How the concavity of reproduction/survival trade-offs impacts the evolution of life history strategies

Alex P. Farrell

Published online: 30 Nov 2020.

Submit your article to this journal ⬀

View related articles ⬀

View Crossmark data ⬀

Taylor & Francis
Taylor & Francis Group

How the concavity of reproduction/survival trade-offs impacts the evolution of life history strategies

Alex P. Farrell

Department of Mathematics, The University of Arizona, Tucson, AZ, USA

ABSTRACT
Previous works using different mathematical techniques, however, show that the concavity of the trade-off relationship can alter the expected life history strategies. Thus we developed a model and found that the concavity of the reproduction–survival curve can still have a large impact on life history strategies in an ecological model with Darwinian evolution.

1. Introduction

Questions about the life history strategies – such as the number and strength of reproductive events – stretch back millennia to Aristotle [9]. One major question is *why does an organism adopt a life history strategy of a single high fecund reproductive event over multiple bouts of lower fecund reproduction?* Although this question is ancient, it is one that remains relevant today to biologists [9] and mathematicians [4] alike.

Traditionally, this question has been answered by considering the post-reproductive survival probability (PRSP), i.e. the probability that an organism will survive the process of birthing new offspring. In this classical view, one may simply classify an organism as semelparous when the PRSP is zero (e.g. Pacific Salmon, *Oncorhynchus tshawytscha*) and as iteroparous when the PRSP is non-zero (e.g. humans, *homo sapiens*). Recently, this view has been challenged in a few ways by Hughes [9], leading to some difficulties when considering the question of semelparity versus iteroparity. In [9], Hughes shows that the binary choices of iteroparity and semelparity fail to capture the entirety of an organism's life history strategy, and that there is a continuum of PRSP with classical semelparity on one end, i.e. zero PRSP, and classical iteroparity, i.e. high PRSP, on the other. We provide two examples (both from [9]) to demonstrate difficulties faced when using the 'classic' binary classification system.

First, consider an organism (e.g. *Boechera fecunda*) that has a small, but non-zero, PRSP. In such a case, every breeding season will likely have at least one specimen that will survive

CONTACT Alex P. Farrell   ✉ alexpfarrell@math.arizona.edu

past reproduction and engage in the next reproductive event for the species, while the vast majority will not survive. This species would not be classically defined as semelparous because the PRSP is non-zero, even though nearly all of the organisms die after reproduction.

Second, consider an organism (e.g. *Misumena vatia*) that will participate in reproductive events until the environment is sufficiently beneficial, whereafter it will have a final larger (and life ending) reproductive event. If such an organism is in a perpetually favourable environment, it will be classically defined as semelparous. If it is a perpetually sub-optimal environment, it will be classically defined as iteroparous.

For more details on these and other examples concerning the parity continuum, see [9].

In [4], an evolutionary game theoretic model is developed to consider the question of semelparity versus iteroparity under the assumption that the reproduction/survival trade-off curve is linear. We expand the work done in [4] by analysing the model's dynamics when the reproduction/survival trade-off curve is either concave or convex. The model here and in [4] assumes Darwinian evolutionary dynamics and uses the framework created in [15]. This framework has been used to study a variety of topics, including cannibalism [7], strong Allee effects [2], the development of corn oil sensitivity in flour beetles [12] and more [1,6,10,16]. This modelling methodology has two main assumptions that somewhat mitigate the issues concerning the parity continuum:

- An individual's vital reproduction and survival rates depend on a phenotypic trait v that is subject to natural selection by Darwinian principles.
- This trait is normally distributed throughout the population with mean u and (constant) variance δ^2.

This modelling methodology aligns well with the first example above. In fact, even in the case of an average PRSP of zero, this is just the *average*; the population will still have many individuals with non-zero PRSP and thus will not be classically defined as semelparous. Even if the average PRSP is positive and somewhat near zero, e.g. on average one out of every 30 individuals would survive a reproductive event, it may be a stretch to say that a species is either 'semelparous' or 'iteroparous'.

The second example above (concerning *Misumena vatia* and others like it) can be considered in two ways. First, we could consider an organism in multiple locations, each with its own unique survival term. Second, we could consider that the organism to be located in a single environment that has changing resource levels that vary with time, although we cannot do so in the model presented here.

Thus, in an attempt to minimize confusion, we will only refer to the average PRSP, and leave its (binary or continuous) interpretation up to the reader. The structure of the paper is as follows: Section 2 contains the basic mathematical structure of the model and our global assumptions, and Section 3 is a dictionary of key quantities seen throughout the paper. In Section 4, we determine existence and stability criteria for extinction equilibria, which are equilibria whose population component is zero. Section 5 shows conditions for equilibria with a positive population component to bifurcate from extinction equilibria, and the stability properties of bifurcating equilibria near the bifurcation. Notably, we find that the shape of the trait dependent fecundity landscape and the reproduction/survival trade-off curve (later denoted f and h respectively) both play critical roles in the potential life history

strategies seen in positive population equilibria. Section 6 is broken into two subsections, each of which makes its own simplifying assumption that yielding additional results. Both subsections have at least one subsection within them, wherein particular functions are chosen and the example is fully analysed. The main body of work is concluded in Section 7, where we further discuss our results and their implications.

Overall our results align well with those of Schaffer and Rosenzweig [13,14], who analysed this question by the mathematical analysis of the expected fecundity of an organism's stage structured life cycle. Broadly speaking, their results say that a concave trade-off function leads to an iteroparous life history strategy while a convex trade-off yields a semelparous life history strategy. Much of our results are obtained through standard eigenvalue analysis, but for readability we removed such details from the main text and place the details in appendices.

2. Model structure

In order to remove any factors that may confound our results concerning how the concavity of the reproduction/survival trade-off function affects the dynamics, we restrict the scope of our study to its most minimal form. By this we mean that we consider only a one-dimensional population model coupled with a one-dimensional trait that evolves by Darwinian principles. We denote the population density at time t as $x(t)$, and the mean trait at time t as $u(t)$. The modelling methodology of evolutionary game theory [15] provides the discrete time equations

$$x(t+1) = r(x(t), v, u(t))|_{v=u(t)}x(t),$$

$$u(t+1) = u(t) + \delta^2 \partial_v r(x(t), v, u(t))|_{v=u(t)}$$

for the population and mean trait where v is the trait of an individual and

$$r(x, v, u) = bf(v)\beta(a_1(v, u)x) + sh(f(v))\sigma(a_2(v, u)x)$$

is the population (per capita) growth rate of the species x. r is the sum of surviving newborns per capita ($bf(v)\beta(a_1(v, u)x)$) and the proportion of adults that survive ($sh(f(v))\sigma(a_2(v, u)x)$) [3,4]. One unit of time is one generation of the population. Thus the term $sh(f(v))\sigma(a_2(v, u)x)$ describes the proportion adults that survive to the next generation, i.e. the PRSP, which includes density effects. If we are concerned with an individual's *heritable* PRSP, which is independent of their density, we only need to consider $sh(f(v))$. b is the maximal density-free fecundity of an adult, $bf(u)$ is the fecundity of an average adult, and β modifies the fecundity, depending on population density x and competition between an individual and an average individual, described by $a_1(v, u)$. $f(v)$ is the (trait dependent) fecundity landscape, which dictates the proportion of the maximal fecundity that an individual achieves, and is dependent on the trait v that is evolving. Analogously, s, $sh(f(v))$, $\sigma(a_2(v, u)x)$ and $a_2(v, u)$ are the maximal density-free survival probability, density-free survival probability of an average adult, density/competition dependent survival probability, and competition for survival respectively. Here h is a function that describes the trade-off between reproduction and post-reproduction survivorship. Finally, δ^2 is the constant variance that is assumed by our modelling methodology [15]. It can also

be though of as 'the speed of evolution' because it modifies how quickly the mean trait can evolve.

To reduce notational clutter, we use ∂_z to denote the partial derivative with respect to the zth component position, e.g.

$$\partial_v r(x, u, u) = \partial_v r(x, v, u)|_{v=u}.$$

Thus we can rewrite the second equation of our model as

$$u(t + 1) = u(t) + \delta^2 \partial_v r(x(t), u(t), u(t)).$$

If multiple partial derivatives are taken, we write $\partial_y \partial_z$ as $\partial_{y,z}$. Further, we use d_z to denote the total derivative with respect to the variable z, e.g.

$$d_u r(x, u, u) = \partial_v r(x, u, u) + \partial_u r(x, u, u).$$

When taking multiple total derivatives, $d_{y_1} d_{y_2}$ will be written as $d_{y_1 y_2}$. Finally, for functions of a single variable, we use the traditional 'prime' notation:

$$d_x g(x) = \partial_x g(x) = g'(x).$$

This allows us to rewrite our model equations as

$$x(t + 1) = r(x(t), u(t), u(t))x(t),$$

$$u(t + 1) = u(t) + \delta^2 \partial_v r(x(t), u(t), u(t)).$$

For the following assumptions, we denote the set of real numbers as $\mathbb{R}$, the set of non-negative real numbers as $\bar{\mathbb{R}}^+$ and the set of positive numbers as $\mathbb{R}^+$. Γ is an open set in $\mathbb{R}$ that contains $\bar{\mathbb{R}}^+$.

(H1) The inherent vital rates satisfy $0 < s < 1$ and $b > 0$. The density terms $\beta(z)$ and $\sigma(z)$ are twice continuously differentiable functions mapping Γ into $\bar{\mathbb{R}}_+$ that satisfy $\beta(0) = \sigma(0) = 1$. Further, we assume that β is strictly deceasing, $\beta(x) > 0$, σ is (non-strictly) decreasing and $\sigma(x) > 0$ for all $x > 0$.

(H2) f and a_i are twice continuously differentiable functions on $\mathbb{R}$ and $\mathbb{R} \times \mathbb{R}$ respectively that satisfy $0 < f(v) \leq 1$, $\lim_{v \to \pm\infty} f(v) = 0$, $a_i(v, u) \geq 0$, $a_i(u, u) = 1$, and $\partial_i a_j(u, u) = 0$ for $i = \{u, v\}, j = 1, 2$. Further, we assume that if $f'(z) = 0$, then $f''(z) \neq 0$. By scaling and/or shifting, we can and do assume without loss of generality that $f'(0) = 0$ and $f(0) = 1$.

(H3) $h(x) : [0, 1] \to [0, 1]$ is twice differentiable with $h(0) = 1, h(1) = 0$ and $h'(x) \leq 0$. Further, h is either strictly concave (i.e. $h''(x) < 0$ for $x \in (0, 1)$, also called 'concave down'), linear (i.e. $h''(x) \equiv 0$ for $x \in (0, 1)$) or strictly convex (i.e. $h''(x) < 0$ for $x \in (0, 1)$, also called 'concave up').

Remark 2.1: By assumption (H1), we know that $0 < \beta(x) < 1$ and $0 < \sigma(x) \leq 1$ for $x > 0$. Furthermore, $0 < s\sigma(x) < 1$ for all $x \in \mathbb{R}_+$.

(H2) implies that for any v such that $f(v) = 1$, we must have $f'(v) = 0$ and $f''(v) < 0$ which ensures the maximum value of inherent reproduction rate is b. Additionally, the assumptions on a_i in (H2) imply that $\partial_u r(x, v, u) \equiv 0$ for any $\text{col}(x, v, u) \in \mathbb{R}_+ \times \mathbb{R}^2$.

By (H3) we know that if $h''(x) = 0$ for any $x \in (0, 1)$ then $h''(z) \equiv 0$ for all $z \in (0, 1)$. Thus, since the concavity of h is guaranteed to be strict, we simply refer to h as being concave or convex respectively. Note that the endpoint restrictions also imply that if h is concave, then $h'(1) < -1 < h'(0)$. If h is convex, then the reverse of these inequalities hold, and if h is linear, then equality holds.

Assumption (H2) implies that at $v = 0$, the reproduction rate is maximized while the PRSP is minimized, and in fact equals zero. The assumption (H1) allows us to consider b and s as the maximal inherent (i.e. when density effects are absent) birth rate and PRSP, respectively. Since $f(v) \neq 0$ for all v, we exclude the possibility for there to be a trait at which fecundity equals 0 (although it can be arbitrarily small).

The assumptions on a_i in (H2) are restrictive, but hold under the commonly made assumption [15] that $a_i(v, u) = \hat{a}_i(v - u)$, with $\hat{a}_i(0) = 1$ and $\hat{a}_i'(0) = 0$, e.g. $a_i(v, u) = \hat{a}_i(v - u) = e^{-w(v-u)^2}$. Biologically, this implies that it is not the value of an individual's trait that determines the competition it experiences, but instead how different the individual's trait is from the typical individual's trait (i.e. the mean population trait, u). This is a concept echoed by Darwin himself. 'It is the most closely allied forms, – varieties of the same species, and species of the same genus or related genera, – … generally come into the severest competition with each other' [8].

Finally, by (H1) and (H3) we know that the PRSP ($sh(f(v))\sigma(x)$) and the heritable PRSP ($sh(f(v))$) can be zero if and only if $f(v) = 1$. Thus, since our primary discussion uses the terms 'zero average PRSP' and 'non-zero average PRSP' we can forgo the distinction between density dependent and heritable PRSP. We do note, however, that even given a high average heritable PRSP, density effects may cause a low average (density dependent) PRSP, and that this distinction requires some knowledge of σ. In particular, if $s\sigma(x)$ is heavily dependent on the environment, then we may see a population that can change parity depending on its location.

With these assumptions, we have the final form of the model:

$$
\begin{aligned}
x(t + 1) &= \big[bf(u(t))\beta(x(t)) + sh(f(u(t)))\sigma(x(t))\big]x(t), \\
u(t + 1) &= u(t) + \delta^2 f'(u(t))\big[b\beta(x(t)) + sh'(f(u(t)))\sigma(x(t))\big].
\end{aligned}
\tag{1}
$$

In general, an equilibrium $\mathrm{col}(x_e, u_e)$ must satisfy the following two algebraic equations:

$$
0 = x_e[bf(u_e)\beta(x_e) + sh(f(u_e))\sigma(x_e)], \quad \text{and} \quad 0 = f'(u_e)\big[b\beta(x_e) + sh'(f(u_e))\sigma(x_e)\big].
$$

Further, we denote the ith eigenvalue of the Jacobian matrix associated with (1) evaluated at the equilibrium $\mathrm{col}(x_e, u_e)$ by $\lambda_i^{(x_e, u_e)}(b, s)$. As indicated, we consider these to be functions of b and s.

2.1. Extinction equilibria

We define an extinction equilibrium of this system to be any equilibrium of the form $\mathrm{col}(0, u_c)$. We can clearly see that $x = 0$ will satisfy the first equation in System (1) regardless of the value of u.

Remark 2.2: $\mathrm{col}(0, u_c)$ is an extinction equilibrium if and only if u_c is a critical trait, i.e. $\partial_v r(0, u_c, u_c) = 0$. That is to say, u_c is a critical point of the *inherent adaptive landscape* $r(0, v, u_c)$ at $v = u_c$.

