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1 **Evolutionary stability under limited population growth:**
2 **Eco-evolutionary feedbacks and replicator dynamics.**

3 K. Argasinski*
4 Department of Mathematics, University of Sussex,
5 Brighton BN1 9QH, UK.
6 K.Argasinski@sussex.ac.uk, tel. 012 73877345

7 M. Broom
8 Department of Mathematics, City, University of London,
9 Northampton Square, London EC1V 0HB, UK.
10 Mark.Broom.1@city.ac.uk

11 *corresponding author

12 **Abstract**

13 This paper further develops a new way of modelling evolutionary game mod-
14 els with an emphasis on ecological realism, concerned with how ecological factors
15 determine payoffs in evolutionary games. Our paper is focused on the impact of
16 strategically neutral growth limiting factors and background fitness components
17 on game dynamics and the form of the stability conditions for the rest points
18 constituted by the intersections of the frequency and density nullclines. It is
19 shown that for the density dependent case, that at the stationary state, the
20 turnover coefficients (numbers of newborns per single dead adult) are equal for
21 all strategies. In addition, the paper contains a derivation of the EESS (eco-
22 evolutionarily stable states) conditions, describing evolutionary stability under
23 limited population growth. We show that evolutionary stability depends on the
24 local geometry (slopes) of the intersecting nullclines. The paper contains exam-
25 ples showing that density dependence induces behaviour which is not compatible
26 with purely frequency dependent static game theoretic ESS stability conditions.
27 We show that with the addition of density dependence, stable states can become
28 unstable and unstable states can be stabilised. The stability or instability of
29 the rest points can be explained by a mechanism of eco-evolutionary feedback.

30 **1 Introduction**

31 Current developments in evolutionary biology emphasize the role of relationships
32 between selection mechanisms and ecological factors (Schoener 2011, Morris

2011, Pelletier et al. 2009). This perspective is very interesting from the point
of view of formal modelling, which can contribute to this research program not
only by quantitative predictions, but also by rigorous conceptualization of the
analyzed mechanisms. Thus, this direction should also be considered in the
development of modelling approaches such as evolutionary game theory. Recent
developments in this field, focused on the realistic modelling of the turnover of
individuals (i.e. the dynamics of the replacement of the dying adult individuals
by newly introduced juveniles), can be useful in pursuing this goal. In this study
we will analyze the interplay between selection dynamics of strategy frequencies
and the ecological dynamics shaping the population size. In addition we will
investigate the relationships between game theoretic equilibrium conditions and
nullclines of the selection and ecological dynamics.

In the classical approach to evolutionary game theory (Maynard Smith 1982,
Hofbauer and Sigmund 1988, 1998), a well-mixed population with clonal repro-
duction and no mutation evolves under natural selection. The strategies are
heritable phenotypic traits or different behavioral patterns and payoff functions
describing their fitness. The merits and limitations of such an approach are
discussed in Maynard Smith (1982) (for interesting general work based upon
similar principles but with an infinite strategy set, see for example Gorban,
2007; Meszina et al., 2006; Oeschler and Riedel, 2001). An abstract “fitness”
is expressed as an infinitesimal growth rate r and described in undefined “units”,
which are the currency in which evolutionary “costs” and “benefits” are counted.
The basic model of the game dynamics of k competing strategies are replicator

dynamics, defined on the $k - 1$ dimensional simplex. Then $q_i = n_i / \sum_j n_j$ (n_i is the number of carriers of the i -th strategy) is the frequency of the i -th strategy and $r_i(q)$ is its payoff function:

$$\dot{q}_i = q_i \left(r_i(q) - \sum_j r_j(q) \right) \quad \text{for } i = 1, \dots, k - 1. \quad (1)$$

45 In the classical approach to evolutionary game modelling there is no explicit
 46 analysis of the impact of limitations of the population size. In more complex
 47 approaches (Cressman 1992, Cressman et al 2001, Cressman and Garay 2003,
 48 Argasinski 2006) density dependence has been taken into consideration. The
 49 specific case of selectively neutral density dependence, which means that the
 50 growth suppression acts on all strategies in the same way, was analyzed in
 51 Argasinski and Kozłowski (2008). It was shown there that the classical approach
 52 (1) can be problematic, when growth limitation, related to the logistic equation,
 53 is implemented. The dynamics stop when the carrying capacity is reached. This
 54 is caused by the fact that both birth and death rates are suppressed, leading
 55 to a population of immortal individuals. This problem can be solved by using
 56 the assumption that only the birth rate is suppressed by juvenile recruitment
 57 survival, which leads to a generalization of the replicator dynamics completed
 58 by the equation for the population size (Argasinski and Broom, 2012). In this
 59 approach payoffs are described explicitly as demographic vital rates (mortality
 60 and fertility), not as an abstract fitness. Thus assume that $W_i(q)$ is the fertility
 61 function, suppressed by the density dependent juvenile recruitment function
 62 $(1 - n/K)$ (where $n = \sum_j n_j$ and K is the carrying capacity describing the
 63 maximal population load, Hui, 2006), and $d_i(q) = 1 - s_i(q)$ is the adult mortality.

64 This leads to the following:

$$\begin{aligned} \dot{q}_i &= q_i \left[\left(W_i(q) - \sum_j W_j(q) \right) \left(1 - \frac{n}{K} \right) - \left(d_i(q) - \sum_j d_j(q) \right) \right] \quad \text{for } i = 1, \dots, k \quad (2) \\ \dot{n} &= n \left(\left(1 - \frac{n}{K} \right) \sum_j W_j(q) - \sum_j d_j(q) \right), \quad (3) \end{aligned}$$

65

66 where the bracketed term from (1) splits into two brackets describing differ-
67 ences in fertilities and mortalities. The replicator system (2) is completed by
68 equation (3) describing the changes of the population size caused by selection of
69 the strategies. A similar method was applied in a number of papers (Hauert et
70 al., 2006; Hauert et al., 2008; Argasinski and Kozłowski, 2008; Zhang and Hui,
71 2011; Argasinski and Broom, 2012; Huang et al., 2015; Gokhale and Hauert,
72 2016). In this approach population size does not converge to an arbitrary car-
73 rying capacity as in many models (for example Cressman and Krivan, 2010;
74 Krivan, 2013) but to a dynamic equilibrium between mortality and fertility
75 (this is often called an emergent carrying capacity, Bowers et al., 2003; Sieber
76 et al., 2014). The general selective properties of this approach were presented in
77 Argasinski and Broom (2013), where the simplified version of (2,3) with payoffs
78 as constants was analyzed. It was shown there that when the population reaches
79 the close neighbourhood of the population size equilibrium (nullcline of the equa-
80 tions for n), then newborns form the pool of candidates from which individuals
81 replacing the dead adults in their nest sites will be drawn. This mechanism
82 was termed the "nest site lottery". This process promotes the strategies that

83 maximize the number of newborns replacing each single dying adult (termed
84 "turnover coefficient"), however among strategies maximizing this quantity it is
85 profitable to maximize the mortality (the number of dead adults) and thus also
86 the number of newborns replacing them. Therefore, we have a two stage fitness
87 measure.

88 The previous paper, Argasinski and Broom (2012), was focused on the de-
89 scription of the above approach using demographic parameters, mortality as the
90 probability of death (or equivalently survival) and fertility as per capita number
91 of offspring. This allows for a description of the abstract and unclear parame-
92 ters such as "fitness" or "growth rate" by clear and measurable parameters. In
93 addition, the new approach is focused on the detailed description of the struc-
94 ture of cause-effect chains underlying the particular interactions. For example,
95 the modelled interaction described by the game theoretic structure can be com-
96 posed of several mortality and fertility stages following each other. This aspect
97 can be illustrated by the simplest case of a single pre-reproductive mortality
98 stage preceding the fertility stage. Then only survivors of the interaction can
99 reproduce, which should be incorporated into the payoff functions. Thus the
100 fertility payoffs $W_i(q)$ will be replaced by the mortality-fertility trade-off func-
101 tion $V_i(q) = \sum_j q_j s_i(e_j) W_i(e_j)$ (where e_j is the vector describing the j -th pure
102 strategy) describing the reproductive success of the survivors. The new concep-
103 tual framework was applied to the classical Hawk-Dove game to illustrate the
104 advantages over the classical approach.

105 The general framework was clarified in a second paper (Argasinski and
106 Broom, submitted) focused on the derivation of the game theoretic model from
107 the general population dynamics model also describing factors other than the
108 modelled type of interaction. For example individuals playing the Hawk-Dove
109 game during the mating conflict (the modelled focal interaction) can also be
110 killed by predators (background interactions without relation to the strategies
111 in the focal game). This leads to a model of a population of individuals playing
112 different types of games describing different interactions occurring at different
113 rates (see Appendix 1 for more details). Thus, by analogy with chemical kinetics
114 (Upadhyay, 2006), the game theoretic structure is equivalent to stoichiometric
115 coefficients describing the outcomes of a single reaction between particles (in our
116 case, interactions between individuals) and the rate of occurrence is equivalent
117 to the reaction rate. The new framework focuses on births and deaths (described
118 by separate payoff functions) as the aggregated outcomes of the physical inter-
119 actions between individuals and the elements of the environment. This is why
120 it was described as the “event-based approach” in the previous papers. This
121 approach is focused on the development of the mechanistic interpretations of the
122 theoretical notions which was emphasized by Geritz and Kisdi (2012). However,
123 in game theoretic analysis we are interested in one particular type of interac-
124 tion referred as a focal game (or a few chosen types affected by an analyzed
125 phenotypic trait in a more general case) while the aggregated outcomes of the
126 other games will constitute the background fitness. In effect (3) should be com-
127 pleted by the background fertility $\Phi(1 - n/K)$ and the background mortality

128 Ψ (see Appendix 1 for details). In addition, the “nest site lottery” operates not
129 only on the demographic outcomes of the modelled game, but on outcomes of
130 all interactions, which means that the aggregated fertility outcomes of events
131 constituting the background fitness (other games played by individuals) are also
132 the subject of this mechanism.

133 The values of the background payoffs can seriously affect the game dynam-
134 ics as shown in Argasinski and Broom (submitted). In Argasinski and Broom
135 (2012) it was also shown that under the influence of neutral density dependence,
136 the behaviour of the system is different from that in the model with unlimited
137 growth. The main difference is that in the model with unlimited growth there
138 are only equations describing the evolution of strategy frequencies, while in the
139 density dependent model there is an additional equation describing the size of
140 the population and fertilities are affected by juvenile mortality described by
141 logistic suppression. In effect, in the density dependent model, the stable fre-
142 quency becomes a function of n describing the nullcline constituting the manifold
143 of game theoretic Nash equilibria (population states with equal growth rates for
144 all strategies). In addition, the equation for the population size leads to another
145 nullcline being a function of the population composition and is affected by back-
146 ground payoffs. This nullcline has a very important biological meaning since it
147 describes the ecological equilibria, conditional on the current strategic compo-
148 sition. In the game theoretic literature it is often referred as the stationary
149 density surface (Cressman et al., 2001; Cressman and Garay, 2003a; Cressman
150 and Garay, 2003b). Thus, the global stationary states are intersections of these

151 nullclines, which can be stable or unstable.

152 The density and frequency nullclines describing the ecological and game
153 theoretic equilibria are important for the mechanistic interpretation of the phe-
154 nomenon in terms of feedbacks. New phenomena can emerge, for example the
155 existence of a stable pure Hawk solution in addition to the stable mixed equilib-
156 rium (Argasinski and Broom, 2012). The additional stable rest point is caused
157 by neutral density dependence. This paper contains a general analysis of system
158 stability and a mechanistic explanation of the interplay between the conver-
159 gence to the selection equilibrium describing the stable population composition
160 (described by the frequency nullcline) and the convergence to the ecological
161 equilibrium describing the stable population size (described by the density null-
162 cline). The study shows when the stability is fully determined by the behaviour
163 along the nullclines and the problem can be reduced to the static game theo-
164 retic analysis limited to simple algebraic inequalities, and when the full dynamic
165 model involving differential equations should be applied.

