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Effects of Density Dependent Sex Allocation on the Dynamics of a Simultaneous Hermaphroditic Population: Modelling and Analysis

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Abstract

In this work we present a mathematical model describing the dynamics of a population where sex allocation remains flexible throughout adult life and so can be adjusted to current environmental conditions. We consider that the fractions of immature individuals acquiring male and female sexual roles are density dependent through non-linear functions of a weighted total population size. The main goal of this work is to understand the role of life-history parameters on the stabilization or destabilization of the population dynamics.

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The model turns out to be a nonlinear discrete model which is analyzed by studying the existence of fixed points as well as their stability conditions in terms of model parameters. The existence of more complex asymptotic behaviours of system solutions is shown by means of numerical simulations.

Females have larger fertility rate than males. On the other hand, increasing population density favours immature individuals adopting the male role. A positive equilibrium of the system exists whenever fertility and survival rates of one of the sexual roles, if shared by all adults, allow population growing while the opposite happens with the other sexual role. In terms of the female inherent net reproductive number, η_F, it is shown that the positive equilibria is stable when η_F is larger and closed to 1 while for larger values of η_F a certain asymptotic assumption on the investment rate in the female function implies that the population density is permanent. Depending on the other parameters values, the asymptotic behaviour of solutions becomes more complex, even chaotic. In this setting the stabilization/destabilization effects of the abruptness rate in density dependence, of the survival rates and of the competition coefficients are analyzed.

Key words: Sex-allocation model, Sex-structured population dynamics, Density dependence, Stability analysis, Bifurcation and chaos

1 Introduction

In many organisms sex is a flexible affair, as it is for hermaphroditic and some gonochoristic species with *environmental sex determination* (ESD), for which

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environmental factors play a crucial role in their strategies of sexual resource allocation. In fact, for these species the traits favored by one sex might be costly to the other [Hosken and Stockley, 2005], what leads to a divergence between male and female fitness and provides in the case of simultaneous hermaphrodites a *gender conflict* [Angeloni, 2003, Anthes et al., 2006]. To mediate this conflict, an evaluation of the current environmental conditions is necessary [Charnov, 1982].

The *Sex Allocation Theory* [Ghiselin, 1969, Charnov, 1982, 1993] is a powerful evolutionary theory that was developed to analyze the gender conflict of such ESD species. This theory describes how the reproduction resources are allocated between male and female components in order to maximize the reproductive value, the *fitness*.

For outcrossing simultaneous hermaphrodites, the available literature [Charnov, 1982, Brauer et al., 2007, Schärer, 2009] shows that the mating group size influences sex allocation. Sex allocation theory for these species predicts a more female-biased investment of reproductive resources when the mating group size decreases [Fischer, 1981, Charnov, 1982, West et al., 2005, Anthes et al., 2006, Shuker et al., 2007]. In relatively small groups individuals need to produce fewer sperms to be successful, thus leaving more resources for the female role [Fischer, 1981, Charnov, 1982, Fischer, 1984]. Often the studies on local mate competition for simultaneous hermaphrodites have focused on the evolutionary adjustment of sex allocation to mating group size. As noted by Brauer et al. [2007], there are, in fact, three different levels at which sex allocation can be adjusted. First level, the allocation strategy can be the result of selection and evolution, and thus be an adaptation to the average mating group size over many generations. In the second case sex allocation is not or not strictly

fixed genetically but it is set during ontogeny and therefore influenced by environmental conditions such as population density (developmental plasticity). Finally, in the third level sex allocation is not fixed neither during evolution nor ontogeny but remains flexible throughout adult life and can be adjusted to current environmental conditions. In this work we represent sex allocation as defined in the third case, therefore considering the density dependence of the sex allocation as an evolutionary stable strategy. More precisely we suppose that, at each reproductive cycle, the gender distribution of the population changes with the fractions of immature individuals acquiring male and female sexual roles being non-linear functions of a weighted total population size. We have to notice that this approach has already been used for some (ESD) gonochoristic species by many authors [Woodward and Murray, 1993] to explain heavily biased sex-ratios, of order 10:1, in favor of females.

The main insights of this work have to do with how the general aspect of sexual gender structures and the density dependence of sexual allocation may lead to complex asymptotic behaviours. Mathematically speaking, we represent the model by means of a structured discrete system with a density-dependent form for immature sexual choice. Our aim is to understand the influence of the intraspecific sexual competition on sex-ratio and population dynamics and to generate information about stabilizing and destabilizing effects.

The paper is organized as follows. Firstly, we present the mathematical model including the relevant biological features described previously. Then we proceed to the analytical study of the nonlinear discrete system by finding out, whenever it is tractable, the existence of fixed points as well as their stability conditions in terms of model parameters. We further discuss the asymptotic behaviour of system solutions through numerical simulations where we observe

a variety of complex chaos-like forms. Finally, we discuss the interpretation of these results for the population dynamics of the referred species.

2 The Model

Let $J(t)$ denote the density of immature individuals, or juveniles, in the population at times $t = 0, 1, 2, \ldots$, where the unit of time is taken to be the duration of a reproductive cycle. At the end of each reproductive cycle a fraction s of juveniles is assumed to keep being at this stage while a fraction π come into the mature stage, adulthood, and adopt either the male or the female functions; the remaining fraction, $0 < 1 - s - \pi \leq 1$, represents thus the juvenile mortality rate per unit of time.

Juveniles when maturing to adulthood are faced to mating opportunities and need to decide about which sexual role to adopt. They have the choice between two genders: male or female. Let $M(t)$ and $F(t)$ denote the density of mature individuals having adopted the male and the female functions respectively. We assume that juveniles invest more in the most profitable sex role, thereby getting a higher fertilization certainty [Anthes et al., 2006]. This investment should then take into account the gender conflict between females, for which multiple mating is advantageous, and males, for which avoiding female multiple mating reduces the risk of competing with rival sperm. The sex allocation is represented in the model through the *investment rate in the female function*, called Φ, being then the investment rate in the male function $1 - \Phi$. As pointed out in the introduction we suppose sex allocation to be dependent on population density through a weighted total population size:

$$W(t) = J(t) + \beta_1 M(t) + \beta_2 F(t), \tag{1}$$

see [Cushing and Li, 1992] for a similar expression in a density dependent juvenile growth model, where positive parameters β_i are competition coefficients that measure the pressure effects of a male or female function individual on the juveniles sexual role choice compare to that of a juvenile individual.

