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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.

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 1 Introduction

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

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

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

16 For outcrossing simultaneous hermaphrodites, the available literature [Charnov,
 17 1982, Brauer et al., 2007, Schärer, 2009] shows that the mating group size in-
 18 fluences sex allocation. Sex allocation theory for these species predicts a more
 19 female-biased investment of reproductive resources when the mating group
 20 size decreases [Fischer, 1981, Charnov, 1982, West et al., 2005, Anthes et al.,
 21 2006, Shuker et al., 2007]. In relatively small groups individuals need to pro-
 22 duce fewer sperms to be successful, thus leaving more resources for the female
 23 role [Fischer, 1981, Charnov, 1982, Fischer, 1984]. Often the studies on local
 24 mate competition for simultaneous hermaphrodites have focused on the evolu-
 25 tionary adjustment of sex allocation to mating group size. As noted by Brauer
 26 et al. [2007], there are, in fact, three different levels at which sex allocation can
 27 be adjusted. First level, the allocation strategy can be the result of selection
 28 and evolution, and thus be an adaptation to the average mating group size
 29 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 $t = 0, 1, 2, \dots$, 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:

$$W(t) = J(t) + \beta_1 M(t) + \beta_2 F(t), \quad (1)$$

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

83 [Fig. 1 about here.]

84 In hermaphroditic species as well as in gonochoristic ones the fecundity of the
 85 female function is limited to the amount of energy available for egg produc-
 86 tion, while male function fecundity is limited to the available eggs (Bateman's
 87 principle) [Bateman, 1948, Charnov, 1979]. Moreover, in relatively smaller
 88 mating groups male individuals need to produce fewer sperm to be successful
 89 in sperm competition, leaving more resources for the female function [Fischer,
 90 1981, Charnov, 1982, Fischer, 1984, Brauer et al., 2007]. Applying these two
 91 principles and assuming that the sizes of the population density and the cor-
 92 responding average mating group are positively correlated, we consider the
 93 investment rate in the female function Φ to be decreasing in terms of the
 94 weighted total population size W , with all juveniles tending to join the female
 95 (resp. male) class at maturation for very low (resp. high) population densities.

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

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

$$\begin{cases} J(t+1) = sJ(t) + f_1M(t) + f_2F(t) \\ M(t+1) = \pi(1 - \Phi(W(t)))J(t) + s_1M(t) \\ F(t+1) = \pi\Phi(W(t))J(t) + s_2F(t) \end{cases} \quad (2)$$

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

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

106 System (2) is an example of nonlinear autonomous matrix equation [Cushing,
 107 1998]. Denoting $X = (J, M, F)$, system (2) can be written as,

$$X(t+1) = P(X(t))X(t) \quad (3)$$

108 where,

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

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

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

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

111 3 Model Analysis

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

114 We use the net reproductive number, $\eta(W)$, of the projection matrix $P(W)$.
115 Matrix $P(W)$ is primitive for every positive W and its strictly dominant
116 eigenvalue $r(W)$ verifies (Th 1.1.3 in [Cushing, 1998]): $r(W) > 1$ if and only
117 $\eta(W) > 1$, $r(W) < 1$ if and only $\eta(W) < 1$ and thus $r(W) = 1$ if and only
118 $\eta(W) = 1$. $\eta(W)$ is the strictly dominant eigenvalue of matrix $F(I - T(W))^{-1}$:

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

119 so

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

120 This expression is simplified by denoting

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

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

$$\eta(W) = \eta_M(1 - \Phi(W)) + \eta_F\Phi(W) \quad (4)$$

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

128 3.1 Trivial equilibrium and extinction of the population.

129 The trivial, or extinction, equilibrium $\mathbf{0} = (0, 0, 0)$ of system (2) always ex-
130 ists. The Jacobian of system (2) at $\mathbf{0}$ is $P(0)$ and thus the facts of $\mathbf{0}$ being
131 asymptotically stable or unstable are directly expressed in terms of parameter
132 $\eta_F = \eta(0)$.

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

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

138 Under the hypothesis $s_1 \leq s_2$, condition $\eta_F < 1$ also implies that the trivial
 139 equilibrium is globally stable, i.e., for any initial condition $(J(0), M(0), F(0)) \in$
 140 $\mathbb{R}_+^3$ the corresponding solution $(J(t), M(t), F(t))$ tends to $\mathbf{0}$ as t goes to infin-
 141 ity.

