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

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Abstract

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

1 Introduction

Current developments in evolutionary biology emphasize the role of relationships 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 reproduction 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; Meszena et al., 2006; Oesschler 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:

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

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

This leads to the following:

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

where the bracketed term from (1) splits into two brackets describing differences in fertilities and mortalities. The replicator system (2) is completed by equation (3) describing the changes of the population size caused by selection of the strategies. A similar method was applied in a number of papers (Hauert et al., 2006; Hauert et al., 2008; Argasinski and Kozłowski, 2008; Zhang and Hui, 2011; Argasinski and Broom, 2012; Huang et al., 2015; Gokhale and Hauert, 2016). In this approach population size does not converge to an arbitrary carrying capacity as in many models (for example Cressman and Krivan, 2010; Krivan, 2013) but to a dynamic equilibrium between mortality and fertility (this is often called an emergent carrying capacity, Bowers et al., 2003; Sieber et al., 2014). The general selective properties of this approach were presented in Argasinski and Broom (2013), where the simplified version of (2,3) with payoffs as constants was analyzed. It was shown there that when the population reaches the close neighbourhood of the population size equilibrium (nullcline of the equations for n), then newborns form the pool of candidates from which individuals replacing the dead adults in their nest sites will be drawn. This mechanism was termed the "nest site lottery". This process promotes the strategies that maximize the number of newborns replacing each single dying adult (termed "turnover coefficient"), however among strategies maximizing this quantity it is profitable to maximize the mortality (the number of dead adults) and thus also the number of newborns replacing them. Therefore, we have a two stage fitness measure.

The previous paper, Argasinski and Broom (2012), was focused on the description of the above approach using demographic parameters, mortality as the probability of death (or equivalently survival) and fertility as per capita number of offspring. This allows for a description of the abstract and unclear parameters such as “fitness” or “growth rate” by clear and measurable parameters. In addition, the new approach is focused on the detailed description of the structure of cause-effect chains underlying the particular interactions. For example, the modelled interaction described by the game theoretic structure can be composed of several mortality and fertility stages following each other. This aspect can be illustrated by the simplest case of **a** single pre-reproductive mortality stage preceding the fertility stage. Then only survivors of the interaction can reproduce, which should be incorporated into the payoff functions. Thus the fertility payoffs $W_i(q)$ will be replaced by the mortality-fertility trade-off function $V_i(q) = \sum_j q_j s_i(e_j) W_i(e_j)$ (where e_j is the vector describing the j-th pure strategy) describing the reproductive success of the survivors. The new conceptual framework was applied to the classical Hawk-Dove game to illustrate the advantages over the classical approach.

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

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

The values of the background payoffs can seriously affect the game dynamics as shown in Argasinski and Broom (submitted). In Argasinski and Broom (2012) it was also shown that under the influence of neutral density dependence, the behaviour of the system is different from that in the model with unlimited growth. The main difference is that in the model with unlimited growth there are only equations describing the evolution of strategy frequencies, while in the density dependent model there is an additional equation describing the size of the population and fertilities are affected by juvenile mortality described by logistic suppression. In effect, in the density dependent model, the stable frequency becomes a function of n describing the nullcline constituting the manifold of game theoretic Nash equilibria (population states with equal growth rates for all strategies). In addition, the equation for the population size leads to another nullcline being a function of the population composition and is affected by background payoffs. This nullcline has a very important biological meaning since it describes the ecological equilibria, conditional on the current strategic composition. In the game theoretic literature it is often referred as the stationary density surface (Cressman et al., 2001; Cressman and Garay, 2003a; Cressman and Garay, 2003b). Thus, the global stationary states are intersections of these nullclines, which can be stable or unstable.

The density and frequency nullclines describing the ecological and game theoretic equilibria are important for the mechanistic interpretation of the phenomenon in terms of feedbacks. New phenomena can emerge, for example the existence of a stable pure Hawk solution in addition to the stable mixed equilibrium (Argasinski and Broom, 2012). The additional stable rest point is caused by neutral density dependence. This paper contains a general analysis of system stability and a mechanistic explanation of the interplay between the convergence to the selection equilibrium describing the stable population composition (described by the frequency nullcline) and the convergence to the ecological equilibrium describing the stable population size (described by the density nullcline). The study shows when the stability is fully determined by the behaviour along the nullclines and the problem can be reduced to the static game theoretic analysis limited to simple algebraic inequalities, and when the full dynamic model involving differential equations should be applied.

2 Results

2.1 Selectively neutral density dependence and the concept of eco-evolutionary feedback

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

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

2.2 General form of the analyzed models

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

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

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

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

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:

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

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

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

2.3 Properties of the stationary points related to the turnover of individuals

In many models $\tilde{q}(n)$ and $\tilde{n}(q)$ defined as the respective nullclines will exist (in some cases they will be attracting nullclines). Expressing q as a function of n (according to the implicit function theorem), the nullcline $\tilde{q}(n)$ is defined by the value of q for which $g(n, q) = 0$ (the right-hand side of equation (6) is 0 for any given n). It is possible that there is more than one such solution, and so more than one such nullcline. Similarly, expressing n as a function of q for $f(n, q) = 0$, the nullcline $\tilde{n}(q)$ is defined by the value of n for which the right-hand side of equation (7) is 0 for any given q. The nullclines, representing the equilibria of interplaying processes (strategic selection and convergence to the ecological equilibrium) will play important roles in the derivation of the static game theoretic conditions (the inequalities for payoffs of the strategies that should be satisfied for evolutionary stability). Those conditions will extend the classical ESS concept to the ecological concept. In addition, on the nullcline representing the equilibria of one process, the dynamics is determined by the opposite process, for example on the density nullcline the dynamics is driven by game dynamics only. The question arises, when can the behaviour of the complicated dynamical system be described by a set of algebraic inequalities?