166 **2 Results**

167 **2.1 Selectively neutral density dependence and the con-** 168 **cept of eco-evolutionary feedback**

169 Now let us focus on the impact of selectively neutral density dependence act-
170 ing as juvenile mortality. The Hawk-Dove example presented in Argasinski and

171 Broom (2012) is a case where there is a single equation for strategy frequen-
172 cies, and the space of the population composition is the unit interval. We are
173 interested in the rest points of the system and their stability. Since we have a
174 system of two equations, one on q and one on n , we can expect two nullclines
175 obtained by calculation of the zero points of the equations.

176 **2.2 General form of the analyzed models**

177 Argasinski and Broom (2012) contains the derivation of both attracting null-
178 clines for frequency, and density equations (described below) for the Hawk-Dove
179 example, and the calculation of their intersections. However, a rigorous stabil-
180 ity analysis was limited to the case when the system is in ecological equilibrium
181 (Theorem 2 of that paper). In this paper we carry out the analysis of the gen-
182 eral stability conditions free from this restriction, find some surprising results,
183 and demonstrate that the previous analysis is insufficient to fully explain the
184 behaviour of the system in some cases.

185 In this section we start from the general dynamical system for two strategies
186 from Argasinski and Broom (2012). Assume that $q = (q_1, 1 - q_1)$ is the vector of
187 frequencies describing the strategic composition of the population. Then $V_i(q)$
188 and $s_i(q) = 1 - d_i(q)$ describe the fertility and adult survival payoffs related
189 to the focal interactions, being the subject of game theoretical analysis. The
190 logistic coefficient $(1 - \frac{n}{K})$ describes the density dependent juvenile survival
191 and background fertility Φ and mortality Ψ describe the impact of other factors
192 (such as other games involving other strategies or phenotypic traits). This leads

193 to the following general set of equations:

$$\dot{q}_1 = q_1 \left((V_1(q) - \sum_j q_j V_j(q)) \left(1 - \frac{n}{K}\right) + (s_1(q) - \sum_j q_j s_j(q)) \right), \quad (4)$$

$$\dot{n} = n \left(\left(\Phi + \sum_i q_i V_i(q) \right) \left(1 - \frac{n}{K}\right) + \sum_i q_i s_i(q) - 1 - \Psi \right), \quad (5)$$

see Appendix 1 for a detailed derivation and description of possible specific modelling approaches that can be considered with the above general framework). Then $\tilde{q}(n)$ is the nullcline of equation (4), $\tilde{n}(q)$ is the nullcline of equation (5) and their intersection is the point (\hat{n}, \hat{q}) . To analyse the underlying dynamics, the above system can be presented in the most general form without the distinction between focal interactions, described by game payoffs, and the background fertility and mortality rates. Then the system **(4,5)** can be denoted in terms of general birth and death rates, $B_1(q) = V_1(q) + \Phi \geq 0$ and $M_1(q) = 1 - s_1(q) + \Psi \geq 0$ (since fecundities and mortalities are always non-negative) describing the demographic outcomes of all interactions (including focal game payoffs and background payoffs Φ and Ψ respectively). Then $\bar{B}(q) = qB_1(q) + (1 - q)B_2(q) \geq 0$ and $\bar{M}(q) = qM_1(q) + (1 - q)M_2(q) \geq 0$ are the mean general fecundity and mortality, respectively. This leads to the system:

$$\dot{q}_1 = g(n, q) = q_1 \left((B_1(q) - \bar{B}(q)) \left(1 - \frac{n}{K}\right) - (M_1(q) - \bar{M}(q)) \right), \quad (6)$$

$$\dot{n} = f(n, q) = n \left(\bar{B}(q) \left(1 - \frac{n}{K}\right) - \bar{M}(q) \right), \quad (7)$$

194 where equation (6) is written focusing on the first strategy; an analogous equa-
195 tion would denote the frequency of the second strategy. We will also use the
196 auxiliary terms (as we see in the associated appendices), $r^u(q) = \bar{B}(q) - \bar{M}(q)$
197 which is the rate of unsuppressed growth and $L = \bar{B}(q)/\bar{M}(q)$ which is the
198 turnover coefficient.

199 **2.3 Properties of the stationary points related to the turnover** 200 **of individuals**

201 In many models $\tilde{q}(n)$ and $\tilde{n}(q)$ defined as the respective nullclines will exist (in
202 some cases they will be attracting nullclines). Expressing q as a function of n
203 (according to the implicit function theorem), the nullcline $\tilde{q}(n)$ is defined by
204 the value of q for which $g(n, q) = 0$ (the right-hand side of equation (6) is 0
205 for any given n). It is possible that there is more than one such solution, and
206 so more than one such nullcline. Similarly, expressing n as a function of q for
207 $f(n, q) = 0$, the nullcline $\tilde{n}(q)$ is defined by the value of n for which the right-
208 hand side of equation (7) is 0 for any given q . The nullclines, representing the
209 equilibria of interplaying processes (strategic selection and convergence to the
210 ecological equilibrium) will play important roles in the derivation of the static
211 game theoretic conditions (the inequalities for payoffs of the strategies that
212 should be satisfied for evolutionary stability). Those conditions will extend the
213 classical ESS concept to the ecological concept. In addition, on the nullcline
214 representing the equilibria of one process, the dynamics is determined by the
215 opposite process, for example on the density nullcline the dynamics is driven

216 by game dynamics only. The question arises, when can the behaviour of the
217 complicated dynamical system be described by a set of algebraic inequalities?

218 Now let us analyze the properties of the stationary points of systems of
219 this type. In classical evolutionary game theory, at the stationary points (a
220 Nash equilibria) there is equality of fitness among all strategies present in the
221 population; we note that this property becomes trivial after the addition of
222 density dependence since all growth rates are equal to zero at the stationary
223 states. The new framework presented here is defined with respect to fertility
224 and mortality separately. Thus the question arises: is there a characterization
225 of the stationary points in the new theory equivalent to the equality of fitness
226 in classical theory? Here the notion of the turnover coefficient $B_i(q)/M_i(q)$,
227 describing the number of newborn candidates replacing a single dead individual,
228 should be recalled. The name “turnover coefficient” was introduced, and the
229 properties of this term were analyzed, in Argasinski and Broom (2013). Similar
230 notions can be found in older papers, for example in Rosenzweig and MacArthur
231 (1963) and Cheng (1981), and an analogous notion describing the ratio of energy
232 allocated to reproduction to mortality can be found in papers related to life
233 history theory (Taylor and Williams, 1984; Kozłowski, 1992 and 1996; Werner
234 and Anholt, 1993; Perrin and Sibly, 1993; for an overview see Kozłowski, 2006).
235 The turnover coefficient can be useful for the characterization of the stationary
236 points of the dynamics even in the general case of k strategies (not only two as
237 in the other results in this paper). This is summarized by Theorem 1 below.

238 **Theorem 1**

239 Any intersection of the nullclines is an equilibrium point, and at such an
 240 intersection:

a) The turnover coefficients of all strategies are equal:

$$\frac{B_i(q)}{M_i(q)} = \frac{B_j(q)}{M_j(q)} = \frac{\bar{B}(q)}{\bar{M}(q)}. \quad (8)$$

241 b) The focal game-specific demographic payoffs $V_i(q)$ and $s_i(q)$ satisfy the
 242 following condition

$$V_i(q) \frac{\bar{M}(q)}{\bar{B}(q)} - (1 - s_i(q)) = V_j(q) \frac{\bar{M}(q)}{\bar{B}(q)} - (1 - s_j(q)). \quad (9)$$

243

244 For a proof see Appendix 2.

245 Condition b) can be interpreted as equality of the suppressed Malthusian
 246 growth rates related to the focal game (and one divided by the population
 247 average turnover coefficient $\bar{M}(q)/\bar{B}(q) = (1 - \bar{s}(q) + \Psi)/(\bar{V}(q) + \Phi)$ is the
 248 density dependent juvenile recruitment survival probability). Note that this
 249 property should be satisfied in general for any number of strategies.

250 **Corollary 1**

If the focal game-specific turnover coefficients satisfy

$$\frac{V_i(q)}{(1 - s_i(q))} = \frac{V_j(q)}{(1 - s_j(q))} = \frac{\bar{B}(q)}{\bar{M}(q)}, \quad (10)$$

251 then the relationship from point b) is satisfied (but not necessarily vice versa).

252 Thus the condition of equality of the turnover coefficients can be extended on
 253 the focal game payoff functions, but it is not general. We can imagine stationary
 254 points where point b) from Theorem 1 is satisfied but there are no equality of
 255 the focal game turnover coefficients. A question arises about the stability of
 256 the stationary points where all strategies have equal turnover coefficient. For
 257 the general case this can be very complex, thus we start from the basic models
 258 and focus on the stability of the stationary states for two competing strategies.
 259 Consider the phase space $q \times n$, consisting of all possible values of q and n . On
 260 the nullclines $\tilde{q}(n)$ and $\tilde{n}(q)$ the right-hand side of the equations (6) and (7)
 261 respectively equals zero, and these nullclines divide the phase space into regions
 262 of growth and decline for q and n . When the right-hand side of equation (6) is
 263 negative we have that $q > \tilde{q}(n)$ is the region of decline for q .

264 We note that in the method of static game theoretic analysis presented in
 265 Argasinski and Broom (2012), the attractor population size $\tilde{n}(q)$ was substi-
 266 tuted into the right hand side of equation (6). Substitution of $\tilde{n}(q)$ into $\tilde{q}(n)$
 267 leads to the inequality $q < (>)\tilde{q}(\tilde{n})$ describing the regions of growth (decline)
 268 of q lying on the density nullcline $\tilde{n}(q)$. In Argasinski and Broom (2012) the
 269 inequality $q \leq \tilde{q}(\tilde{n})$ has the form of a quadratic equation (see Theorem 2 and
 270 Appendix 5 there). Zeros of this equation are intersections of the density and
 271 frequency attracting nullclines. Thus under the assumption of ecological equi-
 272 librium, this method shows which intersection is stable and unstable. This is
 273 a rigorous analysis but it is strictly limited to the attracting density nullcline.
 274 The question arises, when can this reasoning be extended to the neighbourhood

275 of the attracting density nullcline? There are relationships between the density
276 and frequency nullclines, but these cannot necessarily be extrapolated to the
277 general neighbourhood of their intersections. This is summarized by technical
278 Lemma 1 below, where we assume the standard notation for partial derivatives
279 $g_q = \partial g / \partial q$, $g_n = \partial g / \partial n$, $f_q = \partial f / \partial q$ and $f_n = \partial f / \partial n$ of the right hand sides
280 of equations **(6,7)**.

281 **Lemma 1**

282 Assume that the attracting density nullcline and frequency nullcline exist
283 and they intersect. Then:

284 a) if $g_q(n, \tilde{q}(n)) < 0$ (the frequency nullcline is an attractor of the frequency
285 dynamics) then if the intersection is stable (unstable) on the density nullcline,
286 it is stable (unstable) on the frequency nullcline.

287 b) if $g_q(n, \tilde{q}(n)) > 0$ (the frequency nullcline is a repeller of the frequency
288 dynamics) then if the intersection is stable (unstable) on the density nullcline,
289 it is unstable (stable) on the frequency nullcline.

290 For a proof see Appendix 3.

291 Thus in the case when the frequency nullcline is the attractor of the frequency
292 dynamics, which implies that in the density independent case it will be a stable
293 rest point, stability on the attracting density nullcline can be extrapolated to the
294 attracting frequency nullcline. This property can be useful for the derivation
295 of the static conditions for Eco-Evolutionary stability. Part b) of Lemma 1
296 shows that the general situation is more complicated. It shows that in the

297 case of an unstable frequency nullcline the selection process and the ecological
298 process will always act antagonistically. If one process will lead to stabilization
299 of the rest point the second process will act towards destabilization. Thus
300 we need some additional criteria describing this antagonistic relationship. The
301 potential complexity of behaviour will be shown by numerical examples in the
302 next section.