[Fig. 1 about here.]

In hermaphroditic species as well as in gonochoristic ones the fecundity of the female function is limited to the amount of energy available for egg production, while male function fecundity is limited to the available eggs (Bateman's principle) [Bateman, 1948, Charnov, 1979]. Moreover, in relatively smaller mating groups male individuals need to produce fewer sperm to be successful in sperm competition, leaving more resources for the female function [Fischer, 1981, Charnov, 1982, Fischer, 1984, Brauer et al., 2007]. Applying these two principles and assuming that the sizes of the population density and the corresponding average mating group are positively correlated, we consider the investment rate in the female function Φ to be decreasing in terms of the weighted total population size W, with all juveniles tending to join the female (resp. male) class at maturation for very low (resp. high) population densities.

The survival rates of male and female adults are denoted s_1 and s_2 respectively. Let f_2 denote the fertility rate of female adults. Also, assuming that during the mating process an alternation of the sex role may be made by a small number of males into the female role, *Gamete Exchange* [Anthes et al., 2006], we denote f_1 the fertility rate of male adults, which should be much lower than the one of females, i.e. $f_1 \ll f_2$.

Including all the elements defined so far we get the following nonlinear system of difference equations:

$$\begin{cases} J(t+1) = sJ(t) + f_1 M(t) + f_2 F(t) \\ M(t+1) = \pi(1 - \Phi(W(t)))J(t) + s_1 M(t) \\ F(t+1) = \pi\Phi(W(t))J(t) + s_2 F(t) \end{cases} \tag{2}$$

whose parameters are all positive and verify $s + \pi < 1$ and $f_1 \ll f_2$. Finally we assume for function Φ:

$$\Phi \in C^1(\mathbf{R}_+, (0,1]),\ \Phi'(x) \leq 0,\ \Phi(0) = 1 \text{ and } \lim_{x \to +\infty} \Phi(x) = 0.$$

System (2) is an example of nonlinear autonomous matrix equation [Cushing, 1998]. Denoting $X = (J, M, F)$, system (2) can be written as,

$$X(t+1) = P(X(t))X(t) \tag{3}$$

where,

$$P(X(t)) = P(W(t)) = \begin{pmatrix} s & f_1 & f_2 \\ \pi(1 - \Phi(W(t))) & s_1 & 0 \\ \pi\Phi(W(t)) & 0 & s_2 \end{pmatrix}$$

which is the sum, $P(X(t)) = T(W(t)) + F$, of the transition matrix, depending

on the weighted total population size W, and the constant fertility matrix

$$T(W) = \begin{pmatrix} s & 0 & 0 \\ \pi(1-\Phi(W)) & s_1 & 0 \\ \pi\Phi(W) & 0 & s_2 \end{pmatrix} \qquad \text{and} \qquad F = \begin{pmatrix} 0 & f_1 & f_2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

3 Model Analysis

In this section we study the existence and stability of the equilibrium points of system (2).

We use the net reproductive number, $\eta(W)$, of the projection matrix $P(W)$. Matrix $P(W)$ is primitive for every positive W and its strictly dominant eigenvalue $r(W)$ verifies (Th 1.1.3 in [Cushing, 1998]): $r(W) > 1$ if and only $\eta(W) > 1$, $r(W) < 1$ if and only $\eta(W) < 1$ and thus $r(W) = 1$ if and only $\eta(W) = 1$. $\eta(W)$ is the strictly dominant eigenvalue of matrix $F(I-T(W))^{-1}$:

$$F(I-T(W))^{-1} = \begin{pmatrix} \dfrac{\pi f_1(1-\Phi(W))}{(1-s)(1-s_1)} + \dfrac{\pi f_2\Phi(W)}{(1-s)(1-s_2)} & \dfrac{f_1}{1-s_1} & \dfrac{f_2}{1-s_2} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

so

$$\eta(W) = \frac{\pi f_1}{(1-s)(1-s_1)}(1-\Phi(W)) + \frac{\pi f_2}{(1-s)(1-s_2)}\Phi(W)$$

This expression is simplified by denoting

$$\eta_M = \frac{\pi f_1}{(1-s)(1-s_1)} \text{ and } \eta_F = \frac{\pi f_2}{(1-s)(1-s_2)}$$

that can be interpreted as the inherent net reproductive numbers (expected number of offspring per newborn over the course of its lifetime) when only the females reproduce and only the males reproduce respectively. We then have

$$\eta(W) = \eta_M(1-\Phi(W)) + \eta_F\Phi(W) \tag{4}$$

Following the theory and methodology that can be found in [Cushing, 1998] to perform a qualitative analysis of nonlinear autonomous matrix equation like system (2), we study the existence and the stability of its extinction and positive equilibria.

3.1 Trivial equilibrium and extinction of the population.

The trivial, or extinction, equilibrium $\mathbf{0} = (0,0,0)$ of system (2) always exists. The Jacobian of system (2) at $\mathbf{0}$ is $P(0)$ and thus the facts of $\mathbf{0}$ being asymptotically stable or unstable are directly expressed in terms of parameter $\eta_F = \eta(0)$.

Proposition 3.1 *Let* $\mathbf{0} = (0,0,0)$ *be the trivial equilibrium of system (2). If* $\eta_F < 1$, *then* $\mathbf{0}$ *is asymptotically stable and if* $\eta_F > 1$, $\mathbf{0}$ *is unstable.*

Proposition 3.1 yields that $\mathbf{0}$ loses its stability as η_F increases through the critical value 1. We complete this bifurcation result in section 3.2 when considering the positive equilibria.

Under the hypothesis $s_1 \leq s_2$, condition $\eta_F < 1$ also implies that the trivial equilibrium is globally stable, i.e., for any initial condition $(J(0), M(0), F(0)) \in \mathbb{R}^3_+$ the corresponding solution $(J(t), M(t), F(t))$ tends to $\mathbf{0}$ as t goes to infinity.

Proposition 3.2 *Let $s_1 \leq s_2$. If $\eta_F < 1$ then equilibrium $\mathbf{0}$ of system (2) is globally asymptotically stable.*

Proof: see appendix A.1.

3.2 Positive Equilibria

In the next proposition we express in terms of η_M and η_F necessary and sufficient conditions for system (2) to possess a positive equilibrium point $X^* = (J^*, M^*, F^*)$. We also give conditions that ensures X^* stability.