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

144 *Proof: see appendix A.1.*

145 3.2 Positive Equilibria

146 In the next proposition we express in terms of η_M and η_F necessary and
 147 sufficient conditions for system (2) to possess a positive equilibrium point
 148 $X^* = (J^*, M^*, F^*)$. We also give conditions that ensures X^* stability.

149 **Proposition 3.3** *System (2) has a positive equilibrium point $X^* = (J^*, M^*, F^*)$*
 150 *if and only if either $\eta_M < 1$ and $\eta_F > 1$ or $\eta_M > 1$ and $\eta_F < 1$. In the first*
 151 *case, $\eta_M < 1$, X^* is asymptotically stable for values of $\eta_F > 1$ close enough to*
 152 *1 and, in the second case, $\eta_M > 1$, X^* is unstable for values of $\eta_F < 1$ close*
 153 *enough to 1.*

154 *Proof: see appendix A.2.*

155 The positive equilibrium, in both cases, can be explicitly calculated (see ap-
156 pendix A.2) and reads as follows:

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

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

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

164 **Proposition 3.4** *Let $s_1 \leq s_2$ and $\eta_M > 1$. If $(J(t), M(t), F(t))$ is the solution*
165 *of system (2) associated to the non-negative initial condition $(J(0), M(0), F(0)) \neq$*
166 *$(0, 0, 0)$ then $\{(J(t), M(t), F(t)) : t \in \mathbb{N}\}$ is unbounded.*

167 *Proof: see appendix A.3.*

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

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

179 *Proof: see appendix A.4.*

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

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

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

199 **4 Numerical results:**

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

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

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

215 *4.1 The Effect of the abruptness parameter γ :*

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

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

224 [Fig. 2 about here.]

225 We notice that the larger the value of γ the smaller the value of η_F^* , i.e, there
 226 is a clear destabilizing effect produced by an increasing abruptness, the pa-
 227 rameter that governs how rapidly an increase of the weighted total population
 228 density is reflected on sex allocation going towards a more biased male distri-
 229 bution.

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

236 In figure 3(a) it is shown for $\gamma = 1$ the juvenile orbit diagram for values of η_F
 237 near bifurcation point, i.e., for each value of η_F the points in its corresponding
 238 vertical line approximate the long term behaviour of juveniles density $J(t)$,
 239 thus they approximately represent the orbit attractor. It is noticed that for low
 240 values of η_F the asymptotic behaviour corresponds to the juvenile component
 241 J^* of the positive equilibrium. The same is shown in figures 3(b) and 3(c) for
 242 $\gamma = 1.5$ and $\gamma = 2$ respectively.

243 [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

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

268 [Fig. 5 about here.]

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

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

290 [Fig. 6 about here.]

291 4.3 *The effect of the competition coefficients:*

292 As the female role is more expensive in terms of reproductive energy, we
 293 assume in this section that the female competition effect, represented by β_2 , is
 294 larger than the corresponding male effect, β_1 , on juvenile gender choice, *i.e.* ,
 295 $\beta_2 > \beta_1$. The results in previous sections are not affected by this assumption.

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

301 [Fig. 7 about here.]

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

304 [Fig. 8 about here.]

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

309 **5 Discussion and conclusion**

310 In this work we propose a model for the dynamics of an iteroparous out-
 311 crossing 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 $\eta_F \gtrsim 1$ and unstable when $\eta_M > 1$ and $\eta_F \lesssim 1$. Furthermore, 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 Higgins [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.

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

393 A Appendix:

394 A.1 Proof of proposition 3.2

395 $f_1 \leq f_2$ and $s_1 \leq s_2$ imply

$$\begin{cases} J(t+1) = sJ(t) + f_1M(t) + f_2F(t) \leq sJ(t) + f_2(M(t) + F(t)) \\ M(t+1) + F(t+1) = \pi J(t) + s_1M(t) + s_2F(t) \leq \pi J(t) + s_2(M(t) + F(t)) \end{cases} \quad (\text{A.1})$$

396 Considering now the linear system

$$\begin{cases} x(t+1) = sx(t) + f_2y(t) \\ y(t+1) = \pi x(t) + s_2y(t) \end{cases} \quad (\text{A.2})$$