303 **2.4 Numerical examples and their analysis**

304 This section contains numerical simulations of the updated Hawk-Dove game
305 **(52,53)** (see Appendix 4 for details) to show the dynamics induced by the
306 eco-evolutionary feedback mechanism. For simplicity we set the background
307 fertility Φ to be equal to zero. In Theorem 2 in Argasinski and Broom (2012)
308 the local stability of intersections on the stable density nullcline for the Hawk-
309 Dove game was analyzed. However the trajectories of the population away from
310 this nullcline prior to convergence are also interesting and will have ecological
311 interpretations. In Argasinski and Broom (2012) numerical simulations showed
312 the interplay between selection dynamics and the dynamics of the population
313 size. It was shown that ecological dynamics can seriously affect the rules of
314 the game while frequency dynamics determine the population size. This was
315 mechanistically explained in that paper by the impact of density dependent
316 juvenile mortality. In this section we will focus on the relationship between
317 the trajectories, population size and the geometry of the attracting nullclines
318 $\tilde{q}(n)$ and $\tilde{n}(q)$, to reveal new details of this process which were not shown in

319 Argasinski and Broom (2012).

320 FIGURE 1 HERE

321 FIGURE 2 HERE

322 FIGURE 3 HERE

323 FIGURE 4 HERE

324 In Argasinski and Broom (2012) results of the numerical simulations em-
325 phasized the role of the intersections of both nullclines. In this paper we want
326 to show the trajectories prior to convergence. To emphasize the role of both
327 nullclines, in Figures 1-4, model parameters are chosen to set both intersections
328 at values of frequencies q close to 0 and 1. This allows us to maximize the area
329 falling between the nullclines which are very close to each other in the cases
330 when intersections are relatively close (see for example Figure 4). Some of the
331 numerical simulations support the intuition that the dynamics converge to the
332 close neighbourhood of the attracting density nullcline and then trace the equi-
333 librium size value (Figure 1). In this case the assumption from Argasinski and
334 Broom (2012) of the population taking the stable size for a given frequency is
335 justified.

336 However, this happens when both nullclines are placed at relatively high
337 densities. At lower densities the trajectory does not reach a strict neighbour-
338 hood of the attracting density nullcline (Figure 2), but converges to a surface
339 lying between the frequency and density nullclines. At very low densities the
340 trajectories converge to the attracting nullcline which is closer to the frequency

341 attracting nullcline (Figure 3). We note that this effect is suppressed by pop-
342 ulation growth. In some cases the attracting nullcline is located in the close
343 neighbourhood of the frequency attracting nullcline and traces it nearly to the
344 equilibrium (Figure 4). Thus, the assumption that frequency selection occurs
345 on the attracting density nullcline can sometimes be seriously wrong. In the
346 general case the geometry of both nullclines plays an important role in the dy-
347 namics and what happens in the region limited by those surfaces is crucial. At
348 higher densities there is a stronger convergence towards the attracting density
349 nullcline while at lower densities there is a stronger attraction towards the fre-
350 quency attracting nullcline. Therefore, the ecological equilibrium assumption is
351 a simplification of the full problem. In addition, on all figures we can observe
352 the clearly visible convergence of the trajectories to the unique invariant man-
353 ifold. However, the behaviour on these manifolds seems to be compatible with
354 the projection of the vector field on the nullcline $\tilde{n}(q)$ (and also by Lemma 1
355 on the nullcline $\tilde{q}(n)$). This suggests that the stability of the intersection can
356 be described by a simple set of algebraic equations, which will constitute the
357 Eco-Evolutionary static analysis.

358 Note that in the above examples the attracting frequency nullcline represents
359 the set of game theoretic Nash equilibria, conditional on the actual ecological
360 conditions represented by juvenile mortality, determined by population size.
361 However, we have two types of intersection representing the stationary points.
362 One is stable, thus it is compatible with the underlying purely game theoretic
363 notions, while the second is unstable. This means that a point that is a stable

364 equilibrium in the density independent case can be destabilized by ecological
 365 factors. However, we can imagine the opposite situation, where the intersection
 366 of the repelling frequency nullcline (representing the set of invasion barriers con-
 367 ditional on the actual population size) can be stabilized by the impact of density
 368 dependence. This is illustrated by the following phenomenological example:

369 **Example 1: the stabilization of a stationary point by density de-**
 370 **pendent pressure in case of the repelling frequency nullcline.**

Assume that there are two strategies, where the functions

$$B_1(q) = \left(\frac{2}{3}q^2 + \frac{2}{3}q\right) \text{ and } M_1(q) = \left(\frac{7}{9} - \frac{q}{3}\right)$$

are the fertility and mortality of the first strategy, while

$$B_2(q) = \frac{2}{3}q^2 \text{ and } M_2(q) = \left(\frac{4}{9} - \frac{q}{3}\right)$$

are those of the second. This leads to the following replicator equation (see
 Appendix 5 for detailed derivation):

$$\dot{q} = \frac{q}{3}(1-q)((2q-1)), \quad (11)$$

371 where $q = 1/2$ is the unstable rest point (invasion barrier). However when we
 372 extend this model to the density dependent case, the situation is different. We
 373 obtain:

$$\dot{q} = \frac{q}{3}(1-q)(2q(1-n/K)-1), \quad (12)$$

$$\dot{n} = \frac{4}{3}n \left(q^2(1-n/K) - \frac{1}{3} \right). \quad (13)$$

374 Calculation of the frequency and density nullclines gives:

$$375 \tilde{q} = \frac{1}{2(1-n/K)} \text{ and } \tilde{n} = \left(1 - \frac{1}{3q^2}\right) K.$$

376

377 Thus on the density nullcline juvenile mortality is $1 - \hat{n}/K = 1/3q^2$, leading
378 to the stationary state $\hat{q} = 2/3$ and the respective population size $\hat{n} = K/4$
379 (juvenile mortality is $1 - \hat{n}/K = 3/4$). This example clearly shows that the
380 frequency nullcline need not be attracting for the stability of the respective in-
381 tersection with the attracting density nullcline to hold (see Figure 5).

382 FIGURE 5 HERE

383 In this case there is no convergence of the trajectories to the unique manifold.
384 Figure 5 shows that in the neighbourhood of the nullclines there is a spiral at-
385 traction to the intersection. However, below the nullclines there is a huge region
386 of extinction and convergence to the frequency 0. This pattern is caused by the
387 fact that at low densities pressure from the frequency dynamics is stronger than
388 that from the density dynamics. Thus at low population sizes, the frequency
389 nullcline acts as the invasion barrier as in the case of unlimited growth. How-
390 ever, this is caused by the decrease of the population size induced by the density
391 dynamics. This leads to an emergence of the additional boundary between the
392 basins of attraction. This boundary cannot be justified by any existing condition
393 for evolutionary stability. Thus the dynamics can produce patterns that cannot
394 be classified by known static ESS notions, and in this case the full analysis of
395 the dynamic model should be carried out.

396 **2.5 General stability conditions**

The examples presented above suggest the necessity of a general stability analysis. This will enable extrapolation of the stability analysis of the Hawk-Dove example from Argasinski and Broom (2012) to the general neighbourhood of the intersection, not limited to the attracting density nullcline. Coordinates of the intersection are (\hat{n}, \hat{q}) . Stability along the attracting density nullcline is described by the directional derivative (a total derivative expressed in terms of our four partial derivatives)

$$\frac{dg(\tilde{n}(q), q)}{dq} = g_q(\hat{n}, \hat{q}) - g_n(\hat{n}, \hat{q}) \frac{f_q(\hat{n}, \hat{q})}{f_n(\hat{n}, \hat{q})}. \quad (14)$$

397

398 Below, by application of standard linearization methods we will derive the
399 general stability conditions for intersections of the nullclines:

400 **Theorem 2**

401 If for the system described by equations (6) and (7), nullclines $\tilde{q}(n)$ and $\tilde{n}(q)$
402 exist, then:

The intersection is stable if the following EESS (Eco-Evolutionarily Stable State) conditions are satisfied:

a)

$$g_q(\hat{n}, \hat{q}) < |f_n(\hat{n}, \hat{q})|, \quad (15)$$

b)

$$\frac{dg(\tilde{n}(q), q)}{dq} < 0. \quad (16)$$

403

404 For a proof see Appendix 6.

405 **A** question arises about the interpretation of the above stability conditions.
406 Condition a) means that attraction to the density nullcline is stronger than
407 repulsion from the frequency nullcline. This means that in the antagonistic
408 relationship between selection and the ecological process indicated by point b)
409 of Lemma 1, the stabilizing ecological process should be stronger. If the null-
410 cline $\tilde{q}(n)$ is attracting (which means that it consists of stable Nash equilibria)
411 then condition a) is satisfied automatically. Condition b) is equivalent to sta-
412 bility along the density nullcline $\tilde{n}(q)$. Thus for the attracting nullcline $\tilde{q}(n)$
413 the stability of the global equilibrium is equivalent to the behaviour along the
414 nullcline $\tilde{n}(q)$. This justifies the static ESS analysis based on the substitution of
415 the ecological equilibrium $\tilde{n}(q)$ to the dynamics and the analysis of signs of the
416 right hand sides of the q equations as in Theorem 2 in Argasinski and Broom
417 (2012). Note that, according to Lemma 1, condition b) implies instability on
418 the repelling nullcline $\tilde{q}(n)$, representing the game theoretic invasion barriers.
419 However, in this case, if the attraction towards nullcline $\tilde{n}(q)$ is stronger than
420 the repulsion from nullcline $\tilde{q}(n)$, then the intersection can be stable despite
421 this. Note that for the intersection of the repelling frequency nullcline and den-
422 sity nullcline from Example 1, both conditions are satisfied (see Appendix 7
423 for the detailed calculations). According to Lemma 1, satisfying condition b)
424 implies attraction towards the intersection along the attracting frequency null-

425 cline $\tilde{q}(n)$ and repulsion if the frequency nullcline $\tilde{q}(n)$ is repelling. Example
 426 1 supports the results from Lemma 1. The projection of the flow orthogonal
 427 to the density nullcline (see arrows on Figure 6) shows that it will be stable,
 428 while on the frequency nullcline it will be unstable. However the general spiral
 429 dynamics cannot be reduced to convergence along one of the nullclines.

Note that the flow is horizontal on the frequency nullcline and vertical on the density nullcline. Thus the orthogonal projection of the flow is determined by the slope of the respective nullcline. We shall assume that in the neighbourhood of the intersection functions g and f are locally invertible, so that there is a 1-1 correspondence between n and q , at least in the vicinity of a root. This will be true for essentially any biological system, as situations where this is not so, corresponding to nullclines slopes with zero or infinite gradient, are examples of so-called *non-generic games*, see e.g. Broom and Rychtar, 2013). This means that both stability conditions can be interpreted in terms of slopes of the nullclines. The slope of the frequency nullcline is

$$U_q = \frac{dg(g^{-1}(0, \hat{q}), \hat{q})}{dq}, \quad (17)$$

and the slope of the size nullcline is

$$U_n = \frac{df(f^{-1}(0, \hat{q}), \hat{q})}{dq}. \quad (18)$$

430 Then the above conditions are equivalent to the following lemma:

431 **Lemma 2**

432 Provided that the inverses from equations (17) and (18) exist, Condition
 433 a) from Theorem 2 is clearly satisfied when $g_q(\hat{n}, \hat{q}) \leq 0$. For $g_q(\hat{n}, \hat{q}) > 0$, we
 434 require the following condition to be satisfied:

$g_n(\hat{n}, \hat{q})$ is negative (positive) and :

$$U_q < (>) \frac{\hat{n}}{\hat{q}(B_1(\hat{q})/\bar{B}(\hat{q}) - 1)}. \quad (19)$$

435

436 Condition b) is satisfied when $g_n(\hat{n}, \hat{q})$ is negative (positive) and:

$$U_n > (<) U_q. \quad (20)$$

437

438 For a proof see Appendix 8.

439 Note that the right hand side of the condition (19) depends only upon the
 440 fertility stage; the mortality payoffs are not present there.