Proposition 3.3 *System (2) has a positive equilibrium point $X^* = (J^*, M^*, F^*)$ if and only if either $\eta_M < 1$ and $\eta_F > 1$ or $\eta_M > 1$ and $\eta_F < 1$. In the first case, $\eta_M < 1$, X^* is asymptotically stable for values of $\eta_F > 1$ close enough to 1 and, in the second case, $\eta_M > 1$, X^* is unstable for values of $\eta_F < 1$ close enough to 1.*

Proof: see appendix A.2.

The positive equilibrium, in both cases, can be explicitly calculated (see appendix A.2) and reads as follows:

$$X^* = (J^*, \frac{\pi(1-\kappa)}{1-s_1}J^*, \frac{\pi\kappa}{1-s_2}J^*), \tag{5}$$

where $J^* = \Phi^{-1}(\kappa)/(1+\beta_1\frac{\pi(1-\kappa)}{1-s_1}+\beta_2\frac{\pi\kappa}{1-s_2})$ and $\kappa = (1-\eta_M)/(\eta_F-\eta_M)$.

Assuming $s_1 \leq s_2$, it is also hold that $\eta_M < \eta_F$. We have already shown that in this case if $\eta_F < 1$ then the trivial equilibrium is globally stable while for $\eta_F > 1$ is unstable. Concerning the positive equilibrium X^*, the same assumption reduces its existence conditions to $\eta_M < 1 < \eta_F$. In the next proposition we prove that $s_1 \leq s_2$ and $\eta_M > 1$ imply unbounded solutions of system (2).

Proposition 3.4 *Let $s_1 \leq s_2$ and $\eta_M > 1$. If $(J(t), M(t), F(t))$ is the solution of system (2) associated to the non-negative initial condition $(J(0), M(0), F(0)) \neq (0,0,0)$ then $\{(J(t), M(t), F(t)) : t \in \mathbb{N}\}$ is unbounded.*

Proof: see appendix A.3.

After that, we propose a sufficient condition for the permanence of the system (2). We use the definition of permanence found in [Kon et al, 2004] which ensures that the total population density neither explodes nor goes to zero. To prove the permanence of system (2) we apply theorem 3 in [Kon et al, 2004]; for that we need system (2) to be dissipative, i.e., we need to find a compact set $K \subset \mathbb{R}^n_+$ such that for all $X(0) \in \mathbb{R}^n_+$ there exists a $T = T(X(0))$ such that $X(t) \in K$ for all $t \geq T$. In the next proposition we present a condition on the investment rate in the female function, Φ, that ensures system (2) dissipativeness.

Proposition 3.5 *Let $\eta_M < 1$. If $x\Phi(x)$ is bounded on $[0, \infty)$ then system (2) is dissipative.*

Proof: see appendix A.4.

Now, we state in the following proposition sufficient conditions for system (2) permanence which is a direct consequence of theorem 3 in [Kon et al, 2004].

Proposition 3.6 *Let $\eta_M < 1$ and $\eta_F > 1$. If $x\Phi(x)$ is bounded on $[0, \infty)$ then system (2) is permanent.*

In the next section we are presenting a set of simulations to complete the study of those cases where the performed analysis does not help in characterizing the asymptotic behaviour of solutions. These unknown cases correspond to the situation of existence of a unique positive equilibrium point, $X^* = (J^*, M^*, F^*)$, for which it is not known whether it is stable or not. In terms of parameters η_M and η_F, we are dealing with cases with a fixed $\eta_M < 1$ and different values of $\eta_F > 1$. We should also choose a specific form for the allocation function Φ that verifies the condition imposed in proposition 3.6 so that system (2) is permanent. This choice is in a sense robust because it can be proved, see chapter 16 in [Hirsch and Smale, 1974], that if we take a perturbation (C^1) of Φ, i.e., another allocation function $\tilde{\Phi}$ such that $|\Phi(x) - \tilde{\Phi}(x)|$ and $|\Phi'(x) - \tilde{\Phi}'(x)|$ are small for every $x \in \mathbb{R}_+$, the existence of the positive equilibrium X^* in the case of Φ, when it is hyperbolic, imply the existence of a close hyperbolic equilibrium $\tilde{X}^*$ in the case of $\tilde{\Phi}$ which moreover shares the same stability features with X^*.

4 Numerical results:

In this section we pursue the analysis of the asymptotic behaviour of solutions of system (2) by means of numerical simulations.

We use particular forms of function Φ, the investment rate in the female role. In Getz [1996] it is analyzed the influence of abrupt density dependence on the oscillations of a population by means of simple discrete models and using different density-dependent forms. Here we adapt the so-called generalized Ricker function as presented in [Getz, 1996], $\Phi_{R_\gamma}(x) = e^{-x^\gamma}$, where the parameter γ is called the "abruptness" parameter and controls how rapidly density dependence sets in.

In the sequel we study how γ, the abruptness parameter, s_1 and s_2, the adult survival rates, and β_1 and β_2, the competition coefficients, affect the stability of the system. For this, we look for η_F, the female inherent reproductive number, bifurcation values where the positive equilibrium point $X^* = (J^*, M^*, F^*)$ loses its stability as well as the values where the orbits that we calculate get positive Largest Lyapunov Exponents (LLE).

4.1 The Effect of the abruptness parameter γ:

To illustrate the influence of the abruptness parameter γ on the destabilization of the positive equilibrium point X^* we first calculate, figure A.2, the spectral radius of its associated Jacobian matrix for different values of $\gamma \in \{1, 1.5, 2\}$ and $\eta_F \in [1, 14]$ while keeping fixed the rest of parameters values. Let us recall that Proposition 3.3 ensures the asymptotical stability of X^* for $\eta_F \in (1, 1+\varepsilon)$.

It is shown in figure A.2 that this spectral radius is less than 1, i.e., X^* asymptotically stable, for η_F between 1 and a bifurcation value denoted η_F^*. On the other hand, we see that X^* is unstable for $\eta_F > \eta_F^*$.

[Fig. 2 about here.]

We notice that the larger the value of γ the smaller the value of η_F^*, i.e, there is a clear destabilizing effect produced by an increasing abruptness, the parameter that governs how rapidly an increase of the weighted total population density is reflected on sex allocation going towards a more biased male distribution.