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

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

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

402 Using (A.1) we have

$$\begin{cases} J(t+1) \leq sJ(t) + f_2(M(t) + F(t)) \leq sx(t) + f_2y(t) = x(t+1) \\ M(t+1) + F(t+1) \leq \pi J(t) + s_2(M(t) + F(t)) \leq \pi x(t) + s_2y(t) = y(t+1). \end{cases}$$

403 Now, for any initial condition $(J(0), M(0), F(0))$ of system (2), setting $x(0) =$
 404 $J(0)$ and $y(0) = M(0) + F(0)$ as initial conditions of system (A.2), the previous
 405 inequalities imply that $J(t) \leq x(t)$ and $M(t) + F(t) \leq y(t)$ for every $t \geq 0$,
 406 and so we obtain $\lim_{t \rightarrow \infty} (J(t), M(t), F(t)) = (0, 0, 0)$.

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

408 The condition for the existence of a positive equilibrium of system (2) (see
 409 1.2.5 in [Cushing, 1998]) is that $\eta(W) = 1$, i.e., $\eta_M(1 - \Phi(W)) + \eta_F\Phi(W) = 1$
 410 or $\Phi(W) = (1 - \eta_M)/(\eta_F - \eta_M) = \kappa$. Thus, there exists a positive equilibrium
 411 X^* of system (2) if and only if $\kappa \in (0, 1)$. In this case, $X^* = (J^*, M^*, F^*)$ is
 412 unique and can be straightforwardly calculated as the eigenvector of matrix
 413 $P(\Phi^{-1}(\kappa))$ associated to eigenvalue 1 that verifies $\Phi(J^* + \beta_1 M^* + \beta_2 F^*) = \kappa$,
 414 see (5).

415 The proof of proposition 3.3 is a direct consequence of the results in sec-
 416 tion 1.2.2 of [Cushing, 1998]. Writing $P(\eta_F, X(t)) = T(W(t)) + \eta_F \bar{F}$, where
 417 $\bar{F} = \frac{1}{\eta_F} F$, and using η_F as bifurcation parameter, theorem 1.2.4 ensures the
 418 existence of a branch of positive equilibria bifurcating from the equilibrium

419 pair $X = \bar{0}$ and $\eta_F = 1$. The condition of existence of positive equilibria
 420 $\kappa \in (0, 1)$ is equivalent to either $\eta_M < 1$ and $\eta_F > 1$ (bifurcation to the right)
 421 or $\eta_M > 1$ and $\eta_F < 1$ (bifurcation to the left). Now applying theorem 1.2.6 of
 422 [Cushing, 1998], as in our case $w^T Bv = f_2(1 - s)/\eta_F > 0$, we obtain that the
 423 bifurcation is stable if it is to the right and unstable if it is to the left, what
 424 proves the proposition.

425 A.3 Proof of proposition 3.4

426 $f_1 \leq f_2$ and $s_1 \leq s_2$ imply

$$\begin{cases} J(t+1) = sJ(t) + f_1M(t) + f_2F(t) \geq sJ(t) + f_1(M(t) + F(t)) \\ M(t+1) + F(t+1) = \pi J(t) + s_1M(t) + s_2F(t) \geq \pi J(t) + s_1(M(t) + F(t)) \end{cases} \quad (\text{A.3})$$

427 Considering now the linear system

$$\begin{cases} x(t+1) = sx(t) + f_1y(t) \\ y(t+1) = \pi x(t) + s_1y(t) \end{cases} \quad (\text{A.4})$$

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

431 On the other hand, for every $t \geq 0$, $J(t) \geq x(t)$ and $M(t) + F(t) \geq y(t)$ imply
 432 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

$$J(t+1) \geq sJ(t) + f_1(M(t) + F(t)) \geq sx(t) + f_1y(t) = x(t+1)$$

$$M(t+1) + F(t+1) \geq \pi J(t) + s_1(M(t) + F(t)) \geq \pi x(t) + s_1y(t) = y(t+1).$$

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

$$F(t+1) = \pi\Phi(W(t))J(t) + s_2F(t) \leq \pi\Phi(J(t))J(t) + s_2F(t) < \pi K_0 + s_2F(t)$$