441 **2.6 Game theoretic notions revealed by dynamic stability** 442 **conditions**

443 Now let us take the game theoretic perspective and analyze the above statements
 444 from the strategic point of view. To do this we should describe the above
 445 conditions in terms of general payoff functions explicitly and then we should
 446 extract the focal game payoffs from the background payoffs in the conditions
 447 obtained. The following notion known from economics is useful:

Definition 1: The semi-elasticity of the function $f(x)$ at point x is

$$\frac{df(x)/dx}{f(x)}, \quad (21)$$

448 which describes the change in $f(x)$ scaled by its absolute value.

449 This concept can be generalized to the case of convex combination of func-
450 tions $\sum q_i f_i(x)$, as follows.

Definition 2: The partial semi-elasticity of the function $f_i(x)$ with respect
to $\sum q_i f_i(x)$ at point x is

$$\frac{df_i(x)/dx}{\sum q_i f_i(x)}, \quad (22)$$

451 which describes the equivalent scaled change in $\sum q_i f_i(x)$ caused by the
452 component $f_i(x)$.

453 Now we can derive the general stability conditions for the dynamics in the
454 form (6,7) expressed in terms of general demographic payoffs. This is done in
455 the following theorem

456 **Theorem 3**

Condition a) has the form:

$$\hat{q} \left(\frac{(B'_1(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M'_1(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) < \frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})} - 1, \quad (23)$$

457 where $\frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})} - 1$ describes the reproductive surplus, following Definition 1, $\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})}$
458 is the semi-elasticity of \bar{B} and following Definition 2, $\frac{B'_1(\hat{q})}{\bar{B}(\hat{q})}$ is the partial semi-
459 elasticity of \bar{B} with respect to B_1 (for mortalities $M_1(\hat{q})$ and $\bar{M}(\hat{q})$ we have
460 analogous notions).

Condition b) is satisfied when the semielasticities in payoffs satisfy the following condition:

$$\left(\frac{B_1'(\hat{q})}{B_1(\hat{q})} - \frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} \right) - \left(\frac{M_1'(\hat{q})}{M_1(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) < 0. \quad (24)$$

461 where $\frac{B_1'(\hat{q})}{B_1(\hat{q})}$ is the semi-elasticity of B_1 (similarly for M_1).

462 For a proof see Appendix 9.

Note that both conditions resemble the bracket structure of the right hand side of the replicator equations, or rather derivatives of it. The difference is that both conditions are expressed in terms of semi-elasticities and partial semi-elasticities instead of standard derivatives of payoff functions. The above conditions are not expressed with respect to the focal games payoffs. Thus they should be extracted from general payoffs $B_1(\hat{q})$ and $M_1(\hat{q})$. In effect we obtain: $B_1(q) = V_1 + \Phi \geq 0$ and $M_1(q) = 1 - s_1 + \Psi$, so that inequalities (23) and (24) become

$$\hat{q} \left(\frac{(V_1'(\hat{q}) - \bar{V}'(\hat{q}))}{\bar{V}(\hat{q}) + \Phi} + \frac{(s_1'(\hat{q}) - \bar{s}'(\hat{q}))}{1 - \bar{s}(\hat{q}) + \Psi} \right) < \frac{\bar{V}(\hat{q}) + \Phi}{1 - \bar{s}(\hat{q}) + \Psi} - 1 \quad (25)$$

and

$$\left(\frac{V_1'(\hat{q})}{\bar{V}(\hat{q}) + \Phi} - \frac{\bar{V}'(\hat{q})}{\bar{V}(\hat{q}) + \Phi} \right) + \left(\frac{s_1'(\hat{q})}{1 - s_1(\hat{q}) + \Psi} - \frac{\bar{s}'(\hat{q})}{1 - \bar{s}(\hat{q}) + \Psi} \right) < 0. \quad (26)$$

463 Since the background payoffs Φ and Ψ do not depend on the traits under
 464 consideration they should not depend on the frequency of the strategies in the
 465 focal games. In effect they vanish from the derivatives of the general growth
 466 rates B and M . However they are still present in the stability conditions. Thus,

467 the stability in the particular focal type of interaction is determined by the
468 impact of other activities. Since $\Phi = \theta W_B$, $\Psi = \theta m_B$ where θ describes the
469 average number of background events between two focal events, and W_B and
470 m_B are average background events fertility and mortality, parameters Φ and
471 Ψ have a clear interpretation in the purely static *ESS* models too. This result
472 can be important for the research on animal personalities (Dall et al., 2004;
473 Wolf et al., 2007; Wolf and Weissing, 2010; Wolf and Weissing, 2012; Wolf and
474 McNamara, 2012).

475 The above results seriously alter our understanding of the self-regulation
476 mechanism in evolving populations showing the role of density dependent growth
477 limiting factors. They also suggest the relationship between the *ESS* approach
478 and some concepts already present in the debate on evolutionary ecology. We
479 can mechanistically interpret the stable and unstable intersections in terms
480 of eco-evolutionary feedback (Post and Palkovacs, 2009; Kokko and López-
481 Sepulcre, 2007).

482 In the game theoretic framework this concept can be found in Argasinski
483 ski and Kozłowski (2008), Zhang and Hui (2011) and Argasinski and Broom
484 (2012). How does this mechanism work? Perturbation in q (described by
485 Δq) induces convergence towards the respective stable size $\tilde{n}(\hat{q} + \Delta q)$ lying
486 on the attracting density nullcline $\tilde{n}(q)$ which determines the respective fre-
487 quency attractor $\tilde{q}(\tilde{n}(\hat{q} + \Delta q))$ on the frequency attracting nullcline $\tilde{q}(n)$. If
488 $|\tilde{q}(\tilde{n}(\hat{q} + \Delta q)) - \hat{q}| < |\Delta q|$ then negative feedback is induced in a sense that dy-

489 namics chase $\tilde{q}(\tilde{n}(\hat{q} + \Delta q))$ towards \hat{q} . In effect \hat{q} is stable. On the other hand, if
490 $|\tilde{q}(\tilde{n}(\hat{q} + \Delta q)) - \hat{q}| > |\Delta q|$ then a positive feedback is induced and the attractor
491 escapes from \hat{q} . In effect \hat{q} is unstable. See Figure 6 for an illustration.

492 FIGURE 6 HERE

493 **3 Discussion**

494 The results presented in this paper show the importance of the impact of growth
495 limiting factors on selection mechanisms. Using strategically neutral density de-
496 pendence, the results introduced in Argasinski and Broom (2012) and developed
497 in Argasinski and Broom (submitted) have been clarified and completed by rig-
498 orous stability conditions. We have proved that in the case when both the
499 frequency and density nullclines are attracting, results on the local stability of
500 the nullcline intersections on the attracting density nullcline can be extended
501 to the attracting frequency nullcline and vice versa (Lemma 1). In addition,
502 instead of equality of growth rates at the stable points, under the influence of
503 density dependence we have equality of the turnover coefficients (the number of
504 newborn candidates produced per single dead adult individual) as was shown
505 by Theorem 1.

506 Theorem 2 shows the stability conditions. It shows that the stability along
507 the attracting density nullcline can be extrapolated to the neighbourhood of
508 the intersection (Theorem 2 point b). Those conditions show that stability de-

509 pends on the condition similar to the classical ESS notions but expressed in
510 absolute value changes in mortalities and fertilities (Theorem 3). In addition,
511 the stability is determined by the geometry of both nullclines (Lemma 2). It
512 is shown that the dynamics can be attracted by the intersection even in the
513 case when the frequency nullcline is repelling. This can happen when attrac-
514 tion toward the density nullcline is stronger than repulsion from the frequency
515 nullcline. Numerical simulations show a variety of behaviours. Some of these
516 are against intuition based upon the dynamics concentrated on frequencies oc-
517 ccurring on the attracting density nullcline. At low densities there is a stronger
518 attraction towards the attracting frequency nullcline. This is caused by the fact
519 that at high densities differences in fertility are suppressed by density depen-
520 dent juvenile mortality described by the logistic suppression coefficient, while
521 at low densities the impact of fertility on the overall dynamics is significant.
522 Thus both nullclines are important for the dynamics. In particular, the case of
523 convergence to the intersection of the repelling frequency nullcline (which will
524 be an invasion barrier in the case with unlimited growth) with the attracting
525 density nullcline is surprising. In addition, this intriguing pattern coexists with
526 a region of extinction that cannot be easily shown by purely static analysis.

527 The phenomenon of stability and instability of the intersections can be mech-
528 anistically explained by the idea of eco-evolutionary feedbacks, a concept already
529 known in the literature (Post and Palkovacs, 2009; Kokko and López-Sepulcre,
530 2007). The stability or instability of the particular stationary frequency is
531 caused by a shift of the frequency attractor conditional on a corresponding

532 correction of the density attractor. This density attractor is conditional on
533 the perturbation of the frequency, which closes the feedback loop. This is re-
534 lated to the fact that in the framework presented in this paper outcomes of
535 interactions, described by mortality and fertility, are entries of the “nest site
536 lottery” mechanism, when the trajectory reaches a close neighbourhood of the
537 density nullcline. Thus on the density nullcline all newborns introduced to the
538 environment form a pool of candidates from which individuals that substitute
539 dead adults in their nest sites will be randomly drawn. This mechanism in-
540 duces the frequency dependent selection consisting of two stages. At the first
541 stage the strategies maximizing the turnover coefficient (number of newborns
542 produced per single dead adult within a short time interval) are selected. Then
543 every perturbation of the population state (a size decrease caused by natural
544 disaster or invasion of a significant number of suboptimal mutants) leads to an
545 increase of the frequency of the strategy with maximal mortality among those
546 with maximal turnover coefficient. This mechanism was analyzed in Argasinski
547 and Broom (2013). Note that the framework analyzed in this paper collapses to
548 the system analyzed in Argasinski and Broom (2013) under the assumption that
549 all mortality and fertility payoffs are constants. The nest site lottery mechanism
550 was analyzed only for the case when the population is in the neighbourhood of
551 the density nullcline. Thus it is an interesting open question how this mecha-
552 nism works in states far from the density nullcline. It is likely that when there
553 is a shortage of free nest sites the population is subject to a similar mechanism.
554 This fraction increases with convergence to the density attracting nullcline and

555 covers all newborns when the trajectory reaches this nullcline. The importance
556 of the generalization of the nest site lottery mechanism is supported by results
557 from this paper.

558 Our results show an example of the mechanism shaping the ecology of the
559 population according to the aggregated outcomes of particular individual in-
560 teractions of different types. This point of view relies on and provides detailed
561 theoretical justification for the classical ideas proposed by Lomnicki (1988), that
562 ecological and evolutionary reasoning should be based at the level of individuals.
563 Another important aspect of our work is the emphasis on the key role of growth
564 limiting factors in selection mechanisms. This is an important contribution to
565 current developments in evolutionary theory focused on the relationships be-
566 tween selection processes and ecological factors (Schoener, 2011; Morris, 2011;
567 Pelletier et al., 2009). The mechanism of the eco-evolutionary feedback shown
568 in this paper is a good example of the impact of ecological factors, such as
569 growth limitation, on the outcomes of the selection process. The importance
570 of growth limiting mechanisms implies that future research should investigate
571 more detailed mechanistic models of these factors, since the current literature
572 is dominated by the phenomenological logistic approach, which was also used
573 in this paper. Another important direction of research indicated by the results
574 presented in this paper is the generalization of the eco-evolutionary stability
575 conditions to the multidimensional case, describing the competition between
576 more than two strategies. It is likely that significant complexity will arise from
577 these generalizations, which in turn could reveal novel ecological predictions.