From Equation (1), we see that at an extinction equilibrium, u_c must satisfy the following equation:

$$0 = f'(u_c)[b + sh'(f(u_c))]. \tag{2}$$

Thus we have an extinction equilibrium if either $f'(u_c) = 0$ or $b = -sh'(f(u_c))$. Note that roots u_c of the bracketed portion of the equation are dependent, in general, on b and s. We create the following distinction between extinction equilibria:

- $\begin{pmatrix} 0 \\ u_0 \end{pmatrix}$ with $f'(u_0) = 0$ (note u_0 is independent of b and s)
- and
- $\begin{pmatrix} 0 \\ u_n(b, s) \end{pmatrix}$ where

$$b = -sh'(f(u_n(b, s))). \tag{3}$$

The assumption (H2) ensures the existence of the extinction equilibrium $\mathrm{col}(0, 0)$, which we call the trivial extinction equilibrium, although other equilibria of the form $\mathrm{col}(0, u_0)$ may exist.

Remark 2.3: If $f'(u_c(b, s)) = 0$, and $b = -sh'(f(u_c(b, s)))$, then $\mathrm{col}(0, u_c(b, s))$ is a non-hyperbolic equilibrium (see Equation (A2) in the Appendix). We note that this is not the only way for an extinction equilibrium to be non-hyperbolic. For the remainder of the paper, analysis of non-hyperbolic equilibria will be ignored unless we specifically state otherwise. Thus, in general, we do not consider an extinction equilibrium that satisfies both classifications.

Lemma 2.4: *If h is linear, then all extinction equilibria of the form $\mathrm{col}(0, u_n)$ are non-hyperbolic.*

Proof: $h(z) = 1 - z$ is the only linear function that satisfies (H3). Thus $h'(z) = -1$, $h''(z) = 0$ and $b = s$. The second portion of Equation (A2) (in the Appendix) shows that $\lambda_2^{(0, u_n)}(s, s) = 1$. ∎

2.2. Survival equilibria

We define a survival equilibrium of System (1) to be any equilibrium of the form $\mathrm{col}(x_e, u_e)$ with $x_e > 0$. Such equilibria satisfy $r(x_e, u_e, u_e) = 1$ and $0 = \frac{dr}{dv}[r(x_e, v, u_e)|_{v=u_e}$ simultaneously. This is equivalent to satisfying

$$1 = bf(u_e)\beta(x_e) + sh(f(u_e))\sigma(x_e),$$
$$\text{and} \tag{4}$$
$$0 = f'(u_e)\big[b\beta(x_e) + sh'(f(u_e))\sigma(x_e)\big].$$

In a fashion similar to what we did for extinction equilibria, we define two classes of survival equilibria:

$$\begin{pmatrix} x_0 \\ u_0 \end{pmatrix}, \text{ where } f'(u_0) = 0 \text{ and } x_0 > 0,$$

and

$$\begin{pmatrix} x_m \\ u_m \end{pmatrix}, \text{ where } f'(u_m) \neq 0 \text{ and } x_m > 0.$$

Note that to each $\text{col}(x_0, u_0)$ there is an extinction equilibrium $\text{col}(0, u_0)$ with the same u-component. This is not guaranteed to be the case for equilibria whose u component does not satisfy $f'(u) = 0$. More precisely, the existence of $\text{col}(x_m, u_m)$ does not imply that there is a survival equilibrium $\text{col}(0, x_m)$. In fact, the existence of $\text{col}(x_m, u_m)$ does not even guarantee that there exists any extinction equilibrium of the form $\text{col}(0, u_n)$ (e.g. the final bullet of Theorem 6.4).

Assumption (H2) allows us to rearrange the first equation of (4) into

$$b\beta(x_e) = \frac{1 - sh(f(u_e))\sigma(x_e)}{f(u_e)}, \tag{5}$$

which we can substitute into the second equation to get (after some algebraic manipulation)

$$0 = \frac{f'(u_e)}{f(u_e)}\Big[1 - sh(f(u_e))\sigma(x_e) + sh'(f(u_e))f(u_e)\sigma(x_e)\Big]. \tag{6}$$

3. Key quantities

In the analysis in the appendices, we find the repeated use of some key diagnostic quantities and a diagnostic function. For more details, see the appendix. In general, quantities with a subscript '0' relate to equilibria whose u component satisfies $f'(u) = 0$, while those with a subscript 'n' are related to equilibria whose u component satisfies $f'(u) \neq 0$. Notably, extinction equilibria that satisfy Equation (3) are of the 'n' form. See Section 2 for equilibrium classifications. Some important quantities are

$$b_0^*(s) := \frac{1 - sh(f(u_0))}{f(u_0)}, \tag{7}$$

$$b_0^\dagger(s) := -sh'(f(u_0)), \tag{8}$$

$$b_n^m(s) := -sh'(0), \tag{9}$$

$$b_n^M(s) := -sh'(1). \tag{10}$$

Theorem 3.1: $b_n^M(s) < 1$ *if and only if one of the following holds:*

- *h is convex or linear*
- *h is concave and $s \in (0, -h'(1)^{-1})$.*

Proof: Suppose that h is linear. Then $b_n^M(s) = s < 1$.

Suppose that h is convex. Then Remark 2.1 tells us that $-h'(1) < 1$, so $b_n^M(s) = -sh'(1) < 1$.

Finally, if h is concave, then Remark 2.1 tells us that $-h'(1) > 1$, so $b_n^M(s) < 1$ if and only if $s < -h'(1)^{-1}$. ∎

While this result is simple, it becomes extremely useful throughout our analysis, as $b_n^M(s)$ is a frequently used diagnostic quantity.

Corollary 3.2: *If h is concave, then there exists some $s \in (0, 1)$ such that $b_n^M(s) > 1$.*

Proof: From Equation (10), we see that $b_n^M(s) = 1$ if and only if $s = -h'(1)^{-1}$. By excluding this case, we see that $b_n^M(s) > 1$ if and only if $-h'(1)^{-1} < s$. We must ensure, however, that such an s is between 0 and 1, which is accomplished via Remark 2.1, which implies $(-h'(1)^{-1}, 1) \neq \emptyset$. ∎

Lemma 3.3: *Assume (H1)–(H3) and define $\Phi : [0, 1] \to \mathbb{R}$ as*

$$\Phi(z) := h(z) - zh'(z). \tag{11}$$

If $b_n^M(s) > 1$, then there exists a unique $z^*(s) \in (0, 1)$ such that

$$z^*(s) = \Phi^{-1}(1/s). \tag{12}$$

Further, we define

$$b_n^*(s) = -sh'(z^*(s)), \tag{13}$$

with $\lambda_1^{(0,u_n)}(b_n^*, s) = r(0, u_n, u_n) = 1$ for all extinction equilibrium of the form $\mathrm{col}(0, u_n)$. Further, $0 \leq b_n^m(s) < b_n^*(s) < 1 < b_n^M(s)$.

If $b_n^M(s) < 1$, then $\Phi(z) < 1/s$ and $b_n^*(s)$ and $z^*(s)$ do not exist.

Proof: See the Appendix. ∎

Note that if there are multiple equilibria of the form $\mathrm{col}(x_e, u_e)$ with $f'(u_e) = 0$, then there may be multiple values for the '0' subscripted quantities. Importantly, this does not occur for 'n' subscripted quantities, as they do not depend on the value of u_n.

Theorem 3.4: *Consider an extinction equilibrium of the form $\mathrm{col}(0, u_0)$. We have $\lambda_1^{(0,u_0)}(b_0^*, s) = r(0, u_0, u_0) = 1$. Further, we have the following ordering for values of b_0^* when there are multiple extinction equilibria $\mathrm{col}(0, u_0)$:*

- *if $b_n^M(s) < 1$, then the value of $b_0^*(s)$ associated with $\mathrm{col}(0, 0)$ is 1. Further, for all extinction equilibria of the form $\mathrm{col}(0, u_0)$, we have $1 \leq b_0^*(s)$.*
- *if $b_n^M(s) > 1$, then for all extinction equilibria $\mathrm{col}(0, u_0)$ with $h^{-1}(\frac{1-f(u_0)}{s}) < f(u_0) < 1$, the associated value of $b_0^*(s)$ is strictly less than 1.*

Proof: See the Appendix. ∎

We note $b_0^*(s) = 1$ for all extinction equilibria $\mathrm{col}(0, u_0)$ with $f(u_0) = 1$, so a smallest value of $b_0^*(s)$ may not be unique, even if $b_n^M(s) < 1$.

Lemma 3.5: *Assume* (H1)–(H3) *and consider an extinction equilibrium* $\mathrm{col}(0, u_0)$ *with* $f'(u_0) = 0$. *We have the following:*

- *If* $b_n^M(s) < 1$, *then* $b_0^\dagger(s) < b_0^*(s)$.
- *If* $b_n^M(s) > 1$ *and* $f(u_0) < z^*(s)$, *then* $b_0^\dagger(s) < b_0^*(s)$.
- *If* $b_n^M(s) > 1$ *and* $f(u_0) \geq z^*(s)$, *then* $b_0^*(s) \leq b_0^\dagger(s)$.

Proof: See the Appendix. ∎

Note that none of the quantities (eqaaa), (8), (9), (10), (12), or (13), depend on the speed of evolution δ^2.

(H4) Let $b^\odot$ be the maximal birth rate we consider to be biologically reasonable for a particular system in which we are interested. Assume that

$$b^\odot > \max\{b_0^*(s), b_0^\dagger(s), b_n^M(s), b_n^m(s)\},$$

where we emphasize that there may be multiple values for $b_0^*(s)$, and $b_0^\dagger(s)$, as each of these corresponds to a particular $\mathrm{col}(0, u_0)$. Further, let δ^2 be sufficiently small (i.e. the speed of evolution is sufficiently slow) such that all of the following hold:
- For all u_0 such that $f'(u_0) = 0$ and $f''(u_0) < 0$,

$$\delta^2 < \min\left\{\frac{-2}{f''(u_0)(b^\odot - b_0^\dagger(s))}, \frac{-2f(u_0)}{f''(u_0)}\right\}.$$

- For all u_0 such that $f'(u_0) = 0$ and $f''(u_0) > 0$,
  - -- if $b_0^\dagger > 0$, then $\delta^2 < \dfrac{2}{f''(u_0)b_0^\dagger(s)}$.
  - -- if $b_0^\dagger \leq 0$, then there are no additional restrictions on δ^2.
- If h is concave, then

$$\delta^2 < \frac{2}{\max_{z \in (-\infty, \infty)}\{-(f'(z))^2 sh''(f(z))\}}.$$

Remark 3.6: By Lemma 3.3, either $b_n^*(s) < b_n^M(s)$ or $b_n^*(s)$ does not exist. Thus $b^\odot$ is (strictly) greater than all of the diagnostic b values presented in this section. Further, by (H2), we always have that

$$\delta^2 < \frac{-2}{f''(0)\max\{b^\odot - b_n^M(s), 1\}}.$$

4. Extinction equilibria

Recall the definition of an extinction equilibrium in Section 2.1.

Table 1. We emphasize that both b_n^m and b_n^M are functions of s, although this is not included in the table for ease of reading and for space. By Lemma 2.4, a linear h does not need to be considered.

Existence criteria	Restriction	b interval such that the equilibrium exists
Existence of col$(0, u_0)$ type extinction equilibria $f'(u_0) = 0$	$f''(u_0) \neq 0$	$(0, b^\odot)$
Existence of col$(0, u_n)$ type extinction equilibria $b = -sh'(f(u_n))$	Concave h	(b_n^m, b_n^M)
	Convex h	(b_n^M, b_n^m)

Table 2. We emphasize that each of $b_0^*, b_0^\dagger, b_n^m, b_n^M$ and b_n^* are functions of s, although this is not included in the table for ease of reading and for space. Similarly, we remove the arguments from the eigenvalues for space and readability. If $b_n^M < 1$, then b_n^* does not exist (by Lemma 3.3). In this case, we say $\min\{b_n^M, b_n^*\} = b_n^M$ and the interval $(b_n^*, b_n^M) = \emptyset$. If $b_0^\dagger = 0$, we replace any intervals of the form $(0,0)$ with $\emptyset$. By Lemma 2.4, a linear h does not need to be considered. The markers A1, A2, B1 and B2 are for reference to specific rows.

	Restriction	b interval such that			
		$|\lambda_1| < 1$	$|\lambda_2| < 1$	$|\lambda_1| > 1$	$|\lambda_2| > 1$
A. Stability of col$(0, u_0)$ type extinction equilibria					
A1	$f''(u_0) < 0$	$(0, b_0^*)$	$(b_0^\dagger, b^\odot)$	$(b_0^*, b^\odot)$	$(0, b_0^\dagger)$
A2	$f''(u_0) > 0$	$(0, b_0^*)$	$(0, b_0^\dagger)$	$(b_0^*, b^\odot)$	$(b_0^\dagger, b^\odot)$
B. Stability of col$(0, u_n)$ type extinction equilibria		$|\lambda_1| < 1$	$|\lambda_2| < 1$	$|\lambda_1| > 1$	$|\lambda_2| > 1$
B1	Concave h	$(b_n^m, \min\{b_n^M, b_n^*\})$	(b_n^m, b_n^M)	(b_n^*, b_n^M)	$\emptyset$
B2	Convex h	(b_n^M, b_n^m)	$\emptyset$	$\emptyset$	(b_n^M, b_n^m)

Since col$(0, u_0)$ type extinction equilibria only need satisfy $f'(u_0) = 0$, they exist for the maximal b interval we consider, i.e. for $b \in (0, b^\odot)$. By (H2), we also have $f''(u_0) \neq 0$. For col$(0, u_n)$ type extinction equilibria, (H2) and Remark 2.3 allow us to assume that $f(u_n(b, s)) \in (0, 1)$. Thus there is a $u_n(b, s)$ that solves Equation (3) if and only if b is (strictly) between $b_n^m(s)$ and $b_n^M(s)$. By their definitions (Equations (9) and (10)), their ordering is dependent on the sign of h''; if h is concave, then $b_n^m(s) < b_n^M(s)$ and if h is convex, then $b_n^M(s) < b_n^m(s)$.

Table 1 summarizes extinction equilibrium existence conditions. Table 2 summarizes the conditions under which the eigenvalue associated with the Jacobian matrix evaluated at extinction equilibria lie inside the complex unit circle for a given value of s. Details for Table 2 are in the Appendix. We note, again, that the quantities $b_n^m(s)$, $b_n^M(s)$ and $b_n^*(s)$ do not depend on the value of u_n. Thus all extinction equilibria of the form col$(0, u_n)$ have the same stability classification.

Table 2 and Lemma 3.5 yield the following theorem.

Theorem 4.1 (Stability of Extinction Equilibria): *Assume* (H1)–(H4) *and consider an extinction equilibrium* col$(0, u_0)$ *with* $f''(u_0) < 0$.