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

Theorem 1

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

a) The turnover coefficients of all strategies are equal:

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

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

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

For a proof see Appendix 2.

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

Corollary 1

If the focal game-specific turnover coefficients satisfy

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

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

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

We note that in the method of static game theoretic analysis presented in Argasinski and Broom (2012), the attractor population size $\tilde{n}(q)$ was substituted into the right hand side of equation (6). Substitution of $\tilde{n}(q)$ into $\tilde{q}\,(n)$ leads to the inequality $q < (>)\tilde{q}\,(\tilde{n})$ describing the regions of growth (decline) of q lying on the density nullcline $\tilde{n}(q)$. In Argasinski and Broom (2012) the inequality $q \leq \tilde{q}\,(\tilde{n})$ has the form of a quadratic equation (see Theorem 2 and Appendix 5 there). Zeros of this equation are intersections of the density and frequency attracting nullclines. Thus under the assumption of ecological equilibrium, this method shows which intersection is stable and unstable. This is a rigorous analysis but it is strictly limited to the attracting density nullcline. The question arises, when can this reasoning be extended to the neighbourhood of the attracting density nullcline? There are relationships between the density and frequency nullclines, but these cannot necessarily be extrapolated to the general neighbourhood of their intersections. This is summarized by technical Lemma 1 below, where we assume the standard notation for partial derivatives $g_q = \partial g/\partial q$, $g_n = \partial g/\partial n$, $f_q = \partial f/\partial q$ and $f_n = \partial f/\partial n$ of the right hand sides of equations **(6,7)**.

Lemma 1

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

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

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

For a proof see Appendix 3.

Thus in the case when the frequency nullcline is the attractor of the frequency dynamics, which implies that in the density independent case it will be a stable rest point, stability on the attracting density nullcline can be extrapolated to the attracting frequency nullcline. This property can be useful for the derivation of the static conditions for Eco-Evolutionary stability. Part b) of Lemma 1 shows that the general situation is more complicated. It shows that in the case of an unstable frequency nullcline the selection process and the ecological process will always act antagonistically. If one process will lead to stabilization of the rest point the second process will act towards destabilization. Thus we need some additional criteria describing this antagonistic relationship. The potential complexity of behaviour will be shown by numerical examples in the next section.

2.4 Numerical examples and their analysis

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

Argasinski and Broom (2012).

FIGURE 1 HERE

FIGURE 2 HERE

FIGURE 3 HERE

FIGURE 4 HERE

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

However, this happens when both nullclines are placed at relatively high densities. At lower densities the trajectory does not reach a strict neighbourhood of the attracting density nullcline (Figure 2), but converges to a surface lying between the frequency and density nullclines. At very low densities the trajectories converge to the attracting nullcline which is closer to the frequency attracting nullcline (Figure 3). We note that this effect is suppressed by population growth. In some cases the attracting nullcline is located in the close neighbourhood of the frequency attracting nullcline and traces it nearly to the equilibrium (Figure 4). Thus, the assumption that frequency selection occurs on the attracting density nullcline can sometimes be seriously wrong. In the general case the geometry of both nullclines plays an important role in the dynamics and what happens in the region limited by those surfaces is crucial. At higher densities there is a stronger convergence towards the attracting density nullcline while at lower densities there is a stronger attraction towards the frequency attracting nullcline. Therefore, the ecological equilibrium assumption is a simplification of the full problem. In addition, on all figures we can observe the clearly visible convergence of the trajectories to the unique invariant manifold. However, the behaviour on these manifolds seems to be compatible with the projection of the vector field on the nullcline $\tilde{n}(q)$ (and also by Lemma 1 on the nullcline $\tilde{q}(n)$). This suggests that the stability of the intersection can be described by a simple set of algebraic equations, which will constitute the Eco-Evolutionary static analysis.

Note that in the above examples the attracting frequency nullcline represents the set of game theoretic Nash equilibria, conditional on the actual ecological conditions represented by juvenile mortality, determined by population size. However, we have two types of intersection representing the stationary points. One is stable, thus it is compatible with the underlying purely game theoretic notions, while the second is unstable. This means that a point that is a stable equilibrium in the density independent case can be destabilized by ecological factors. However, we can imagine the opposite situation, where the intersection of the repelling frequency nullcline (representing the set of invasion barriers conditional on the actual population size) can be stabilized by the impact of density dependence. This is illustrated by the following phenomenological example:

Example 1: the stabilization of a stationary point by density dependent pressure in case of the repelling frequency nullcline.

Assume that there are two strategies, where the functions
$B_1(q) = \left(\frac{2}{3}q^2 + \frac{2}{3}q\right)$ and $M_1(q) = \left(\frac{7}{9} - \frac{q}{3}\right)$
are the fertility and mortality of the first strategy, while
$B_2(q) = \frac{2}{3}q^2$ 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):

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

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

$$\begin{aligned} \dot{q} &= \frac{q}{3}(1-q)\left(2q(1-n/K)-1\right), && (12) \\ \dot{n} &= \frac{4}{3}n\left(q^2(1-n/K)-\frac{1}{3}\right). && (13) \end{aligned}$$

Calculation of the frequency and density nullclines gives:
$\tilde{q} = \frac{1}{2(1-n/K)}$ and $\tilde{n} = \left(1 - \frac{1}{3q^2}\right)K$.