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700 **Table 1: Important symbols.**

n	population size
q_i	frequency of the i -th strategy
K	carrying capacity (maximal environmental load)
$W_i(q)$	fertility payoff of the i -th strategy
$s_i(q)$	prereproductive survival payoff function of the i -th strategy
$V_i = \sum_j q_j s_i(e_j) W_i(e_j)$	mortality-fertility trade-off function (example of fertility payoff)
τ_1	rate of occurrence (intensity) of the game event
τ_2	rate of occurrence of the background event
W_B	average background event fertility
$m_B = 1 - b_B$	average background event mortality
$\theta = \tau_2/\tau_1$	average number of background events between two focal events
$\Phi = \theta W_B$	rate of the average background fertility
$\Psi = \theta m_B$	rate of background mortality
⁷⁰¹ $g(n, q)$	Function describing the right hand side of the frequency equation
$f(n, q)$	Function describing the right hand side of the population size equation
$V_1(q)$	General fertility payoff related to the focal events of the first strategy
$s_1(q)$	General survival payoff related to the focal events of the first strategy
$B_1(q) = V_1 + \Phi$	General fertility factor of all events of the first strategy
$M_1(q) = 1 - s_1 + \Psi$	General mortality factor of all events of the first strategy
$\bar{B}(q) = qB_1 + (1 - q)B_2$	Average fertility factor
$\bar{M}(q) = qM_1 + (1 - q)M_2$	Average mortality factor
$r^u(q) = \bar{B}(q) - \bar{M}(q)$	Rate of the unsuppressed growth
S	Hawk-Dove example survival payoff matrix
$F = WP$	Hawk-Dove example fertility payoff matrix
$d = 1 - s$	probability of death during a contest in a Hawk-Dove game
$\tilde{q}(n)$	frequency nullcline
$\tilde{n}(q)$	density nullcline

702 Appendix 1

703 This section contains some details from Argasinski and Broom (2012) and Ar-
704 gasinski and Broom (submitted). $W_i(q)$ is the focal game fertility payoff function
705 of the i -th strategy, $s_i(q)$ is the pre-reproductive mortality payoff function of the
706 i -th strategy. Further, $V_i(q) = \sum_j q_j s_i(e_j) W_i(e_j)$ is the mortality-fertility trade-
707 off function for the case when s_i and W_i are frequency dependent, although more
708 complicated functions are also possible (Argasinski and Broom, 2012). In Ar-
709 gasinski and Broom (2012) the classical approach to the background fitness was
710 generalized to the case of two demographic payoff functions. It was described
711 by the phenomenological elements of the payoffs (additive fertility and mul-
712 tiplicative post-reproductive mortality), which affect the dynamics. However,
713 in this paper we will use an alternative approach from Argasinski and Broom
714 (submitted) which has clear mechanistic interpretation and better describes the
715 distribution of the background interactions in time. Assume that the modelled
716 interaction described by the game theoretic structure occurs at intensity τ_1 .
717 Other events shaping the fertility and mortality occur at the separate intensity
718 τ_2 and during the average background event W_B newborns are produced and
719 adult individuals die with probability m_B . This leads to the following general
720 growth equations:

$$\dot{n}_i = n_i \tau_1 V_i(q) \left(1 - \frac{n}{K}\right) - n_i \tau_1 (1 - s_i(q)) + n_i \tau_2 W_B \left(1 - \frac{n}{K}\right) - n_i \tau_2 m_B \quad (27)$$

721

$$= n_i \tau_1 \left(V_i(q) \left(1 - \frac{n}{K} \right) - (1 - s_i(q)) + \frac{\tau_2}{\tau_1} W_B \left(1 - \frac{n}{K} \right) - \frac{\tau_2}{\tau_1} m_B \right). \quad (28)$$

722

723 Then by change of timescale $\tilde{t} = t\tau_1$ and substitution using $\Phi = \frac{\tau_2}{\tau_1} W_B$ and

724 $\Psi = \frac{\tau_2}{\tau_1} m_B$, we obtain:

$$\dot{n}_i = n_i \left[V_i(q) \left(1 - \frac{n}{K} \right) - (1 - s_i(q)) + \Phi \left(1 - \frac{n}{K} \right) - \Psi \right], \quad (29)$$

which leads to the general system of equations (4,5) and to the nullcline for population size:

$$\tilde{n}(q) = K \left(1 - \frac{\Psi + 1 - \sum_i q_i s_i(q)}{\Phi + \sum_i q_i V_i(q)} \right). \quad (30)$$

725 It is attracting since the right hand side of (5) is a decreasing function
 726 of n . Thus the game theoretic stage can be very complex, since payoffs in a
 727 modelled game V_i and s_i can have a structure describing several causal stages
 728 of the interaction (as was shown in Argasinski and Broom 2012). However
 729 all models of the basic and extended types can be presented in the following
 730 simplified general form, which are equations (4) and (5) where $V_i(q)$ and $s_i(q)$
 731 describe potentially complicated fertility and mortality payoffs related to the
 732 focal interactions. This allows us to keep a distinction between focal game and
 733 background payoffs.

734 **Appendix 2**

735 Proof of Theorem 1:

736 Assume a generalized n -dimensional version of system (6,7), where we have
 737 n individual strategies and the frequency dynamics defined on $n - 1$ dimensional
 738 strategy simplex is completed by the following single equation for the population
 739 size:

$$\frac{dn}{dt} = f(n, q) = n \left(\bar{B}(q) \left(1 - \frac{n}{K} \right) - \bar{M}(q) \right). \quad (31)$$

The bracketed term in equation (31) equals zero when

$$\left(1 - \frac{n}{K} \right) = \frac{\bar{M}(q)}{\bar{B}(q)}, \quad (32)$$

which leads to

$$\tilde{n} = \left(1 - \frac{\bar{M}(q)}{\bar{B}(q)} \right) K. \quad (33)$$

740 Here we substitute this expression into equation (6), when the right hand
 741 side becomes

$$\frac{dq_i}{dt} = q_i \left((B_i(q) - \bar{B}(q)) \left(\frac{\bar{M}(q)}{\bar{B}(q)} \right) - (M_i(q) - \bar{M}(q)) \right) \quad (34)$$

$$= q_i \bar{M}(q) \left(\frac{B_i(q)}{\bar{B}(q)} - \frac{M_i(q)}{\bar{M}(q)} \right). \quad (35)$$

Thus at the intersection of the nullclines the bracketed term from equation
 (35) should be equal to zero. This is satisfied when

$$\frac{B_i(q)}{M_i(q)} = \frac{\bar{B}(q)}{\bar{M}(q)}, \quad (36)$$

742 which means that the turnover coefficients of all strategies should be equal.

743 Thus point a) is proved.

Now focus on the role of the outcomes of the focal game. Then equality of the turnover coefficients can be described as

$$\frac{V_i(q) + \Phi}{1 - s_i(q) + \Psi} = \frac{V_j(q) + \Phi}{1 - s_j(q) + \Psi} = \frac{\bar{B}(q)}{\bar{M}(q)}. \quad (37)$$

744 Assume auxiliary notation $d_i(q) = 1 - s_i(q)$. This implies that when $V_i(q) -$
745 $V_j(q) = x_V$ and $d_i(q) - d_j(q) = x_s$, we have

$$\frac{V_i(q) + \Phi}{d_i(q) + \Psi} = \frac{V_i(q) + x_V + \Phi}{d_i(q) + x_s + \Psi} \Rightarrow \quad (38)$$

$$\frac{V_i(q) + \Phi}{d_i(q) + \Psi} x_s = x_V. \quad (39)$$

Thus from (37) and (39) we have

$$V_i(q) - V_j(q) = \frac{\bar{B}(q)}{\bar{M}(q)} (d_i(q) - d_j(q)) \quad (40)$$

leading to the following general condition which can be interpreted as equality of focal game specific suppressed Malthusian growth rates:

$$V_i(q) \frac{\bar{M}(q)}{\bar{B}(q)} - d_i(q) = V_j(q) \frac{\bar{M}(q)}{\bar{B}(q)} - d_j(q). \quad (41)$$

746 This is the proof of point b).

747 **Appendix 3**

748 Proof of Lemma 1:

Assume that the dynamics is limited to the frequency attracting nullcline. If we substitute the equilibrium of the size equation into the frequency equation then the derivative of the right side of the frequency equation can be presented

as the directional derivative along the vector $(\frac{d\tilde{n}}{dq}, 1)$ tangent to the attracting density nullcline. Since $f : (n, q) \rightarrow z$ is the function assigning the value of the derivative z to each pair (n, q) describing the population state, then the inverse function $f^{-1} : (z, q) \rightarrow n$ assigns size n to the respective pair (z, q) and can be denoted as $n(z, q)$. On the nullcline $\tilde{n}(q)$ we have $z = 0$, and thus we obtain the derivative $\frac{d\tilde{n}}{dq}$ in the following way. Since along the nullcline $f(\tilde{n}(q), q) = 0$ the derivative of it will also be equal to zero, leading to:

$$\frac{df(\tilde{n}(q), q)}{dq} = f_q + f_n \frac{d\tilde{n}(q)}{dq} = 0 \Rightarrow \quad (42)$$

$$\frac{d\tilde{n}(q)}{dq} = -\frac{f_q}{f_n}. \quad (43)$$

Therefore, for the intersection point it will describe the derivative of the attracting density nullcline \tilde{n} (a level set with $z = 0$). Thus the directional derivative mentioned above can be presented as:

$$\frac{dg(\tilde{n}(q), q)}{dq} = g_q - g_n \frac{f_q}{f_n}. \quad (44)$$

If we assume that the dynamics is limited to the attracting density nullcline, then by analogous derivation we can obtain:

$$\frac{df(n, \tilde{q}(n))}{dn} = f_n - f_q \frac{g_n}{g_q}. \quad (45)$$

749 Note that the former derivative is just the latter multiplied by $\frac{g_q}{f_n}$. Since
 750 f_n is always negative, the sign of this factor is determined by the sign of g_q .
 751 Thus if $g_q < 0$ (the frequency nullcline is attracting) then if the intersection
 752 is stable (unstable) on the density nullcline then it is stable (unstable) on the
 753 frequency nullcline. However, if $g_q > 0$ (the frequency nullcline is repelling)

754 then if the intersection is stable (unstable) on the density nullcline then it is
 755 unstable (stable) on the frequency nullcline.

756 Appendix 4

A Hawk-Dove example was used to illustrate the above, using the payoff matrices
 S (the mortality payoff) and P , where the fertility matrix is $F = WP$, as follows

$$S = \left(\begin{array}{c|cc} & H & D \\ \hline H & s & 1 \\ D & 1 & 1 \end{array} \right), \quad P = \left(\begin{array}{c|cc} & H & D \\ \hline H & 0.5 & 1 \\ D & 0 & 0.5 \end{array} \right),$$

757

758

where $s < 1$ is the survival probability of a fight between Hawks, and the
 fertility matrix containing the expected number of newborns W produced from
 the interaction. When we substitute the above matrix payoffs into equations
 (4) and (5) as the general fertility payoff $V(v, q) = vS \cdot Pq^T$ and the pre-
 reproductive survival payoff $s(v, q) = vSq^T$ respectively (where \cdot is elementwise
 multiplication of matrix entries) leading to strategy payoffs $V_i(v, q) = e_i S \cdot Pq^T$
 and $s_i(v, q) = e_i Sq^T$. In effect we obtain the following system:

$$\dot{q}_h = q_h \left(\left(1 - \frac{n}{K} \right) W (e_1 S \cdot Pq^T - qS \cdot Pq^T) + (e_1 Sq^T - qSq^T) \right) \quad (46)$$

and

$$\dot{n} = n \left((\Phi + qS \cdot Pq^T W) \left(1 - \frac{n}{K} \right) + qSq^T - 1 - \Psi \right), \quad (47)$$

759 where the matrix operations are as follows (Argasinski Broom 2012):

$$e_1 S q^T = s q_h + 1 - q_h = q_h (s - 1) + 1, \quad (48)$$

$$e_1 S \cdot P q^T = 0.5 s q_h + 1 - q_h, \quad (49)$$

$$q S q^T = q_h (q_h (s - 1) + 1) + (1 - q_h) = 1 - q_h^2 (1 - s), \quad (50)$$

$$q S \cdot P q^T = q_h (0.5 s q_h + 1 - q_h) + 0.5 (1 - q_h)^2 = 0.5 (1 - q_h^2 (1 - s)) \quad (51)$$