- If $b_n^M(s) < 1$, then $\mathrm{col}(0, u_0)$ is locally asymptotically stable (LAS) for $b \in (b_0^\dagger(s), b_0^*(s))$ and unstable for $b \in (0, b_0^\dagger(s)) \cap (b_0^*(s), b^\odot)$.
- If $b_n^M(s) > 1$ and $f(u_0) < z^*(s)$, then $\mathrm{col}(0, u_0)$ is LAS for $b \in (b_0^\dagger(s), b_0^*(s))$ and unstable for $b \in (0, b_0^\dagger(s)) \cap (b_0^*(s), b^\odot)$.
- If $b_n^M(s) > 1$ and $f(u_0) \geq z^*(s)$, then $\mathrm{col}(0, u_0)$ is unstable for all $b \in (0, b^\odot)$.

Since the trivial extinction equilibrium $\mathrm{col}(0,0)$ always exists, we show how Theorem 4.1 applies to it. To do so we note that $0 < z^*(s) < 1 = f(0)$ and that, by (H2), $b_0^*(s) = 1$, and $b_0^\dagger(s) = b_n^M(s)$ for the trivial extinction equilibrium.

Corollary 4.2: *Assume* (H1)–(H4).
If $b_n^M(s) < 1$, then the extinction equilibrium $\mathrm{col}(0,0)$ is locally asymptotically stable for $b \in (b_n^M(s), 1)$.
If $b_n^M(s) > 1$, then $\mathrm{col}(0,0)$ is unstable for all $b \in (0, b^\odot)$.

5. Bifurcation and basic analysis of survival equilibria

Recall the definition of a survival equilibrium in Section 2.2. We see that Equation (6) is satisfied if $f'(u_e) = 0$ and by (H2) we know that $f'(0) = 0$. Substituting $u_e = 0$ into Equation (5) we see that $\beta(x_e) = b^{-1}$. If $b^\odot < \lim_{x \to \infty}(\beta(x))^{-1}$, then since β is strictly decreasing and $\beta(0) = 1$, we have that the survival equilibrium $(\beta^{-1}(1/b), 0)$ exists for $b \in (1, b^\odot)$.

We will use the technique developed in [5] to show when survival equilibria bifurcate from extinction equilibria and the stability properties of both equilibira.

Theorem 5.1: *Consider an extinction equilibrium $\mathrm{col}(0, u_c(b, s))$. Assume* (H1)–(H4)*, and that there is some $\hat{b}$ such that at $b = \hat{b}$, $r(0, u_c(b, s), u_c(b, s)) = 1$ and either $f'(u_c(b, s)) \neq 0$ or $b \neq -sh'(f(u_c(b, s)))$.*

Then, as b increases through $\hat{b}$, a survival equilibrium bifurcates from $\mathrm{col}(0, u_c(b, s))$.

Further, if $|\lambda_2^{(0, u_c(\hat{b}, s))}(\hat{b}, s)| < 1$, then as b increases through $\hat{b}$, the bifurcating survival equilibrium is locally asymptotically stable.

If $|\lambda_2^{(0, u_c(\hat{b}, s))}(\hat{b}, s)| > 1$, then as b increases through $\hat{b}$, the bifurcating survival equilibrium is unstable.

Proof: See the appendix. ∎

Armed with Theorem 5.1, Table 2 can now be used to determine the stability of a bifurcating survival equilibrium.

Theorem 5.2: *Assume* (H1)–(H4). *If $b_n^M(s) < 1$, then for all $b \in (0, b^\odot)$ there are no survival equilibria of the form $\mathrm{col}(x_m, u_m)$.*
If $b_n^M(s) > 1$, then there exists some $\varepsilon > 0$ such that for $b \in (b_n^*(s), b_n^*(s) + \varepsilon)$ there exists a survival equilibrium of the form $\mathrm{col}(x_m, u_m)$.

Proof: See the Appendix. ∎

Corollary 5.3: *Suppose* (H1)–(H4).

If $b_n^M(s) < 1$ and h is concave, then all extinction equilibria of the form $\mathrm{col}(0, u_n)$ *are locally asymptotically stable for $b \in (b_n^m, b_n^M)$.*

If $b_n^M(s) < 1$ and h is convex, then all extinction equilibria of the form $\mathrm{col}(0, u_n)$ *are saddles for $b \in (b_n^M, b_n^m)$.*

If $b_n^M(s) > 1$, then all extinction equilibria of the form $\mathrm{col}(0, u_n)$ *are locally asymptotically stable for $b \in (b_n^m, b_n^*)$ and saddles for $b \in (b_n^*, b_n^M)$. Further, there is a bifurcation of survival equilibria from extinction equilibria of the form* $\mathrm{col}(0, u_n)$ *at $b = b_n^*(s) < 1$ and the bifurcating survival equilibria are locally asymptotically stable near the bifurcation.*

Proof: The first result is seen by combining Table 2 and Lemma 3.3. The second follows directly from Table 2. The third assertion follows from Theorem 5.1, Lemma 3.3 and Table 2. ∎

By Lemma 2.4, we do not need to consider when h is linear. We see that Corollaries 3.2 and 5.3 together imply that so long as h is concave and s is sufficiently large, there will be a bifurcation of survival equilibria from extinction equilibria of the form $\mathrm{col}(0, u_n)$. Notably, Corollary 5.3 provides the potential for survival equilibria with a non-zero average PRSP to exist at a lower b values than zero average PRSP survival equilibria.

Corollary 5.4: *Suppose* (H1)–(H4).

If $b_n^M(s) < 1$, then at $b = 1$ a locally asymptotically stable survival equilibrium bifurcates from $\mathrm{col}(0, 0)$. *No other bifurcations from extinction equilibria occur for $b < 1$.*

If $b_n^M(s) > 1$, then a locally asymptotically stable survival equilibrium bifurcates from an extinction equilibrium for b values less than 1.

Proof: For the first result, we see that no survival equilibria will bifurcate before $b = 1$ by Lemma 3.3 and Theorem 3.4. Further, Lemma 3.5 and Table 2 allow us to use Theorem 5.1 for the result. Corollary 5.3 provides the second result. ∎

The first portion of Corollary 5.4 implies that for a convex or linear h, the first survival equilibrium to bifurcate from an extinction equilibrium will have a zero average PRSP. The second tells us that if $b_n^M(s) > 1$ (and so h must be concave by Theorem 3.1), at least one non-zero average PRSP survival equilibrium will bifurcate from a survival equilibrium at a b value less than 1. Theorem 3.4 and Lemma 3.3 provide details as to the extinction equilibria from which the survival equilibria bifurcate.

By Theorem 5.2, $b_n^M(s) < 1$ implies that all survival equilibria are critical values of the fecundity landscape, i.e. $\mathrm{col}(x_e, u_e)$ with $f'(u_e) = 0$. Thus there may still be a non-zero average PRSP survival equilibria, but the existence, or lack thereof, of such equilibria is fully determined by the shape of f.

If $b_n^M(s) < 1$, multiple maxima of f do not guarantee that there are heritable average PRSPs (i.e. the average PRSP without considering losses due to density) that are significantly different from zero. The heritable average PRSP of the population is $sh(f(u))$, so if f has maxima at or near 1, then *all* such values of u still correspond to a near-zero species average PRSP. Further, the shape of h can make extreme differences in potential life history

strategies. For example, let $h(z) = (1-z)^n$, where $n \geq 1$ is an integer. Then

$$b_n^M(s) = -sh'(1) = 0 < 1,$$

and for any given value of $0 < f(u) \leq 1$ the species average PRSP can be made to be as close to zero as desired by selecting a sufficiently large n.

Theorem 5.5: *Assume* (H1)–(H4) *and consider a survival equilibrium of the form* $\text{col}(x_m, u_m)$. *Any such equilibrium satisfies* $f(u_m) \geq z^*(s)$.

Proof: See the Appendix. ∎

From this theorem, we can see that, with respect to the parameter b, the reproduction rate modifier at a survival equilibrium (i.e. $f(u_m)$) is minimized at the bifurcation point. Since h is decreasing, this also implies that the species average PRSP (i.e. $sh(f, u_m)$)) is maximized at the bifurcation point. Thus, as b grows, the survival equilibrium $\text{col}(x_m, u_m)$ cannot become 'more iteroparous' in the sense that it cannot increase its PRSP from its near extinction value.

6. Examples

Under additional, and somewhat specific, assumptions more analytical results can be found. After we complete the development of the theory under an additional assumption, specific functions are chosen as an example and a complete description of the dynamics is given. We explore two special cases: $\sigma(x) \equiv 1$ and $\sigma(x) = \beta(x)$. The biological meaning of each of these assumptions is detailed in its respective section below.

In Section 6.1, we assume that $\sigma(x) \equiv 1$ and find that the life history strategies of survival equilibria are independent of b and the associated population density x at equilibrium. Further, it shows the potential for a non-zero average PRSP survival equilibria to exist before a zero average PRSP equilibria. Section 6.1.1 chooses specific functions and fully analyses the model, displaying a range of potential equilibrium configurations with changes in b and s. In Section 6.1.2, new functions are chosen, with an emphasis on the role that f can play in overall dynamics.

$\sigma(x) = \beta(x)$ is assumed in Section 6.2, which implies that the life history strategy (i.e. the u component of the equilibrium) seen in a survival equilibrium is also seen in an extinction equilibrium. Further, for sufficiently large b, the population component of all survival equilibria satisfies $f'(x) = 0$. The further specialized example in Section 6.2.1 shows these concepts more concretely.

6.1. $\sigma(x) \equiv 1$

Under this assumption, we ignore the effects of density on the PRSP. Equivalently, we are assuming that the density effects on birth rates are significantly more important than those on death rates, to the point that density-dependent effects on death are effectively non-existent.

Then Equation (6), which must be satisfied by survival equilibria, becomes

$$0 = \frac{f'(u_e)}{f(u_e)}\big[1 - sh(f(u_e)) + sh'(f(u_e))f(u_e)\big]. \tag{14}$$

Note neither b nor x_e appear in this equation, so the trait component u_e of survival equilibria does not depend on either of these quantities. In fact, u_e is either a solution to $f'(u_e) = 0$ or $\Phi(f(u_e)) = 1/s$. As a result, changes is the inherent birth rate b do not affect life history strategies of the survival equilibrium populations in this model.

With these observations, we can easily classify the stability of survival equilibria in some cases. Recall the definition of $z^*(s)$ from Equation (12).

Theorem 6.1: *Assume (H1)–(H4), that h is concave, and $\sigma(x) \equiv 1$. Consider a survival equilibrium* $\mathrm{col}(x_0, u_0)$ *with $f'(u_0) = 0$.*

If $b_n^M(s) < 1$ and $f''(u_0) > 0$, then $\mathrm{col}(x_0, u_0)$ *is unstable for all $b \in (0, b^{\odot})$.*

If $b_n^M(s) > 1, f''(u_0) < 0$, and $f(u_0) \geq z^*(s)$, then $\mathrm{col}(x_0, u_0)$ *is unstable for all $b \in (0, b^{\odot})$.*

Proof: See the Appendix. ∎

Recall that by H2 we have $f'(0) = 0$ and Theorem 6.1 implies the following corollary.

Corollary 6.2: *Assume (H1)–(H4), that h is concave, and $\sigma(x) \equiv 1$. Let*

$$b^{\sharp} = \min\{b^{\odot}, \lim_{x\to\infty} (\beta(x))^{-1}\}.$$

Then the survival equilibrium $\mathrm{col}(x_0, 0)$ *exists for all $1 < b < b^{\sharp}$ with $x_e = \beta^{-1}(1/b)$.*

If $b_n^M(s) > 1$, then $\mathrm{col}(x_0, 0)$ *is unstable for all $1 < b < b^{\sharp}$.*

Proof: Since $r(0, 0, 0) = b$, Theorem 5.1 implies that $\mathrm{col}(x_e, 0)$ bifurcates from $\mathrm{col}(0, 0)$ at $b = 1$.

Using $f(0) = 1$ and $h(1) = 0$, Equation (5) simplifies to

$$b\beta(x_e) = 1.$$

Finally, note that $0 < z^*(s) < 1 = f(0)$. Applying Theorem 6.1 yields the result. ∎

Theorem 6.3: *Suppose (H1)–(H4), that h is concave, $f(v)$ has a single critical point at $v = 0$, $s \in (-h'(1)^{-1}, 1)$,*

$$b^{\odot} < \lim_{x\to\infty} \frac{b_n^*(s)}{\beta(x)} \quad \text{and} \quad \frac{2}{1 + b_n^*(s)} > -x\frac{\beta'(x)}{\beta(x)} \quad \text{for all } x \in (0, \infty).$$

If $b \in (0, b_n^*(s))$, then there are no survival equilibria.

If $b \in (b_n^*(s), 1)$, then there exists a survival equilibrium $\mathrm{col}(x_m, u_m)$ *that is locally asymptotically stable.*

If $b \in (1, b^{\odot})$, then there exists a survival equilibrium $\mathrm{col}(x_m, u_m)$ *that is locally asymptotically stable and a survival equilibrium* $\mathrm{col}(x_0, 0)$ *that is unstable.*

Proof: See the Appendix. ∎

The conditions on β are feasible. First, note that $b_n^*(s) < 1$, which implies that $\frac{2}{1+b_n^*(s)} > 1$. Now, consider $\beta(x) = (1+x)^{-n}$ for $n \in (0,1]$. Then, for $x \in [0,\infty)$,

$$-x\frac{\beta'(x)}{\beta(x)} = -x\frac{(-n)(1+x)^{-n-1}}{(1+x)^{-n}} = \frac{nx}{1+x} < n \le 1 < \frac{2}{1+b_n^*(s)}$$

See Theorem 6.4 for a full example. Theorem 6.3 shows an interesting biological phenomenon, namely that under some conditions, a higher intrinsic survival rates ($s \in (-h'(1)^{-1}, 1)$) allow for a stable survival equilibrium with a non-zero average PRSP can exist in a parameter region ($b \in (b_n^*(s), 1)$) that excludes the potential for a zero average PRSP survival equilibrium to exist. Further, even when $b > 1$ the zero average PRSP survival equilibrium exists but is not stable.

6.1.1. Furthering the example: h is concave

For this example, we choose

$$f(v) = e^{-v^2}, \quad h(z) = 1 - z^2, \quad \beta(x) = \frac{1}{x+1}, \quad \text{and} \quad \sigma(x) \equiv 1, \tag{15}$$

and calculate extinction equilibria:

$$\begin{pmatrix} 0 \\ u_0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 0 \\ u_n^{\pm} \end{pmatrix} = \begin{pmatrix} 0 \\ \pm\sqrt{\ln\left(\frac{2s}{b}\right)} \end{pmatrix} \tag{16}$$

and survival equilibria:

$$\begin{pmatrix} x_0 \\ u_0 \end{pmatrix} = \begin{pmatrix} b-1 \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} x_m \\ u_m^{\pm} \end{pmatrix} = \begin{pmatrix} \frac{b}{2s\sqrt{1/s-1}} - 1 \\ \pm\sqrt{\frac{-1}{2}\ln(1/s-1)} \end{pmatrix}. \tag{17}$$

Theorem 6.4: *Suppose our model is described in Equation* (1) *with the function definitions in* (15). *Choose*

$$b^{\odot} > \begin{cases} 1, & s \le 1/2, \\ 2s, & s \ge 1/2, \end{cases} \quad \text{and} \quad \delta^2 < \frac{1}{\max\left\{b^{\odot} - 2s, 2se^{-1}\right\}}.$$

For the exact expressions of the equilibria, see Equations (16) *and* (17).
Assume $s < 1/2$.