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

FIGURE 5 HERE

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

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)

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

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

Theorem 2

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

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

a)

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

b)

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

For a proof see Appendix 6.

A question arises about the interpretation of the above stability conditions. Condition a) means that attraction to the density nullcline is stronger than repellence from the frequency nullcline. This means that in the antagonistic relationship between selection and the ecological process indicated by point b) of Lemma 1, the stabilizing ecological process should be stronger. If the nullcline $\tilde{q}(n)$ is attracting (which means that it consists of stable Nash equilibria) then condition a) is satisfied automatically. Condition b) is equivalent to stability along the density nullcline $\tilde{n}(q)$. Thus for the attracting nullcline $\tilde{q}(n)$ the stability of the global equilibrium is equivalent to the behaviour along the nullcline $\tilde{n}(q)$. This justifies the static ESS analysis based on the substitution of the ecological equilibrium $\tilde{n}(q)$ to the dynamics and the analysis of signs of the right hand sides of the q equations as in Theorem 2 in Argasinski and Broom (2012). Note that, according to Lemma 1, condition b) implies instability on the repelling nullcline $\tilde{q}(n)$, representing the game theoretic invasion barriers. However, in this case, if the attraction towards nullcline $\tilde{n}(q)$ is stronger than the repellence from nullcline $\tilde{q}(n)$, then the intersection can be stable despite this. Note that for the intersection of the repelling frequency nullcline and density nullcline from Example 1, both conditions are satisfied (see Appendix 7 for the detailed calculations). According to Lemma 1, satisfying condition b) implies attraction towards the intersection along the attracting frequency nullcline $\tilde{q}(n)$ and repellence if the frequency nullcline $\tilde{q}(n)$ is repelling. Example 1 supports the results from Lemma 1. The projection of the flow orthogonal to the density nullcline (see arrows on Figure 6) shows that it will be stable, while on the frequency nullcline it will be unstable. However the general spiral 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

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

and the slope of the size nullcline is

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

Then the above conditions are equivalent to the following lemma:

Lemma 2

Provided that the inverses from equations (17) and (18) exist, Condition 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 require the following condition to be satisfied:

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

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

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

$$U_n > (<) U_q. \tag{20}$$

For a proof see Appendix 8.

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

2.6 Game theoretic notions revealed by dynamic stability conditions

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

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

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

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

This concept can be generalized to the case of convex combination of functions $\sum q_i f_i(x)$, 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

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

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

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

Theorem 3

Condition a) has the form:

$$\hat{q}\left(\frac{\left(B_1'(\hat{q}) - \bar{B}'(\hat{q})\right)}{\bar{B}(\hat{q})} - \frac{\left(M_1'(\hat{q}) - \bar{M}'(\hat{q})\right)}{\bar{M}(\hat{q})}\right) < \frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})} - 1, \tag{23}$$

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

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

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

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

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

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

and

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

Since the background payoffs Φ and Ψ do not depend on the traits under consideration they should not depend on the frequency of the strategies in the focal games. In effect they vanish from the derivatives of the general growth rates B and M. However they are still present in the stability conditions. Thus, the stability in the particular focal type of interaction is determined by the impact of other activities. Since $\Phi = \theta W_B$, $\Psi = \theta m_B$ where θ describes the average number of background events between two focal events, and W_B and m_B are average background events fertility and mortality, parameters Φ and Ψ have a clear interpretation in the purely static *ESS* models too. This result can be important for the research on animal personalities (Dall et al., 2004; Wolf et al., 2007; Wolf and Weissing, 2010; Wolf and Weissing, 2012; Wolf and McNamara, 2012).

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

In the game theoretic framework this concept can be found in Argasinski and Kozłowski (2008), Zhang and Hui (2011) and Argasinski and Broom (2012). How does this mechanism work? Perturbation in q (described by Δq) induces convergence towards the respective stable size $\tilde{n}(\hat{q} + \Delta q)$ lying on the attracting density nullcline $\tilde{n}(q)$ which determines the respective frequency attractor $\tilde{q}(\tilde{n}(\hat{q} + \Delta q))$ on the frequency attracting nullcline $\tilde{q}(n)$. If $|\tilde{q}(\tilde{n}(\hat{q} + \Delta q)) - \hat{q}| < |\Delta q|$ then negative feedback is induced in a sense that dynamics chase $\tilde{q}(\tilde{n}(\hat{q}+\Delta q))$ towards $\hat{q}$. In effect $\hat{q}$ is stable. On the other hand, if $|\tilde{q}(\tilde{n}(\hat{q}+\Delta q))-\hat{q}|>|\Delta q|$ then a positive feedback is induced and the attractor escapes from $\hat{q}$. In effect $\hat{q}$ is unstable. See Figure 6 for an illustration.

FIGURE 6 HERE

3 Discussion

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

Theorem 2 shows the stability conditions. It shows that the stability along the attracting density nullcline can be extrapolated to the neighbourhood of the intersection (Theorem 2 point b). Those conditions show that stability depends on the condition similar to the classical ESS notions but expressed in absolute value changes in mortalities and fertilities (Theorem 3). In addition, the stability is determined by the geometry of both nullclines (Lemma 2). It is shown that the dynamics can be attracted by the intersection even in the case when the frequency nullcline is repelling. This can happen when attraction toward the density nullcline is stronger than repellence from the frequency nullcline. Numerical simulations show a variety of behaviours. Some of these are against intuition based upon the dynamics concentrated on frequencies occurring on the attracting density nullcline. At low densities there is a stronger attraction towards the attracting frequency nullcline. This is caused by the fact that at high densities differences in fertility are suppressed by density dependent juvenile mortality described by the logistic suppression coefficient, while at low densities the impact of fertility on the overall dynamics is significant. Thus both nullclines are important for the dynamics. In particular, the case of convergence to the intersection of the repelling frequency nullcline (which will be an invasion barrier in the case with unlimited growth) with the attracting density nullcline is surprising. In addition, this intriguing pattern coexists with a region of extinction that cannot be easily shown by purely static analysis.