After calculations and the substitution $d = 1 - s$ the following equations were obtained

$$\dot{q}_h = q_h (1 - q_h) \left(0.5 W (1 - q_h d) \left(1 - \frac{n}{K} \right) - q_h d \right), \quad (52)$$

$$\dot{n} = n \left(\left(\Phi + (1 - q_h^2 d) 0.5 W \right) \left(1 - \frac{n}{K} \right) - q_h^2 d - \Psi \right). \quad (53)$$

760 Two rest points of this system are $q_h = 0$ and 1. A nontrivial rest point,
761 which becomes the attracting nullcline for the density dependent case, (for de-
762 tailed calculation see Argasinski and Broom, submitted) is given by

$$\tilde{q}_h(n) = \frac{0.5 W \left(1 - \frac{n}{K} \right)}{d \left(0.5 W \left(1 - \frac{n}{K} \right) + 1 \right)}. \quad (54)$$

There is a stable population size at either $\tilde{n} = 0$ or the following positive rest point which is conditional on the actual hawk strategy frequency (describing the attracting nullcline parametrized by q_h)

$$\tilde{n}(q_h) = K \left(1 - \frac{1 + \Psi - (1 - q_h^2 d)}{\Phi + 0.5 W (1 - q_h^2 d)} \right). \quad (55)$$

763 The intersections of the above nullclines constitute the rest-points of the
764 system. For the above Hawk-Dove game there are two intersections. If it exists,
765 the first one is the stable mixed equilibrium which has the form

$$\hat{q}_h = (1 + \Psi) - \sqrt{(1 + \Psi)^2 - \frac{4\Psi}{d}}, \quad (56)$$

766 and the second (unstable) intersection is an invasion barrier for a stable pure
 767 Hawk equilibrium (where q_h converges to Hawk if and only if $q_h > \check{q}_h$),

$$\check{q}_h = (1 + \Psi) + \sqrt{(1 + \Psi)^2 - \frac{4\Psi}{d}}. \quad (57)$$

768 Appendix 5

769 Let us derive the replicator equations for Example 1. For the density indepen-
 770 dent case we have the following Malthusian growth rates

$$\begin{aligned} 771 \quad r_1^u(q) &= B_1(q) - M_1(q) = \frac{2}{3}q^2 + q - \frac{7}{9}, \\ 772 \quad r_2^u(q) &= B_2(q) - M_2(q) = \frac{2}{3}q^2 + \frac{q}{3} - \frac{4}{9}. \end{aligned}$$

773 This leads to the following replicator equation:

$$774 \quad \dot{q} = q(1 - q)(r_1^u(q) - r_2^u(q)) = \frac{q}{3}(1 - q)(2q - 1)$$

775 where $q = 1/2$ is the unstable rest point (invasion barrier). However when we

776 extend this model to the density dependent case, the situation is different. Then

777 the density dependent Malthusian growth rates are:

$$\begin{aligned} 778 \quad r_1(q, n) &= \left(\frac{2}{3}q^2 + \frac{2}{3}q\right)(1 - n/K) - \left(\frac{7}{9} - \frac{q}{3}\right), \\ 779 \quad r_2(q, n) &= \frac{2}{3}q^2(1 - n/K) - \left(\frac{4}{9} - \frac{q}{3}\right). \end{aligned}$$

780 This leads to the replicator dynamics:

$$781 \quad \dot{q} = q(1 - q)(r_1 - r_2) = \frac{q}{3}(1 - q)(2q(1 - n/K) - 1).$$

782 Further we obtain the following equation for the mean payoff

$$783 \quad r = qr_1 + (1 - q)r_2 = \frac{4}{3}q^2(1 - n/K) - \frac{4}{9},$$

784 leading to the differential equation for the population size:

$$\dot{n} = nr = \frac{4}{3}n \left(q^2(1 - n/K) - \frac{1}{3} \right).$$

785

786 After calculation of the frequency and density nullclines we obtain:

$$787 \quad \hat{q} = \frac{1}{2(1 - n/K)} \quad \text{and} \quad \hat{n} = \left(1 - \frac{1}{3q^2} \right) K.$$

788

789 Thus on the density nullcline juvenile mortality is $1 - n/K = 1/3q^2$. The
790 intersection of the nullclines satisfies the equation $q = \frac{3q^2}{2}$. The stationary
791 state is thus $\hat{q} = 2/3$ and respective population size $\hat{n} = \frac{K}{4}$ (juvenile mortality
792 is $1 - \hat{n}/K = \frac{3}{4}$).

793 Appendix 6

794 Here we prove Theorem 2: in particular giving a derivation of general formulae
795 for conditions a) and b) from the theorem.

We consider the system in equations (6) and (7). Standard linearization techniques can be applied. At the critical points \hat{n}, \hat{q} we have $f(\hat{n}, \hat{q}) = g(\hat{n}, \hat{q}) = 0$. We need to consider each of the derivatives of f and g with respect to each of q and n at the critical points, and in particular the Jacobian matrix

$$\begin{pmatrix} f_n(\hat{n}, \hat{q}) & f_q(\hat{n}, \hat{q}) \\ g_n(\hat{n}, \hat{q}) & g_q(\hat{n}, \hat{q}) \end{pmatrix}$$

796 and its eigenvalues. The eigenvalues of the Jacobian are found as follows.

$$\begin{vmatrix} f_n(\hat{n}, \hat{q}) - \lambda & f_q(\hat{n}, \hat{q}) \\ g_n(\hat{n}, \hat{q}) & g_q(\hat{n}, \hat{q}) - \lambda \end{vmatrix} = \lambda^2 + A\lambda + Z \quad (58)$$

797 where $A = -(f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q}))$ (which leads to the condition from point b)

798 and $Z = f_n(\hat{n}, \hat{q})g_q(\hat{n}, \hat{q}) - f_q(\hat{n}, \hat{q})g_n(\hat{n}, \hat{q})$. Thus:

$$\lambda_{1,2} = \frac{-A \pm \sqrt{A^2 - 4Z}}{2}.$$

799 For stability we need either two negative eigenvalues or two complex eigen-
800 values with negative real parts. This occurs when $A > 0$ and $Z > 0$.

801 The condition $Z > 0$ is just condition b) from Theorem 2 and can be pre-
802 sented in the form

$$803 \quad f_n(\hat{n}, \hat{q}) \left(g_q(\hat{n}, \hat{q}) - g_n(\hat{n}, \hat{q}) \frac{f_q(\hat{n}, \hat{q})}{f_n(\hat{n}, \hat{q})} \right) > 0.$$

804 Thus it is a product of $f_n(\hat{n}, \hat{q}) < 0$ and the directional derivative along
805 the attracting density nullcline $\frac{dg(\tilde{n}(q), q)}{dq}$ (see equation (44)) from Appendix
806 3. Thus the condition b) is satisfied when this derivative is negative, i.e. the
807 intersection is an attractor on the density nullcline (and, by Lemma 1, on the
808 frequency attracting nullcline). This constitutes point b).

809 The condition $A > 0$ occurs if $f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q}) < 0$. The first of these
810 two terms is negative; the second of these being negative is the condition for
811 stability in density independent models. Thus, for example, the Hawk-Dove

812 game which has a mixed ESS for its density independent version (the classical
813 game) automatically satisfies this condition. However, the condition $A > 0$ can
814 be satisfied even in the case when the frequency nullcline is repelling, which
815 implies $g_q(\hat{n}, \hat{q}) > 0$. Then this condition leads to $g_q(\hat{n}, \hat{q}) < |f_n(\hat{n}, \hat{q})|$, since
816 $f_n(\hat{n}, \hat{q})$ is negative, which is condition a) from Theorem 2. Thus our conditions
817 $A > 0$ and $Z > 0$ are precisely those from Theorem 2 as required.

818 Appendix 7

819 Below we will analyze stability in Example 1. The respective derivatives are:

$$820 \quad g_q(q, n) = \frac{1}{3} [(4q - 6q^2)(1 - n/K) - (1 - 2q)],$$

$$821 \quad g_n(q, n) = \frac{-2q^2(1 - q)}{3K},$$

$$822 \quad f_q(q, n) = \frac{4}{3} (2qn(1 - n/K)),$$

$$823 \quad f_n(q, n) = \frac{4}{3} \left(q^2 (1 - 2n/K) - \frac{1}{3} \right).$$

824 After substitution of the rest points, we obtain:

$$825 \quad g_q(\hat{q}, \hat{n}) = \frac{1}{9} > 0,$$

$$826 \quad g_n(\hat{q}, \hat{n}) = -\frac{8}{81K},$$

$$827 \quad f_q(\hat{q}, \hat{n}) = \frac{K}{3},$$

$$828 \quad f_n(\hat{q}, \hat{n}) = \frac{4}{3} \left(\frac{2}{9} - \frac{1}{3} \right) = -\frac{4}{27}.$$

829 Now the stability conditions a) $A = -(f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q})) > 0$ and b)

$$830 \quad g_q(\hat{n}, \hat{q}) - g_n(\hat{n}, \hat{q}) \frac{f_q(\hat{n}, \hat{q})}{f_n(\hat{n}, \hat{q})} < 0 \text{ from Theorem 2 should be checked.}$$

831 a) $-\left(-\frac{4}{27} + \frac{3}{27}\right) = \frac{1}{27} > 0,$

832 b) $\frac{1}{9} + \frac{8}{81K} \left(-\frac{27K}{12}\right) = -\frac{1}{9} < 0.$

833 Thus in the density dependent case the intersection of the invasion barrier
 834 and the attracting density nullcline is stable.

835 **Appendix 8**

836 Proof of Lemma 2:

837 The four derivatives, necessary for the following work, are given by the following
 838 expressions:

839 $f_n(n, q) = \bar{B}(q) \left(1 - \frac{2n}{K}\right) - \bar{M}(q),$

840 $f_q(n, q) = n \left(\bar{B}'(q) \left(1 - \frac{n}{K}\right) - \bar{M}'(q)\right),$

841 $g_n(n, q) = \frac{-q(B_1(q) - \bar{B}(q))}{K},$

842 $g_q(n, q) = \left((B_1(q) - \bar{B}(q)) \left(1 - \frac{n}{K}\right) - (M_1(q) - \bar{M}(q))\right)$

843 $+q \left((B_1'(q) - \bar{B}'(q)) \left(1 - \frac{n}{K}\right) - (M_1'(q) - \bar{M}'(q))\right),$

844 where $B_i'(q)$ is the derivative of $B_i(q)$ w.r.t q , and similarly $M_i'(q)$ is the
 845 derivative of $M_i(q)$ w.r.t q , for $i = 1, 2$ and for the non-indexed averaged payoffs.

846

For stability we require (Condition A from Appendix 6) that

$$f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q}) < 0. \quad (59)$$

On the density nullcline $f_n(\hat{n}, \hat{q}) < 0$ thus for $g_q(\hat{n}, \hat{q}) \leq 0$ the condition (59) is always satisfied. For $g_q(\hat{n}, \hat{q}) > 0$ we require $g_q(\hat{n}, \hat{q}) < -f_n(\hat{n}, \hat{q})$. Dividing (59) by $-g_n(\hat{n}, \hat{q})$ we have the following conditions, when $g_n(\hat{n}, \hat{q})$ is negative (positive),

$$-\frac{g_q(\hat{n}, \hat{q})}{g_n(\hat{n}, \hat{q})} < (>) \frac{f_n(\hat{n}, \hat{q})}{g_n(\hat{n}, \hat{q})}. \quad (60)$$

847 This leads to:

$$\frac{f_n(\hat{n}, \hat{q})}{g_n(\hat{n}, \hat{q})} = \frac{\bar{B}(\hat{q}) \left(1 - \frac{2\hat{n}}{K}\right) - \bar{M}(\hat{q})}{-\hat{q} (B_1(\hat{q}) - \bar{B}(\hat{q})) / K} = \frac{\bar{B}(\hat{q})\hat{n}}{\hat{q} (B_1(\hat{q}) - \bar{B}(\hat{q}))} = \frac{\hat{n}}{\hat{q}} / (B_1(\hat{q})/\bar{B}(\hat{q}) - 1)$$

since we know that $\bar{B}(\hat{q}) \left(1 - \frac{\hat{n}}{K}\right) - \bar{M}(\hat{q}) = 0$ meaning the original denominator reduces to $-\frac{\hat{n}}{K}\bar{B}(\hat{q})$. This leads to the condition

$$\frac{dg(g^{-1}(0, \hat{q}), \hat{q})}{dq} < (>) \frac{\hat{n}}{\hat{q}} / (B_1(\hat{q})/\bar{B}(\hat{q}) - 1), \quad (61)$$

848 leading to condition a).