- $b < 2s$ *implies the extinction equilibria* $\mathrm{col}(0, u_m^{\pm})$ *are both locally asymptotically stable and the extinction equilibrium* $\mathrm{col}(0, u_0)$ *is unstable. There are no survival equilibria.*
- $2s < b < 1$ *implies* $\mathrm{col}(0, u_0)$ *is the only equilibrium, is an extinction equilibrium and is locally asymptotically stable.*
- $1 < b < b^{\odot}$ *implies the survival equilibrium* $\mathrm{col}(x_0, 0)$ *is locally asymptotically stable and the extinction equilibrium* $\mathrm{col}(0, u_0)$ *is unstable.*

If instead s > 1/2, then

- $b < 2\sqrt{s - s^2}$ *implies the extinction equilibria* $\mathrm{col}(0, u_m^{\pm})$ *are both locally asymptotically stable and the extinction equilibrium* $\mathrm{col}(0, u_0)$ *is unstable. There are no survival equilibria.*
- $2\sqrt{s - s^2} < b < 1$ *implies that the survival equilibria* $\mathrm{col}(x_m, u_m^{\pm})$ *are both locally asymptotically stable and the extinction equilibria* $\mathrm{col}(0, u_n^{\pm})$ *and* $\mathrm{col}(0, u_0)$ *are unstable.*
- $1 < b < 2s$ *implies the survival equilibria* $\mathrm{col}(x_m, u_m^{\pm})$ *are both locally asymptotically stable, and that the survival equilibrium* $\mathrm{col}(x_0, u_0)$ *and extinction equilibria* $\mathrm{col}(0, u_n^{\pm})$ *and* $\mathrm{col}(0, u_0)$ *are unstable.*
- $2s < b < b^{\odot}$ *implies the survival equilibria* $\mathrm{col}(x_m, u_m^{\pm})$ *are both locally asymptotically stable, and that the survival equilibrium* $\mathrm{col}(x_0, u_0)$ *and extinction equilibria* $\mathrm{col}(0, u_0)$ *are unstable.* $\mathrm{col}(0, u_n^{\pm})$ *do not exist.*

Proof: See the Appendix. ∎

We note that for concrete values of $b^{\odot}$ and δ^2, (H4) can be satisfied by choosing $b^{\odot} = 2$ and $\delta^2 = 0.25$.

Recalling Theorem 6.3, it seems that this particular model (Equation 15) favours organisms with more iteroparous life history strategies for a sufficiently large value of s. This can be seen in the second row of subfigures in Figure 1.

Each subfigure in Figure 1 shows the phase plane for a bullet of Theorem 6.4. The bifurcation information is summarized in Figure 2.

6.1.2. Another example: h is linear

For another example, we choose

$$f(v) = e^{-v^2 - v^2(1-v^2)/0.05}, \quad h(z) = 1 - z, \quad \beta(x) = \frac{1}{x+1}, \quad \text{and} \quad \sigma(x) \equiv 1. \quad (18)$$

The reproduction function f for this example is selected from [4] and has two maxima, as seen in Figure 3. A priori, a reproduction (or more generally, fitness) landscape with multiple maxima may appear to be a purely mathematical exercise rather than the modelling of a biological system. Contrary to this, however, [11] states that multiple maxima on fitness landscapes are common and 'may account for much of life's diversity' by allowing for rapid niche diversification.

Choosing h to be linear simplifies much of the previous work; however, choosing a more complex f increases the difficulty. We find the following extinction equilibria:

$$\begin{pmatrix} 0 \\ u_0^1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} 0 \\ u_0^2 \end{pmatrix} \approx \begin{pmatrix} 0 \\ 0.5564 \end{pmatrix}, \quad \text{and} \quad \begin{pmatrix} 0 \\ u_0^3 \end{pmatrix} \approx \begin{pmatrix} 0 \\ 0.9436 \end{pmatrix}, \quad (19)$$

and the survival equilibria:

$$\begin{pmatrix} x_0^1 \\ u_0^1 \end{pmatrix} = \begin{pmatrix} b - 1 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} x_0^2 \\ u_0^2 \end{pmatrix} \approx \begin{pmatrix} \dfrac{0.2170b}{1 - 0.7830s} - 1 \\ 0.5564 \end{pmatrix}, \quad \begin{pmatrix} x_0^3 \\ u_0^3 \end{pmatrix} \approx \begin{pmatrix} \dfrac{0.3879b}{1 - 0.6121s} - 1 \\ 0.9436 \end{pmatrix}. \quad (20)$$
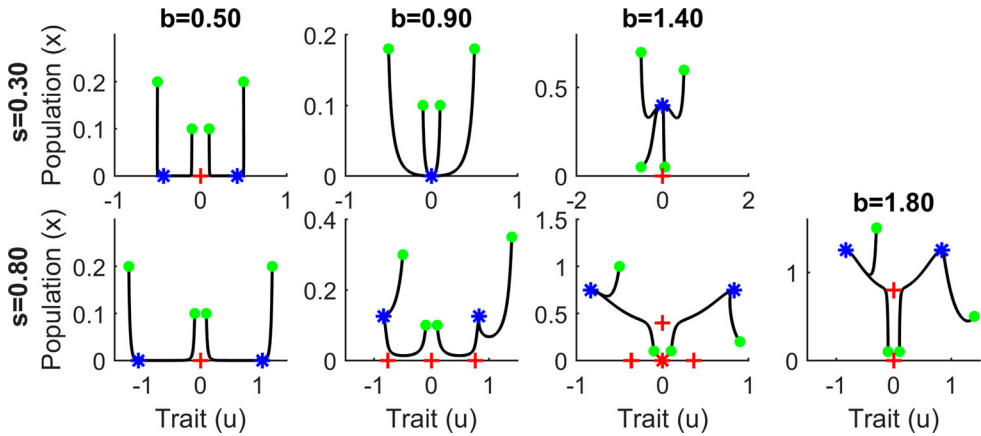
Figure 1. Simulations of the model defined by Equations (1) and (15). Each green dot is an initial condition, with a black line corresponding to its trajectory. A blue star indicates a locally asymptotically stable equilibrium, a red star an unstable node and a red plus a saddle. The value of s is on the left, while the value of b is on top. The top row corresponds to the first three bullets of Theorem 6.4 and the bottom four figures to the final four bullets. When $s = 0.8$, $2\sqrt{s - s^2} = 0.8$ as well. $b^{\odot}$ and δ are chosen to be 2 and 0.25 respectively.

Each survival equilibrium (x_0^i, u_0^i) bifurcates from its respective extinction equilibrium $(0, u_0^i)$ at

$$b_0^* = \frac{1 - s}{f(u_0^i)} + s = f(u_0^i)^{-1} + s(1 - f(u_0^i)^{-1}).$$

For convenience, we define the following:

$$F_2 := f(u_0^2) = f\left(\frac{3}{4} - \sqrt{\frac{3}{80}}\right) \approx 0.2170,$$

$$F_3 := f(u_0^3) = f\left(\frac{3}{4} + \sqrt{\frac{3}{80}}\right) \approx 0.3879.$$

$$(21)$$

Theorem 6.5: *Assume $b^{\odot}$ and δ^2 are chosen to satisfy* (H4) *and that our system is defined using the function definitions in* (18). *Refer to Equations* (20) *and* (19) *for definitions of the equilibria mentioned below.*

- *If $b < s$, then $\text{col}(0, u_0^2)$ is locally asymptotically stable and both $\text{col}(0, u_0^1)$ and $\text{col}(0, u_0^3)$ are unstable. None of $\text{col}(x_0^i, u_0^i)$ have $x_0^i > 0$.*
- *If $s < b < 1$, then both $\text{col}(0, u_0^1)$ and $\text{col}(0, u_0^3)$ are locally asymptotically stable and $\text{col}(0, u_0^2)$ is unstable. None of $\text{col}(x_0^i, u_0^i)$ have $x_0^i > 0$.*
- *If $1 < b < F_3^{-1} + s(1 - F_3^{-1})$, then both $\text{col}(0, u_0^1)$ and $\text{col}(0, u_0^2)$ are unstable, and both $\text{col}(x_0^1, u_0^1)$ and $\text{col}(x_0^3, u_0^3)$ are locally asymptotically stable. $\text{col}(x_0^2, u_0^2)$ and $\text{col}(x_0^3, u_0^3)$ do not have $x_0^i > 0$.*
- *If $F_3^{-1} + s(1 - F_3^{-1}) < b < F_2^{-1} + s(1 - F_2^{-1})$, then both $\text{col}(x_0^1, u_0^1)$ and $\text{col}(x_0^3, u_0^3)$ are locally asymptotically stable and $\text{col}(0, u_0^i)$ are unstable for $i = 1, 2, 3$. $\text{col}(x_0^2, u_0^2)$ does not have $x_0^2 > 0$.*
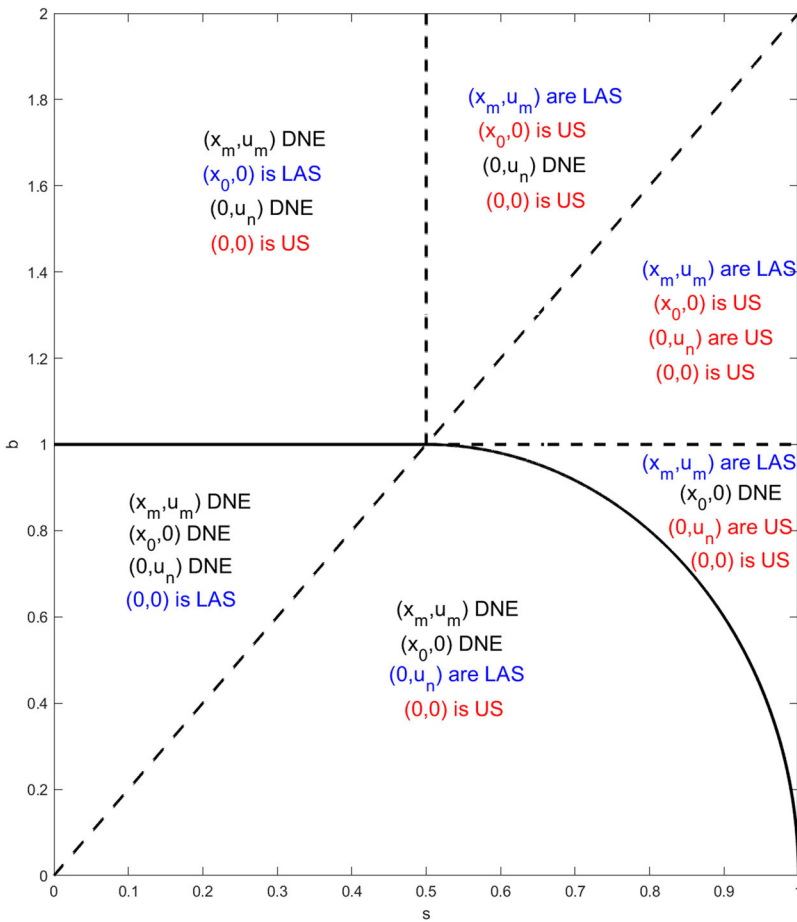
Figure 2. For a parameter pair (b, s) below the solid black line, there are no survival equilibria. Above the solid black line, there exists a survival equilibrium that is (locally asymptotically) stable. LAS (blue) stands for locally asymptotically stable, US (red) stands for unstable and DNE (black) stands for does not exist.

- If $F_2^{-1} + s(1 - F_2^{-1}) < b < b^{\odot}$, then both $\operatorname{col}(x_0^1, u_0^1)$ and $\operatorname{col}(x_0^i, u_0^3)$ are locally asymptotically stable and all of $\operatorname{col}(x_0^2, u_0^2)$ and $\operatorname{col}(0, u_0^i)$ are unstable for $i = 1, 2, 3$.

Proof: See the Appendix. ∎

We note that (H4) can be satisfied by choosing $b^{\odot} > 5$ and $\delta^2 = \min\{0.01, s/7.5\}$. Each subfigure in Figure 4 shows the phase plane for a bullet of Theorem 6.5.

We note that in the model using Equation (18), there exists a locally asymptotically stable survival equilibrium for all $b > 1$. For $b < F_3^{-1} + s(1 - F_3^{-1})$, the only survival equilibrium is $\operatorname{col}(x_0^1, u_0^1) = \operatorname{col}(x_0^1, 0)$, so a zero average PRSP life history strategy develops for smaller b values than a non-zero average PRSP life history strategy. From the expressions of x_0^i in Equation (20), we see that the relationship $x_0^3 < x_0^2 < x_0^1$ holds whenever the respective survival equilibria exist. This has two implications: first is that the stable manifold of
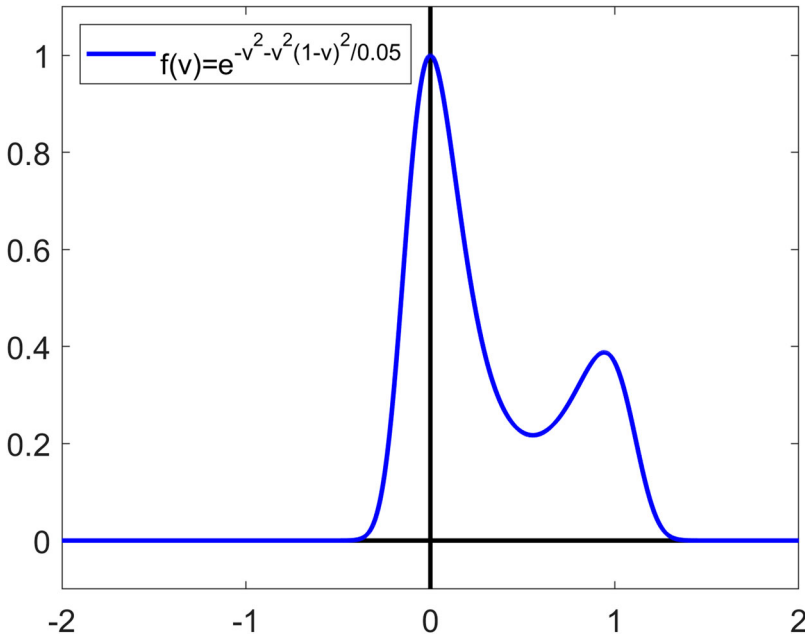
Figure 3. The function $f(v) = \exp(-v^2 - v^2(1-v)^2/0.05)$ has three extrema: a global maximum at (0,1), a local maximum at approximately (0.9436,0.3879), and a local minimum at approximately (0.5564,0.2170).

$\text{col}(x_0^2, u_0^2)$ (or $\text{col}(0, u_0^2)$, if $b < F_2^{-1} + s(1 - F_2^{-1})$) forms a separatrix between the basins of attraction of $\text{col}(x_0^1, u_0^1)$ and $\text{col}(x_0^3, u_0^3)$. Second, in the case when a locally asymptotically stable non-zero average PRSP life history strategy exists, it will have a smaller equilibrium population than the zero average PRSP equilibrium population level. This provides a stark contrast to the results of Theorem 6.4, which uses the same function as Theorem 6.5, except $h(z)$ and $f(v)$ (which are $1 - z^2$ and $\exp(-v^2)$ respectively).