The phenomenon of stability and instability of the intersections can be mechanistically explained by the idea of eco-evolutionary feedbacks, a concept already known in the literature (Post and Palkovacs, 2009; Kokko and López-Sepulcre, 2007). The stability or instability of the particular stationary frequency is caused by a shift of the frequency attractor conditional on a corresponding correction of the density attractor. This density attractor is conditional on the perturbation of the frequency, which closes the feedback loop. This is related to the fact that in the framework presented in this paper outcomes of interactions, described by mortality and fertility, are entries of the “nest site lottery” mechanism, when the trajectory reaches a close neighbourhood of the density nullcline. Thus on the density nullcline all newborns introduced to the environment form a pool of candidates from which individuals that substitute dead adults in their nest sites will be randomly drawn. This mechanism induces the frequency dependent selection consisting of two stages. At the first stage the strategies maximizing the turnover coefficient (number of newborns produced per single dead adult within a short time interval) are selected. Then every perturbation of the population state (a size decrease caused by natural disaster or invasion of a significant number of suboptimal mutants) leads to an increase of the frequency of the strategy with maximal mortality among those with maximal turnover coefficient. This mechanism was analyzed in Argasinski and Broom (2013). Note that the framework analyzed in this paper collapses to the system analyzed in Argasinski and Broom (2013) under the assumption that all mortality and fertility payoffs are constants. The nest site lottery mechanism was analyzed only for the case when the population is in the neighbourhood of the density nullcline. Thus it is an interesting open question how this mechanism works in states far from the density nullcline. It is likely that when there is a shortage of free nest sites the population is subject to a similar mechanism. This fraction increases with convergence to the density attracting nullcline and covers all newborns when the trajectory reaches this nullcline. The importance of the generalization of the nest site lottery mechanism is supported by results from this paper.

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

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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
$g(n, q)$	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

Appendix 1

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

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

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

Then by change of timescale $\tilde{t} = t\tau_1$ and substitution using $\Phi = \frac{\tau_2}{\tau_1}W_B$ and $\Psi = \frac{\tau_2}{\tau_1}m_B$, we obtain:

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

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

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

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

Appendix 2

Proof of Theorem 1:

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

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

The bracketed term in equation (31) equals zero when

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

which leads to

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

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

$$\begin{aligned}\frac{dq_i}{dt} &= q_i\left(\big(B_i(q)-\bar{B}(q)\big)\left(\frac{\bar{M}(q)}{\bar{B}(q)}\right) - \big(M_i(q)-\bar{M}(q)\big)\right) & (34)\\ &= q_i\bar{M}(q)\left(\frac{B_i(q)}{\bar{B}(q)} - \frac{M_i(q)}{\bar{M}(q)}\right). & (35)\end{aligned}$$

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

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

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

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

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

$$\begin{aligned}\frac{V_i(q)+\Phi}{d_i(q)+\Psi} &= \frac{V_i(q)+x_V+\Phi}{d_i(q)+x_s+\Psi}\Rightarrow & (38)\\ \frac{V_i(q)+\Phi}{d_i(q)+\Psi}x_s &= x_V. & (39)\end{aligned}$$

Thus from (37) and (39) we have

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

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

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

This is the proof of point b).

Appendix 3

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:

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

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

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:

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

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

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

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

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

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

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 $V_i(v,q) = e_iS \cdot Pq^T$ and $s_i(v,q) = e_iSq^T$. In effect we obtain the following system:

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

and

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

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

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

$$e_1 S \cdot P q^T = 0.5 s q_h + 1 - q_h, \tag{49}$$

$$q S q^T = q_h\left(q_h(s-1)+1\right) + (1-q_h) = 1 - q_h^2(1-s), \tag{50}$$

$$q S \cdot P q^T = q_h\left(0.5 s q_h + 1 - q_h\right) + 0.5(1-q_h)^2 = 0.5\left(1 - q_h^2(1-s)\right). \tag{51}$$

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

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

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

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

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

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)

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

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

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

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

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

Appendix 5

Let us derive the replicator equations for Example 1. For the density independent case we have the following Malthusian growth rates

$r_1^u(q) = B_1(q) - M_1(q) = \frac{2}{3}q^2 + q - \frac{7}{9},$

$r_2^u(q) = B_2(q) - M_2(q) = \frac{2}{3}q^2 + \frac{q}{3} - \frac{4}{9}.$

This leads to the following replicator equation:

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

where $q = 1/2$ is the unstable rest point (invasion barrier). However when we extend this model to the density dependent case, the situation is different. Then the density dependent Malthusian growth rates are:

$r_1(q,n) = \left(\frac{2}{3}q^2 + \frac{2}{3}q\right)(1-n/K) - \left(\frac{7}{9} - \frac{q}{3}\right),$

$r_2(q,n) = \frac{2}{3}q^2(1-n/K) - \left(\frac{4}{9} - \frac{q}{3}\right).$

This leads to the replicator dynamics:

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

Further we obtain the following equation for the mean payoff

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

leading to the differential equation for the population size:

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

After calculation of the frequency and density nullclines we obtain:

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

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

Appendix 6

Here we prove Theorem 2: in particular giving a derivation of general formulae 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

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

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

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

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

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

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

The condition $Z > 0$ is just condition b) from Theorem 2 and can be presented in the form

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

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

The condition $A > 0$ occurs if $f_n(\hat{n},\hat{q}) + g_q(\hat{n},\hat{q}) < 0$. The first of these two terms is negative; the second of these being negative is the condition for stability in density independent models. Thus, for example, the Hawk-Dove game which has a mixed ESS for its density independent version (the classical game) automatically satisfies this condition. However, the condition $A > 0$ can be satisfied even in the case when the frequency nullcline is repelling, which 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 $f_n(\hat{n}, \hat{q})$ is negative, which is condition a) from Theorem 2. Thus our conditions $A > 0$ and $Z > 0$ are precisely those from Theorem 2 as required.

Appendix 7

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

$$g_q(q, n) = \frac{1}{3}\left[(4q - 6q^2)(1 - n/K) - (1 - 2q)\right],$$
$$g_n(q, n) = \frac{-2q^2(1 - q)}{3K},$$
$$f_q(q, n) = \frac{4}{3}\left(2qn(1 - n/K)\right),$$
$$f_n(q, n) = \frac{4}{3}\left(q^2\left(1 - 2n/K\right) - \frac{1}{3}\right).$$

After substitution of the rest points, we obtain:

$$g_q(\hat{q}, \hat{n}) = \frac{1}{9} > 0,$$
$$g_n(\hat{q}, \hat{n}) = -\frac{8}{81K},$$
$$f_q(\hat{q}, \hat{n}) = \frac{K}{3},$$
$$f_n(\hat{q}, \hat{n}) = \frac{4}{3}\left(\frac{2}{9} - \frac{1}{3}\right) = -\frac{4}{27}.$$

Now the stability conditions a) $A = -(f_n(\hat{n}, \hat{q}) + g_q(\hat{n}, \hat{q})) > 0$ and b) $g_q(\hat{n}, \hat{q}) - g_n(\hat{n}, \hat{q})\dfrac{f_q(\hat{n}, \hat{q})}{f_n(\hat{n}, \hat{q})} < 0$ from Theorem 2 should be checked.

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

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

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

Appendix 8

Proof of Lemma 2:

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

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

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

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

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

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

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

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

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

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),

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

This leads to:

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

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

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

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

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

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

Appendix 9

Proof of Theorem 3:

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

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

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

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

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

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

since the first bracketed term equals zero.

Let us calculate concrete forms of conditions A and Z:

Condition A:

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

Then $A > 0$ when

$$\frac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})} - 1 > \hat{q}\left(\frac{\left(B_1'(\hat{q}) - \bar{B}'(\hat{q})\right)}{\bar{B}(\hat{q})} - \frac{\left(M_1'(\hat{q}) - \bar{M}'(\hat{q})\right)}{\bar{M}(\hat{q})}\right). \tag{63}$$

Condition Z:

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

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

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

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

$$\left.\left.- \frac{\left(M_1'(\hat{q}) - \bar{M}'(\hat{q})\right)}{\bar{M}(\hat{q})}\right)\right].$$

Thus $Z > 0$ if

$$\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})}\right)\frac{\left(B_1(\hat{q}) - \bar{B}(\hat{q})\right)}{\bar{B}(\hat{q})} > \left(\frac{\left(B_1'(\hat{q}) - \bar{B}'(\hat{q})\right)}{\bar{B}(\hat{q})} - \frac{\left(M_1'(\hat{q}) - \bar{M}'(\hat{q})\right)}{\bar{M}(\hat{q})}\right) \Rightarrow$$

$$\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})}\right)\frac{\left(B_1(\hat{q}) - \bar{B}(\hat{q})\right)}{\bar{B}(\hat{q})} > \left(\frac{B_1'(\hat{q})}{\bar{B}(\hat{q})} - \frac{M_1'(\hat{q})}{\bar{M}(\hat{q})}\right) - \left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})}\right) \Rightarrow$$

$$\left(\frac{\bar{B}'(\hat{q})}{\bar{B}(\hat{q})} - \frac{\bar{M}'(\hat{q})}{\bar{M}(\hat{q})}\right) > \left(\frac{B_1'(\hat{q})}{B_1(\hat{q})} - \frac{M_1'(\hat{q})\bar{B}(\hat{q})}{\bar{M}(\hat{q})B_1(\hat{q})}\right).$$

From equality of the turnover coefficients at the rest point we have that $L = B_1(\hat{q})/M_1(\hat{q}) = \bar{B}(\hat{q})/\bar{M}(\hat{q})$. This leads to $\dfrac{\bar{B}(\hat{q})}{\bar{M}(\hat{q})B_1(\hat{q})} = \dfrac{L}{B_1(\hat{q})} = \dfrac{1}{M_1(\hat{q})}$. Thus formula Z can be presented as:

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

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

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

End of proof.