Condition $Z > 0$ is satisfied when $g_n(\hat{n}, \hat{q})$ is negative (positive) if

$$-\frac{f_q(\hat{n}, \hat{q})}{f_n(\hat{n}, \hat{q})} > (<) -\frac{g_q(\hat{n}, \hat{q})}{g_n(\hat{n}, \hat{q})}$$

which is equivalent to

$$\frac{df(f^{-1}(0, \hat{q}), \hat{q})}{dq} > (<) \frac{dg(g^{-1}(0, \hat{q}), \hat{q})}{dq} \quad (62)$$

849 (this is possible when there is a 1-1 correspondence between n and q , at least
850 in the vicinity of a root).

851 **Appendix 9**

852 Proof of Theorem 3:

853 Here we give a derivation of the detailed form of the formulae A and Z leading
854 to the stability conditions expressed in terms of the payoff functions.

855 The necessary derivatives are given in Appendix 8. After substitution of the
856 stationary points \hat{q} and $\hat{n} = \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})}\right) K$, we have

857
$$f_n(\hat{n}, \hat{q}) = -r^u(\hat{q}),$$

858
$$f_q(\hat{n}, \hat{q}) = \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})}\right) K \left(\bar{B}'(\hat{q}) \left(\frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})}\right) - \bar{M}'(\hat{q})\right)$$

859
$$= \bar{M}(\hat{q}) \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})}\right) K \left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})}\right),$$

860
$$g_n(\hat{n}, \hat{q}) = \frac{-\hat{q}(B_1(\hat{q}) - \bar{B}(\hat{q}))}{K},$$

861
$$g_q(\hat{n}, \hat{q}) = \hat{q} \left((B_1'(\hat{q}) - \bar{B}'(\hat{q})) \left(\frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})}\right) - (M_1'(\hat{q}) - \bar{M}'(\hat{q})) \right)$$

862
$$= \hat{q} \bar{M}(\hat{q}) \left(\frac{(B_1'(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M_1'(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right),$$

863 since the first bracketed term equals zero.

864 Let us calculate concrete forms of conditions A and Z :

865 Condition A :

866
$$A = - \left(\bar{M}(\hat{q}) - \bar{B}(\hat{q}) + \hat{q} \bar{M}(\hat{q}) \left(\frac{(B_1'(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M_1'(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) \right) =$$

867
$$= \bar{B}(\hat{q}) - \bar{M}(\hat{q}) \left(1 + \hat{q} \left(\frac{(B_1'(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M_1'(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) \right).$$

Then $A > 0$ when

$$\frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})} - 1 > \hat{q} \left(\frac{(B'_1(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M'_1(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right). \quad (63)$$

868 Condition Z :

$$869 \quad Z = f_n(\hat{n}, \hat{q})g_q(\hat{n}, \hat{q}) - f_q(\hat{n}, \hat{q})g_n(\hat{n}, \hat{q}) \Rightarrow$$

$$\begin{aligned} 870 \quad Z &= - \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})} \right) \bar{B}(\hat{q})\hat{q}\bar{M}(\hat{q}) \left(\frac{(B'_1(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M'_1(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) \\ 871 \quad &+ \bar{M}(\hat{q}) \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})} \right) \left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) \hat{q} (B_1(\hat{q}) - \bar{B}(\hat{q})) = \\ 872 \quad &= \bar{M}(\hat{q})\hat{q} \left(1 - \frac{\bar{M}(\hat{q})}{\bar{B}(\hat{q})} \right) \left[\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) (B_1(\hat{q}) - \bar{B}(\hat{q})) - \bar{B}(\hat{q}) \left(\frac{(B'_1(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} \right. \right. \\ 873 \quad &\left. \left. - \frac{(M'_1(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) \right]. \end{aligned}$$

874 Thus $Z > 0$ if

$$\begin{aligned} 875 \quad &\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) \frac{(B_1(\hat{q}) - \bar{B}(\hat{q}))}{\bar{B}(\hat{q})} > \left(\frac{(B'_1(\hat{q}) - \bar{B}'(\hat{q}))}{\bar{B}(\hat{q})} - \frac{(M'_1(\hat{q}) - \bar{M}'(\hat{q}))}{\bar{M}(\hat{q})} \right) \Rightarrow \\ 876 \quad &\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) \frac{(B_1(\hat{q}) - \bar{B}(\hat{q}))}{\bar{B}(\hat{q})} > \left(\frac{B'_1(\hat{q})}{\bar{B}(\hat{q})} - \frac{M'_1(\hat{q})}{\bar{M}(\hat{q})} \right) - \left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) \Rightarrow \\ 877 \quad &\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) > \left(\frac{B'_1(\hat{q})}{B_1(\hat{q})} - \frac{M'_1(\hat{q})\bar{B}(\hat{q})}{\bar{M}(\hat{q})B_1(\hat{q})} \right). \end{aligned}$$

878 From equality of the turnover coefficients at the rest point we have that

$$879 \quad L = B_1(\hat{q})/M_1(\hat{q}) = \bar{B}(\hat{q})/\bar{M}(\hat{q}). \text{ This leads to } \frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})B_1(\hat{q})} = \frac{L}{B_1(\hat{q})} = \frac{1}{M_1(\hat{q})}.$$

880 Thus formula Z can be presented as:

$$881 \quad \frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} > \frac{B'_1(\hat{q})}{B_1(\hat{q})} - \frac{M'_1(\hat{q})}{M_1(\hat{q})}$$

882 In effect we obtain the classical condition but expressed in terms of semi-
883 elasticities:

$$\left(\frac{B'_1(\hat{q})}{B_1(\hat{q})} - \frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} \right) - \left(\frac{M'_1(\hat{q})}{M_1(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})} \right) < 0. \quad (64)$$

884

885 End of proof.

886 FIGURE CAPTIONS

887 Figure 1: The dynamics of a Hawk-Dove population. Initial conditions
888 ($q_h(0) = 0.02, n(0) = 250$), ($q_h(0) = 0.3, n(0) = 200$) and ($q_h(0) = 0.7, n(0) = 300$).
889 Model parameters: $W = 7, d = 0.5, \Psi = 0.01$. The trajectories converge to a
890 nullcline lying in the very close neighbourhood of the attracting density null-
891 cline and follows it converging to the mixed equilibrium $\hat{q}_h = 0.0202$. The Hawk
892 invasion barrier is $\check{q}_h = 0.9897$. Thus in a stable mixed equilibrium there is ap-
893 proximately one Hawk per 50 Doves and Hawks can take over a population if
894 their number exceeds 100 per single Dove. The general flow is indicated by the
895 arrows. Note that the orthogonal projection of the arrows lying on both null-
896 clines will show the direction, along the respective nullcline, towards the stable
897 intersection. This illustrates point a) from Lemma 1.

898 Figure 2: The dynamics of a Hawk-Dove population. Initial conditions
899 ($q_h(0) = 0.02, n(0) = 147$), ($q_h(0) = 0.3, n(0) = 147$) and ($q_h(0) = 0.6, n(0) = 147$).
900 Model parameters: $W = 7, d = 0.8, \Psi = 0.06$. At lower densities conver-
901 gence to the attracting density nullcline is not strong. The frequency attracting
902 nullcline is passed by the trajectories which converge to the attracting surface
903 placed between the density and frequency nullclines. The mixed equilibrium is
904 $\hat{q}_h = 0.0762$, while the Hawk invasion barrier is $\check{q}_h = 0.9837$. The flow indicated
905 by the arrows, as in the previous figure, supports the predictions from point a)
906 of Lemma 1.

907 Figure 3: The dynamics of a Hawk-Dove population. Initial conditions

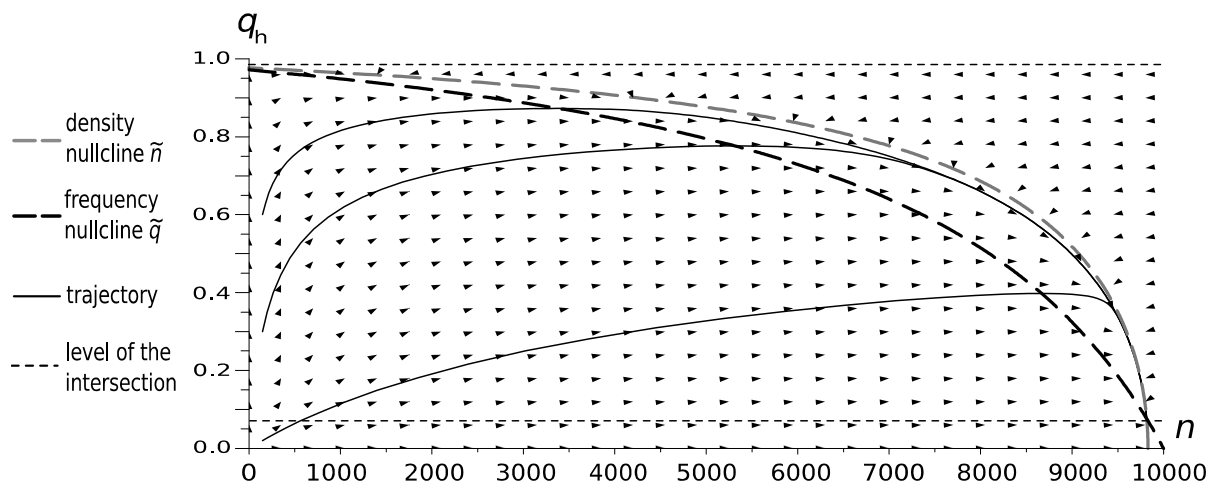
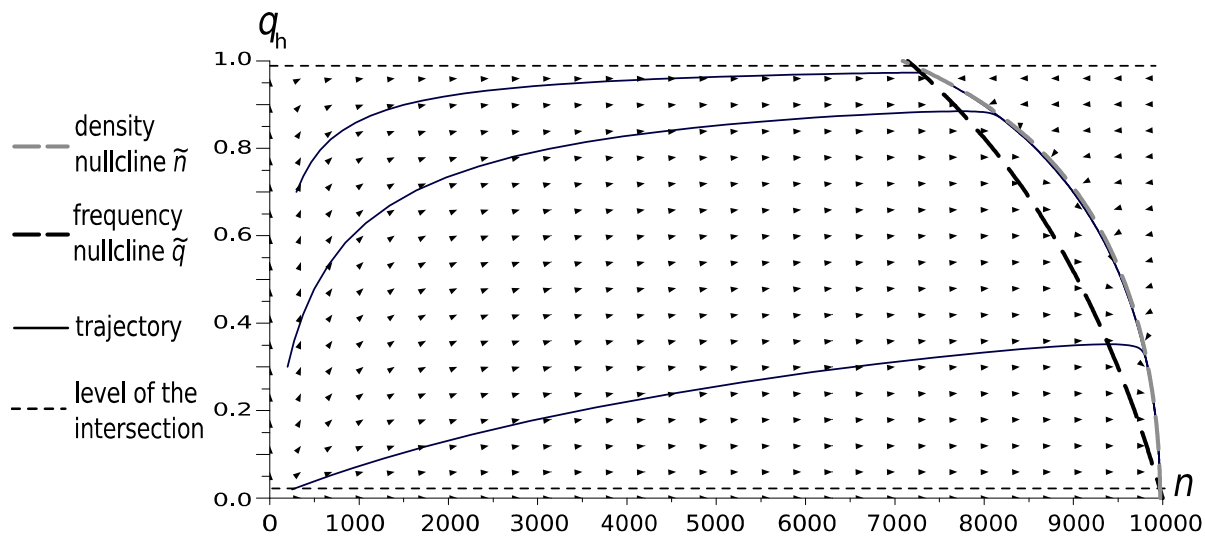
908 $(q_h(0) = 0.02, n(0) = 147)$, $(q_h(0) = 0.3, n(0) = 147)$ and $(q_h(0) = 0.89, n(0) = 147)$.
 909 Model parameters: $W = 0.8$, $d = 0.5$, $\Psi = 0.01$. In this case, the attracting
 910 nullcline lies close to the frequency nullcline at low densities but becomes closer
 911 to the density nullcline with an increase of the population size. At the beginning
 912 the trajectories pass the attracting density nullcline and converge to the stable
 913 surface in the neighbourhood of the attracting frequency nullcline, but then
 914 the trajectory leaves it slowly converging to the density nullcline. The mixed
 915 equilibrium is $\hat{q}_h = 0.0202$, while the Hawk invasion barrier is $\check{q}_h = 0.9897$. The
 916 flow indicated by the arrows, as in the previous figures, supports the predictions
 917 from point a) of Lemma 1.