Remark 6.6: We note that if in Equation (18) h was chosen to be a convex function, then the overall dynamics of such a system would be extremely similar to those described in Theorem 6.5. The only difference is that some extinction equilibria $\text{col}(0, u_n)$ would exist, with the number of such equilibria and their existence interval depending on the specific h chosen. Such extinction equilibria will always be unstable (see Table 2), and so the global dynamics will be largely unaffected by their presence.

If instead h is concave, then these dynamics would also include the survival equilibria $\text{col}(x_m, u_m)$ for $s > 1/2$. Further, there exists an interval of s such that, for a sufficiently large b value, 4 survival equilibria of the form $\text{col}(x_m, u_m)$ would exist.

6.2. $\sigma(x) = \beta(x)$

The assumption $\sigma(x) = \beta(x)$ can be biologically interpreted in either of two ways.

From one perspective, we consider β as the density-dependent survival term of newborns that reach maturity. Here, β does not affect the birth rate, just the survivorship of
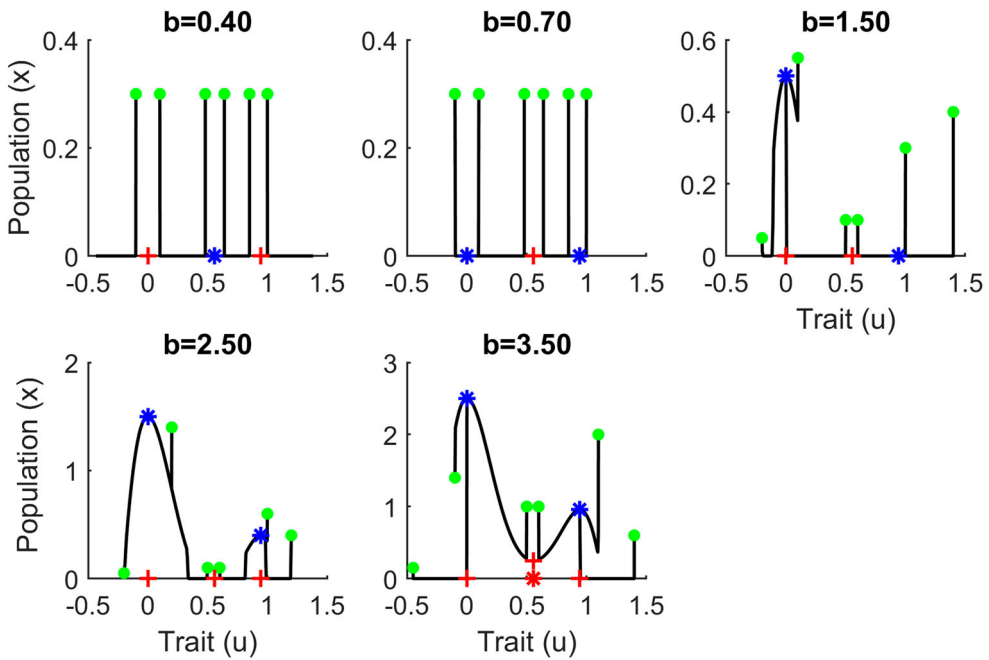
Figure 4. Simulations of the model defined by Equations (1) and (18). Each green dot is an initial condition, with a black line corresponding to its trajectory. A blue star indicates a locally asymptotically stable equilibrium, a red star an unstable node and a red plus a saddle. The value of $s = 0.5$ throughout and the value of b is on top of each subfigure, allowing us to obtain each of the bullets in Theorem 6.5. We find that $F_3^{-1} + s(1 - F_3^{-1}) \approx 1.789$ and $F_2^{-1} + s(1 - F_2^{-1}) \approx 2.8$. We choose $b^\odot = 6$. δ is chosen to be 0.009, which causes the trait (u) dynamics are significantly slower than the population (x) dynamics. Recall that $\delta < 0.01$ must hold to satisfy (H4).

juveniles. Thus $\beta(x) \equiv \sigma(x)$ assumes that density effects newborns and adults in the same way.

From another perspective, we can consider the equality of β and σ to say that density effects apply to birthrates and adult survivorship equally, and that all juveniles survive to adulthood.

No matter our biological perspective, this assumption transforms our system into

$$x(t+1) = \left[f(u(t)) + sh(f(u(t)))\right]\beta(x(t))x(t),$$

$$u(t+1) = u(t) + \delta^2\left[1 + sh'(f(u(t)))\right]\beta(x(t))f'(u(t)).$$

Then our equations for survival equilibria (Equation 4) simplify to

$$\beta(x_e) = \frac{1}{bf(u_e) + sh(f(u_e))}$$

and

$$0 = f'(u_e)\left[b + sh'(f(u_e))\right].$$

(22)

Remark 6.7: From the first equation in Equation (22) and (H1), we have that survival equilibria cannot exist if

$$\frac{1}{bf(u_e(b,s)) + sh(f(u_e(b,s)))} > 1.$$

When considering survival equilibria of the form $\mathrm{col}(x_0, u_0)$, this is equivalent to $b > b_0^*$.

Further, we note that the second equation of (22) is the same as Equation (2). This gives us the following theorem.

Theorem 6.8: *Suppose that $\beta(x) = \sigma(x)$. Then, for any survival equilibria of the form $\mathrm{col}(x_e, u_e)$, there exists an extinction equilibria of the form $\mathrm{col}(0, \hat{u})$ with $\hat{u} = u_e$.*

Corollary 6.9: *Suppose that $\beta(x) = \sigma(x)$ and $b > b_n^M(s)$. Then there are no survival equilibria of the $\mathrm{col}(x_m, u_m)$ type.*

Proof: By Theorem 5.2, we can assume $b_n^M(s) > 1$, which implies that h is concave by Theorem 3.1. By Table 1, there are no equilibria of the form $\mathrm{col}(0, u_n)$ when $b > b_n^M$. The contrapositive of Theorem 6.8 yields the result. ∎

The next theorem provides conditions under which survival equilibria of the form $\mathrm{col}(x_0, u_0)$ exist and are unstable. Without choosing a specific function for β, the stability conditions are somewhat unwieldy.

Theorem 6.10: *Assume (H1)–(H3), that $\sigma(x) \equiv \beta(x)$ and*

$$\lim_{x \to \infty} \beta(x) \le \min_{u_0 : f'(u_0) = 0} [b^{\odot} f(u_0) + sh'(f(u_0))]^{-1}.$$

Consider u_0 such that $f(u_0) = 0$. Then for all $b \in (b_0^*, b^{\odot})$, there exists a unique x_0 that solves the first equation of (22), thus defining a survival equilibrium $\mathrm{col}(x_0, u_0)$.

Further, this equilibrium is unstable if any one of the following hold:

- *$f''(u_0) > 0$ and $b_n^M(s) < 1$,*
- *$f''(u_0) > 0$, $b_n^M(s) > 1$ and $f(u_0) < z^*(s)$,*
- *$f''(u_0) > 0$, $b_n^M(s) > 1$, $f(u_0) \ge z^*(s)$ and $b_0^{\dagger} < b$.*
- *$f''(u_0) < 0$, $b_n^M(s) > 1$, $f(u_0) > z^*(s)$, and $b < b_0^{\dagger}$.*

We note that the condition on β is easily satisfied if $\lim_{x \to \infty} \beta(x) = 0$.

Proof: See the Appendix. ∎

6.2.1. Furthering the example: h is concave

For a more complete example, we choose

$$f(v) = e^{-v^2}, \quad h(z) = 1 - z^2, \quad \text{and} \quad \beta(x) = \sigma(x) = e^{-x}. \tag{23}$$

We find the following extinction equilibria:

$$\begin{pmatrix} 0 \\ u_0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 0 \\ u_n^{\pm} \end{pmatrix} = \begin{pmatrix} 0 \\ \pm\sqrt{\ln\left(\frac{2s}{b}\right)} \end{pmatrix} \tag{24}$$

and the following survival equilibria:

$$\begin{pmatrix} x_0 \\ u_0 \end{pmatrix} = \begin{pmatrix} \ln b \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} x_m \\ u_m^{\pm} \end{pmatrix} = \begin{pmatrix} \ln\left(\frac{b^2 + 4s^2}{4s}\right) \\ \pm\sqrt{\ln\left(\frac{2s}{b}\right)} \end{pmatrix}. \tag{25}$$

Theorem 6.11: *Assume that $b^{\odot} = e^2$, $\delta^2 < (e^2 - 2s)^{-1}$ and suppose that our system is defined using function definitions in (23). For the expressions of the equilibria, see Equations (24) and (25).*

Consider when $s < 1/2$.

- *$b < 2s$ implies that the extinction equilibria $\mathrm{col}(0, u_m^{\pm})$ are both locally asymptotically stable and the extinction equilibrium $\mathrm{col}(0, u_0)$ is unstable. There are no survival equilibria with positive population components.*
- *$2s < b < 1$ implies that $\mathrm{col}(0, u_0)$ is the only equilibrium, is an extinction equilibrium and is locally asymptotically stable.*
- *$1 < b < e^2$ implies that the survival equilibrium $\mathrm{col}(x_0, 0)$ is locally asymptotically stable and the extinction equilibrium $\mathrm{col}(0, u_0)$ is unstable.*

If instead $s > 1/2$, then

- *$b < 2\sqrt{s - s^2}$ implies that the extinction equilibria $\mathrm{col}(0, u_m^{\pm})$ are both locally asymptotically stable and $\mathrm{col}(0, u_0)$ is unstable. There are no survival equilibria.*
- *$2\sqrt{s - s^2} < b < 1$ implies that the survival equilibria $\mathrm{col}(x_m, u_m^{\pm})$ are both locally asymptotically stable, and the extinction equilibria $\mathrm{col}(0, u_n^{\pm})$ and $\mathrm{col}(0, u_0)$ are unstable. $\mathrm{col}(x_0, u_0)$ does not have $x_0 > 0$.*
- *$1 < b < 2s$, then the survival equilibria $\mathrm{col}(x_m, u_m^{\pm})$ are both locally asymptotically stable. The survival equilibrium $\mathrm{col}(x_0, u_0)$ and the extinction equilibria $\mathrm{col}(0, u_n^{\pm})$ are unstable. The extinction equilibrium $\mathrm{col}(0, u_0)$ is an unstable node.*
- *$2s < b < e^2$, then $\mathrm{col}(x_0, u_0)$ is locally asymptotically stable and $\mathrm{col}(0, u_0)$ is unstable. The extinction equilibrium $\mathrm{col}(0, u_n^{\pm})$ do not exist and the survival equilibria $\mathrm{col}(x_m, u_m^{\pm})$ do not have $x_m > 0$.*

Proof: See the Appendix. ∎
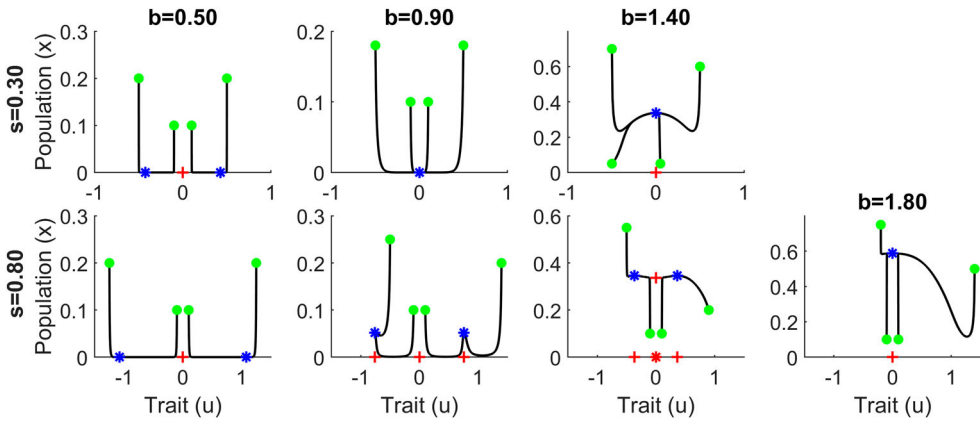
Figure 5. Simulations of the model defined by Equations (1) and (23). Each green dot is an initial condition, with a black line corresponding to its trajectory. A blue star indicates a locally asymptotically stable equilibrium, a red star an unstable node and a red plus a saddle. The value of s is on the left, while the value of b is on top. The top row corresponds to the first three bullets of Theorem 6.11 and the bottom four figures to the final four bullets. When $s = 0.8$, $2\sqrt{s - s^2} = 0.8$ as well. $b^{\odot}$ and δ are chosen to be e^2 and 0.14 respectively.

Remark 6.12: Note that the choice of β (and σ) is from the classical Ricker map, which is known to have chaotic behaviour, and has an initial bifurcation at $b > e^2$, hence our choice of $b^{\odot}$ (which could have been any number greater than 1 if $s < 1/2$ or greater than $2s$ if $s > 1/2$). Our analysis indicates that this may still hold for this evolutionary model as well, as $\lambda_1^{(x_m, u_m)}(b, s)$ passes through -1 as b increases through e^2, which leads to period doubling.

Each subfigure in Figure 5 shows the phase plane for a bullet of Theorem 6.11. Figure 6 shows a parameter map for Theorem 6.11. A stark contrast to the results in Theorem 6.4, we see that for $\max\{1, 2s\} < b < e^2$, the only survival equilibrium has a zero average PRSP life history strategy, i.e. $\mathrm{col}(x_0, 0)$.

In fact, when $\beta(x) = \sigma(x)$ in general (more specifically, independent of our choices in Equation 23), Corollary 6.9 shows that survival equilibria of the form $\mathrm{col}(x_m, u_m)$ (i.e. with $f'(u_m) \neq 0$) will no longer exist when $b > b_n^M$. Thus the only survival equilibrium life history strategies that will be seen for large b values are the critical values of f. An important caveat to this is that stable non-equilibrium dynamics, and perhaps even chaos, may be present in such a system for large b values.

7. Discussion

From our analysis of a basic discrete population model that has Darwinian evolution, we see quite interesting and diverse findings. We proved conditions for existence and stability of all extinction equilibria as well as the conditions for a bifurcation of survival equilibria from an extinction equilibrium. Our examples showed that fairly complex dynamics can arise from a relatively simple, low dimensional evolutionary model.