FIGURE CAPTIONS

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

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

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

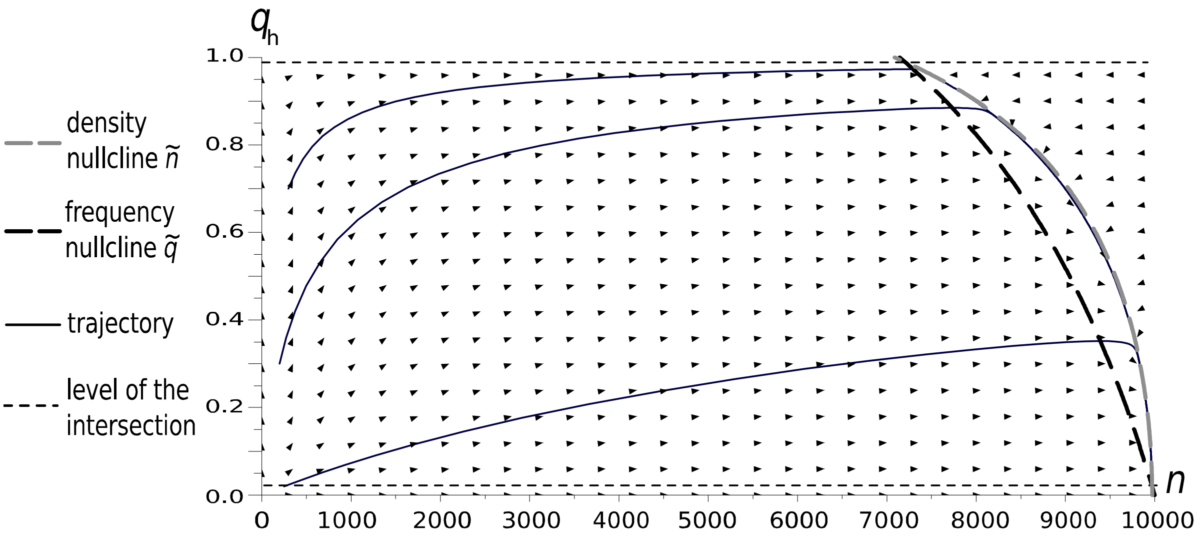
$(q_h(0) = 0.02, n(0) = 147)$, $(q_h(0) = 0.3, n(0) = 147)$ and $(q_h(0) = 0.89, n(0) = 147)$. Model parameters: $W = 0.8$, $d = 0.5$, $\Psi = 0.01$. In this case, the attracting nullcline lies close to the frequency nullcline at low densities but becomes closer to the density nullcline with an increase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

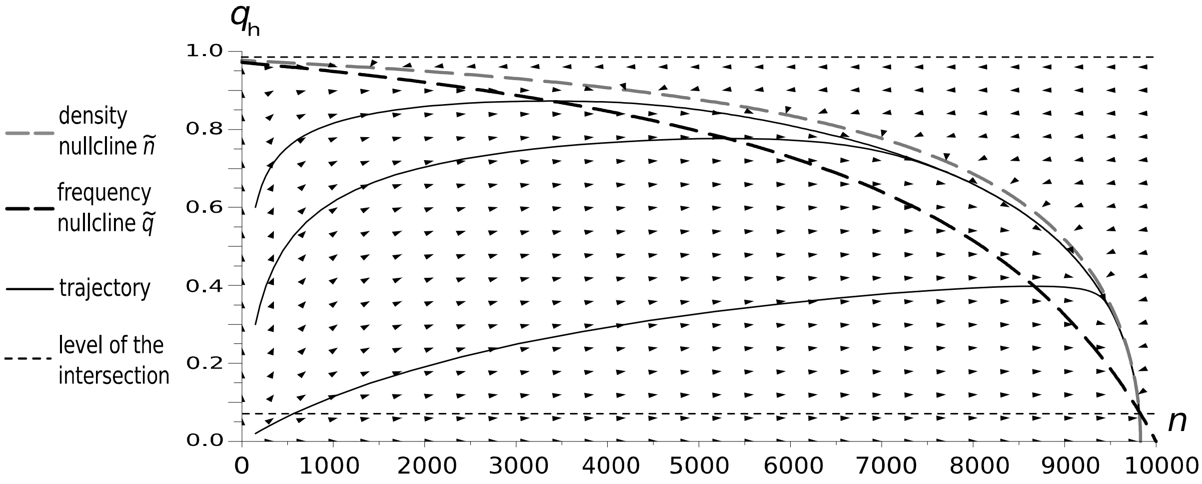
Figure 4: The dynamics of a Hawk-Dove population. Initial conditions $(q_h(0) = 0.2, n(0) = 20)$, $(q_h(0) = 0.87, n(0) = 2000)$ and $(q_h(0) = 0.9, n(0) = 450)$. Model parameters: $W = 3$, $d = 0.9$, $\Psi = 0.4$. In this case the attracting nullcline lies in the very close neighbourhood of the attracting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

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

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

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


q_h
1.0
0.8
0.6
0.4
0.2
0.0
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
n
density nullcline $\tilde{n}$
frequency nullcline $\tilde{q}$
trajectory
level of the intersection