To illustrate what happens once the positive equilibrium loses its stability we use the results of a number of numerical simulations. We calculate orbits of system (2), with initial conditions $X(0) = (J(0), M(0), F(0)) = (20, 15, 10)$, three different values of $\gamma \in \{1, 1.5, 2\}$, $\eta_F \in [0, 80]$ and the rest of parameters values being the same as those previously used. We also calculate the LLE of each of these orbits.

In figure 3(a) it is shown for $\gamma = 1$ the juvenile orbit diagram for values of η_F near biffurcation point, i.e., for each value of η_F the points in its corresponding vertical line approximate the long term behaviour of juveniles density $J(t)$, thus they approximately represent the orbit attractor. It is noticed that for low values of η_F the asymptotic behaviour corresponds to the juvenile component J^* of the positive equilibrium. The same is shown in figures 3(b) and 3(c) for $\gamma = 1.5$ and $\gamma = 2$ respectively.

[Fig. 3 about here.]

In figure A.4, using η_F as a parameter, the LLE of the orbits represented in figure A.3 are plotted for the three different values of the abruptness parameter $\gamma \in \{1, 1.5, 2\}$.

[Fig. 4 about here.]

To quantify the destabilizing effects of γ we use, on the one hand, the lowest value of η_F from which positive Lyapunov exponents appear, henceforth denoted η_F^∞ (Fig. A.4), and, on the other hand, the amplitude of the orbit attractors (Fig. A.3). We observe that increasing γ entails decreasing η_F^∞ while there is an increase of the orbits attractors amplitude. We can then conclude that an increase of parameter γ promotes instability and chaotic-like oscillations in the population and that this kind of behaviour is reinforced as long as the value of η_F is increased. Larger sensibility to density dependence of sex allocation together with larger female inherent rate reproductive number implies more complex population dynamics.

4.2 The effect of the adult survival rates:

The survival rates s_1 and s_2 constitute important parameters of the model since they characterize species iteroparity. To see their influence on the stability of the population dynamics we perform a numerical study analogous to that already done for γ in the previous section.

The first index we use to assess the stability of the population is η_F^*, the bifurcation value of η_F where the positive equilibrium X^* of system (2) loses its stability. We calculate η_F^* for the different values of the survival rates s_1 and s_2 in $[0.1, 0.9]$, with $s_1 < s_2$, and fixed values of the rest of parameters. In

figure A.5 it is shown a 2D representation of η_F^* in terms of s_1 and s_2.

[Fig. 5 about here.]

Understanding an increase of η_F^* as a population stability rise, we notice the clear stabilization effect of increasing the female survival rate. In fact, for any fixed value of s_1 we see that the larger s_2 the bigger η_F^*. This is not the case of s_1, as we can see that for certain values of s_2 the largest values of η_F^* are found for intermediate values for s_1 while the lowest values of η_F^* are found for either small or large values of s_1. This is certainly due to the asymmetric roles of males and females.

Once the positive equilibrium X^* loses its stability, our index to assess the complexity of population dynamics are the values of η_F^∞, that represent where orbits start to possess positive Lyapunov exponents. We identify increasing η_F^∞ with a gain in population stability. To obtain η_F^∞ we calculate the orbits of system (2), with the same conditions on $X(0)$ and η_F as previously and for the different values of s_1 and s_2 in $[0.1, 0.9]$, and fixed values of the rest of parameters. The 2D representation of η_F^∞ in terms of s_1 and s_2 is shown in figure A.6, where we notice that the complexity of population dynamics increases as a result of low survival rates. High values of s_1 and s_2 imply that very high values of η_F are needed to get chaotic-like behaviour of system orbits. This stabilization effect of the dynamical system can be assimilated to iteroparity [Demetrius, 1971, Getz, 1996]: the repeated production of offspring throughout the life cycle *versus* semelparity, where each individual reproduces only once during its life.

[Fig. 6 about here.]

4.3 The effect of the competition coefficients:

As the female role is more expensive in terms of reproductive energy, we assume in this section that the female competition effect, represented by β_2, is larger than the corresponding male effect, β_1, on juvenile gender choice, *i.e.* , $\beta_2 > \beta_1$. The results in previous sections are not affected by this assumption.

We calculate η_F^* for the different values of the competition coefficients β_1 and β_2 in $[0, 50]$, with $\beta_1 < \beta_2$, and fixed values of the rest of parameters as before. In figure A.7, similarly to figure A.5, it is shown a 2D representation of η_F^* in terms of β_1 and β_2. We notice that the lowest values of η_F^* are found for β_1 either small or close to β_2.

[Fig. 7 about here.]

The results of the calculation of η_F^∞, as done in previous sections, are shown in figure A.8.

[Fig. 8 about here.]

We note a clear destabilizing pattern, η_F^∞ decreasing, directly related to the increase of the male competition coefficient β_1. The fact that males and females are comparable in terms of reproductive energy entails a more complex population dynamics.

5 Discussion and conclusion

In this work we propose a model for the dynamics of an iteroparous outcrossing simultaneous hermaphroditic population whose life cycle consists of

a juvenile growth stage followed by a reproductive one with two different adult sexual roles. At maturation period, the transition to the reproductive stage depends on population density through a weighted total population size that differentiates by gender the competition between juvenile and adult stages.

This approach suppose that sex allocation is not fixed during evolution but remains flexible throughout adult life and can be adjusted to current environmental conditions, this was already proved by many authors [Schärer, 2009], our goal is to study the implication at a population dynamics level of this fact.

Apart from the parameters directly appearing in system (2) we have introduced η_M and η_F, the male and female inherent net reproductive numbers. We have proved that the system (2) has a positive equilibrium point $X^* = (J^*, M^*, F^*)$ if and only if either $\eta_M < 1$ and $\eta_F > 1$ or $\eta_M > 1$ and $\eta_F < 1$. Moreover, it exists a branch of non-extinction equilibrium pairs (η_F, X^*), which bifurcates from the point $(\eta_F, X^*) = (1, \mathbf{0})$ which results stable when $\eta_M < 1$ and $\eta_F \gtrapprox 1$ and unstable when $\eta_M > 1$ and $\eta_F \lessapprox 1$. Further more, under condition $s_1 \leq s_2$, we proved that if $\eta_M > 1$ the population grows unboundedly and if $\eta_F < 1$ the population gets extinct. In the rest of the discussion we assume $\eta_M < 1$ and $\eta_F > 1$, where we proved the permanence of the system (2) provided that $x\Phi(x)$ be a bounded function for $x \in [0, \infty)$, which is the case for the generalized Ricker function $\Phi_{R_\gamma}(x) = e^{-x^\gamma}$ used in the numerical simulations of section 4.