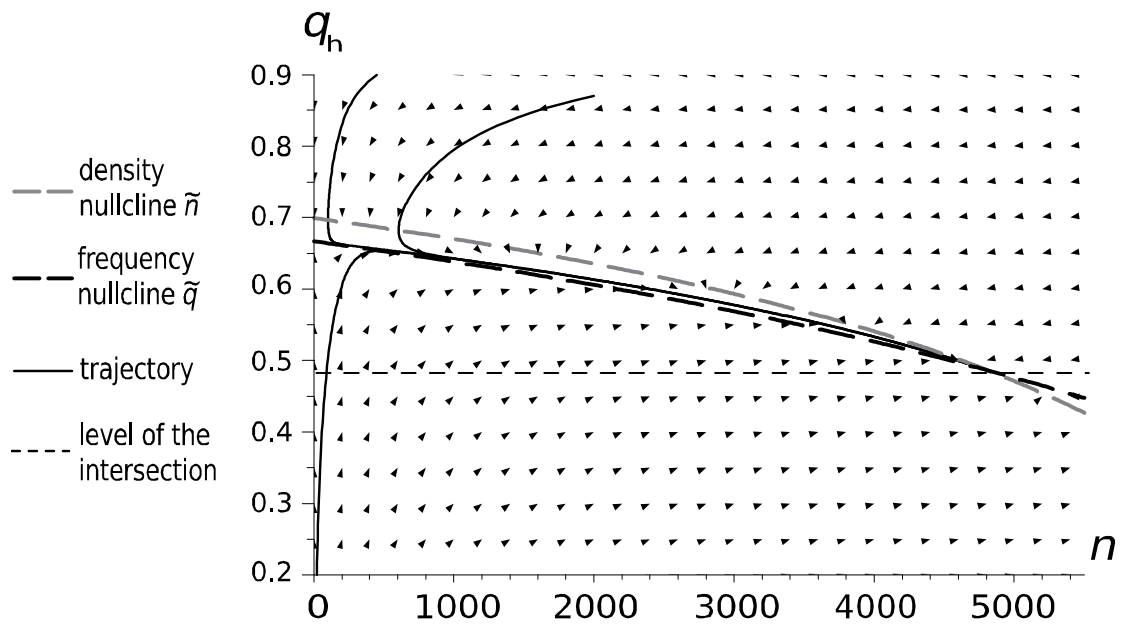
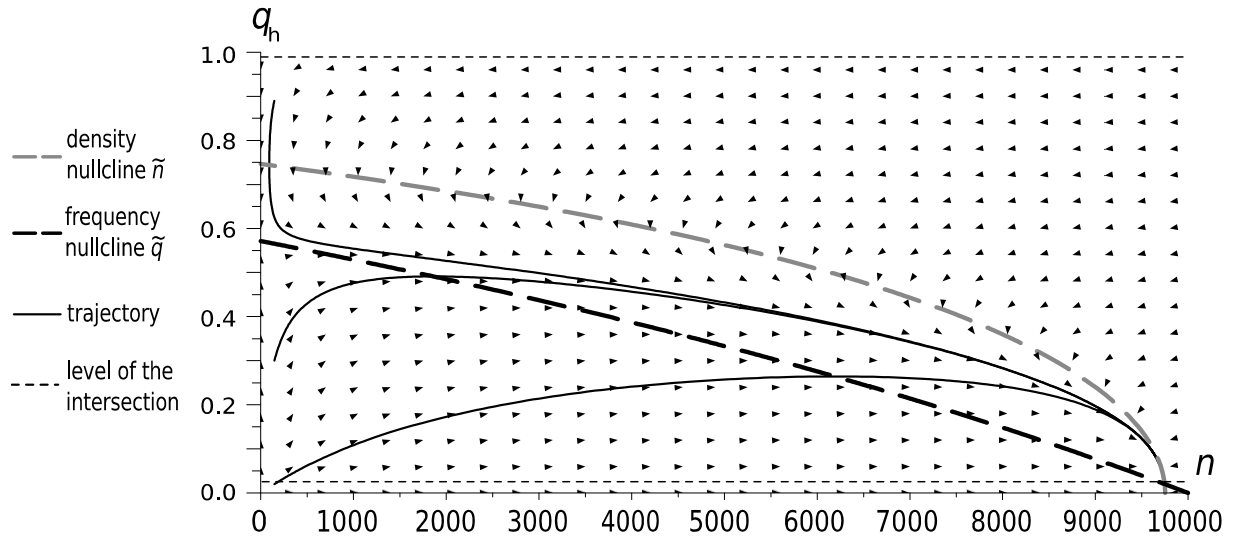
918 Figure 4: The dynamics of a Hawk-Dove population. Initial conditions
 919 $(q_h(0) = 0.2, n(0) = 20)$, $(q_h(0) = 0.87, n(0) = 2000)$ and $(q_h(0) = 0.9, n(0) = 450)$.
 920 Model parameters: $W = 3$, $d = 0.9$, $\Psi = 0.4$. In this case the attracting null-
 921 cline lies in the very close neighbourhood of the attracting frequency nullcline
 922 and follows it almost to the mixed equilibrium $\hat{q}_h = 0.4865$. The Hawk invasion
 923 barrier is $\check{q}_h = 0.9134$. The flow indicated by the arrows, as in the previous
 924 figures, supports the predictions from point a) of Lemma 1.

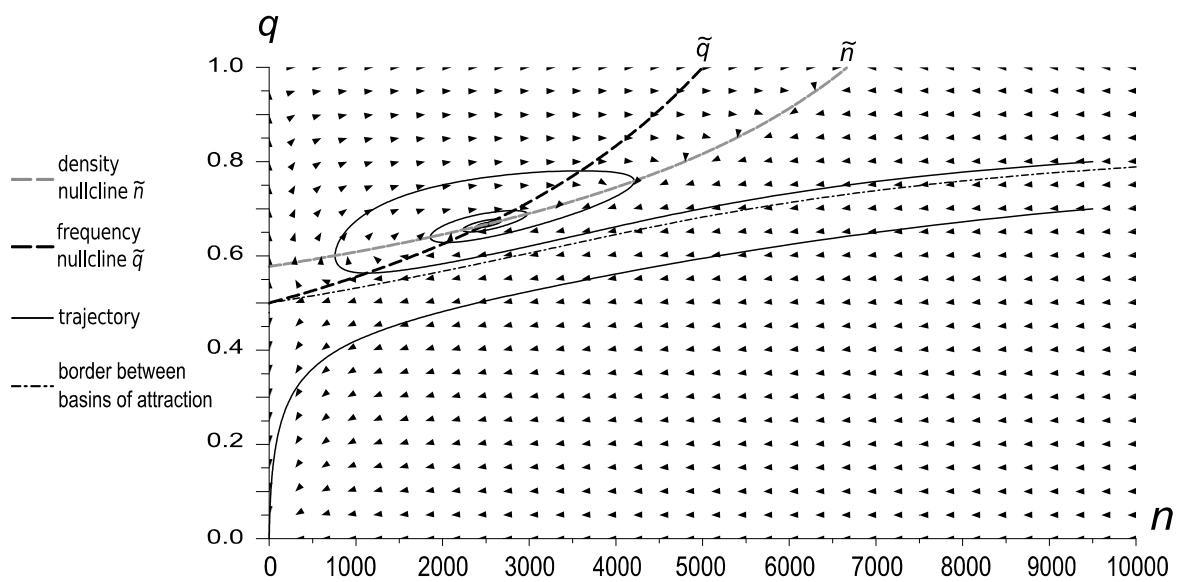
925 Figure 5: Trajectories of example 1, with an repelling frequency nullcline
 926 (evolutionarily unstable state for purely frequency dependent approach). In
 927 this case there are two basins of attraction: one is the intersection of the null-
 928 clines (the trajectory converges spirally) and the second is a region of extinction
 929 (convergence to $n = 0$ and $q = 0$). The border between the basins of attraction

930 was calculated numerically. Note that in this case, the orthogonal projection
931 of the flow (indicated by the arrows) on the density nullcline shows a direction
932 towards the stable intersection while the projection on the repelling frequency
933 nullcline shows the opposite direction This illustrates point b) from Lemma 1.

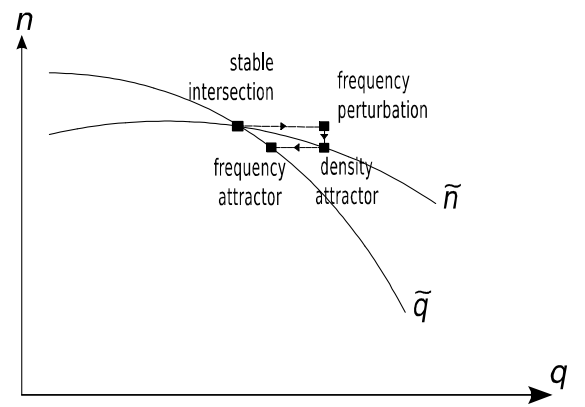
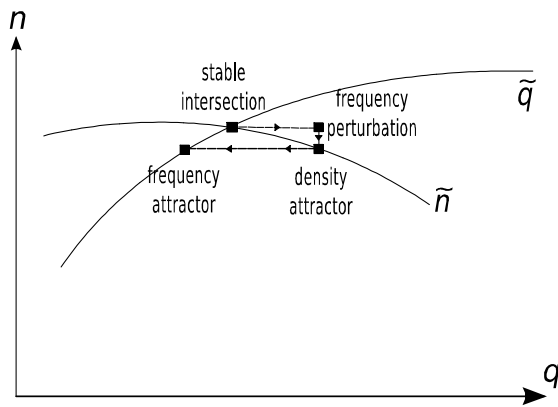
934 Figure 6: Presentation of the eco-evolutionary feedback mechanism. Posi-
935 tive or negative feedback, caused by frequency perturbation Δq , is induced by
936 the position of the density and frequency attractors $\tilde{n}(\hat{q} + \Delta q)$ and $\tilde{q}(\tilde{n}(\hat{q} + \Delta q))$
937 towards the stationary point (intersection) \hat{q}, \hat{n} . Note that we consider a continu-
938 ous system and not a sequential discrete system, and this figure is an illustration
939 only. Other figures show that at relatively high densities attraction towards the
940 attracting density nullcline is much stronger than attraction towards the at-
941 tracting frequency nullcline.







negative feedback



positive feedback