q_h
1.0
0.8
0.6
0.4
0.2
0.0
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1000
2000
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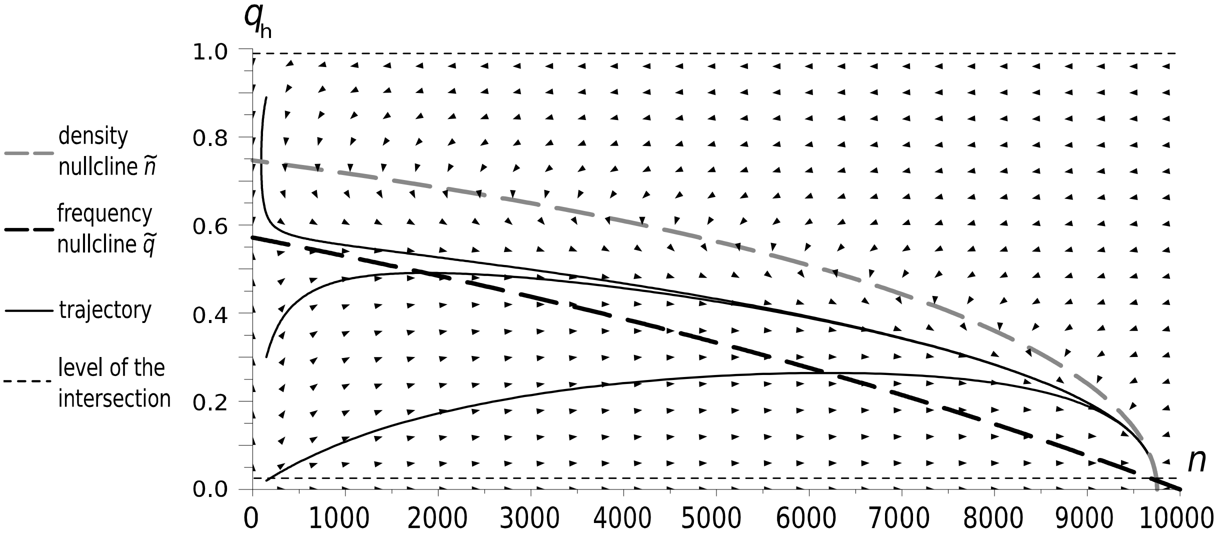
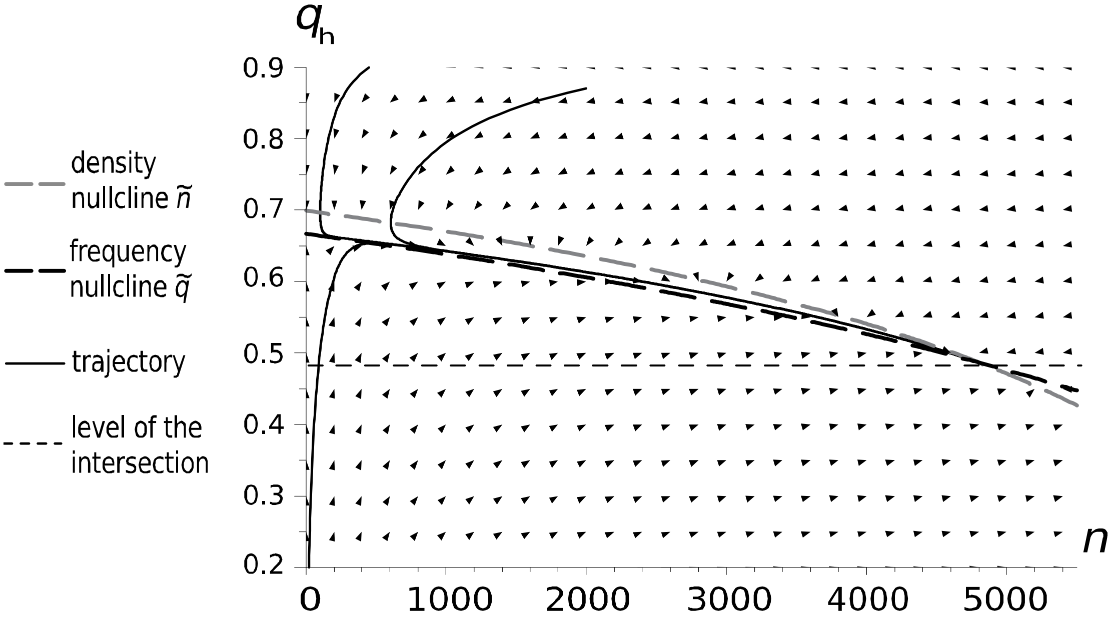
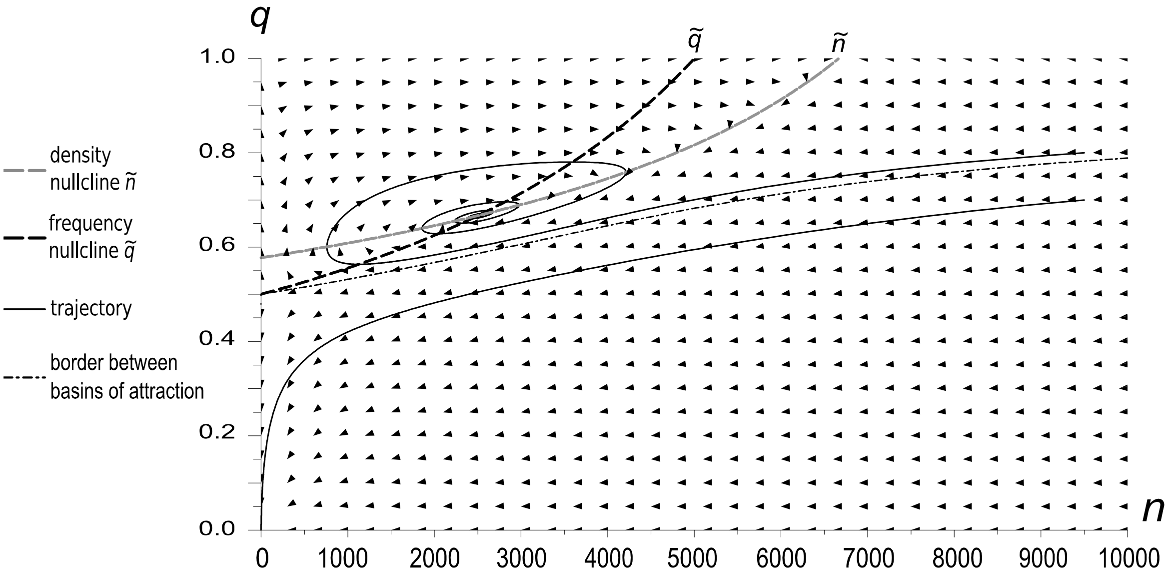
9000
10000
n
density nullcline $\tilde{n}$
frequency nullcline $\tilde{q}$
trajectory
level of the intersection