Parameter η_F close to 1 represents, through X^*, low population density and also female biased sex allocation due to density dependence effects. We proved that X^* is locally asymptotically stable whenever η_F is bigger and close to 1, that is, a low population density implies a stabilization of the population with

a sex allocation almost completely biased towards the female role. Density dependent sexual allocation protects hermaphroditic species from extinction.

Parameter η_M close to 1 or high values of parameter η_F represent high population density at equilibrium X^* what entails a decrease of the female investment rate. This situation corresponds to a loss of stability of the population dynamics which, depending on other parameters values, may become chaotic. In this context we studied the influence of density dependence through the abruptness parameter γ. We found that the more severe the effects of density dependence are, i.e., the larger the parameter γ, the more complex the population dynamics becomes. We have also studied the influence of survival rates obtaining that the complexity of population dynamics increases if they are low while high values of s_1 and specially of s_2 imply that very high values of η_F are needed to get chaotic-like behaviour of system orbits. An important applied consequence of the last point is that selective mortality might have a destabilization effect on exploited simultaneous hermaphroditic species. Concerning competition parameters we also found a destabilizing effect when the male coefficient β_1 is high, that is, when the reproductive energy consumed by males and females is comparable.

We have shown, following the schema in Higgens [Higgins et al., 1997], that the population dynamics shows a sensibility to changes in life history parameters and in sex allocation patterns. Numerical simulations reveal the existence of chaotic-like long-term behaviour of the population dynamics for certain domains of parameters values. In this sense iteroparity and abruptness parameters have opposite effects. The latter is prone to imply chaotic behaviour whereas the former promotes stability. Complex dynamics implies a strong variability in the densities of male and female adults what induces also a

strong variation in sex ratio. This variation involves an increase of the number of sex role changes per individual with the corresponding energy expenses. In the case that this energy cannot be allocated, the concerned species has an evolutionary constraint in avoiding complex dynamics which should be counteracted by means of life history parameters such as η_F, s, s_1 and s_2.

It is implicit in model (2) that sex-allocation is regulated by two mechanisms acting at two different time scales. The first one is an evolutionary mechanism reflected in the existence of a sex-allocation function in terms of population density and the second one has to do with the population dynamics derived from this sex-allocation function. We proved, as the inherent rate reproductive number increases, that this dynamics can be very complex to the point of exhibiting chaotic-like attractors. However, we have to note that few experimental works exhibit these dynamical phenomena, perhaps because they suppose that population density remains constant or absolute fitness values are measured as the breeding number instead of using the inherent net reproductive rate, [Caswell, 2001], as we do. Integrating model (2) into an adaptative dynamics model for the traits β_1 and β_2 , or s_1 and s_2, could help understanding the relationships between the mentioned two times scales.

In general, sex allocation responses to environmental variability occurs at the individual level. In our model, the study scale is at the population level and, therefore, the response of the population to environmental changes should be considered as the average of individual responses. To perform the study at the individual level we could use a computational model like an IBM (individual based model) which would allow subsequently a very interesting comparison between both macroscopic and microscopic approaches.

Finally, we have to note that the same sex allocation behaviour is observed for some sequential hermaphroditic species. An analogous modelling approach could be used in this case provided that the model integrates a new adult class representing asexual individuals and the corresponding transitions from the female and male classes to the asexual one after the reproductive period.

A Appendix:

A.1 Proof of proposition 3.2

$f_1 \leq f_2$ and $s_1 \leq s_2$ imply

$$\begin{cases} J(t+1) = sJ(t) + f_1 M(t) + f_2 F(t) \leq sJ(t) + f_2(M(t) + F(t)) \\ M(t+1) + F(t+1) = \pi J(t) + s_1 M(t) + s_2 F(t) \leq \pi J(t) + s_2(M(t) + F(t)) \end{cases} \tag{A.1}$$

Considering now the linear system

$$\begin{cases} x(t+1) = sx(t) + f_2 y(t) \\ y(t+1) = \pi x(t) + s_2 y(t) \end{cases} \tag{A.2}$$

we find that $\eta_F < 1$ implies that the strictly dominant eigenvalue of the associated matrix is less than 1 and so for any initial condition $(x(0), y(0))$ the corresponding solution verifies $\lim_{t\to\infty}(x(t), y(t)) = (0, 0)$.

On the other hand, for every $t \geq 0$, $J(t) \leq x(t)$ and $M(t) + F(t) \leq y(t)$ imply

that $J(t+1) \leq x(t+1)$ and $M(t+1) + F(t+1) \leq y(t+1)$:

Using (A.1) we have

$$\begin{cases} J(t+1) \leq sJ(t) + f_2(M(t)+F(t)) \leq sx(t) + f_2 y(t) = x(t+1) \\ M(t+1) + F(t+1) \leq \pi J(t) + s_2(M(t)+F(t)) \leq \pi x(t) + s_2 y(t) = y(t+1). \end{cases}$$

Now, for any initial condition $(J(0), M(0), F(0))$ of system (2), setting $x(0) = J(0)$ and $y(0) = M(0)+F(0)$ as initial conditions of system (A.2), the previous inequalities imply that $J(t) \leq x(t)$ and $M(t) + F(t) \leq y(t)$ for every $t \geq 0$, and so we obtain $\lim_{t\to\infty}(J(t), M(t), F(t)) = (0, 0, 0)$.

A.2 Proof of proposition 3.3 and equation (5)

The condition for the existence of a positive equilibrium of system (2) (see 1.2.5 in [Cushing, 1998]) is that $\eta(W) = 1$, i.e., $\eta_M(1 - \Phi(W)) + \eta_F \Phi(W) = 1$ or $\Phi(W) = (1 - \eta_M)/(\eta_F - \eta_M) = \kappa$. Thus, there exists a positive equilibrium X^* of system (2) if and only if $\kappa \in (0, 1)$. In this case, $X^* = (J^*, M^*, F^*)$ is unique and can be straightforwardly calculated as the eigenvector of matrix $P(\Phi^{-1}(\kappa))$ associated to eingevalue 1 that verifies $\Phi(J^* + \beta_1 M^* + \beta_2 F^*) = \kappa$, see (5).