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

$$J(t+1) = sJ(t) + f_1M(t) + f_2F(t) < sJ(t) + f_1M(t) + f_2K_1$$

$$M(t+1) = \pi(1 - \Phi(W(t)))J(t) + s_1M(t) < \pi J(t) + s_1M(t)$$

444 and thus

$$\begin{pmatrix} J(t+1) \\ M(t+1) \end{pmatrix} < \begin{pmatrix} s & f_1 \\ \pi & s_1 \end{pmatrix} \begin{pmatrix} J(t) \\ M(t) \end{pmatrix} + \begin{pmatrix} f_2K_1 \\ 0 \end{pmatrix}$$

445 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

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

$$\begin{pmatrix} J(t) \\ M(t) \end{pmatrix} < \left[\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \begin{pmatrix} s & f_1 \\ \pi & s_1 \end{pmatrix} \right]^{-1} \begin{pmatrix} f_2K_1 \\ 0 \end{pmatrix} = \frac{\eta_F K_0}{1 - \eta_M} \begin{pmatrix} 1 \\ \frac{\pi}{1 - s_1} \end{pmatrix}$$

447 what completes the proof.

448 References

- 449 Angeloni L., 2003. Sexual selection in a simultaneous hermaphrodite with
 450 hypodermic insemination: body size, allocation to sexual roles and paternity.
 451 *Animal Behaviour*, 66(3):417–426.
 452 Anthes N., Putz A., Michiels N. K., 2006. Sex role preferences, gender con-

- 453 flict and sperm trading in simultaneous hermaphrodites: a new framework.
 454 *Animal Behaviour*, 72(1):1–12.
- 455 Bateman A. J., 1948. Intra-sexual selection in drosophila. *Heredity*, 2:349–368.
- 456 Brauer V. S., Scharer L., Michiels N. K., 2007. Phenotypically flexible sex
 457 allocation in a simultaneous hermaphrodite. *Evolution*, 61(1):216–222.
- 458 Caswell H., 2001. *Matrix Population Models*. Sinauer Associates Inc., Sunder-
 459 land, Massachusetts.
- 460 Charnov E. L., 1979. Simultaneous hermaphroditism and sexual selection.
 461 *Proc Natl Acad Sci U S A*, 76(5):2480–2484.
- 462 Charnov E. L., 1982. *The theory of sex allocation*. *Monogr. Popul. Biol.*, Vol.
 463 18, Princeton University Press.
- 464 Charnov E. L., 1993. *Life History Invariants: Some Explorations of Symmetry*
 465 *in Evolutionary Ecology (Broch)*. *Oxford Series in Ecology & Evolution*,
 466 Oxford University Press.
- 467 Cushing J. M., 1998. *An Introduction to Structured Population Dynamics*.
 468 CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 71,
 469 SIAM, Philadelphia.
- 470 Cushing J. M., Li J., 1992. Intra-specific competition and density dependent
 471 juvenile growth. *Bulletin of mathematical biology*, 54:503–519.
- 472 Demetrius L., 1971. Primitivity conditions for growth matrices. *Mathematical*
 473 *Biosciences*, 12:53–58.
- 474 Fischer E. A., 1981. Sexual allocation in a simultaneously hermaphroditic
 475 coral reef fish. *Amer. Nat*, 117:64–82.
- 476 Fischer E. A., 1984. Local mate competition and sex allocation in simultaneous
 477 hermaphrodites. *The American Naturalist*, 124(4):590–596.
- 478 Getz W. M., 1996. A hypothesis regarding the abruptness of density depen-

- 479 dence and the growth rate of populations. *Ecology*, 77(7):2014–2026.
- 480 Ghiselin M., 1969. The evolution of hermaphroditism among animals. *The*
481 *Quarterly Review. of Biology*, 44:189–208.
- 482 Higgins K., Hastings A., Botsford L. W., 1997. Density dependence and age
483 structure: Nonlinear dynamics and population behavior. *The American*
484 *Naturalist*, 149(2):247–269.
- 485 Hirsch M. W., Smale S., 1974, Academic Press, Inc.: *Differential Equations,*
486 *Dynamical Systems, and Linear Algebra*. San Diego.
- 487 Hosken D. J., Stockley P. 2005. Sexual conflict. *Current Biology*, 15(14):
488 535–536.
- 489 Kon R., Saito Y., Takeuchi Y. 2004, Permanence of single-species stage-
490 structured models. *Mathematical Biology*, 48(5):515–528.
- 491 Schärer L. 2009. Tests of Sex Allocation Theory in Simultaneously
492 Hermaphroditic Animals. *Evolution*, 63(6):1377–1405.
- 493 Shuker D. M., Reece S. E., Lee A., Graham A., Duncan A. B., West S. A.,
494 2007. Information use in space and time: sex allocation behaviour in the
495 parasitoid wasp *nasonia vitripennis*. *Animal Behaviour*, 73(6):971–977.
- 496 Stewart G.W., Sun Ji-guang, 1990, Academic Press, Inc.: *Matrix Perturbation*
497 *Theory*. Boston.
- 498 West S. A., Shuker D. M., Sheldon B. C., 2005. Sex-ratio adjustment when
499 relatives interact: A test of constraints on adaptation. *Evolution*, 59(6):
500 1211–1228.
- 501 Woodward D. E., Murray J. D., 1993. On the Effect of Temperature-
502 Dependent Sex Determination on Sex Ratio and Survivorship in Crocodil-
503 ians. *Proceedings of the Royal Society B: Biological Sciences*, 252:149–155.