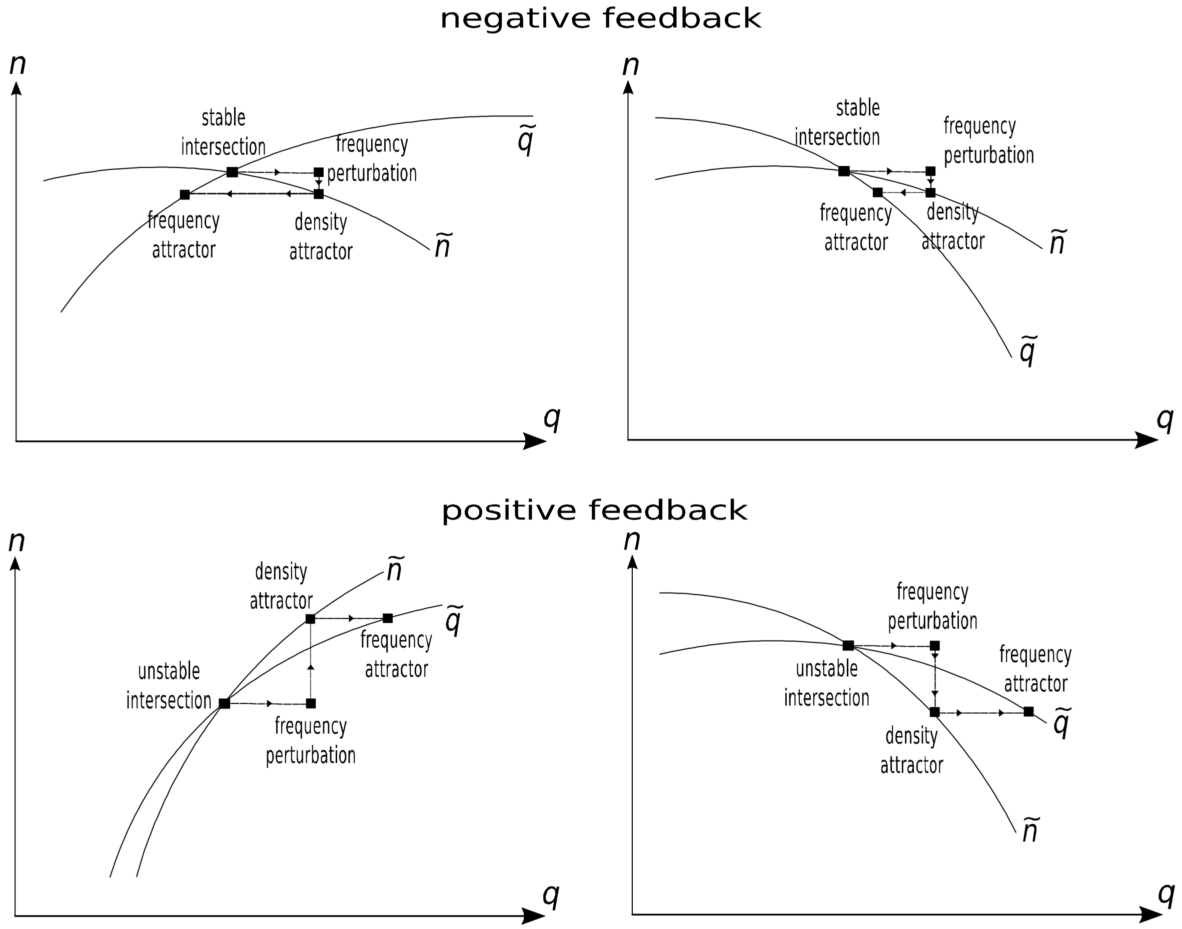


q_h
1.0
0.8
0.6
0.4
0.2
0.0
density nullcline $\tilde{n}$
frequency nullcline $\tilde{q}$
trajectory
level of the intersection
n
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000



q_h
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
density nullcline $\tilde{n}$
frequency nullcline $\tilde{q}$
trajectory
level of the intersection
n
0
1000
2000
3000
4000
5000


q
1.0
0.8
0.6
0.4
0.2
0.0
n
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
$\tilde{q}$
$\tilde{n}$
density nullcline $\tilde{n}$
frequency nullcline $\tilde{q}$
trajectory
border between basins of attraction


negative feedback
n
stable intersection
frequency perturbation
frequency attractor
density attractor
$\tilde{q}$
$\tilde{n}$
q
n
stable intersection
frequency perturbation
frequency attractor
density attractor
$\tilde{n}$
$\tilde{q}$
q
positive feedback
n
density attractor
$\tilde{n}$
$\tilde{q}$
frequency attractor
unstable intersection
frequency perturbation
q
n
frequency perturbation
unstable intersection
frequency attractor
$\tilde{q}$
density attractor
$\tilde{n}$
q