The proof of proposition 3.3 is a direct consequence of the results in section 1.2.2 of [Cushing, 1998]. Writing $P(\eta_F, X(t)) = T(W(t)) + \eta_F \bar{F}$, where $\bar{F} = \frac{1}{\eta_F} F$, and using η_F as bifurcation parameter, theorem 1.2.4 ensures the existence of a branch of positive equilibria bifurcating from the equilibrium

pair $X = \bar{0}$ and $\eta_F = 1$. The condition of existence of positive equilibria $\kappa \in (0,1)$ is equivalent to either $\eta_M < 1$ and $\eta_F > 1$ (bifurcation to the right) or $\eta_M > 1$ and $\eta_F < 1$ (bifurcation to the left). Now applying theorem 1.2.6 of [Cushing, 1998], as in our case $w^T B v = f_2(1-s)/\eta_F > 0$, we obtain that the bifurcation is stable if it is to the right and unstable if it is to the left, what proves the proposition.

A.3 Proof of proposition 3.4

$f_1 \leq f_2$ and $s_1 \leq s_2$ imply

$$\begin{cases} J(t+1) = sJ(t) + f_1 M(t) + f_2 F(t) \geq sJ(t) + f_1(M(t) + F(t)) \\ M(t+1) + F(t+1) = \pi J(t) + s_1 M(t) + s_2 F(t) \geq \pi J(t) + s_1(M(t) + F(t)) \end{cases} \tag{A.3}$$

Considering now the linear system

$$\begin{cases} x(t+1) = sx(t) + f_1 y(t) \\ y(t+1) = \pi x(t) + s_1 y(t) \end{cases} \tag{A.4}$$

Condition $\eta_M > 1$ implies that the strictly dominant eigenvalue of the associated matrix is larger than 1 and so for any initial condition $(x(0), y(0)) \neq (0,0)$ the corresponding solution verifies $\lim_{t\to\infty}(x(t), y(t)) = (+\infty, +\infty)$.

On the other hand, for every $t \geq 0$, $J(t) \geq x(t)$ and $M(t) + F(t) \geq y(t)$ imply that $J(t+1) \geq x(t+1)$ and $M(t+1) + F(t+1) \geq y(t+1)$:

433 Using (A.4) we have

$$J(t+1) \geq sJ(t) + f_1(M(t)+F(t)) \geq sx(t) + f_1 y(t) = x(t+1)$$

$$M(t+1) + F(t+1) \geq \pi J(t) + s_1(M(t)+F(t)) \geq \pi x(t) + s_1 y(t) = y(t+1).$$

434 Now, for any non-negative initial condition $(J(0), M(0), F(0)) \neq (0,0,0)$ of
435 system (2), setting $x(0) = J(0)$ and $y(0) = M(0) + F(0)$ as initial conditions
436 of system (A.4), the previous inequalities imply that $J(t) \geq x(t)$ and $M(t) +$
437 $F(t) \geq y(t)$, for every $t \geq 0$, and so that $\{(J(t), M(t), F(t)) : t \in \mathbb{N}\}$ is
438 unbounded.

439 *A.4 Proof of proposition 3.5*

440 Let $K_0 > 0$ be such that $x\Phi(x) < K_0$ for all $x \geq 0$.

441 For every solution $X(t) = (J(t), M(t), F(t)) \in \mathbf{R}^3_+$ of system (2) we have

$$F(t+1) = \pi\Phi(W(t))J(t) + s_2 F(t) \leq \pi\Phi(J(t))J(t) + s_2 F(t) < \pi K_0 + s_2 F(t)$$

442 Since $0 < s_2 < 1$, there exists $T_1 = T_1(X(0)) > 0$ such that for $t \geq T_1(X(0))$

$$F(t) < \frac{\pi K_0}{1 - s_2} = K_1$$

443 Now we have for all $t \geq T_1(X(0))$ that

$$J(t+1) = sJ(t) + f_1 M(t) + f_2 F(t) < sJ(t) + f_1 M(t) + f_2 K_1$$

$$M(t+1) = \pi(1 - \Phi(W(t))J(t) + s_1 M(t) < \pi J(t) + s_1 M(t)$$

444 and thus

$$\begin{pmatrix} J(t+1) \\ M(t+1) \end{pmatrix} < \begin{pmatrix} s & f_1 \\ \pi & s_1 \end{pmatrix} \begin{pmatrix} J(t) \\ M(t) \end{pmatrix} + \begin{pmatrix} f_2 K_1 \\ 0 \end{pmatrix}$$

Since $\eta_M < 1$ we have that the spectral radius of matrix $\begin{pmatrix} s & f_1 \\ \pi & s_1 \end{pmatrix}$ is less than

445

446 1 and so we can find $T_2(X(0)) > T_1(X(0))$ such that for all $t \geq T_2(X(0))$

$$\begin{pmatrix} J(t) \\ M(t) \end{pmatrix} < \left[\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \begin{pmatrix} s & f_1 \\ \pi & s_1 \end{pmatrix} \right]^{-1} \begin{pmatrix} f_2 K_1 \\ 0 \end{pmatrix} = \frac{\eta_F K_0}{1 - \eta_M} \begin{pmatrix} 1 \\ \frac{\pi}{1 - s_1} \end{pmatrix}$$

447 what completes the proof.

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List of Figures

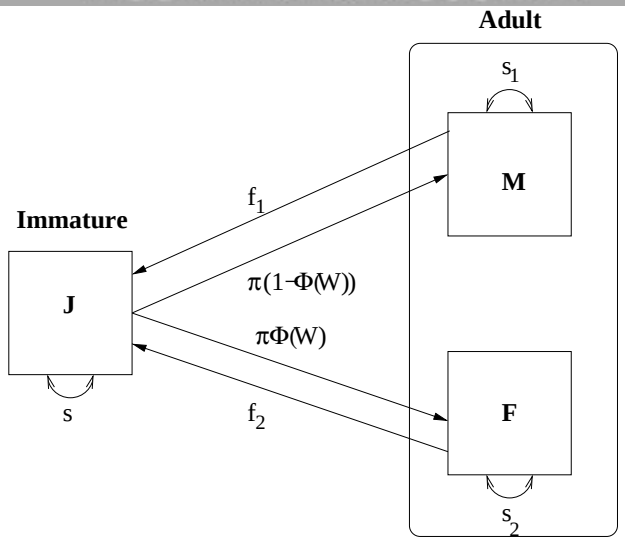


Fig. A.1. Conceptual model.