505	A.1 Conceptual model.	29
506	A.2 The spectral radius of the Jacobian matrix associated to the	
507	equilibrium point $X^* = (J^*, M^*, F^*)$ of system (??) is shown	
508	for three different values of $\gamma \in \{1, 1.5, 2\}$, as η_F increases from	
509	1 to 14, with $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$,	
510	$f_2 = \eta_F(1 - s)(1 - s_2)/\pi$, $\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x^\gamma}$.	
511	η_F^* represents the bifurcation value where X^* loses its stability.	30
512	A.3 Using the female inherent reproductive number η_F as	
513	a parameter, orbit diagrams for the juvenile density	
514	J are shown for system (??) with parameter values	
515	$s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$,	
516	$f_2 = \eta_F(1 - s)(1 - s_2)/\pi$, $\beta_1 = 1$ and $\beta_2 = 1.5$, initial conditions	
517	$X(0) = (J(0), M(0), F(0)) = (20, 15, 10)$, and $\Phi(x) = e^{-x^\gamma}$: (a)	
518	$\gamma = 1$, (b) $\gamma = 1.5$ and (c) $\gamma = 2$ (note the different vertical	
519	scales).	31
520	A.4 The largest Lyapunov exponents (LLE) of the orbit of system	
521	(??) is shown for three different values of $\gamma \in \{1, 1.5, 2\}$, as	
522	η_F increases from 0 to 22, with parameters values and initial	
523	conditions as in Fig. ?? . η_F^∞ represents the largest value of η_F	
524	such that the LLE of the orbit is negative for $\eta_F \leq \eta_F^\infty$.	32
525	A.5 The value η_F^* , value of η_F for which the positive equilibrium	
526	point $X^* = (J^*, M^*, F^*)$ of system (??) loses its stability,	
527	is shown for $s_1 \in [0.1, 0.9]$ and $s_2 \in [s_1, 0.9]$, with $s = 0.05$,	
528	$\pi = 0.6$, $f_1 = 0.01$, $\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x}$.	33
529	A.6 The value η_F^∞ , smallest value of η_F starting from which	
530	the corresponding orbit has a positive LLE, is shown for	
531	$s_1 \in [0.1, 0.9]$, $s_2 \in [s_1, 0.9]$, with $s = 0.05$, $\pi = 0.6$, $f_1 = 0.01$,	
532	$\beta_1 = 1$, $\beta_2 = 1.5$ and $\Phi(x) = e^{-x}$.	34
533	A.7 The value η_F^* , value of η_F for which the positive equilibrium	
534	point $X^* = (J^*, M^*, F^*)$ of system (??) loses its stability,	
535	is shown for $\beta_1 \in [0, 50]$ and $\beta_2 \in [\beta_1, 50]$, with $s = 0.05$,	
536	$s_1 = 0.25$, $s_2 = 0.4$, $\pi = 0.6$, $f_1 = 0.01$ and $\Phi(x) = e^{-x}$.	35
537	A.8 The value η_F^∞ , smallest value of η_F starting from which	
538	the corresponding orbit has a positive LLE, is shown for	
539	$\beta_1 \in [0, 50]$ and $\beta_2 \in [\beta_1, 50]$, with $s = 0.05$, $s_1 = 0.25$, $s_2 = 0.4$,	
540	$\pi = 0.6$, $f_1 = 0.01$ and $\Phi(x) = e^{-x}$.	36

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 $\Phi(x) = e^{-x}$.