Our work also showed a basic distinction of overall expectations based on the concavity of h. If h is convex or linear, the life history of all survival equilibria can be determined
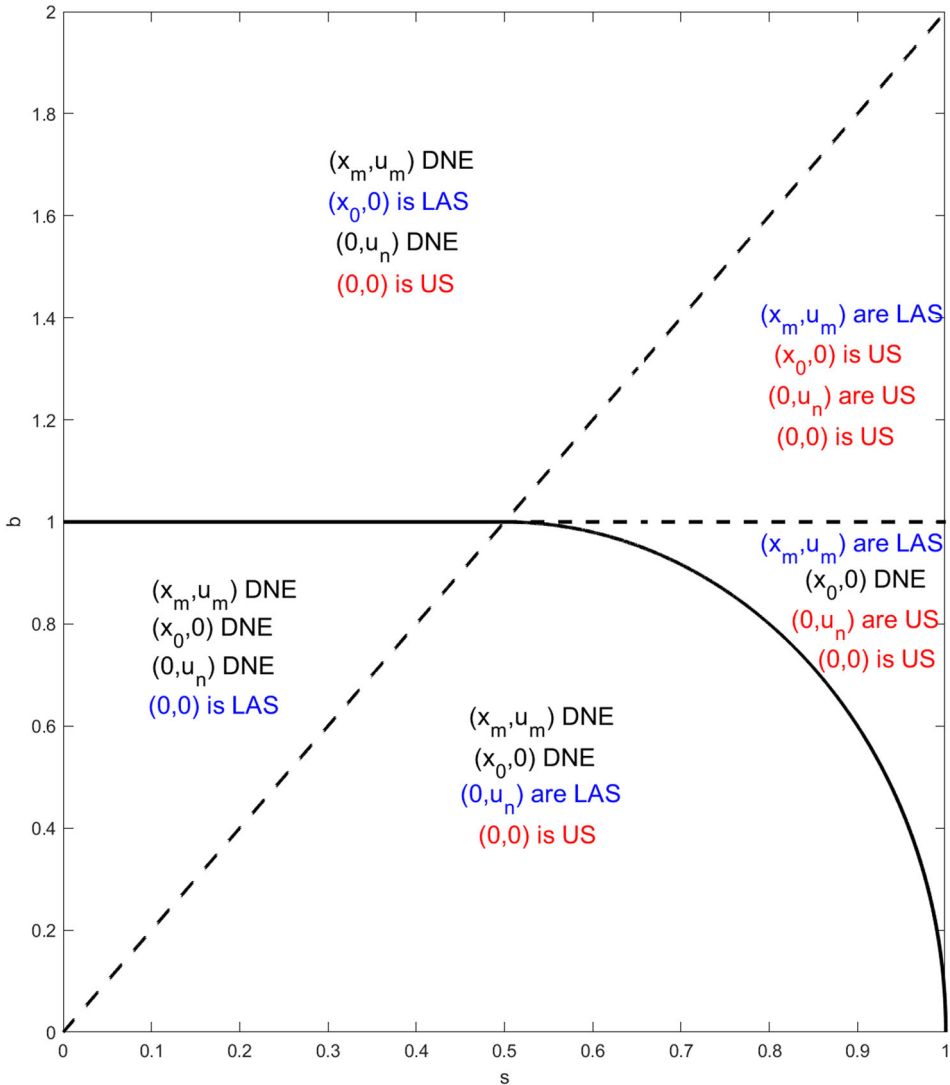
Figure 6. For a parameter pair (b, s) below the solid black line, there are no survival equilibria. Above the solid black line, there always exist an survival equilibrium that is (locally asymptotically) stable. LAS (blue) stands for locally asymptotically stable, US (red) stands for unstable and DNE (black) stands for does not exist.

directly by f (Theorem 5.2). If h is concave and survival is sufficiently large (specifically $s > -h'(1)^{-1}$), then survival equilibria with non-zero PRSP will exist (Corollary 5.3), although we note that they may not exist for a large interval of b values, as seen in Theorem 6.11.

Previous studies using different mathematical techniques show that a concave trade-off function implies an iteroparous life history strategy while a convex trade-off implies that semelparity is the most likely outcome [13,14]. Although we avoid the polarizing terms of 'iteroparity' and 'semelparity', our results align fairly well with the overarching ideas from [13] and [14]. Recall that Corollary 5.3 implies that if h is concave there will be a bifurcation of a survival equilibrium from a *non-zero* average PRSP extinction equilibrium (i.e. 'semelparity'), and that Corollary 5.4 implies that if h is linear or convex then at $b = 1$,

a survival equilibrium will bifurcate from col$(0, 0)$ (i.e. 'iteroparity'). In fact, in our model the general concept follows from a geometric standpoint as well: considering $h(f(v))$ near $v = 0$ (or $f(v) = 1$), a small change in the trait v produces larger changes in survivorship $h(f(v))$ when h is concave than when it is convex. Thus a concave h provides an easier evolutionary route to a higher PRSP (i.e. more iteroparous) life history strategy.

Moreover, [13] and [14] state that using more realistic reproduction and growth curves can generate outcomes with multiple stable strategies, potentially one being semelparous and the other iteroparous. This also matches well with our results, as seen in Theorem 6.5 where the reproduction curve has multiple local maxima, which is a realistic assumption [11], and the long-term dynamics include both a zero and a non-zero PRSP. Interestingly, the dynamics implied by Theorem 6.5 will be relatively unchanged by the shape of h for large values of b (e.g. $b \in (2, e^2)$), though this is under the assumption $\sigma(x) = \beta(x)$.

Even if the functions f, h, β and σ are chosen for mathematical simplicity, however, survival equilibria with non-zero PRSP can exist if h is concave. Importantly, the non-zero PRSP survival equilibria can exist for smaller b values than the zero PRSP survival equilibria, as seen in Theorem 6.4. This implies that a more semelparous life history may be advantageous at low birth rates. In fact, Theorem 3.4 implies that so long as h is not concave, survival equilibria with zero PRSP will exist for smaller b values than any other survival equilibria.

Also, we wish to point out that changes in the maximal survival probability s can cause the existence or lack of survival equilibria with a non-zero PRSP. In particular, suppose that we study a particular species that lives in two distinct, disconnected locations and that only s differs in each location. By applying this model to each location separately, we can obtain results consistent with the second example in the introduction concerning *Misumena vatia*. By Corollary 5.4, if one location has a sufficiently low s, we expect to see a locally asymptotically stable zero average PRSP equilibrium to bifurcate at $b = 1$ and no other equilibria to bifurcate for $b < 1$. If at the other location s were sufficiently large, we would be guaranteed to have a locally asymptotically stable non-zero average PRSP equilibrium to bifurcate at $b = b_n^*(s) < 1$ and no other equilibria to bifurcate for smaller b values.

Though our analysis agrees with previous work, there are still limitations in our work worth keeping in mind. In (H2) we assume that $\partial_i a_j(u, u) = 0$; however this may not be accurate for all species. For example larger individuals may feel less competition for being larger than the typical individual, leading to an non-zero derivative. Indeed [5] considers the dynamics born out of violating this assumption (while also assuming h is linear). Further, it may not be realistic to assume that h'' is of one sign.

Relaxing any of the assumptions in (H1)–(H3) provides an excellent opportunity for future research. As seen in the increased complexity between the original model [4] and ours, there may be a wealth of potential dynamics in such future works.

Acknowledgments

Disclosure statement

ORCID

Alex P. Farrell http://orcid.org/0000-0001-5702-3906

References

[1] J.M. Cushing, *An evolutionary Beverton–Holt model*, in *Theory and Applications of Difference Equations and Discrete Dynamical Systems*, Springer, 2014, pp. 127–141.

[2] J.M. Cushing, *The evolutionary dynamics of a population model with a strong Allee effect*, Math. Biosci. Eng. 12(4) (2015), pp. 643–660.

[3] J.M. Cushing, *Difference equations as models of evolutionary population dynamics*, J. Biol. Dyn. 13(1) (2019), pp. 103–127.

[4] J.M. Cushing, *Discrete time Darwinian dynamics and semelparity versus iteroparity*, Math. Biosci. Eng. 16(4) (2019), pp. 1815–1835.

[5] J.M. Cushing, *A bifurcation theorem for Darwinian matrix models with an application to the evolution of reproductive life history strategies*, J. Biol. Dyn. 17(1) (2020), pp. 1–13.

[6] J. Cushing and S.M. Stump, *Darwinian dynamics of a juvenile–adult model*, Dynamics 30(32) (2013), p. 33.

[7] J.M. Cushing, S.M. Henson, and J.L. Hayward, *An evolutionary game-theoretic model of cannibalism*, Nat. Resour. Model. 28(4) (2015), pp. 497–521.

[8] C. Darwin, *On the origin of species: A facsimile of the first edition*, Harvard University Press, Cambridge, MA, 1964.

[9] P.W. Hughes, *Between semelparity and iteroparity: empirical evidence for a continuum of modes of parity*, Ecol. Evol. 7(20) (2017), pp. 8232–8261.

[10] V. Křivan, *The Lotka–Volterra predator–prey model with foraging–predation risk trade-offs*, Amer. Natur. 170(5) (2007), pp. 771–782.

[11] C.H. Martin and P.C. Wainwright, *Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild*, Science 339(6116) (2013), pp. 208–211.

[12] R. Rael, T.L. Vincent, R.F. Costantino, and J.M. Cushing, *Evolution of corn oil sensitivity in the flour beetle*, in *Advances in Dynamic Game Theory*, Springer, 2007, pp. 367–376.

[13] W.M. Schaffer, *Selection for optimal life histories: the effects of age structure*, Ecology 55(2) (1974), pp. 291–303.

[14] W.M. Schaffer and M.L. Rosenzweig, *Selection for optimal life histories. II: multiple equilibria and the evolution of alternative reproductive strategies*, Ecology 58(1) (1977), pp. 60–72.

[15] T.L. Vincent, J.S. Brown, *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*, Cambridge University Press, Cambridge, England, 2005.

[16] T.L. Vincent and R.A. Gatenby, *An evolutionary model for initiation, promotion, and progression in carcinogenesis*, Int. J. Oncolog. 32(4) (2008), pp. 729–737.

Appendices

Appendix 1. Overview

In the following appendices, we mainly use straightforward eigenvalue analysis.

Using $0 = \partial_v r(x^*, u^*, u^*)$ and Remark 2.1 the Jacobian matrix for System (1) evaluated at a general equilibrium $\mathrm{col}(x^*, u^*)$ simplifies to

$$J(x^*, u^*) = \begin{pmatrix} r(x^*, u^*, u^*) + x\partial_x r(x^*, u^*, u^*) & 0 \\ \delta^2 \partial_{x,v} r(x^*, u^*, u^*) & 1 + \delta^2 \partial_{v,v} r(x^*, u^*, u^*) \end{pmatrix}. \tag{A1}$$

Thus, for any equilibria $\mathrm{col}(x^*, u^*)$, the eigenvalues of the Jacobian matrix are

$$\lambda_1^{(x^*, u^*)}(b, s) := r(x^*, u^*, u^*) + x\partial_x r(x^*, u^*, u^*)$$
$$= bf(u^*)\beta(x^*) + sh(f(u^*))\sigma(x^*) + x^*\big(bf(u^*)\beta'(x^*) + sh(f(u^*))\sigma'(x^*)\big)$$

$$\lambda_2^{(x^*,u^*)}(b,s) := 1 + \delta^2 \partial_{v,v} r(x^*, u^*, u^*)$$

$$= 1 + \delta^2 \Big[f''(u^*)\big(b\beta(x^*) + s\sigma(x^*)h'(f(u^*))\big) + s\sigma(x^*)h''(f(u^*))[f'(u^*)]^2 \Big]. \quad \text{(A2)}$$

Appendix 2. Some lemmas concerning Φ

From Equation (11), we note the following properties of Φ:

- $\Phi(0) = 1 < 1/s$.
- $\Phi(1) = h'(1)$.
- $\Phi'(z) = -zh''(z)$.

From this information, we can make a few useful lemmas.

Lemma A.1: *If h is convex or linear, then $\Phi(z) < 1/s$ for all $z \in (0,1)$.*

Proof: Suppose that h is linear. Then $\Phi(z) \equiv 1 < 1/s$.
   Suppose that h is convex. Then Φ is strictly decreasing and $\Phi(z) \leq \Phi(0) = 1 < 1/s$. ∎

Lemma A.2: *If h in concave, then there is a unique solution to*

$$\Phi(z^*(s)) = 1/s,$$

with $z^*(s) \in (0,1)$, if and only if $b_n^M(s) > 1$.

Proof: We see that Φ is strictly increasing with $\Phi(0) = 1 < 1/s$. Thus there exists a unique solution to $\Phi(z) = 1/s$, with $z \in (0,1)$ if any only if $\Phi(1) = -h'(1) > 1/s$. From Equation (10), we see that this is equivalent to $b_n^M(s) > 1$. ∎

Appendix 3. Table tab2 and related lemmas

Row A1

Considerations of λ_1: For $(0, u_0)$, the first equation of (A2) yields

$$\lambda_1^{(0,u_0)}(b,s) := bf(u_0) + sh(f(u_0)). \quad \text{(A3)}$$

By design, we have defined b_0^* in Equation (eqaaa) such that $\lambda_1^{(0,u_0)}(b_0^*,s) = 1$. By (H1) and (H3), we can conclude that $0 < sh(f(u_0)) < 1$, so this b_0^* is unique and positive. Clearly $\lambda_1^{(0,u_0)}(b,s)$ is a linear (increasing) function of b. Therefore, since $\lambda_1^{(0,u_0)}(b_0^*(s),s) = 1$, $0 < \lambda_1^{(0,u_0)}(b,s) < 1$ for $b < b_0^*(s)$, and $\lambda_1^{(0,u_0)}(b,s) > 1$ when $b_0^*(s) < b$.
   Considerations of λ_2:
   For $(0, u_0)$, the second equation of (A2) yields

$$\lambda_2^{(0,u_0)}(b,s) := 1 + \delta^2 f''(u_0)(b + sh'(f(u_0))).$$

For each u_0 and a given s, we have defined Equation (8) and define

$$b_0^\delta(s) := \frac{-2}{\delta^2 f''(u_0)} - sh'(f(u_0)) = \frac{-2}{\delta^2 f''(u_0)} + b_0^\dagger(s), \quad \text{(A4)}$$

so that $\lambda_2^{(0,u_0)}(b_0^\dagger(s),s) = 1$ and $\lambda_2^{(0,u_0)}(b_0^\delta(s),s) = -1$. Thus, since $\lambda_2^{(0,u_0)}(b,s)$ is linear in b, we know that if b is between $b_0^\dagger(s)$ and $b_0^\delta(s)$, then $|\lambda_2^{(0,u_0)}(b,s)| < 1$.

   By (H4), we know that $b_0^\delta(s) > b^\odot$, thus $|\lambda_2^{(0,u_0)}(b,s)| < 1$ when $b \in (b_0^\dagger(s), b^\odot)$ and $|\lambda_2^{(0,u_0)}(b,s)| > 1$ when $b < b_0^\dagger(s)$. Note that it is possible for $b_0^\dagger$ to be negative, in particular when h is increasing, so $b < b_0^\dagger(s)$ may not be possible for all models.

Row A2

Considerations of λ_1: The results for Row A1 hold here. *Considerations of* λ_2: Equations (8) and (A4) have the same significance here as they did in A.1. Now (H4) implies $b_0^\delta(s) < 0$, so $|\lambda_2^{(0,u_0)}(b,s)| < 1$ when $b \in (0, b_0^\dagger(s))$ and $|\lambda_2^{(0,u_0)}(b,s)| > 1$ when $b > b_0^\dagger(s)$.

