-stage-structured fluctuating environments case (section B.2). Unlike the non-stage-structured case, if all the survivorship functions are convex the entire sum is *guaranteed* to be made up of convex functions.
Repeating this logic shows each element the top row of $\bar{L}$ can be written as a function which features a patchwork fitness landscape similar to the non-stage-structured fluctuating environments case. As in the constant environment stage-structured case, the $\mathbf{r_i}$ are independent so we can find the vector which maximizes the weighted sum for each stage.
However, as discussed in the text, natural selection likely maximizes the much harder to calculate $\ln \lambda_s$ rather than $\ln \mu$.