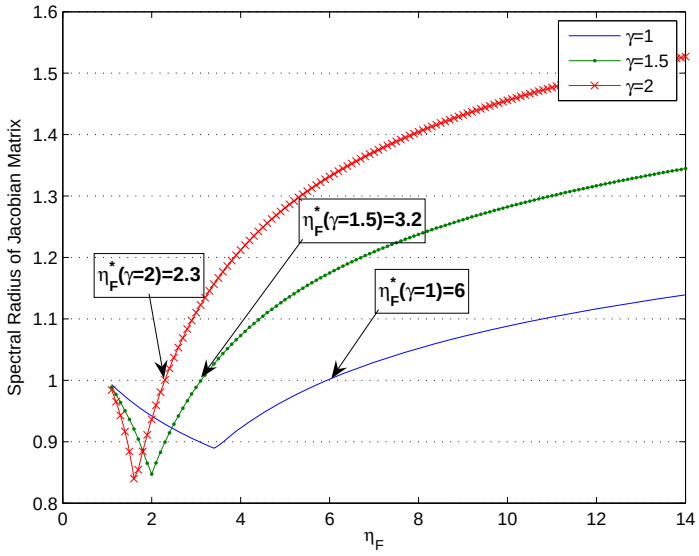
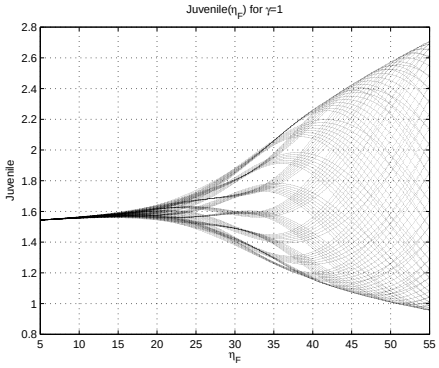
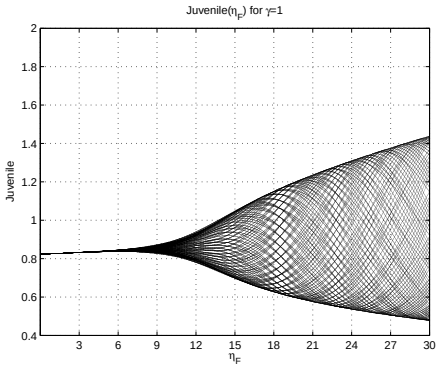


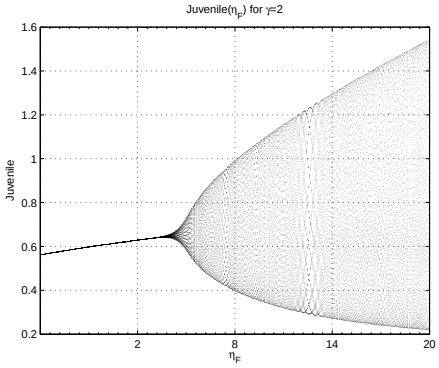
Fig. A.2. The spectral radius of the Jacobian matrix associated to the equilibrium point $X^* = (J^*, M^*, F^*)$ of system (2) is shown for three different values of $\gamma \in \{1, 1.5, 2\}$, as η_F increases from 1 to 14, with $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$, $f_2 = \eta_F(1-s)(1-s_2)/\pi$, $\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x^\gamma}$. η_F^* represents the bifurcation value where X^* loses its stability.



(a) $\gamma = 1$



(b) $\gamma = 1.5$



(c) $\gamma = 2$

Fig. A.3. Using the female inherent reproductive number η_F as a parameter, orbit diagrams for the juvenile density J are shown for system (2) with parameter values $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$, $f_2 = \eta_F(1-s)(1-s_2)/\pi$, $\beta_1 = 1$ and $\beta_2 = 1.5$, initial conditions $X(0) = (J(0), M(0), F(0)) = (20, 15, 10)$, and $\Phi(x) = e^{-x^\gamma}$: (a) $\gamma = 1$, (b) $\gamma = 1.5$ and (c) $\gamma = 2$ (note the different vertical scales).

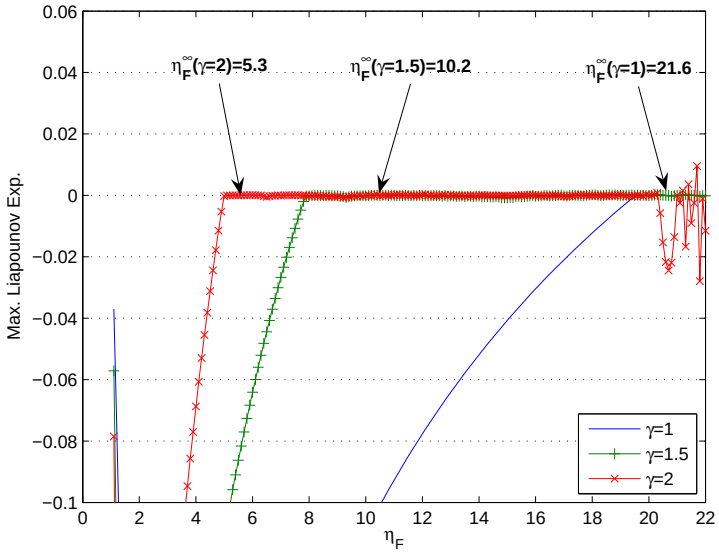


Fig. A.4. The largest Lyapunov exponents (LLE) of the orbit of system (2) is shown for three different values of $\gamma \in \{1, 1.5, 2\}$, as η_F increases from 0 to 22, with parameters values and initial conditions as in Fig. A.3. η_F^∞ represents the largest value of η_F such that the LLE of the orbit is negative for $\eta_F \leq \eta_F^\infty$.