Row B1 and Part of Lemma 3.3

Considerations of λ_1: For $(0, u_n)$ type equilibria, we have

$$\lambda_1^{(0,u_n)}(b,s) := bf(u_n(b,s)) + sh(f(u_n(b,s))).$$

Assume that s is given. We make the following, implicit, definition of $b_n^*(s)$:

$$b_n^*(s) := \frac{1 - sh(f(u_n(b_n^*,s)))}{f(u_n(b_n^*,s))}, \tag{A5}$$

which defines $b_n^*(s)$ such that $\lambda_1(b_n^*(s), s) = 1$. We note that $b_n^*(s)$ has a non-implicit definition (Equation 13) that will be derived from Equation (A5) in the proof of Lemma 3.3. From Equation (A5) alone, it is not clear if or when $b_n^*(s)$ exists, or, given that it does exist, if it is unique. These questions are answered in the proof of Lemma 3.3.

proof of Lemma 3.3: Using the definition of u_n (Equation 3), we can rewrite equation (A5) as

$$- sf(u_n(b_n^*,s))h'(f(u_n(b_n^*,s))) = 1 - sh(f(u_n(b_n^*,s))), \tag{A6}$$

which is equivalent to solving $\Phi(f(u_n(b_n^*,s))) = 1/s$. Note that we need not consider $f(u_n(b_n^*,s)) = 0$ by (H2) or $f(u_n(b_n^*,s)) = 1$ by Remark 2.3. Combining Lemmas A.1 and Lemma A.2 implies that such a solution exists if and only if h is concave and $b_n^M(s) > 1$. Using $z^*(s) = f(u_n(b_n^*,s))$ and Equation (3), we obtain Equation (13).

Focusing on $z^*(s)$ as a function of s, and we see by implicit differentiation of $\Phi(z^*(s)) = 1/s$ that

$$d_s z^*(s) = \frac{1}{z^*(s)h''(z^*(s))s^2} < 0,$$

so z^* is a decreasing function of s. Finally, we note that when $b_n^M(s) = 1$ (i.e. $s = -(h'(1))^{-1}$), $\Phi(1) = 1/s$. Thus we can say that if $b_n^M > 1$, then b_n^* exists and $0 \le b_n^m < b_n^* < 1 < b_n^M$. ■

We see from Equation (A3) that

$$\begin{aligned}
\partial_b \lambda_1^{(0,u_n)}(b,s) &= f(u_n(b,s)) + f'(u_n(b,s))\big[b + sh'(f(u_n(b,s)))\big]\partial_b[u_n(b,s)] \\
&= f(u_n(b,s)) > 0,
\end{aligned} \tag{A7}$$

so $\lambda_1^{(0,u_n)}(b,s)$ is an increasing function of b. Lemma 3.3 shows that $\lambda_1^{(0,u_n)}(b_n^*(s),s) = 1$, and so $\lambda_1^{(0,u_n)}(b,s) < 1$ if $b < b_n^*(s)$. Similarly, $\lambda_1^{(0,u_n)}(b,s) > 1$ if $b > b_n^*(s)$.

Considerations of λ_2: When considering col$(0, u_n)$, we have

$$\lambda_2^{(0,u_n)}(b,s) := 1 + (\delta f'(u_n(b,s)))^2 sh''(f(u_n(b,s))),$$

which is less than 1 since h is concave. Assumption (H4) implies that $\lambda_2^{(0,u_n)}(b,s) > -1$ for all $(b,s) \in (0, b^\circ) \times (0,1)$. Thus $|\lambda_2^{(0,u_n)}(b,s)| < 1$ whenever col$(0, u_n)$ exists.

Row B2

Considerations of λ_1: Recall that $\lambda_1^{(0,u_n)}(b,s) := bf(u_n(b,s)) + sh(f(u_n(b,s)))$.

By Equation (A7), Theorem 3.1 and Lemma 3.3, we know that $0 < \lambda_1^{(0,u_n)}(b,s) < 1$ whenever col$(0, u_n)$ exists (i.e. for all $s \in (0,1)$ and $b \in (b_n^m(s), b_n^M(s))$).

Considerations of λ_2: Recall that $\lambda_2^{(0,u_n)}(b,s) := 1 + (\delta f'(u_n(b,s)))^2 sh''(f(u_n(b,s)))$. Since h is convex, $\lambda_2^{(0,u_n)}(b,s) \geq 1$ for all $b,s \geq 0$.

Theorem 3.4

proof of Theorem 3.4: We first consider b_0^* as a function of $f \in (0,1]$ and note that

$$\partial_f b_0^* = \partial_f \frac{1 - sh(f)}{f} = \frac{1}{sf^2}[\Phi(f) - 1/s].$$

Thus by Lemma 3.3 we know that if $b_n^M < 1$ then $\Phi(f(u_0)) - 1/s < 0$. Therefore $\partial_{f(u_0)} b_0^*$ is always negative, so the minimum value of b_0^* occurs when $f(u_0) = 1$. By (H2), this occurs for col$(0,0)$. We note that this occurs for all u_0 such that $f(u_0) = 1$, so this may not be unique.

If h is concave and $b_n^M > 1$, then $\Phi(f(u_0)) - 1/s > 0$ for $f(u_0) > z^*(s)$. This implies that there exists some $\omega \in (0, z^*(s))$ and $\psi \in (-\infty, \infty)$ such that $b_0^* = 1$ for an equilibrium col$(0, \psi)$ with $f(\psi) = \omega$. Thus for any equilibria col$(0, u_0)$ with $f(u_0) \in (\omega, 1)$, $b_0^* < 1$. ∎

Lemma 3.5

We note that it is possible for $b_0^*(s) \leq b_0^\dagger(s)$. Using their definitions, Equations (eqaaa) and (8), the inequality is equivalent to

$$1/s \leq h(f(u_0)) - f(u_0)h'(f(u_0)).$$

The right-hand side of this equation is $\Phi(f(u_0))$ from Equation (11). If Φ is strictly increasing, then Lemma 3.3 tells us when $\Phi(z) = 1/s$, providing the following result:

Lemma A.3: *Suppose that $b_n^M(s) < 1$. Then by Lemma 3.3, $\Phi(z) < 1/s$ for all $z \in (0,1)$, i.e. $0 > h(f(u_0)) - f(u_0)h'(f(u_0)) - 1/s$ for all u_0. This is equivalent to $b_0^\dagger(s) < b^*(s)$.*

Suppose that $b_n^M(s) > 1$. Then by Lemma 3.3, $\Phi(z^*(s)) = 1/s$. By Theorem 3.4 and Lemma A.2, Φ is increasing, $\Phi(z) \geq 1/s$ for all $z \geq z^*(s)$ and $\Phi(z) < 1/s$ for all $z < z^*(s)$. The remaining conclusions follow from this.

Appendix 4. Bifurcation and basic analysis of survival equilibria

To explore bifurcations of survival equilibria from extinction equilibria of the form col$(0, u_c(b,s))$, we consider the following transformed system:

$$
\begin{aligned}
x(t+1) &= r(x(t), \hat{u}(t) + u_c(b,s), \hat{u}(t) + u_c(b,s))x(t), \\
\hat{u}(t+1) &= \hat{u}(t) + \delta^2 \partial_v r(x(t), \hat{u}(t) + u_c(b,s), \hat{u}(t) + u_c(b,s)),
\end{aligned}
\tag{A8}
$$

where $\hat{u}(t) = u(t) - u_c(b,s)$. Now our transformed system has an equilibrium at col$(0,0)$ for all values of b that the equilibrium col$(0, u_c(b,s))$ exists.

proof of Theorem 5.1: WLOG, via the transformed system, we consider the extinction equilibrium col$(0,0)$ of System A8.

To prove the existence of a bifurcating equilibrium, we seek to apply Theorem 2 from [5] to the transformed system (A8), and so we check its hypotheses. We choose b (equivalently μ in [5]) as our bifurcation parameter, so $\hat{b}$ is equivalent to μ_0. We also choose Ω_μ to be an open neighbourhood of $\hat{b}$ such that col$(0, u_c(b,s))$ exists for all $b \in \Omega_\mu$.

(A1): By Remark 2.1, we have

$$\nabla_u p_{ij}(\mu, 0, u, v) = \partial_u r(0, v, u) = 0.$$

(A2): Here $M = \delta^2$ is a 1×1 matrix that is symmetric, positive semi-definite, diagonally dominant, and non-singular.

(A3): Note that, by (H2)

$$\partial_v r(0, u_c(\hat{b}, s), u_c(\hat{b}, s)) = f'(u_c(\hat{b}, s))(b + sh'(f(u_c(\hat{b}, s)))).$$

By Equation (2), this is zero.

(A4): We see (removing the arguments of $u_c(\hat{b}, s)$ for space and noting that $H(\mu, \hat{0}, \hat{u}_0, \hat{u}_0)$ is $H(b, 0, u_0, u_0)$) that at $b = \hat{b}$,

$$H(\hat{b}, 0, u_0, u_0) = \partial_{v,v} r(0, u_c, u_c) = f''(u_c)\big(\hat{b} + sh'(f(u_c))\big) + sh''(f(u_c))[f'(u_c)]^2. \quad \text{(A9)}$$

We need to show that H is non-singular, which, in this case, is equivalent to $H \neq 0$. We split the analysis of this case into $\text{col}(0, u_0)$ and $\text{col}(0, u_n)$ type equilibria.

$\text{col}(0, u_0)$ type equilibria: Here $f'(u_0) = 0$, so by (H2) $f''(u_0) \neq 0$. Further, by our hypothesis, we have $\hat{b} + sh'(f(u_c(b, s))) \neq 0$. This shows that $H \neq 0$.

$\text{col}(0, u_n)$ type equilibria: Here we have $\hat{b} + h'(f(u_c(b, s))) = 0$ and by our hypotheses we also have $f'(u_n) \neq 0$. Finally, we note that if $h''(x)$ is zero, then $h'(f(u_c(b, s))) = -1$ for all $u_c(b, s)$. Notably, this holds for $u_c(b, s) = 0$, however $f'(0) = 0$, contradicting our hypothesis. Thus we do not consider when $h''(x) = 0$, and we can see that $H \neq 0$.

Thus, since we are not considering non-hyperbolic equilibria, we know that H is non-singular.

(A5): We see that, by (H2),

$$\partial_b r(0, u_c(b, s), u_c(b, s)) = f(u_c(b, s)) + f'(u_c(b, s))\partial_b u_c(b, s)[b + sh'(f(u_c(b, s)))] = f(u_c(b, s)),$$

which, when viewed as a 1×1 matrix, has left and right eigenvectors $\tilde{w}_L^T = \tilde{w}_R = 1$. Thus, by (H2), the quantity $d := \tilde{w}_L^T \partial_\mu P(\mu_0, 0, 0, 0)\tilde{w}_R = f(u_c(b, s)) > 0$.

We now calculate $\kappa = -\tilde{w}_L^T[\nabla_x r(0, u_c(b, s), u_c(b, s))\tilde{w}_R]\tilde{w}_R$ at $b = \hat{b}$.

$$\begin{aligned}
\kappa &= -\tilde{w}_L^T[\nabla_x r(0, u_c(b, s), u_c(b, s))\tilde{w}_R]\tilde{w}_R \\
&= -\partial_x r(0, u_c(b, s), u_c(b, s)) \\
&= -\hat{b}f(u_c(b, s))\beta'(0) - sh(f(u_c(b, s)))\sigma'(0).
\end{aligned}$$

By (H1) κ is positive.

Now we can apply Theorem 2 from [5] with $d > 0$ and $\kappa > 0$, which proves that there is a bifurcation of an equilibrium with positive population from the extinction equilibrium, and this bifurcation is forward.

To show the stability of the bifurcating equilibrium, we now apply Theorem 3 from [5]. We first show that the matrix $P(\mu_0, 0, u_0, u_0) = r(0, u_c, u_c)$ is primitive at $b = \hat{b}$. This clearly holds, since $r(0, u_c, u_c) = 1$ when $b = \hat{b}$.

From Equations (A2) and (A9), we can see that

$$\lambda_2^{(0, u_c)}(\hat{b}, s) = 1 + \delta^2 H(b, 0, u_0, u_0).$$

Note that (H4) forces δ to be small enough to ensure that $\lambda_2^{(0, u_c)}(\hat{b}, s) > -1$. Thus either $\lambda_2^{(0, u_c)}(\hat{b}, s) \in (-1, 1)$ or $\lambda_2^{(0, u_c)}(\hat{b}, s) > 1$, depending on the sign of $H(b, 0, u_0, u_0)$. Due to this dichotomy, $\lambda_2^{(0, u_c)}(\hat{b}, s) > 1$ is equivalent to $|\lambda_2^{(0, u_c)}(\hat{b}, s)| > 1$. Note that this shows that our δ (equivalently σ in [5]) is 'sufficiently small' to apply Lemma 2 in [5], as this is equivalent to our assumption (H4). Therefore $H(b, 0, u_0, u_0) < 0$ (i.e. H is negative definite) if and only if $|\lambda_2^{(0, u_c)}(\hat{b}, s)| < 1$. ∎

Proof of Theorem 5.2: Suppose $b_n^M(s) < 1$. Then by Remark 2.1 and Lemma 3.3 we have

$$\Phi(f(u_e)) < \frac{1}{s} \leq \frac{1}{s\sigma(x_e)}.$$

However the bracketed portion of Equation (6) is equivalent to $1 - s\sigma(x_e)\Phi(f(u_e))$. Therefore, there are no solutions to Equation (6).

Suppose $b_n^M(s) > 1$. Then by Lemma 3.3, $\lambda_1^{(0,u_n)}(b_n^*(s), s) = 1$, and so we can apply Theorem 5.1 to show that a survival equilibrium of the form $\mathrm{col}(x_m, u_m)$ bifurcates from an extinction equilibrium of the form $\mathrm{col}(0, u_n)$. ∎

Proof of Theorem 5.5: Note that the existence of a survival equilibrium $\mathrm{col}(x_m, u_m)$ implies that h is concave by Theorem 5.2. Since h is concave, Appendix A implies that $\Phi(z)$ is strictly increasing.

Since σ is decreasing and $\sigma(0) = 1$,

$$\Phi(f(u_m)) = \frac{1}{s\sigma(x_m)} \geq \frac{1}{s\sigma(0)} = \frac{1}{s} = \Phi(z^*(s)).$$

Thus, since Φ is strictly increasing, $f(u_m) \geq z^*(s)$. ∎

Appendix 5. Examples

A.1 $\sigma(x) \equiv 1$

Proof of Theorem 6.1: For general survival equilibria with $f'(u_e) = 0$, we see (using Equations 5 and A2)

$$\lambda_1^{(x_0,u_0)}(b, s) := 1 + x_0 b f(u_0)\beta'(x_0),$$

$$\lambda_2^{(x_0,u_0)}(b, s) = 1 + \delta^2 \frac{f''(u_0)}{f(u_0)}\left[1 - s\Phi(f(u_0))\right].$$

Suppose $b_n^M < 1$: By Lemma 3.3, we know that $b_n^M < 1$ implies $0 < 1 - s\Phi(z)$ for all $z \in (0, 1)$. Thus if $f''(u_0) > 0$, then so $\lambda_2^{(x_0,u_0)}(b, s)$ is greater than 1 and $\mathrm{col}(x_0, 0)$ is unstable.

Suppose $b_n^M > 1$: Now, by Lemma 3.3, we know that $b_n^M < 1$ implies $1 - s\Phi(z) > 0$ if $z \geq z^*(s)$. Thus if $f''(u_0) < 0$ and $f(u_0) \geq z^*(s)$, then $\lambda_2^{(x_0,u_0)}(b, s)$ is positive. ∎

Proof of Theorem 6.3: By our assumption on f, $f'(u_e) = 0$ is solved only by $u_e = 0$. Corollary 4.2 implies all of the results concerning $\mathrm{col}(x_0, 0)$.

Consider a survival equilibrium $\mathrm{col}(x_m, u_m)$. From Lemma 3.3, we have $b_n^*(s) = -sh'(\Phi^{-1}(1/s))$ < 1. From Equation (4) and after some rearranging, an interior equilibrium can be found by solving

$$\Phi(f(u_m)) = 1/s \quad \text{and} \quad \beta(x_m) = \frac{-sh'(f(u_m))}{b}.$$

Note that $\beta(x_m) = \frac{b_n^*(s)}{b}$, which has a unique solution if and only if $b_n^*(s) < b < b^{\odot}$ since β is strictly decreasing and

$$b^{\odot} < \frac{b_n^*(s)}{\lim_{x \to \infty}(\beta(x))}.$$

This also implies that there are no survival equilibria for $b < b_n^*(s)$. Next, we note the following inequalities, which hold for all $x > 0$:

$$\frac{2}{1 + b_n^*(s)} > -x\frac{\beta'(x)}{\beta(x)}.$$

In particular, it holds for and x_m. Using $f(u_m) = \Phi^{-1}(1/s) = z^*$ and Equation (13), this inequality is equivalent to

$$-1 < 1 + x_m\frac{\beta'(x_m)}{\beta(x_m)}(1 - sh'(f(u_m))).$$

By Equation (5), the right-hand side is equal to $1 + bx_m f(u_m)\beta'(x_m) = \lambda_1^{(x_m,u_m)}(b, s)$. The above combined with β being strictly decreasing yields $|\lambda_1^{(x_m,u_m)}(b, s)| < 1$. (H4) ensures that $|\lambda_2^{(x_m,u_m)}(b, s)| < 1$. Therefore, $\mathrm{col}(x_m, u_m)$ is stable whenever it exists ∎

An Example: h is Concave

Proof of Theorem 6.4: It is easily verifiable that the functions for this model satisfy (H1)–(H3). The local stability of extinction equilibria can be found in Table 2, so we only need to show the stability results for the survival equilibria. Here, our key quantities are $b_0^\dagger(s) = b_n^M(s) = 2s$, $b_0^*(s) = 1$, $b_n^m = 0$ and, if $s > 1/2$, $b_n^*(s) = s\sqrt{s - s^2}$ (note that the key quantities pertaining to col$(0, u_n^\pm)$ are the same for both of them). We also note that our restrictions on $b^\odot$ and δ satisfy (H4).

Assume $s < 1/2$. Then col(x_0, u_0) will exist for $b > 1$, so we assume that this holds. No other survival equilibria exist for $s < 1/2$. From Equation (A2), we find

$$\lambda_1^{(x_0, u_0)}(b, s) = \frac{1}{b},$$

$$\lambda_2^{(x_0, u_0)}(b, s) = 1 - 2\delta^2 [1 - 2s].$$

Clearly $0 < \lambda_1^{(x_0, u_0)}(b, s)$ and by (H4) $\lambda_2^{(x_0, u_0)}(b, s) < 1$. Further, for $b > 1$, $\lambda_1^{(x_0, u_0)}(b, s) < 1$. (H4) also ensures that $\delta^2 < \frac{-2f(0)}{f''(0)} = 1$, which implies that $1 - 2\delta^2[1 - 2s]$ is bounded below by -1. Thus we have local asymptotic stability of col(x_0, u_0) in this case.

Assume $1/2 < s$. We can see from our above considerations that $\lambda_2^{(x_0, u_0)}(b, s) < -1$ for $s > 1/2$, so col(x_0, u_0) is unstable whenever it exists.

For col(x_m, u_m), we can see from Equation (A2) that

$$\lambda_2^{(x_m, u_m)}(b, s) = 1 + [\delta f'(u_m)]^2 sh''(f(u_m)) < 1,$$

and by (H4) we also have $\lambda_2^{(x_m, u_m)}(b, s) > -1$. Recall that $\lambda_1^{(x_m, u_m)}(2\sqrt{s - s^2}, s) = 1$. Then we see

$$\lim_{b \to \infty} \lambda_1^{(x_m, u_m)}(b, s) = 2s - 1 > -1 \quad \text{and} \quad \frac{\partial}{\partial b} \lambda_1^{(x_m, u_m)}(b, s) = -\frac{4(1 - s)}{b^2} < 0,$$

so such equilibria will be always be stable whenever they exist. ∎

Another Example: h is Linear

Proof of Theorem 6.5: It is easily verifiable that the functions for this model satisfy (H1)–(H3). Now we have multiple equilibria of the form col$(0, u_0)$ and col(x_0, u_0), so we must be careful with our key quantities. Because h is linear, $h'(z) = -1$ for all z, thus $b_0^\dagger = s$ for all col$(0, u_0)$. We can also see that for col$(0, u_0^1)$, $b_0^*(s) = 1$, for col$(0, u_0^2)$, $b_0^*(s) = \frac{1-s}{0.2170} + s$, and for col$(0, u_0^3)$, $b_0^*(s) = \frac{1-s}{0.3879} + s$. From this, we can use Table 2 to find the stability of each of the survival equilibria.

Now we only need to show the stability of survival equilibria. We begin by using Equation (A10):

$$\lambda_1^{(x_0^i, u_0^i)}(b, s) := 1 - \frac{x_0 b f(u_0^i)}{(1 + x_0)^2},$$

$$\lambda_2^{(x_0^i, u_0^i)}(b, s) = 1 + \delta^2 \frac{f''(u_0)}{f(u_0^i)} \left[1 - s\Phi(f(u_0^i)) \right].$$

Clearly $\lambda_1^{(x_0^i, u_0^i)}(b, s) < 1$ for all b. For each of col(x_0^i, u_0^i) we note that x_0^i is a linear function of b, i.e. $x_0^i = \alpha_i(s)b - 1$, where

$$\alpha_i(s) = \frac{f(u_0^i)}{1 - s(1 - f(u_0^i))},$$

so we can rewrite λ_1 as

$$\lambda_1^{(x_0^i, u_0^i)}(b, s) := 1 - \frac{(a_i(s)b - 1)f(u_0^i)}{a_i(s)^2 b}.$$

We can see that near their respective bifurcation points, $x_0^i \approx 0$, so $\lambda_1^{(x_0^i, u_0^i)}(b_0^*(s), s) \approx 1$. We also note that

$$\lim_{b \to \infty} \lambda_1^{(x_0^i, u_0^i)}(b, s) = 1 - \frac{f(u_0^i)}{a_i(s)} = s(1 - f(u_0^i)) > 0.$$

Finally, we note that

$$\frac{\partial}{\partial b} \lambda_1^{(x_0^i, u_0^i)}(b, s) = -\frac{f(u_0^i)}{a_i(s)^2 b^2} < 0,$$

thus, since $\lambda_1^{(x_0^i, u_0^i)}(b, s)$ is monotonically decreasing, we know that

$$0 < \lambda_1^{(x_0^i, u_0^i)}(b, s) < 1$$

for all b and s such that $\mathrm{col}(x_0^i, u_0^i)$ exists. Since h is linear, we see that $\Phi(f(u_0^i)) = 1$, simplifying the second equation to:

$$\lambda_2^{(x_0^i, u_0^i)}(b, s) = 1 + \delta^2 \frac{f''(u_0^i)}{f(u_0^i)}(1 - s).$$

Further, by (H4) and since $s \in (0, 1)$, we can conclude that $\lambda_2^{(x_0^i, u_0^i)}(b, s) > -1$ for $i = 1, 2, 3$. Thus only the sign of $f''(u_0^i)$ will determine if $\lambda_2^{(x_0^i, u_0^i)}(b, s)$ is greater or less than 1.

For $\mathrm{col}(x_0^1, u_0^1)$: Since $f''(u_0^1) < 0$, $\mathrm{col}(x_0^1, u_0^1)$ exists and is locally asymptotically stable for $b > 1$.

For $\mathrm{col}(x_0^2, u_0^2)$: Here, since $f''(u_0^2) > 0$, $\mathrm{col}(x_0^2, u_0^2)$ exists and is unstable for $b > F_2^{-1} + s(1 - F_2^{-1})$.

For $\mathrm{col}(x_0^3, u_0^3)$: Here, since $f''(u_0^3) < 0$, $\mathrm{col}(x_0^3, u_0^3)$ exists and is locally asymptotically stable for $b > F_3^{-1} + s(1 - F_3^{-1})$. ∎

A.2　$\sigma(x) = \beta(x)$

Using Equation (22) with Equation (A2), we have

$$\lambda_1^{(x_0, u_0)}(b, s) := 1 + x_0 \frac{\beta'(x_0)}{\beta(x_0)}$$
$$\lambda_2^{(x_0, u_0)}(b, s) := 1 + \delta^2 \beta(x_0) f''(u_0) \Big[b + sh'(f(u_0)) \Big] \tag{A10}$$

and

$$\lambda_1^{(x_m, u_m)}(b, s) := 1 + x_m \frac{\beta'(x_m)}{\beta(x_m)}$$
$$\lambda_2^{(x_m, u_m)}(b, s) := 1 + [\delta f'(u_m)]^2 \beta(x_m) sh''(f(u_m)). \tag{A11}$$

Proof of Theorem 6.10: From Remark 6.7, such an equilibrium can only exist if $b > b_0^*$. Combined with the hypothesis on β, we have that there is a solution to Equation (22) for all $b \in (b_0^*, b^\odot)$.

From the second equation of (A10), we have

$$\lambda_2^{(x_0, u_0)}(b, s) = 1 + \delta^2 \beta(x_0) f''(u_0) \Big[b + sh'(f(u_0)) \Big].$$

We will have $\lambda_2^{(x_0, u_0)}(b, s) > 1$ if and only if $f''(u_0)[b + sh'(f(u_0))] > 0$. Equivalently, we can write this as $f''(u_0)[b + b_0^\dagger] > 0$.

Suppose $f''(u_0) > 0$. Then so long as $b > b_0^\dagger$, $\lambda_2^{(x_0, u_0)}(b, s) > 1$. By Lemma 3.5, we can see when $b_0^\dagger < b_0^*$, which implies that $\mathrm{col}(x_0, u_0)$ is unstable. If Lemma 3.5 would imply $b_0^\dagger < b_0^*$, then we enforce the condition directly.

Similarly we find the conditions on $f''(u_0) < 0$. ∎

An Example: h is Concave

Proof of Theorem 6.11: It is easily verifiable that the functions for this model satisfy (H1)–(H3).

The key quantities are $b_n^M(s) = b_0^\dagger(s) = 2s, b_0^*(s) = 1$, and $b_n^m(s) = 0$, thus, since $b^\odot = e^2 > 1$ and $\delta^2 < (e^2 - 2s)^{-1} = \frac{1}{\max\{e^2 - 2s, 1, 4e^{-1}\}}$ satisfies (H4).

The only $\mathrm{col}(0, u_0)$ equilibrium of this system is $\mathrm{col}(0, 0)$, which has $b_0^\dagger = b_n^M$ and $b_0^* = 1$. The $\mathrm{col}(0, u_n)$ equilibria have $b_n^m = 0, b_n^M = 2s$ and, if $s > 1/2, b_0^* = 2\sqrt{s - s^2}$. In all cases, the local stability of the extinction equilibria can be found in Table 2. Thus we only need to prove the results for interior equilibria.

Note that $\mathrm{col}(x_0, u_0) = \mathrm{col}(x_0, 0)$ exists for $b > 1$. From Equations (A10), we see

$$\lambda_1^{(x_0, u_0)}(b, s) := 1 - \ln(b),$$

$$\lambda_2^{(x_0, u_0)}(b, s) := 1 + \delta^2 f''(u_0)\left[1 - 2s/b\right].$$

In general, $\lambda_1^{(x_0, u_0)}(b, s) < 1$. We can also see that $\lambda_1^{(x_0, u_0)}(b, s) > -1$ if and only if $b < e^2$.

Suppose that $s < 1/2$, and assume that $b > 1$. By (H4) we have

$$\frac{-2f(0)}{\delta^2 f''(0)} > 1 \iff -1 < 1 + \delta^2 f''(0),$$

and $1 + \delta^2 f''(0) < 1 + \delta^2 f''(0)[1 - 2s/b]$. Thus $|\lambda_2^{(x_0, u_0)}(b, s)| < 1$.

From the above, we know that $|\lambda_1^{(x_0, u_0)}(b, s)| < 1$.

Suppose that $1/2 < s$. If $b \in (2\sqrt{s - s^2}, 2s)$, then $\mathrm{col}(x_m, u_m^\pm)$ exist. Considering Equation (A11), we have

$$\lambda_1^{(x_m, u_m)}(b, s) := 1 - \ln\left(\frac{b^2 + 4s^2}{4s}\right)$$

$$\lambda_2^{(x_m, u_m)}(b, s) := 1 - [\delta f'(u_m)]^2 \frac{8s^2}{b^2 + 4s^2}.$$

We note that $\lambda_1^{(x_m, u_m)}(b, s) > -1$ for $s > 1/2$ and $b \in (2\sqrt{s - s^2}, 2s)$. By (H4), we have that $\delta^2 < \frac{-2f(0)}{f''(0)} = 1$. Further, we find that for $b \in (2\sqrt{s - s^2}, 2s), 1 < \frac{8s^2}{b^2 + 4s^2} < 2s$ and $[f'(v)]^2 \leq 2e^{-1}$. Thus

$$[\delta f'(u_m)]^2 \frac{8s^2}{b^2 + 4s^2} < 4se^{-1}\delta^2 < 4e^{-1} < 1.$$

This implies

$$-1 < 0 < 1 - [\delta f'(u_m)]^2 \frac{8s^2}{b^2 + 4s^2},$$

so $|\lambda_2^{(x_m, u_m)}(b, s)| < 1$.

Since $1 < \frac{8s^2}{b^2 + 4s^2} < 2s$, we have

$$0 < \ln\left(\frac{8s^2}{b^2 + 4s^2}\right) < \ln(2s) < 1,$$

so

$$|\lambda_1^{(x_m, u_m)}(b, s)| < 1.$$

Therefore, $\mathrm{col}(x_m, u_m)$ is locally asymptotically stable whenever it exists. From our considerations when $s \in (0, 1/2)$, we can see that $\mathrm{col}(x_0, u_0)$ will be unstable for $b < 2s$ and locally asymptotically stable for $2s < b$. ∎