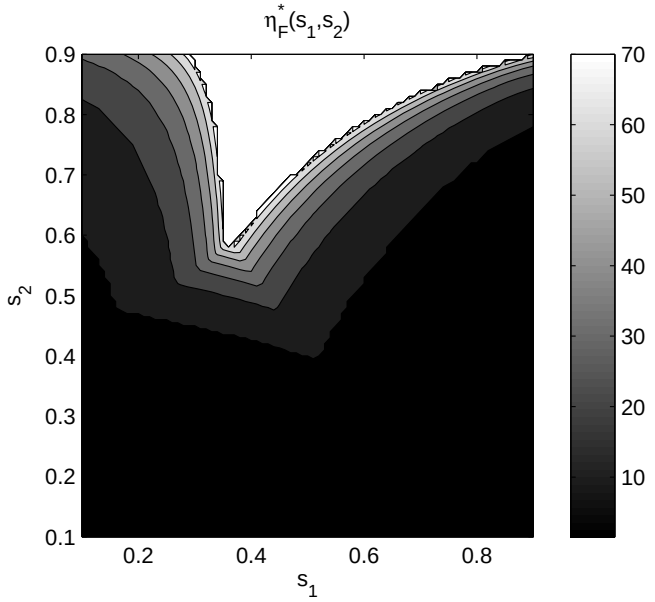


Fig. A.5. The value η_F^*, value of η_F for which the positive equilibrium point $X^* = (J^*, M^*, F^*)$ of system (2) loses its stability, is shown for $s_1 \in [0.1, 0.9]$ and $s_2 \in [s_1, 0.9]$, with $s = 0.05$, $\pi = 0.6$, $f_1 = 0.01$, $\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x}$.

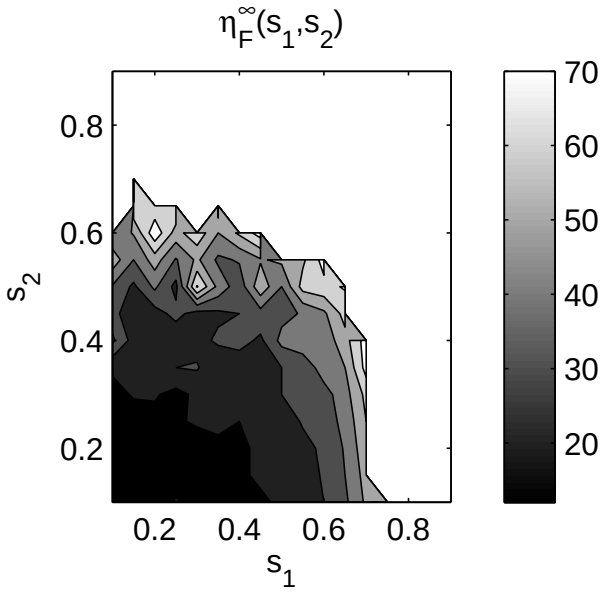


Fig. A.6. The value η_F^∞, smallest value of η_F starting from which the corresponding orbit has a positive LLE, is shown for $s_1 \in [0.1, 0.9]$, $s_2 \in [s_1, 0.9]$, with $s = 0.05$, $\pi = 0.6$, $f_1 = 0.01$, $\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x}$.

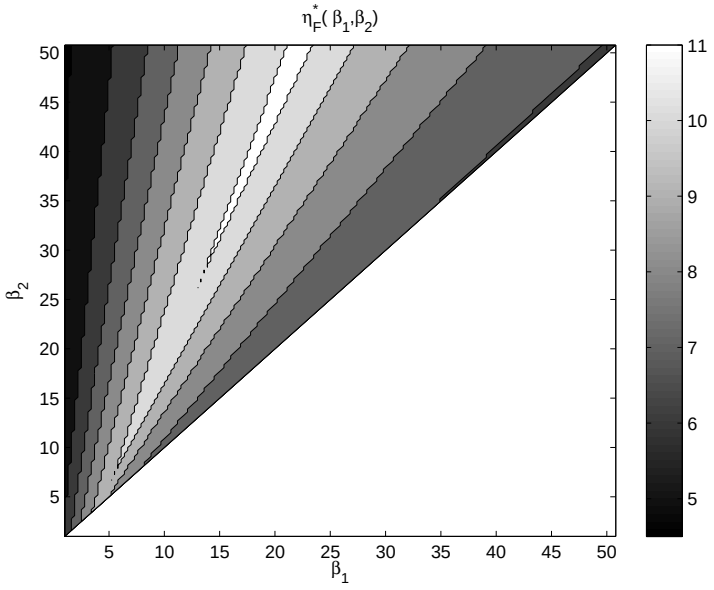


Fig. A.7. The value η_F^*, value of η_F for which the positive equilibrium point $X^* = (J^*, M^*, F^*)$ of system (2) loses its stability, is shown for $\beta_1 \in [0, 50]$ and $\beta_2 \in [\beta_1, 50]$, with $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$ and $\Phi(x) = e^{-x}$.

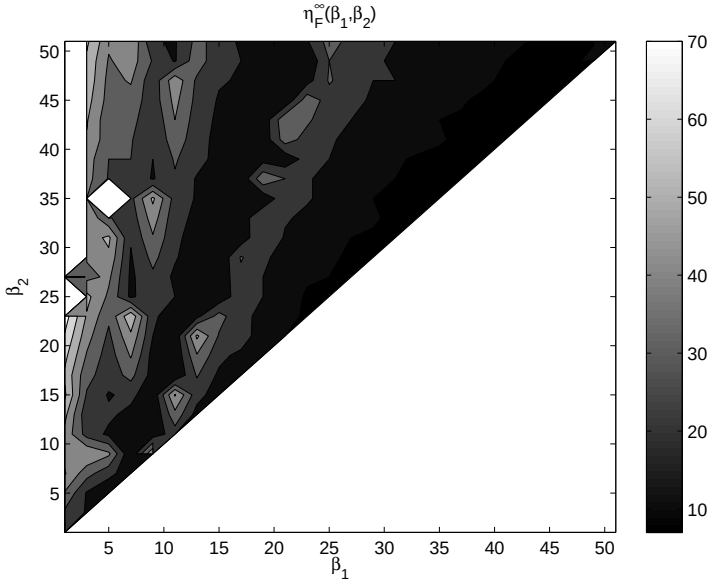


Fig. A.8. The value η_F^∞, smallest value of η_F starting from which the corresponding orbit has a positive LLE, is shown for $\beta_1 \in [0, 50]$ and $\beta_2 \in [\beta_1, 50]$, with $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$ and $\Phi(x) = e^{-x}$.